

# The importance of fine-scale studies for integrating paleogenomics and archaeology

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There has been an undercurrent of intellectual tension between geneticists studying human population history and archaeologists for almost 40 years. The rapid development of paleogenomics, with geneticists working on the very material discovered by archaeologists, appears to have recently heightened this tension. The relationship between these two fields thus far has largely been of a multidisciplinary nature, with archaeologists providing the raw materials for sequencing, as well as a scaffold of hypotheses based on interpretation of archaeological cultures from which the geneticists can ground their inferences from the genomic data. Much of this work has taken place in the context of western Eurasia, which is acting as testing ground for the interaction between the disciplines.

Perhaps the major finding has not been any particular historical episode, but rather the apparent pervasiveness of migration events, some apparently of substantial scale, over the past ~5000 years, challenging the prevailing view of archaeology that largely dismissed migration as a driving force of cultural change in the 1960s. However, while the genetic evidence for 'migration' is generally statistically sound, the description of these events as structured behaviours is lacking, which, coupled with often over simplistic archaeological definitions, prevents the use of this information by archaeologists for studying the social processes they are interested in. In order to integrate paleogenomics and archaeology in a truly interdisciplinary manner, it will be necessary to focus less on grand narratives over space and time, and instead integrate genomic data with other form of archaeological information at the level of individual communities to understand the internal social dynamics, which can then be connected amongst communities to model migration at a regional level. A smattering of recent studies have begun to follow this approach, resulting in inferences that are not only helping ask questions that are currently relevant to archaeologists, but also potentially opening up new avenues of research.

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## Introduction

It is arguably Luigi Luca Cavalli-Sforza's work analyzing frequencies of classical genetic markers (blood groups and other protein allozymes) and some limited mitochondrial DNA (mtDNA) in modern populations from across the world [1–3], culminating in his opus *A History and Geography of Human Genes* [4], that first brought geneticists and archaeologist into conflict. By relating their data with information from other disciplines (linguistic phylogenies and distributions of archaeological culture), Cavalli-Sforza and colleagues attempted to reconstruct how people had colonized the world in past societies. However this work drew a number of critiques from researchers from other fields at the time [5–8], and, despite massive improvements in both the generating of genetic data (from uniparental markers, to SNP arrays, through to whole genomes) and its analysis, an intellectual tension has remained between human genetics and archaeology [9,10,11\*,12\*,13]. Until recently, it was somewhat easy for archaeologists to dismiss or at least question the work emanating from genetics, arguing that the results obtained from modern DNA (even using genomic-level data) relied on critical assumptions about how populations were distributed and structured in the past, while finding the estimates of timings of demographic events to have confidence intervals so wide (because of inherent uncertainty when modelling genealogical processes as well mutation rates and generation times) so as to be essentially useless.

However, the recent ability to reliably obtain ancient genomes from past people of interest (the field of paleogenomics), rather than extrapolating from modern populations, largely overcomes these issues, and now potentially confronts archaeologists with a paradigm shift.

Archaeologists can no longer take a back seat or avoid (not that they necessarily actively wish too) the findings arising from the field, as it is genetic data generated from their own samples that must now be interpreted, in particular the apparent evidence of substantial migration over the last 5000 years. In this paper, I first detail the major findings from human paleogenomics over the past five or so years and the major theme that these inferences fit into. I follow this with my opinion of why these results are not being readily accepted by the archaeological community, and finally detail a potential approach that will allow these two fields to work in a truly interdisciplinary fashion.

### The arrival of paleogenomics

During the early period of paleogenomics, the primary focus of research was on sequencing archaic hominins such as Neanderthals to look for evidence of potential introgression with anatomically modern humans [14,15] and investigating to what extent hunter-gatherers in Europe had been replaced by incoming Neolithic farmers from the Near East [16–18], the very question Cavalli-Sforza and colleagues had attempted to examine in their early classical studies [1] and that had generated such debate for over 40 years using various type of genetic [19–23]. The general picture that emerged largely fit with the views of Ammerman, Cavalli-Sforza, Colin Renfrew and others of a large replacement during this transition (i.e. demic rather than cultural diffusion), with a clear shift in the genetic ancestry of individuals sampled from Europe within Paleolithic/Mesolithic versus Neolithic contexts. However, what was perhaps more surprising is that Early Neolithic individuals showed very little resemblance to modern Europeans, except Sardinians [16–18]. This left the question of what had happened since the Early Neolithic. To what extent were other migrations a factor in shaping the modern European gene pool [24], and might such migrations correlate in some way with particular archaeological cultures [25]?

Therefore the past three years has seen efforts shift towards better understanding the genetic ancestry of people sampled later in the Neolithic and into the Bronze Age (though work continues to be done elucidating the origins of the original farmers that moved into Europe [18,26–30]). The first major finding (discovered by two groups independently) was the identification of an additional genetic ancestry component introduced into Europe from Ukraine/Russia that was associated with the early Bronze Age Yamnaya steppe herder culture [31,32], who were later shown themselves to be a mixture of eastern and Caucasus hunter-gatherers and early Neolithic Iranians [33]. A similar genetic input was observed moving in an eastern direction into Central Asia, and it appears that at this point in time the major genetic ancestry types had been introduced such that later Bronze Age populations began to increasingly resemble modern

Eurasian population genetic structure. What has followed is a series of papers over the past two years sequencing individuals associated with different Late Neolithic, Bronze Age and Iron Age archaeological cultures in order to examine to what extent the proportions of putative ancestral genetic ancestry types are changing such that this may indicate some kind of migration (either connecting similar archaeological cultures in different regions or indicating a replacement of one material culture by another in the same region). In this regard, archaeology is very much a back seat driver in this process, acting simply as the a source of material for DNA extraction and providing some kind of hypothesis framework that geneticists can hang their models of migration, which is also likely responsible for some resentment between the disciplines.

An almost dizzying array of potential migrations, invasions and replacements have been described in Eurasia beginning ~5000 years ago using this general approach: eastern Caucasus-related ancestry into Minoans in Crete and northern steppe ancestry into Mycenaean Greeks; steppe ancestry related to the Beaker culture into continental Neolithic farmer individuals and then (with ~90% turnover) into Britain [34] and even Ireland [35]; eastern ancestry into post-Bronze Age Northern Europeans [36]; a Scythian expansion from the eastern to central steppes, followed by the Xiongnu-Hunnic invasion and replacement of Asian Scythians [37\*]. This migrationist emphasis has recently been extended to more recent periods such as (perhaps not surprisingly) the European Migration Period (eastern Europeans moving into Bavaria [38], mainland Europeans moving into Britain [39,40]), as well as other continents (ancient Eurasian back migration into Africa [41], Papuan ancestry replacing indigenous East Asian ancestry in remote Oceania [42,43] and Neolithic and then Bronze Age migrants entering southeast Asia and replacing indigenous residents [44]).

### Is paleogenomics as currently applied relevant to the work of archaeologists?

So what is it about this recent body of paleogenomics work that has archaeologists so on edge to the extent that it drew the attention of a recent Nature News article [12\*]? Despite being hotly contested over decades, the finding of evidence of a population replacement of Paleolithic/Mesolithic hunter-gatherers by Neolithic farmers is not likely to be the key factor. The reason this topic has garnered such interest is there is substantial archaeological evidence that this population transition may have happened, and in many ways the genetic data has simply helped confirm one hypothesis over the other. Instead, it seems that it is the finding of evidence of so many new migration events in the Late Neolithic/Bronze Age and later that is proving most troubling (though not perhaps in the way geneticists may think). Formalized by Kossina and then Childe, archaeologist have historically been

interested in migration as an agent of cultural change, but the arrival of processual archaeology led, particularly in Britain, to the subject largely being ignored for decades [45] (partly because migration was so difficult to identify and incorporate [46]) in favour of investigating internal social dynamics. A refocus back on migration and certainly mobility has seen somewhat of a resurgence over the last couple of decades [47], but this is still within a framework that involves fairly few migrants and very little biological or genetic impact, with the impact of large-scale migrations generally met with skepticism.

However, the recent paleogenomic work appears to demonstrate that migration has been pervasive during a period of significantly increasing societal and cultural complexity. This makes migration as a subject incredibly hard to now ignore for archaeologists (indeed, two of the main proponents for the importance of migration in archaeology, David Anthony and Kristian Kristianson [48], are now key collaborators with high profile paleogenomics groups). Yet, it is unlikely that the current presentation of these ideas in the paleogenomic literature will embolden current or future archaeologists to embrace these findings more generally. There are two major, somewhat intertwined, problems that currently exist.

First, archaeologists are not critiquing whether the migrations identified by paleogenomics using sophisticated population genetic machinery are actually occurring. Instead, the technical criticism arrives in terms of how these migrations are being ascribed to specific cultures. In many paleogenomic papers, there is a tendency (and often an analytical and technical need) to associate samples with particular archaeological cultures, for which all samples are then treated as possessing some kind homogeneous and pervasive social identity that is bound in space and time. The major critiques of this thus far have been directed to those studies examining Corded-Ware and Bell-Beaker-related individuals and their potential relationship to the Yamnaya [9,11\*,49\*], but are applicable to many other 'migration' scenarios described in the recent literature. This is compounded by the use of sometimes small numbers of samples to represent certain cultures from a particular geographic area as representatives of the entire culture at a supra-regional level. Yet often these archaeological cultures such as Corded-Ware and Bell-Beaker themselves show considerable variability in space and time, and even within cemeteries [9,50], which is not factored into the genetic analysis.

From a population geneticists point of view, this kind of simplification is somewhat understandable and will often likely have very little impact on the final analysis, given that the primary goal is usually to use ancient samples to better understand modern genetic variation. Though there may be a specific historical interest in some of these past events, I would argue that the aim for most

population geneticists at a higher level is to try and fit modern patterns of genetic variation using the simplest models possible that take into account past demographic events (for example fitting *f-statistics* using the ADMIXTUREGRAPH approach [51]), as this is how we are trained [52]. Although sharing an archaeological culture may not mean that a set of individuals are part of the same homogeneous social group in reality, this approach may be a good enough heuristic to find broad genetic connections compared to another group represented by a different culture, which can then ultimately help understand and model modern human population structure. However, for an archaeologists interested in the ancient individuals themselves and their social identity, this lumping is unsatisfactory, where sophisticated narratives of the individual migrants and their ancient communities are the intended goal.

The second related problem is that 'migration' in the sense used currently in the paleogenomics literature lacks sufficient detail to be of much use for an archaeologists attempting to disentangle the complex social dynamics within and between communities. To truly understand the role of migration as a social process and its contribution towards cultural changes, it is necessary to describe it as a structured behaviour [46,53], rather than treating it as an explanatory 'black box' [47]. Are the migrations occurring as a result of short range waves-of-advance movements, or as long-distance movements via leapfrogging models or stream migrations along established routes dependent on key kinship networks. Are there return migrants, and are some subset of individuals more predisposed to migration driving the signals? Although such models were implemented in past studies (even with classical markers [1]) and are part of the population genetics literature [54–56], they are lacking in the current paleogenomics literature when discussing migration. The finding that there is an increase of 12.3% of ancestry type X in population A compared to the preceding population B that is suggestive of a migration, is not particularly useful for examining these kind of models. It is also unclear to what degree standard population genetic parameters estimated from genomic data such as effective population size,  $N_e$ , and gene flow are relevant to models studied in archaeology, given they reflect (somewhat undefined) long-term population sizes and average rates of movements over time, rather than reflecting any kind of reality of census size and mobility in the ancient communities the archaeologists are actually attempting to study.

### A way forward

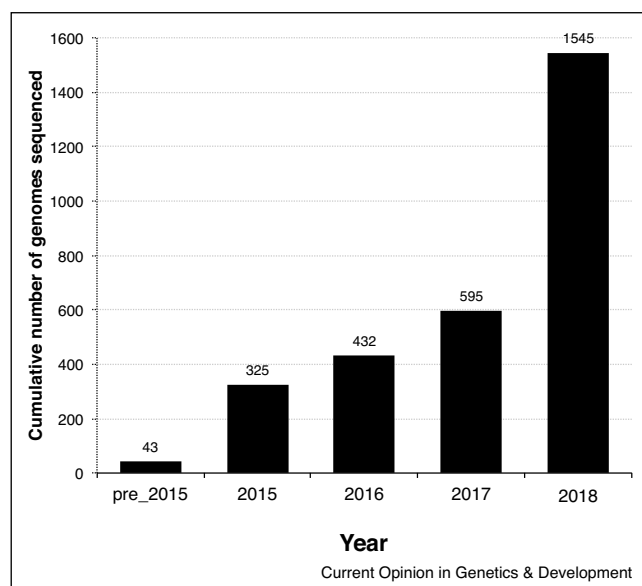
Given the issues discussed above, how can we progress such that paleogenomic data can be utilized in a manner that is truly interdisciplinary. As suggested recently by Furholt [11\*], to answer the kind of questions about migration that archaeologists are interested, systematic

investigation of local ancient communities will be required (for example as represented by individuals sampled from single cemeteries). These communities need thorough characterization not only to define levels of genetic relatedness, but also in terms of material culture, age, sex, stress and activity indicators, stable isotopes for diet reconstruction (nitrogen,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , carbon,  $^{13}\text{C}/^{12}\text{C}$ ) and strontium and oxygen isotopes for mobility ( $^{87}\text{Sr}/^{86}\text{Sr}$ ,  $\delta^{18}\text{O}$ ). Where possible, sites should be examined over multiple generations. In addition it will be incredibly useful to characterize the impact of disease in these communities, which is also proving to be a highly fruitful realm for paleogenomics [57–59].

Such data will provide detailed information on the social processes in play within these ancient communities. These fine-grained social dynamics can then be contextualized within networks of other such local systems, providing rich material to truly model migration as a structural process at both local and regional levels and allowing a thorough assessment of how it has contributed to change in culture that takes into account the full variability of the archaeological record.

No published work has yet to fully realize this framework. Though the amount of ancient genomes being produced is increasing at an astonishing rate (we have gone from 43 Eurasian ancient genomes since before 2015 to more than 1500 in the published literature at present, Figure 1), the emphasis has very much been on broad geographic

Figure 1



Barplot showing cumulative number of ancient Eurasian genomes published on a yearly basis up to 8th July 2018. Includes samples undergoing both whole genome shotgun and SNP capture sequencing.

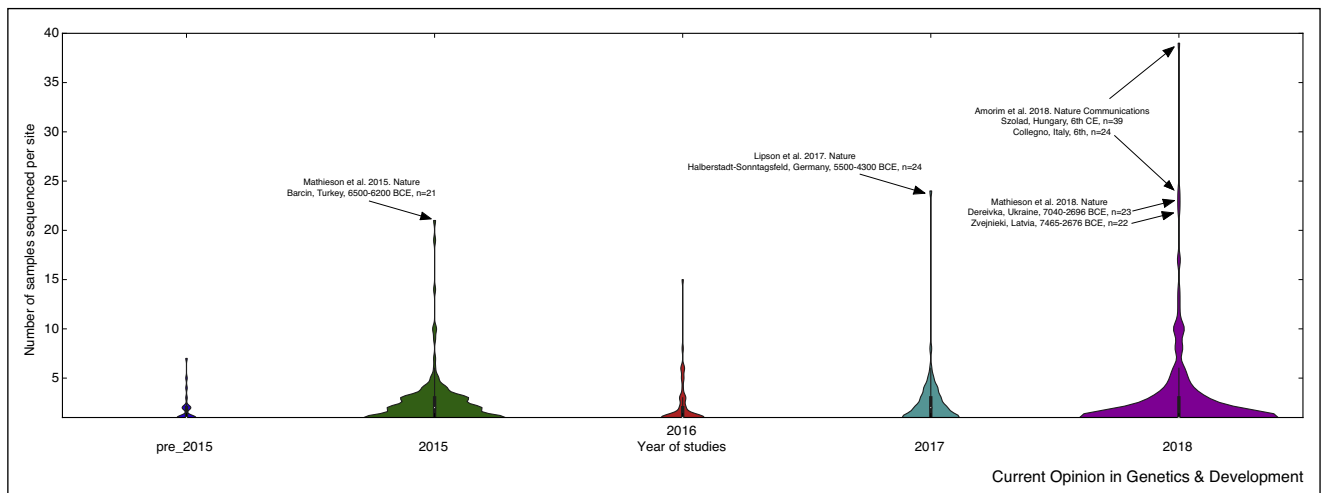
and temporal coverage, and the actual number of individuals sequenced per any particular archaeological site has not notably increased. There are only 24 archaeological sites where the number of ancient individuals sampled is 10 or greater, and only 6 where it is 20 or greater (the mean is 2.6 individuals sampled per site, Figure 2). Fortunately, there a couple of recent notable studies that provide a glimpse of the kind of insights we might expect to observe based on more community-focused sampling.

Though only examining mtDNA, Knipper *et al.* [60] focused their analysis on 84 individuals from a small region in Bavaria, Germany, spanning the period associated with Bell Beaker Complex (2500–2150 BC) to the Early Bronze Age (2150–1700/1650 BC). By combining full mitogenome haplotypes with  $^{87}\text{Sr}/^{86}\text{Sr}$ , and  $\delta^{18}\text{O}$  data they were able to find evidence of significant non-local adult female migration into the region accompanied with an increase in matrilineal genetic diversity, suggesting that these communities had practised patrilineal residential rules, with female exogamy and mobility perhaps being the ‘driving force of regional and supraregional communication and knowledge transmission’ in the region. In addition they identified potential biological kinship persisting across the apparent change in archaeological culture in the region.

Myself and colleagues also recently performed a study which we believe can act as a model to future community-level paleogenomics work, focusing our attention on characterizing the genomes of all individuals in two 6th century Migration Period cemeteries, Szólád in western Hungary and Collegno in Northern Italy, that have been associated with the proposed Lombard migration from historical texts [61]. We obtained genomic DNA using a combination of whole shotgun sequencing and a 1.2 million SNP capture protocol from 39 (out of 45) and 24 (out of 57) graves at these two sites, making Szólád the cemetery with highest number of samples characterized from a single archaeological site to date (Figure 2). By combining this genomic data with a full description of the cemetery’s funerary practices and grave goods as well as diet and mobility isotope data, we were able to make a number of inferences about the social organization of these two communities. One of the more striking features that could only truly emerge with the application of dense paleogenomic data such as this was the organization of both cemeteries around two large male-dominated biological kinship groups spanning three generations, both of which possessed genetic ancestry that would not typically be found in the region, rich protein-based diets and an abundance of grave goods compared to other people buried in the cemetery. In addition  $^{87}\text{Sr}/^{86}\text{Sr}$  data demonstrated that the first generation individuals in the large kindred in Collegno were likely non-local, unlike the second and third generation individuals. The presence of prominent kin groups (not necessarily biologically



Figure 2



Violin plot showing number of ancient Eurasian genomes published per specific archaeological site on a yearly basis up to 8th July 2018. Includes samples undergoing both whole genome shotgun and SNP capture sequencing. Locations with more than 20 individuals are indicated on the figure.

defined) is an important part of many long-distance models of migration, though future work applying our framework to other cemeteries surrounding Szólád and Collegno geographically and temporally will be key to obtaining a full understanding of social organization and dynamics in the region, and linking this to archaeological models of migration.

## Conclusion

Paleogenomic studies shaped around narratives of long distance migrations and population replacements are undoubtedly attractive, often garnering high profile papers with substantial press coverage, while it is not clear fine-scale inferences of social dynamics at the single cemetery level will receive as much attention. In addition, I appreciate the actual availability of samples may limit this kind of approach as we move further back in time. However, the transition from ‘top down’ geographically and temporally broad culture-based paleogenomic studies to more ‘bottom up’, community-focused studies is a necessary transition if the field is to move beyond being purely descriptive, to one that helps archaeologists study social processes in past people. Whether this transition is made will depend somewhat on whether the scientific community and funding bodies recognize the intellectual value of such work. However, the potential is huge, and if geneticists and archaeologists endeavour to promote such interdisciplinary work, involving true integration of methods and ideas with equal partnerships, then exciting new fields of research are likely to arise in the future.

## Conflict of interest statement

Nothing declared.

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