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Following the herd

*Population genetics of European sheep in time and
space*

PEDRO MORELL MIRANDA



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Abstract

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Sheep, which were domesticated in the Fertile Crescent about 10,000-12,000 years ago, have been a key resource for human populations ever since. We, however, know little about how they were domesticated, and what happened to them after their initial expansion from their domestication area into all corners of Eurasia and later Africa and the Americas. In this thesis I use state-of-the-art methods in population genetics and archaeogenetics to try to elucidate how sheep have evolved into the big diversity of modern breeds we see today and what demographic events shaped modern sheep genetic landscape in Europe. We were able to characterize the demographic history of three key locations in Europe for sheep: Iberia, the Baltic region and the Mediterranean islands. Our results confirm that the initial Neolithic expansion into Europe followed two independent routes, through the Danube-Rhine axis in Central Europe and sailing through the Mediterranean, and that mouflons from Corsica and Sardinia descend from this last early domestic sheep. We were also able to identify two independent expansions into Europe of Eastern ancestry, one related with archaic long wool, a phenotype retained by primitive European sheep breeds, and a later one associated with more modern woolly phenotypes. This last expansion, that occurred slightly before or during the Roman period in Iberia, didn't reached the Baltic region, whose breeds are still to this day displaying primitive phenotypes. Lastly, we were able to describe the phylogeny of modern wild and feral mouflons from the Mediterranean and the Middle East. My thesis highlight the dynamic nature of the demographic history of sheep, and how responsive it has been to human demographic and cultural changes.

Keywords: Sheep, Population Genetics, Ancient DNA, Wool, Demography, Wool, Mouflon

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A Andrea. Por la paciencia, el apoyo y el cariño que ha aportado a esta tesis.

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I **Morell Miranda, P.**, Soares, A.E.R., and Günther, T. (2023).
Demographic Reconstruction of the Western Sheep Expansion from Whole-Genome sequences. *G3 Genes|Genomes|Genetics*.
- II **Morell Miranda, P.**, Galindo-Pellicena, M.A., Mereu, P., Iriarte, E., Kaptan, D., Moreno-García, M., Antolino, J.A., Pirastru, M., Vural, K.B., Columbano, N., Tejedor, C., Arsuaga, J.L., Leoni, G.G., Royo Guillén, J.I., Naitana, S., de Gaspar, I., Rojo-Guerra, M., Smith, C., Barbato, M., Carretero, J.M., Somel, M., Özer, F., Valdiosera, C. and Günther, T. Ancient genomes reveal 7000 years of interconnected Demographic History between Sheep and Humans in Iberia.
Manuscript
- III Mereu, P.*, Pirastru, M.*, **Morell Miranda, P.***, Atağ, G., Columbano, N., Vural, K.B., Wilkens, B., Kaptan, D., Zedda, M., Barbato, M., Güler, M.N., Altinişik, E., Yazici, T.D., Eker, E., Togan, I., Naitana, S., Hadjisterkotis, E., Leoni, G.G., Somel, M., Özer, F. and Günther, T. Matrilineal phylogeographic structure of wild and feral sheep from the Mediterranean and the Middle East. *Manuscript*
- IV Larsson, M. N.*, **Morell Miranda, P.***, Pan, L., Başak Vural, K., Kaptan, D., Elias, A., Soares, R., Kivikero, H., Kantanen, J., Somel, M., Özer, F., Johansson, A. M., Storå, J. and Günther, T. (2023). Ancient Sheep Genomes reveal four Millennia of North European Short-Tailed Sheep in the Baltic Sea region. *BioRxiv*, 2023.06.26.544912. *In Review*

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The following papers were also published during my graduate studies but are not part of this dissertation.

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1. Introduction

Since the Last Glacial Maximum, European human populations have experienced several big events of population migration, admixture and replacement. There was, however, none as impactful as the Neolithic Expansion. This migration of people from the region known as the Fertile Crescent, on the Eastern coast of the Mediterranean and the Middle East, exported a set of cultural and technological assets that changed significantly how humans lived and how they interacted with their environment. Before leaving the Fertile Crescent, these Neolithic populations developed a set of novel tools and techniques to exploit more efficiently their surroundings. Important examples of this are bow-drills [1], wells [2] and pottery [3]. There is, however, a key single technical development that allowed all of the latter changes to happen: domestication.

The ability to control the evolution of another species was not new for human populations. Dogs, the first domestic species, domesticated between 18,000 and 35,000 years ago [4], were already ubiquitous in Eurasia when the first groups of Middle Eastern hunter-gatherers started trying to control other species' evolution [5]. However, our association with dogs, as successful and longstanding as it has been, could not have the impact of the ones that harboured the Neolithic Revolution for one simple reason: dogs were not a reliable food source. While cynophagy (dog-eating) has been extensively documented in Europe (including on one of the sites studied in this thesis) [6, 7], dogs require higher quality food than livestock species to produce a smaller amount of meat. During the Early Neolithic these hunter-gatherers started domesticating some of the local species they had been exploiting seasonally, like wheat, barley, chickpea, sheep and goats [8, 9, 10]. This translated into those early small groups of nomadic hunter-gatherers becoming more sedentary and larger groups that were less dependent on seasonal migrations of prey and the availability of plants to forage. This transition into sedentarism also meant they could build more permanent structures and more complicated tools that they could store, which allowed them to develop better stone-carving techniques, pottery, more complex cultural artifacts (figurines, carvings, etc.) and a megalithic culture with burials and ceremonial/ritual sites marked by large stone structures (e.g. Göbekli Tepe) [11].

The initial techniques and technologies associated with growing and caring for the early domesticates expanded fast from the early domestication sites to conquer all of the Fertile Crescent, where other species, like linen, cattle and pigs were also domesticated [9]. At some point around 8,000 years ago, these Neolithic farmers expanded from the Fertile Crescent both eastwards and

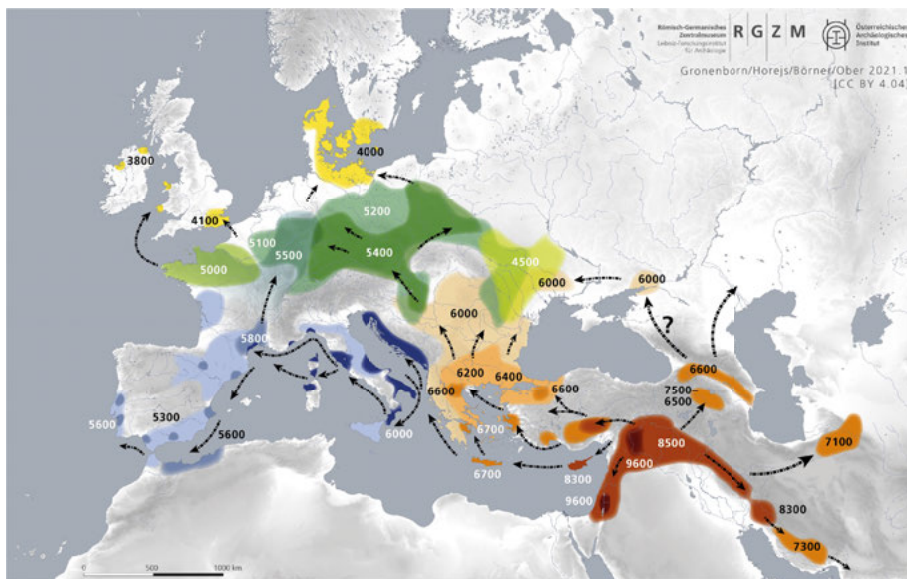


Figure 1.1. Map of the Neolithic Expansion. Arrows represent inferred main migratory routes and the color gradient represents simplified isochrones for said expansions. Dates based on direct dating from different studies, and presented in cal BCE [12] [CC BY 4.04]

westwards. In Europe, this expansion followed two independent routes: following the Danube-Rhine axis inland across Central and Northern Europe, and through the islands and Northern coast of the Mediterranean into what nowadays are Greece, Italy, Spain and Portugal [13]. The expansion inland was quite slow, taking several thousand years to reach Scandinavia, the British Isles and Ireland [14, 15], while the expansion through the Mediterranean was significantly faster, which most scholars agree strongly supports that this expansion occurred by sea [16, 17, 18, 19].

This has not been the only time domesticating another species has translated into big technological and demographic changes. Other regions of the world have had their own independent Neolithic revolutions [20, 21, 22]. There is a later domestication event, however, that had singular consequences for most populations in Eurasia: the domestication of the horse [23]. This domestication, which recent analyses suggest happened in the Volga-Don basin, has been associated with the expansion of a culture from the Pontic steppes, known as the Yamnaya [24], and its expansion into the East [25]. For some time the Western expansion of this Steppe ancestry was also assumed to have been initiated by being able to ride horses and carts, but the same study that identified the domestication origin showed that the expansion westwards of the human Steppe ancestry started before the domestication of horses [24]. Burials of the Corded Ware Culture in Central and Northern Europe [26] presented

already Yamnaya ancestry by 4,900 years ago, while the domestic ancestry did not expand outside the Pontic steppes until a few centuries later. This association of the expansion of this ancestry in humans and the arrival of domestic horses may be explained by the fact that they expanded quickly into Europe after that. Horses led then the expansion of Steppe ancestry into the other western cultures associated with this ancestry, such as the Bell Beaker culture [24, 23, 27].

Since its domestication between 12,000 and 10,000 years ago, sheep has been one of the most popular livestock species in Neolithic settlements [28, 29, 30], and nowadays they are a domesticate that has been exported to all continents but Antarctica and has adapted to hundreds of different environments. This continued importance through millennia of human exploitation not only makes sheep evolution and demographic history interesting on their own merit, but places them as a useful proxy for studying fine-scale patterns of population movements in the human past. Having that in mind, sheep and other domesticates have been extensively studied by zooarchaeologists. There are, however, limits to what morphometrics and other classical methods can tell us about ancient animals, as most material is incomplete and fragmentary. Molecular approaches, on the other hand, have proved in several species to be extremely useful when combined with archaeology and other fields to untangle the recent (and not so recent) past, and population genetics have had a particularly relevant role in most of these studies [31, 32, 33, 34, 35, 36].

1.1 Iberia since the Neolithic

Iberia, the peninsula that lies at the Western extreme of Europe, was reached by the Early Cardial culture of Neolithic farmers soon after they left the Fertile Crescent. The first Iberian settlements can be found in the North-East, and date to up to 7700 before present (BP) [37]. These Early Neolithic Iberian settlers started expanding, using the coast and river basins of the Ebro, Guadalquivir and Guadiana to ease their expansion [38, 39, 40, 16]. The total neolithization of inland areas of Iberia took more than a millennium of expansion by land into the Northwestern region, which suggests that the harsher sea and smaller river basins of the Northwestern coast acted as a barrier while the Eastern and Southern ones did not [41]. Since their early arrival, sheep have been one of the most popular livestock species [42, 43], with massive sheep herd movements (sometimes of hundreds of kilometers) that can be traced to the Roman period or, according to some authors, even to the Neolithic era [44]. Sheep became particularly important in Iberia during the late Middle Ages, with the development of the fine wool Merino breed, which displaced Italian and British wool in the European Medieval market as the preferred wool of the wealthy [45].

1.2 Scandinavia, the Baltic Sea and modern North European Short-Tail breeds

Scandinavia and the Baltic region were one of the last regions to receive the Neolithic farmers, who arrived to this region following the Danube-Rhine route, around 6000 BP [46]. While this region is not characterized by an extensive presence of sheep, at some point between the Bronze Age and the Iron ages, wool production became one of the main local industries, producing from clothing to boat sails [47, 48]. In modern times only a few regions are densely populated with sheep (e.g. Gotland), while most of the Baltic Sea and Scandinavia is pepper-sprayed with small populations of local breeds, or landraces, of sheep belonging to the North European Short-Tail (NEST) group. These sheep, which can be found not only on the Baltic, but also in some regions associated with Viking activity during the Iron Age [49], have been proposed by some authors as displaying the original phenotype of domestic sheep in Europe [50, 51]. Other authors, however, have linked their phenotype with a secondary expansion related to wool [52].

1.3 The Mediterranean islands

The seafaring first farmers that left the Fertile Crescent during the Neolithic Expansion in the Mediterranean quickly populated some of the biggest islands, such as Cyprus, Corsica and Sardinia [53, 54]. Cyprus seems to have been reached soon during the early Neolithic. Sardinia and Corsica, however, only got populated by farmers once they left the Fertile Crescent. These islands are now characterized by local production breeds and landraces, but also for small populations of free-ranging, wild-looking mouflons. These were thought to be remnants of a wild European ovid, but several lines of evidence seem to agree in the fact that all three populations were introduced by humans [53, 55, 56, 57]. While the feral nature of the Corsican and Sardinian mouflons is now commonly accepted [57, 58, 59, 45], the relationship between the Cyprus mouflon and domestic sheep is not clear [60, 61, 55].

2. Population Genetics

Mammals are diploid organisms. This means that for each chromosome, we have two copies; one from the mother, and one from the father, so we can have two different alleles at the same time, which drove Gregor Mendel to postulate his Three Laws of Inheritance [62]. Those inheritance laws, however, only apply to certain types of inheritance and there are other processes not covered by them. Now, we understand the chemical and structural processes that drive how we inherit our characteristics (to a decent extent, at least). This has led us not only to be able to track how a concrete mutation (or changes in the DNA sequence) is inherited inside a family, in what is known as a pedigree, but also to start tracking down these mutations through entire populations thanks to mathematical models that allowed to combine genetics with Darwin's Evolution Theory [63, 64, 65]. These models introduced concepts such as genetic drift, or the random processes not derived from selection that can alter the allele frequencies of a population over time. This effect is population size dependent and is stronger in small populations than in bigger ones, where the individual randomness of each reproductive event has less impact on the population's gene pool. The study of this drift is informative of the relationship between different populations. Two populations that have been separated will drift independently and through quantitative methods we can estimate how much time has passed since they started diverging. Other demographic events such as migration, bottlenecks (fast reductions of the size of a population) admixture between populations, or strong selection have an effect on the allele frequencies of the population that can be detected hundreds or thousands of generations later. These changes can be used to reconstruct the evolution and demographic history of the populations of study in a range from hundreds to hundreds of thousands of years.

During several decades since its inception, population genetics remained mainly a theoretical field, studying how mutations (or novel allele variants) behave under an evolutionary framework. This changed as our knowledge of how genetic information was encoded in our cells grew [66, 67, 68, 69] and we became able to access the actual sequence of DNA [70, 71]. It was, however, the sequencing of the first whole genome of a human and the associated technologies developed to achieve such a feat that pushed population genetics into the spotlight [72]. With almost a hundred years of accumulated statistical methods for describing genetic variation over time and a fastly decreasing cost of producing sequencing data due to the development of Next Generation Sequencing (NGS), suddenly we were not looking at single loci anymore, but

analyzing hundreds, thousands or even millions of loci all over the genome for tens, hundreds or thousands of samples. This offered new possibilities for population genetics methods, as now we had many recombining loci, which could act as somewhat independent “samples” of the same process that we would describe before looking only at one locus. This was a big improvement, as it allowed us to overcome the stochasticity of a single locus, to a certain extent, and allowed us to develop tools to describe common patterns across the whole genome which will be discussed in the Methods section. Consequently, this has substantially increased resolution and allowed us to infer more complex processes, such as the demographic history of a set of populations with several waves of gene flow from different sources (or even different species) [73, 74].

2.1 Ancient DNA

While applying population genomics to whole genome data has allowed us to describe the genetic variability of modern populations of several species all over the world and trace evolution and demographic history [75, 76], this approach soon showed conflicting results when trying to trace the past [77], as some demographic events mask past signals left in the genome. To circumvent this issue, genetic material has been extracted directly from ancient bone samples of up to 1.4 million years of age [36], and for ancient sediments of over 2 million years [78]. This genetic material, while fragmented and damaged, has been pivotal in describing past demographic and selective events in humans [79, 34] and non-human animals alike [35, 80, 10, 81]. Since the first attempts at extracting ancient sequences in the 1980s [82, 83] to the first whole genome of a human [84], the development of Next Generation Sequencing changed completely the amount and quality of data we were able to obtain from ancient samples. In 2023 the milestone of 10,000 ancient human whole genome SNP capture sequences was reached [85], with several hundreds of individuals whose whole genome have also been shotgun sequenced. While no other species can compare to this fast rate of sequencing, other popular species, such as horses, can count their published ancient genomes in the hundreds [24], and new sequences are being published every year for more and more species [86].

Ancient DNA (aDNA) brings, however, a whole lot of new issues to consider. DNA is not a stable molecule, so it degrades with time, the action of the elements (especially heat), or by the enzymatic activity of other organisms [87] and its own intracellular processes. This means that ancient remains will yield low amounts of DNA sequences while sequenced, and these sequences will be fragmented and damaged in several ways. It also means that ancient samples are extremely susceptible to contamination, both modern (from soil during excavation, from the researchers etc.) and ancient (organisms that may have left their DNA in the sample during deposition). All these features of

ancient DNA mean that it needs to be treated differently from modern DNA so we can make use of it in our analysis.

Nowadays, the preparation of libraries for sequencing is done in clean labs with extreme precautions and after thorough cleaning of the samples to avoid as much contamination as possible [88]. Sampling from optimal locations that have not been exposed to big temperature changes, as caves (e.g. Sima de los Huesos or Denisova Cave) [89, 73] or directly from frozen individuals in glaciers [90] or in the arctic permafrost have proved that, in ideal conditions, ancient DNA can be useful for hundreds of thousands or even millions of years [33, 91, 36, 78]. We also target the bones that are more likely to have preserved DNA, such as the petrous bone of the inner ear and the cementum of teeth [92, 93]. Down to a certain length range, DNA fragmentation have not been such big of an issue, as the most common sequencing methods in the second wave of NGS technologies use short read lengths [94]. However, if DNA is too fragmented, it will not be useful for downstream analysis, as fragments that are too short are extremely hard to uniquely map to a reference genome. This means that, while we can use short-read sequencing to deal with this fragmentation to a certain extent, if a sample is too fragmented, its sequencing yield will still not allow us to map it and analyze it with enough confidence in our results.

2.1.1 aDNA Damage

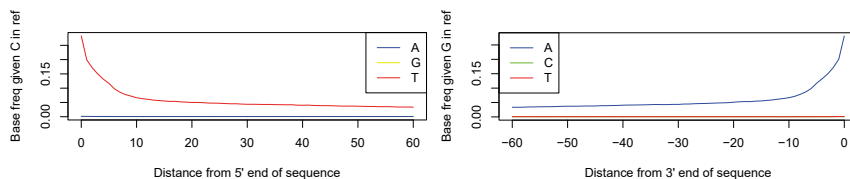


Figure 2.1. Deamination plots characteristic of ancient DNA. In the plots we can see an increase in the frequency of C-T substitutions towards the 5' end of each read, and G-A substitutions in the 3' ends. The frequencies depicted in these plots correspond to a sheep sample from El Portalón, in Northern Iberia, that lived during the Bronze Age period (dated to 3703 ± 123 Cal BP). These plots are part of Supplementary Figure 1 in Paper II

With the degradation of biological material after the death of the individual the genome loses its mechanisms of repair [95]. Hydrolytic and oxidative processes may change DNA molecules in several ways that can compromise our ability to sequence them. Hydrolytic processes can cause either the deamination of cytosine into uracil or convert a methylated cytosine into thymine [95]. Less common hydrolytic processes, such as guanine to adenosine substi-

tutions may also occur. These substitutions happen mostly at the terminal ends of the fragmented DNA sequence, which are more frequently single-stranded and more exposed to hydrolysis [96]. Oxidative processes can cause misincorporations of nucleotides, because of the “attack” of free radicals that the cell can no longer eliminate. Guanine is especially susceptible to the action of these free radicals [96]. After undergoing PCR amplification, this damage results into specific patterns of DNA damage (C to T changes in the 5’ end, and G to A changes in the 3’ end, as can be seen in Figure 2.1) that allow us to identify ancient sequences and check if there is modern contamination in our samples.

2.1.2 Contamination and authentication of aDNA

From the fragmented and altered nature of ancient DNA derives the fact that it is quite susceptible to contamination, both from environmental sources and from the researchers sampling it [88]. Even if bioinformatics is now capable to discriminate between contaminant and endogenous DNA using statistical frameworks to estimate the proportion of contamination [97] and even to filter our non-endogenous sequences [98], contamination is still a heavy burden, as the more contaminant DNA is present in the sample, the smaller fraction of endogenous DNA will return from sequencing.

Once we have sequenced our ancient DNA samples, best practices include filtering the data, aligning our reads to our organism’s reference genome to keep only the reads of endogenous DNA, and checking for damage patterns and fragmentation. This is done to check that we have sequenced ancient DNA and not modern DNA from the same species. While this may not be an important risk for extinct megafaunal projects, for example, past experiences have shown the importance when studying species that are still alive nowadays, especially in humans, making it a standard procedure nowadays [99, 100, 101, 102, 103].

3. Sheep (*Ovis aries*) as a domestic species

3.1 Domestication

Sheep were domesticated in the fertile crescent, probably in Eastern Anatolia or the Zagros mountain range, in North-Western Iran [9] from wild Asiatic Mouflons (*Ovis gmelini*). We start seeing clear evidence of exploitation of domestic sheep in the Early Neolithic settlements of Çatal Höyük [104] and Aşıklı Höyük [28, 105, 29], in Anatolia. The oldest levels of these sites already show the presence of sheep and goat pens and remains, with a clear preference for the first over the latter. This suggests that ovicaprids were already common domestic animals by 9000 BP. While the presence of these species in pens has been interpreted as confirmation that domestication happened before these settlements started to flourish, some researchers have suggested that domestication may have happened as they established, matured and grew in population [29]. This hypothesis is based on slaughter patterns at different levels in Aşıklı Höyük, where it seems that in early stages most of the sheep were wild youngsters that were kept in pens for slaughtering through the year, while in later levels there is a change in the ratio of young vs old and male vs female, which was interpreted by the researchers as evidence of an increase of domestic reproduction and a reduction of wild captures. This aligns with the results of early archaeozoological studies, which used morphological markers, such as the reduction of general body and cranium size as a clear sign for domestication [101], which timed the domestication of sheep and goats at around 10,000-9,500 BP.

These dates, however, have been contested by more recent studies, as their results show that this correlation is more likely explained by a change in culling strategies (focusing on young males instead of old animals), instead of a fast morphological change due to domestication [106, 107]. This change in methodology lead to new and more subtle markers for studying domestication. Some of these markers that were especially informative were sexual dimorphism and prey demographic composition, which showed that domestication may have started way sooner. In Iraq and southeastern Anatolia, unusual profiles of sheep bone assemblages were found, dating to 12,000 BP, that may suggest early attempts at manipulating herd demographics in order to increase production while assuring the viability of prey populations [108]. This pattern is believed to appear due to a change in hunting tactics, targeting male individuals, as a response to the stresses suffered by herbivore populations during the Younger Dryas climatic event [108]. This pattern has been interpreted as an initiation

of the "Prey Domestication Pathway" [109], a process in which hunters' management of wild populations gradually increases until they end up as domestic herds. This is the most supported hypothesis for how sheep, goat and cattle were domesticated.

After their domestication, sheep were transported as livestock, first to all of the Fertile Crescent, and then along the expansion of Neolithic farmers through Europe and Central Asia. The expansion into Europe followed two independent routes: from the Balkans and up the Danube [110] and by sea following northern coast of the Mediterranean [110, 19, 111, 54]. By 7450 BP we can find the earliest sheep bones from Western Iberia in Sintra, Portugal [16], way sooner than other regions of inland Europe. How this affected the initial population structure of European sheep is, however, poorly understood [112, 30].

This maritime expansion also affected the islands of the Mediterranean, with the first sheep arriving to Cyprus by 10,000 BP [53]. This early presence of free-roaming sheep in the island has always begged the question of whether modern Cyprus mouflons' origin was wild or they came from a domestic stock.

Later on, once the Neolithic farmers started expanding West, they also arrived to other islands, such as Corsica and Sardinia, where we also can find modern free-roaming individuals. While these sheep present a similar phenotype to their wild relatives, they seem to descend from already domestic sheep and are now considered to be a remnant of Neolithic sheep that became feralized in the predator-free environments of the islands [57, 113, 56].

3.2 Later expansions reshaped European sheep populations

As mentioned before, Neolithic sheep looked way more like their wild ancestors than like modern European improved breeds. Thousands of years of artificial selection have changed them severely (see Figure 3.1). There are, however, a few key traits that archaeological evidence suggests were not first selected in Europe. The most important is, without a doubt, wool. Wild and feral mouflons have a short under-layer of primary fibers of wool and an over-layer of thick, hard kemp [52]. This is a common phenotype for mammals of temperate climates, as they can shed the under-layer every spring to stay fresh during the hot season and regrow it for the cold one. Both direct remains of skin and wool and wool industry remains (the tools used to process wool) suggest that the long wool we associate with most sheep breeds today appeared somewhere in the Middle East or Central Asia [52, 45, 114]. This trait became popular quite soon after and by the Early Bronze Age (aprox. 4,000-2500 years ago) we have wool fabric remains in archaeological contexts in Northern and Central Europe and Northern Iran [52, 114]. These findings, along with the spread of tools associated with wool processing during the late Chalcolithic and Early Bronze Age, have been interpreted as a secondary expansion into

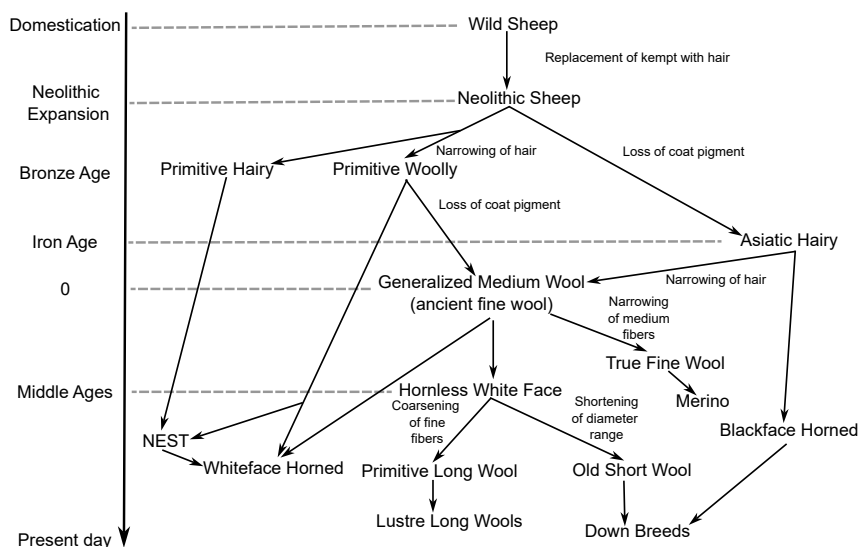


Figure 3.1. Evolution of wool. Adapted from Ryder, 1964 [52]. This hypothesis for the evolution of wool, while probably inaccurate and too "British-centric", highlights the complexity of wool evolution and the diversity of modern woolly phenotypes.

Europe of sheep with longer wool and thinner hair. This is also the period when we see a change in how humans exploited their animals in Europe from using them just for slaughter to produce meat and skins to develop "secondary uses", such as traction, milk, or, in the case of sheep, wool. This change is known as the Secondary Product Revolution [115, 116].

These Bronze Age fabrics, however, were still archaic in comparison to modern wool, with most of the samples still showing some medium hairs (Ryder, 1964 assumed that most of them were extracted manually during processing of the wool) [52] and that the wool had been shed or plucked out of the animal, not sheared as modern wool for most breeds [52]. While there are still European sheep with medium hair and some that also are able to shed their wool seasonally, those breeds tend to be associated with isolated island populations and not with production breeds that have been actively selected for their wool production. Modern European woolly sheep breeds have been classified depending on their wool quality (coarse and fine, long and short wool), length (short and long wool), the color of their faces (whitefaces and blackfaces), the tail (fat, thin, long and short), and by the presence or absence of horns in females or in both sexes [52, 117]. Most of these novel traits have been assumed to develop once woolly sheep were in Europe, with long wool being one of the main raw material exports of England in the Early Middle Ages, mainly pro-

duced by Cotswold sheep, until the fine wool Spanish Merino took the crown as Europe's favourite wool in the late Middle Ages [52, 118].

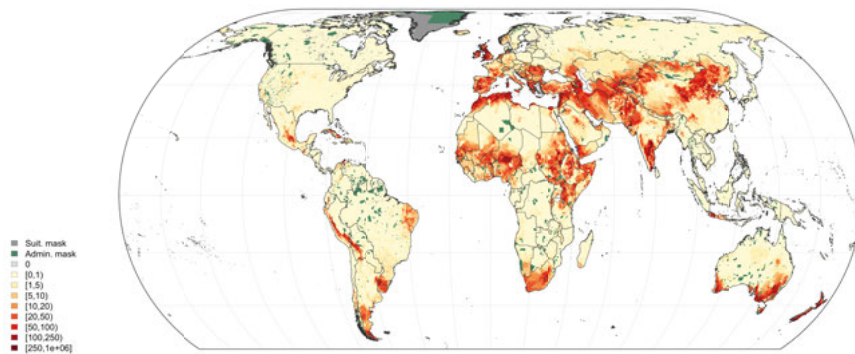


Figure 3.2. Map of the distribution of sheep around the world in 2010. Data from the Gridded Livestock of the World 2010 (GLW3) [119] [CC0 1.0]

3.3 Sheep genetics

Sheep are still today one of the most important livestock species in most regions of Eurasia (see Figure 3.2), with breeds adapted to cold and hot, and humid and arid environments alike. While this is an extremely popular and economically relevant species, until recently its genetic variability was not as well studied as other, more charismatic species, such as the dog or the horse. With only a handful of studies using a few genetic markers such as the matrilineally inherited mitochondrial DNA [120, 121, 122] or the patrilineal Y chromosome [123, 124], only broad patterns of diversity could be described. Modern sheep display 4 different haplogroups on the paternal Y chromosome, with yA being the most common in modern European commercial breeds and yC in European archaic ones [125]. On the maternally inherited mitochondrial DNA, 5 different and somewhat geographically structured mitochondrial haplogroups have been described [120, 57, 113] (mtA is the most common one in Asia and the Middle East, while mtB is prevalent in Europe and European mouflons), while Cyprus mouflons belong to a lineage related to wild mouflons from Anatolia and Iran, but is also part of the domestic mtC - mtE haplogroup complex [60, 61, 55].

It seems these haplogroups diverged before domestication, which has been presented as evidence of up to three independent domestication events [121]. This, coupled with the fact that sheep show higher levels of genetic diversity in comparison with other domesticates [76], has puzzled researchers for years, as most domestication events and posterior expansions meant severe bottlenecks on the domestic populations [126]. This pattern, however, could be explained

by multiple domestications, by early admixture of the recent domesticated population with wild individuals, or by the first domesticates being recruited from a diverse and structured wild population. Or a combination of all three phenomena.

One study, using retroviruses nested in sheep's genome at specific regions, was able to identify a secondary expansion of ancestry into Europe and Africa from the East after the original expansion [50]. This second wave massively reshaped the distribution of the retrotypes of most modern European sheep, while the archaic breeds and mouflons shared a more primitive retrotype. The authors of the study interpreted this as the expansion of wool during the Secondary Product Revolution, in contrast to the more archaic, coarse wool sheep presenting the original Neolithic phenotype. This interpretation, however, does not take into account the phenotypical differences between feral mouflons in the Mediterranean and those primitive breeds (e.g. coat color, kemp vs hair or short vs long wool). These phenotypical differences, added to the lack of proper dating of this expansion of the retrotype associated with modern breeds (enJSRV18), allows for the possibility of the detected expansion not being the secondary expansion related with wool production, but a later one associated with more modern phenotypes [45].

It was not until the first publications with the Ovine50kSNP beadchip that big patterns of genetic diversity could be described [76, 127, 59]. These studies, however, mostly highlighted the complex demographic history of this species, which could only start to be untangled using big whole genome data [128, 129, 125, 130, 131, 132].

If we look at modern sheep's overall genetic structure, several studies have shown that modern breeds form a cline between Eastern and Western ancestry, with Middle Eastern and African breeds in the middle, and little gene flow with wild mouflons [59, 132]. This does not mean that some populations did not admix with their wild relatives, especially in areas where local adaptations were needed to survive. As with other species, adaptive introgression and general admixture with wild animals have occurred wherever newly arrived domestic and locally adapted wild sheep met [133, 134, 135, 132]. In Europe, as there is no direct evidence of any wild ovid prior to the arrival of Neolithic farmers, this was not the case. Some domestic sheep populations, however, admixed at some point in their history with feral European mouflons [127, 59]. A recent study pointed out that feral European mouflon, now living only on the islands of Corsica and Sardinia, may have been admixed with a close relative to Snow and Bighorn sheep (*Ovis nivicola* and *O. canadensis*, respectively), two ovid species from eastern Siberia and North America [131]. This signal suggests the presence in Europe of some kind of basal ovid or close relative to the genus. With no fossil evidence of such a species, however, it is hard to tell if this is a real signal or an artifact caused by basal ancestry retained by the Mediterranean mouflons that the Asiatic mouflon samples have lost or masked by admixing with modern sheep.

As described above, genetic studies on modern DNA have helped us describe the actual genetic diversity of the species, but have highlighted also a lot of unknowns around the domestication and posterior demographic history of sheep. Ancient DNA has been successful in answering similar questions in other species, such as horses, demonstrating that the first known domesticated horse population is not the ancestor of modern horses, but of the feral Przewalski horses of the Eastern steppes, and that modern horses descend from a secondary domestication in the Volga-Don region [23, 24]. Pig’s demographic history has also benefited from the increased temporal resolution offered by aDNA. This species’ modern DNA suggested European pigs had been domesticated independently from their Fertile Crescent counterparts [136], even if archaeology pointed at the Fertile Crescent as the domestication origin [9]. Ancient DNA studies, on the other hand, contradicted this interpretation, as Neolithic European pig share almost all of their ancestry with those of the Fertile Crescent. This, however, changed over time as pigs admixed with their wild relatives in Europe, causing an almost complete genetic turnover [137, 80]. In goats, aDNA was able to offer evidence for a complex mosaic domestication, with several distant wild populations contributing to the original domestic gene pool [10] and also study how these domestication events developed in the Zagros region [138]. In comparison to all these domesticates, genome-wide ancient sheep sequences are still few in number and mostly from samples with poorly preserved DNA [139, 30]. This has hindered a proper investigation of how this early domestication happened and how modern morphological and phenotypic diversity developed. Yurtman et al., 2021 [30] found out that the geographical cline described in modern populations [127, 59, 132] can already be seen in the Early Neolithic, with Anatolian Neolithic samples showing higher levels of genetic affinity to modern Europeans while the Neolithic samples from Obishir, in modern Kyrgyzstan [139] had higher affinity for Eastern breeds. The poor DNA preservation, however, made it difficult to describe any fine-scale patterns within Anatolia. The only example of a well preserved ancient genome, from a mummified leg of a sheep from the Sasanian Empire (approx. 400 CE, in modern Iran) [140] is not close enough temporally to study these processes, nor inform us of continental gene flow that probably happened way before this individual was alive. Lastly, there are no proper time-series data available that covers long periods of time with several cultural backgrounds (other than the low-coverage Neolithic dataset from Yurtman et al. 2021[30]). This kind of dataset can be informative to track demographic changes, and specially on the extreme ends of population movements. While putative source regions such as the Fertile Crescent can present several lineages with little divergence moving in different directions, populations on the extremes of the different expansions will receive markedly drifted lineages with each migration.

The limitations of the available data only highlight the need for further sampling of medium and high-coverage genomes from relevant geographical and

temporal ranges to disentangle the complex demographic history and evolution of domestic sheep in Europe and other regions.

4. Methods

Disentangling the demographic history of a species using ancient genomes must comply with specific methodologies and the highest quality standards in order to obtain trustworthy and useful results. While there are variations and alternatives to the methods described in this chapter, I will focus on the methods used to produce the results described in this dissertation. Some methods are also mentioned due to their popularity within the ancient DNA literature, even if they were not applied in any of the projects listed in this dissertation, as to describe the state-of-the-art of ancient DNA research.

4.1 Sample collection and preparation

While modern samples can be obtained *in-situ* at farms or in the field (both from intrusive means, such as blood or tissue, or from non-intrusive ones, such as hair and scat), ancient DNA samples are obtained from archaeological excavations and museum collections. Before sampling, bones are studied to look for viable candidates. This includes the bone type (e.g. petrous bone and teeth have proven to preserve ancient DNA better than other, longer bones [92]), the aspect of the bone and, sometimes, if it weights what it should [88].

Once samples have been selected, and destructive sampling has been approved, samples are moved into a clean, dedicated lab prepared to avoid contamination from modern sources. These labs are actively “decontaminated” with bleach, ethanol, and UV lights and have HEPA-filtered positive air pressure systems to prevent contamination from airborne sources. Lab personnel must wear protective suits, two layers of gloves, and masks, and follow strict protocols to avoid contamination [141].

In order to minimize environmental and modern contamination, the sample is radiated with UV light and then its external layer is removed with a drill. After the mechanical removal of putative contaminants, the exposed surface is wiped with bleach before being radiated again with UV light [88].

Ancient samples for this thesis were collected from archaeological collections from Sweden, Finland, Sardinia and Spain. All available samples were inspected in-house for external signs of poor preservation, and those samples that did not comply were excluded from further preparations. Samples that passed the inspection were decontaminated as described above. Samples for whom teeth and jaw were available were sampled independently.

4.2 aDNA extraction, library building and sequencing

Extraction of ancient DNA was performed by the SciLifeLab aDNA unit, at Uppsala University using a silica-based extraction protocol by Yang et al [142], with modifications described in the Papers. Ancient DNA methods normally use silica-based columns to minimize the co-extraction of inhibitors of downstream steps, such as library building and amplification [143]. Extraction and library blanks were added every 10 samples as negative controls.

The most popular approaches for producing aDNA sequences since the development of NGS data are target-enrichment and shotgun sequencing. While shotgun approaches aim at building "libraries" of short segments of DNA, and then amplifying and sequencing all of them, target-enrichment approaches selectively capture known regions of interest from the library before amplification and sequencing (e.g. mitogenomes [144] or a wide arrange of SNPs over the whole genome [145]). Shotgun sequencing has several advantages, as it also captures previously unknown variation particular to that sample, but if the proportion of endogenous DNA is low, most of what is sequenced is not going to be our sample's genome. This translates into a higher sequencing cost, as more resequencing will need to be done. Potentially, this may also mean more material from the original remains will need to be destroyed, if we want to bring our sample to an acceptable level of depth of coverage. Enrichment methods, on the other side, work well with poorly preserved samples where the endogenous DNA content is quite low. In humans, a popular capture panel, developed to target 1.24 million SNPs for ancestry analyses has been used in almost 70% of the published ancient genomes [145, 146], while other capture panels have been used, for example, for capturing specific pathogens [147]. These methods, however, are always exposed to certain limitations related with the enrichment for known SNPs: difficulty to compare with other data, as only overlapping regions can be compared [148], increased clonality and reduced data complexity [149] and, most importantly, ascertainment bias, particularly if the sample's population is distant or drifted from the ones used to design the capture panel [150]. Some studies use chemical treatments in combination with shotgun sequencing to repair the deaminations associated with aDNA (e.g. uracil-DNA-glycosylase, or UDG) [151, 152]. This process, however, increases the cost of sequencing and requires extra lab procedures.

All data generated for this dissertation is composed of shotgun sequenced whole genomes. This technique requires DNA extracts to be converted into sequencing libraries, which then are used for untargeted cluster amplification for parallel sequencing. Single-stranded blunt-end libraries have been proven to work better at amplifying short and degraded fragments of DNA, but the increased cost and complex implementation in comparison with double-stranded blunt-end library preparation made us side with the latter. Double-stranded library building is done using a modified version of the Illumina protocol [153],

adapted to include indexes for each sample that is going to be analyzed in the same lane. First, DNA fragments are repaired by the extension of overhanging single strands at the extremes. Adapters are then ligated to these blunt-end fragments, and a fill-in step matches the adapter's sequence with its complementary. Indexing oligos are added once the double-stranded libraries are prepared to be able to identify each sample. The ligation of adapters is what facilitates the sequence to attach to the solid flow cell of the sequencer machine, and adding these indexes allows us to pool together several samples in the same sequencing run, decreasing time and money invested on each genome [153].

One of the most popular NGS methods, especially in aDNA studies, is the one developed by Illumina (Illumina/Solexa company). This method is based on fixing the fragments of DNA to a glass support (known as a flow cell), followed by several cycles of amplification and denaturalization of the oligos to create clusters of complementary sequences. Once the clusters are formed, fluorescent nucleotides are added, so that the order of the sequencing can be recorded by a camera.

4.3 Data processing

Using different sequencing platforms and bioinformatic pipelines can lead to subtle biases that can imitate fine-scale demographic or evolutionary patterns. One way to avoid this methodological issue is to be as consistent as possible with the sequencing and preprocessing of the data. This includes pipelines for both ancient samples and modern reference panels and datasets.

For this thesis, modern data for Paper I was gathered from publicly available sources such as the International Sheep Genome Consortium (ISGCv2) [154] for domestic breeds and the NEXTGEN project for wild mouflons [128]. The NEXTGEN data is distributed as raw FASTQ files, while the ISGCv2 data is distributed as preprocessed VCF files, so the wild mouflon data was processed following the same pipeline. For Papers II and IV, another dataset of publicly available modern sequences of domestic genomes was assembled from publicly available data [130, 129, 125]. As this dataset was going to be compared with ancient samples and a significant amount of the modern samples belonged to commercial breeds and/or highly drifted populations, the dataset was reduced to genotypes ascertained on wild and feral ovids. This was done to reduce the bias induced by using reference populations that have suffered a significant diversity loss in recent years due to modern breeding and selective practices. For Paper IV an additional dataset comprised of genotypes from the OvineSNP50 bead chip (Illumina), focused on local Northern European and Russian populations, was used for comparison due to the lack of any suitable publicly available whole genome data for these breeds.

Ancient reads were trimmed of the adaptors using *Cutadapt* [155], and then forward and reverse reads were merged using *FLASH* [156] where an overlap of at least 11 base pairs was found. This last step is not so common anymore for processing NGS data, but it is still used in highly fragmented sequences, such as aDNA, as it increases the length of the reads, which makes them easier to map to a reference genome, as we do with aDNA, or to create a *de novo* assembly, especially when working with modern bacteria [156]. Then the merged reads were comparatively mapped using *FastQ Screen* [157] to a set of reference genomes including human, mouse, sheep and goat, in order to validate that our sequences belonged to our target species.

The merged reads were mapped to the Texel reference genome versions Oar3.1 (Papers I and IV) and a modified version of Oar4.0 that included the mitochondrial chromosome reference (NCBI Accession NC_001941.1) (Papers II and IV). Unlike with modern data, genotype calling on aDNA data is quite complicated. The damaged nature of the sequences, along with the generally low amount of them (which translates into a significantly lower genome coverage) makes standard approaches for this step unreliable [158]. To circumvent this unreliability, a lot of studies avoid this issue by calling haploid genotypes instead, either selecting a random variant from each site or by consensus between the sequences. Other methods have been developed to try to account for this issue, for example by using Bayesian probabilistic methods to calculate genotype probabilities [159], using a frequentist iterative approach [160] or using Machine Learning methods [161] to try to avoid the uncertainty associated with this damage. All these methods, however, work significantly better with higher coverage data than most samples can produce.

This limitation of aDNA is not only an issue during variant calling. In addition to undetected contamination (e.g. from modern individuals of the same species), postmortem deamination being interpreted as actual genetic variation or the lack of overlapping data on highly fragmented genomes, low coverage will be an issue with most population genetics analyses, and our methods have to be adapted accordingly.

4.4 Sex Determination

For sex determination of ancient human samples, the most common approach is to use the method described in Skoglund et al., 2013 [162]. This method uses the ratio of sequences aligned to X or Y chromosomes to infer the sex of each sample. This simple approach has proved to be quite robust, working even with highly degraded samples, and is contamination-sensitive by tracking damage patterns in the sequences. However, the sheep reference genome does not include the Y chromosome. In those cases, the most common approach is to just compare the average depth of coverage for sites in autosomal regions versus in the X chromosome. As males in mammals only have one X chromosome,

the depth of this region should be around half of that of autosomal regions. Recently, a statistical method was developed to formally test if the autosomal and X chromosome coverage is different, known as the Rx ratio [163, 164]. As the X and autosomal chromosomes are significantly bigger than the Y one, this method allowed for sex determination with even lower amounts of data than the comparison between the coverages of X and Y, both in humans and in species where the assembly does not include the Y chromosome. All our ancient sheep's biological sex was inferred using this method.

4.4.1 Mitogenome sequence alignment

Mitochondrial DNA has been extensively used in population genetics in general and within aDNA research in particular. As the number of mitochondria is several orders of magnitude higher than cell nuclei in any given sample, it is easier to sequence enough data from this region even in samples with poor nuclear DNA preservation. There are two main approaches to reconstruct the mitogenome of a sample from shotgun whole genomes: extract the mitochondrial consensus sequence from the whole genome alignment (e.g. with *ANGSD -doFasta* option [165]) or by aligning reads to a reference mitochondrial sequence. The first option is fast and can be done in parallel with the whole genome data processing. The alternative approach, that of assembling the mitochondrial reads specifically to a reference, is often favoured in cases where the whole genome reference assembly may not be an accurate reference. The *Mapping Iterative Algorithm (MIA)* [100] is a reference-based iterative algorithm that was developed to assemble the mitochondrial genome and other short regions of the Neanderthal genome using an appropriate reference, and to evaluate putative contamination from modern humans. It can be used with the standard substitution matrix, or use custom ones to take aDNA damage into account.

4.5 Population genetic data analysis

4.5.1 Dimensionality Reduction

Genomic data is, by nature, highly dimensional. This means that, for a species that understands the world in three dimensions such as humans, it is impossible to visualize the relationship between different samples. Therefore, we use different mathematical methods to reduce the number of dimensions relevant to our data. Principal Component Analysis (PCA) is a data summary technique for dimensionality reduction that linearly transforms the data into a new coordinate system that maximizes the variability of the data described by the first dimension, called Principal Component 1 (or PC1), then PC2, then PC3, etc. This in practice means that the first few components condense the majority of the variability, and as we go up, the less informative those are. This

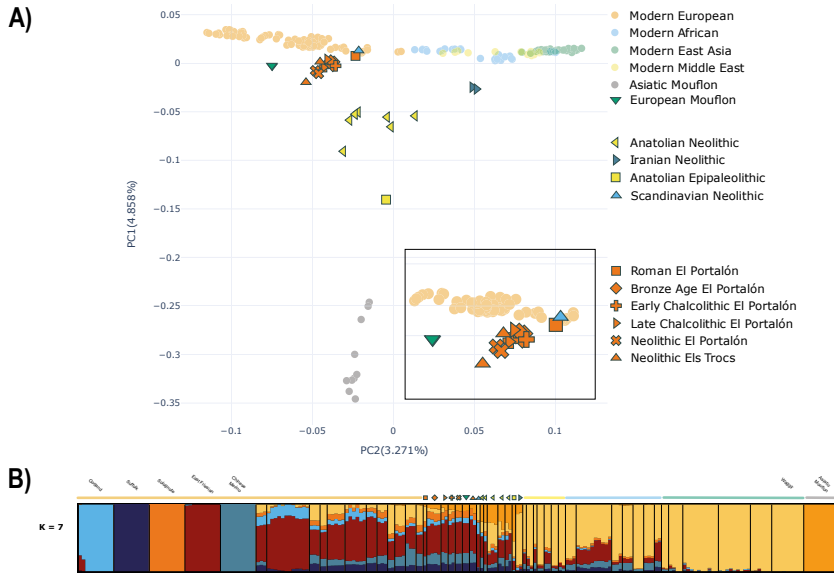


Figure 4.1. Examples of two of the most common data analyses to visualize population structure using genetic data. A) PCA of a global modern sheep dataset with projected ancient samples (highlighted). B) *ADMIXTURE* plot of modern and ancient data (marked with the same symbols as in the PCA). Adapted from Paper II.

transformation allows us to obtain a lower-dimensional representation while preserving as much variability as possible on the first components, allowing us to summarize and explore the data visualizing only the first few dimensions of the dataset. The result is a scatterplot in which each axis represents one of these new components (see Figure 4.1A). This is an easy way to condense complex relationships between samples in a graphical way.

As ancient samples are characterized by lower coverages and higher missingness than modern samples, they cannot be directly compared with modern data. PCA transformation of the dataset's multidimensionality is based on the variance of allele frequencies among pairs of individuals. This makes discrepancies in pairwise overlap a big issue when calculating the scores. The relative distances between scores are used to infer genetic similarity, which means that comparing fragmented, haploid data with high missingness and potentially higher error rates to modern high-coverage samples is going to distort and bias the results [166]. This data, however, can be projected into a PCA space defined by modern high-coverage samples to compare them with modern genetic variation. High-coverage ancient samples may still be used in PCA, even if some of the other issues of aDNA may still affect them. The more common software for Principal Component Analysis of genetic data are *PLINK* [167]

and *EIGENSOFT* [168, 169], and then the results are represented using *R* or *Python*.

An alternative method to PCA that is also popular in Population Genetics is Multidimensional Scaling (MDS). This technique uses a distance matrix of dissimilarities between samples to create a hypothetical N-dimensional space that retains this dissimilarity, but on a lower dimensional level. For most cases, $N=2$, so we can represent its results in the same way as a PCA. MDS can be directly applied to genomic data using, for example, *SC-MDS* [170]. Both methods, however, can also be applied to summary statistics or any other dissimilarity or similarity metrics (e.g. F-Statistics) [5].

4.5.2 F-Statistics

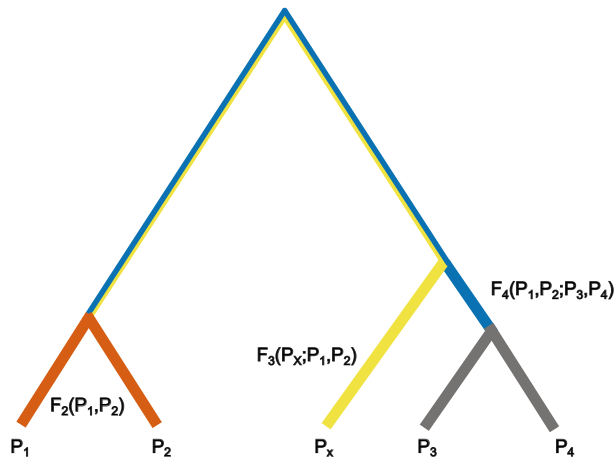


Figure 4.2. A population phylogeny with branches corresponding to the F_2 (orange), F_3 (yellow) and F_4 (blue). Adapted from Peter 2016 [171].

One of the most popular methods to study genetic variation between different populations is F-Statistics. This set of mathematical equations, presented by Reich et al, 2009 [172] and summarized by Patterson et al, 2012 [173], are based on calculating the amount of shared genetic drift. This amount of genetic drift can be represented as the branch length of a coalescent or phylogenetic tree, as represented in Figure 4.2, as the path of an admixture graph or the length of the internal branches of gene genealogies [171]. F-Statistics are labeled according to the number of populations considered (F_2 , F_3 and F_4). F_2 is simply a measure of the amount of drift that occurred between two populations. This value can be used to study different relationships between two populations (e.g. isolation and inbreeding) [171], as a measure of the covariance between two populations or to accelerate other computations [174, 175]. F_3 measures

the amount of drift from a private branch to the internal node where the other branches coalesce. This equation has two main uses: to measure the amount of common drift between P_1 and P_2 by using a known outgroup for P_x (this is also called Outgroup F_3 for this reason) or to test if P_2 is admixed with P_x by testing how well P_2 adjust to the topology described in Figure 4.2. If the F_3 value is negative, then the simple tree is rejected in favour of a model with gene flow between the branches [171]. The last and more complex statistic is F_4 , a test for how well our data adjust to the 4 population topology. Deviations of this basic model can indicate gene flow, which allows us to explore admixture hypotheses and complex gene flow models [171]. This functions have been implemented in several software packages, such as *Admixtool*, *Admixtools2* or *admixr*.

4.5.3 Model Based Clustering

Bar plots of admixture estimates are another way we can represent visually the genetic relationship between populations. These plots represent this relationship as common ancestry components, or “clusters”, based on the inferred genetic ancestry of samples [176, 177]. *ADMIXTURE* [178, 177] estimates allele frequencies in clusters and then assigns ancestry proportions to each genotype using a simple model-based approach. This software assumes a certain number of clusters, that must be defined by the user, to infer and assign the fraction of ancestry components for each individual. The clustering, however, has to be interpreted with care, as in cases where we have small sample sizes and/or have undergone little population specific drift of their own, they can appear as a mix of multiple drifted groups. This is especially relevant for ancient samples, as they can appear as a mix of ancestral populations younger than the sample is [179] (see Figure 4.1B). To visualize *ADMIXTURE* results we can use *Python* or *R*, or specific visualization software such as *PONG* [180].

4.5.4 Admixture Graph

Admixture graphs are a Graph Theory approach to describe the ancestral relationships between populations, both present and past. Similar to other tree-like representations, they display a basal topology of the genetic relationship between the different populations, but also allow us to model migrations and population merges by means of gene flow [181].

There are several methods, such as *TreeMix* [182], *OrientAGraph* [183] or *qpGraph* [173, 175] to create directed, acyclic graphs (represented normally as trees with edges connecting some of the branches) to describe these relationships based on different correlation metrics (such as F-Statistics or covariance matrices) to explore the graph space while adding migration/admixture edges. In general, a tree-like representation is often a poor reflection of the different

demographic processes we are trying to describe. As the graph search space is so big, and the number of competing topologies within the coalescent processes of whole genomes is so complex to summarize, we end up with a single model that fits the data as well as possible. These trees may not be the "true" model or even the best possible explanation, but at least they are an approximation for interpretation and, in some cases, storytelling.

4.5.5 Demographic inference

Using modern and ancient samples for inferring the movements and interactions of past populations has proven to be a powerful tool to add an extra layer of information to archaeological and historical sources for interpretation and have been key in confirming and/or contradicting several long-held hypotheses about humans and other animal and plant species. Up until now, the methods described above focused on data exploration, while demographic inference focuses on hypothesis testing and modeling. Some of the challenges when we try to infer demographic changes from genomic data that we must deal with are the gigantic amount of data and the probabilistic space of possible demographic models, which both are high-dimensional by nature, adding statistical and computational challenges to make the analysis feasible with nowadays computational resources. One way to reduce the dimensionality and sheer amount of data used in the analysis is to work with summary statistics. These statistics have been used traditionally to estimate population structure, split times, effective population sizes (N_e), gene flow, etc., and one of the most popular summary statistics is the joint Sample Frequency Spectrum (SFS) [184]. This statistic represents a multidimensional histogram of mutant allele counts of some DNA sequences from different populations, and it can be used both by frequentist and probabilistic methods to estimate complex demographic histories. For Paper I, we used *Momi2* [185], a maximum likelihood (ML) method that efficiently estimates complex topologies, including bottlenecks, admixture pulses and population growth using SFS as a summary statistic assuming a Moran Model [186]. This method offers an efficient and easy to interpret tool for inferring past demographic events using a likelihood framework. A probabilistic alternative to *Momi2* is the extremely popular Approximate Bayesian Computation [187, 188, 189], a family of methods that use different summary statistics (which can include or be derived from the SFS) and simulations of different demographic models (e.g. using *msprime* [190, 191] or *SLiM 3* [192]) to both choose the most probable model and estimate the parameters of this model that better fit the data (such as split times and N_e for each population along time).

These methods, however, depend on user-defined models and quickly increase computation time as the models get more complex. Other methods have been developed to estimate the individual parameters described before

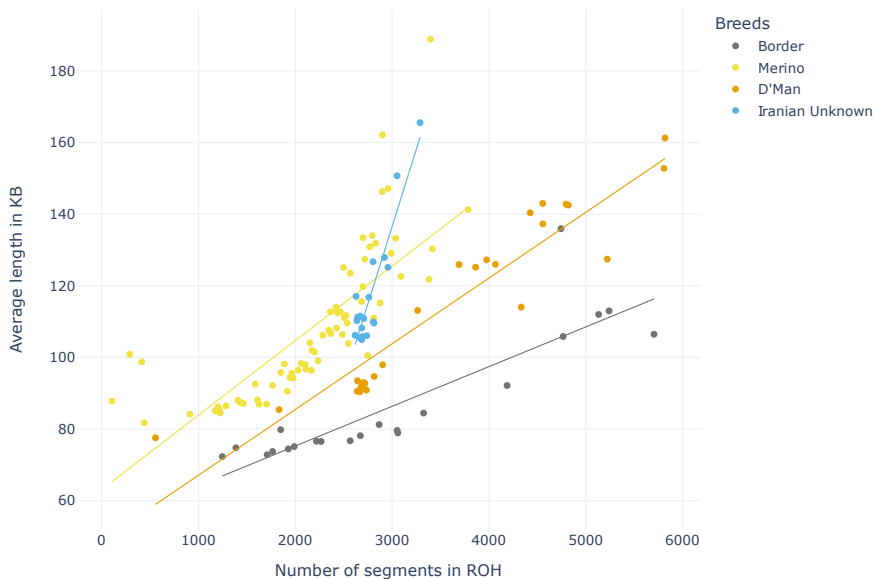


Figure 4.3. Runs of Homozygosity of 4 domestic sheep populations. Adapted from Paper I.

without assuming a specific demographic model. One approach that can be quite informative on N_e and how this has changed in the past is estimating how heterozygosity and homozygosity are distributed across genomes in our populations. Heterozygosity can be used as a proxy for the measure of a population's genetic diversity. In Papers II and IV we used the pairwise mismatch probability, or the chance of picking two alleles at random from the whole population and finding a mismatch, as a measure of heterozygosity. Low genetic diversity is associated with low effective population sizes. This metric can be used as a proxy of the historical population size, but it offers no information of when changes occurred.

Runs of homozygosity (ROHs) [193], on the other side, are stretches of the genome that are found in homozygosity. This happens when both parental haplotypes are identical, and it can be caused by recent inbreeding and/or small effective population sizes. These two events, however, leave different signals in the genome. While recent inbreeding is characterized by very long stretches of homozygosity, as closely related parents will share most of their genetic sequences, a small population or a population with low genetic diversity will produce an increased number of short ROHs distributed along the genome. This pattern can be seen in Figure 4.3, where some samples of Merino (yellow) and Iranian Unknown (cyan) are enriched for the number of long ROHs, while

the Border Leicester (grey) has a higher number of shorter ROHs. This last result agrees with other analyses, that suggest a strong bottleneck in the past followed by fast population recovery for this breed (see Paper I). This pattern of homozygosity will dilute and change over recombination events if there is new gene flow (for example, by admixing with members of another population) or if the N_e of the population increases. This allows us to make inferences of the demographic history of the population in a similar way linkage disequilibrium-based (LD-based) N_e methods do.

PSMC (Pairwise Sequentially Markovian Coalescent) [194] is a method that compares how the distribution of heterozygous sites is distributed across each pair of chromosomes in a diploid genome, reflecting periods of constant Time to the Most Recent Common Ancestor (TMRCA), which are separated by historical recombination events that the method can quantify. While this is an extremely popular algorithm for the analysis of modern genomes, it has several limitations. First and foremost, it's a pairwise comparison of one individual's chromosomes, which means we need high quality data for which we can do diploid calling. This means *PSMC* struggles dealing with recent effective population changes, as the number of recombination events in one pair of chromosomes is too small to offer enough statistical power. *MSMC (Multiple Sequentially Markovian Coalescent)* [195] solved this issue by allowing us to compare more than two chromosomes, and by that adding extra samples per population and extra resolution in more recent times. Both methods, however, are complicated to work with, as they are quite susceptible to low quality data with low coverages, the presence of repetitive sites and/or high missingness [196, 197], and if we want to use more than one individual in *MSMC*, we need to phase our genomes (*MSMC* can work with unphased sequences if run with only one sample), and *MSMC* can only work with a few samples per population. *SMC++* [198] uses the same sequentially Markovian coalescent model, but without the need to phase our data and allowing us to use more samples. This approach, while offering even more resolution in recent times, still struggles with very recent events [197]. For really recent effective population size changes methods using LD offer better results. These methods, instead of looking at the recombination events, focus on the distribution of sites in LD (or sites that have not recombined randomly), which is another way of evaluating the amount of recombination events, but with a genome-wide approach. These methods, like *SNeP* [58] or *GONE* [199], offer information on the recent N_e changes up to 100-200 generations, losing power as more and more recombination events accumulate. All these methods focus on estimating N_e changes over time assuming population continuity, so violations of this assumption, like admixture, can produce false values/artifacts.

Lastly, we can also use recombination and LD to estimate split-times and times of admixture events. Recently admixed populations will have long stretches of SNPs in LD, even orders of magnitude longer than unadmixed populations. As LD decays over time due to recombination, methods such as *ALDER* [200]

and *MALDER* [201] (*ALDER* adapted to consider more than one admixture event) can establish a relationship between the strength of the LD signal and the distance between the different genetic markers to date when this admixture event happened.

4.6 Phylogenetic analysis

Population genetics and phylogenetics are very similar in their goals, but differ significantly in their methods and scale. While population genomics are focused on how different alleles are distributed within populations to study recent evolutionary changes within a species and how demography, selection, gene flow and other processes shape them, phylogenetics focuses on describing the deep-time evolutionary processes that lead to speciation to describe the relationship between different groups. The basic phylogenetic analysis is performed by aligning orthologous sequences (homologous sequences that split by a speciation event and have since evolved independently) in order to compare them, and reconstruct their phylogeny, traditionally in the form of a phylogenetic tree. This does not mean population genetic studies cannot benefit from phylogenetic approaches. While gene flow and recombination may add uncertainty or directly violate some of the assumptions of phylogenetic methods [202], we can still use these methods by targeting non-recombinant regions of the genome (e.g. mitochondria or the Y chromosome). As most of the questions relevant for population genetics involve a shorter time-frame than phylogenetics, a smaller number of mutations separate the sequences and most of the differences between groups are not fixed. This means more individuals from each population are needed to estimate the frequency of certain variants and properly describe the relationships between different groups while some branches may be difficult to resolve. Phylogenetic trees, however, are a useful tool to describe the population structure of a population and its relationship with closely related clades.

There are several mathematical approaches to reconstruct a phylogeny. While all methods are based on tracing the amount of changes on the aligned orthologous sequences, each type of algorithm uses a series of assumptions. The simplest one is known as Maximum Parsimony [203], and reconstructs the phylogeny following the principle that the simplest explanation (the one with the least changes) is the most likely one. This is a naive approach, which can be misleading in several scenarios [204], and has been substituted by more complex models. The three most common approaches for reconstructing a phylogeny are Neighbour-Joining [205], Maximum Likelihood and Bayesian methods. Neighbour-Joining-derived methods are also quite simple in their approach. They are based on creating pairs of "operating taxonomic units" that minimize the branch length of the tree. By clustering these closely related units, a phylogeny can be reconstructed in a more nuanced way than follow-

ing the most parsimonious approach. This method, however, is quite naive in its assumptions. While Neighbour-Joining algorithms are still common for reconstructing the phylogeny of a species (e.g. using Neighbour-Joining networks), Maximum Likelihood and Bayesian phylogenetics are considered as the gold-standard for reconstructing phylogenies. Both approaches use models of nucleotide substitution to estimate the evolutionary distances between sequences, but Maximum Likelihood uses a frequentist approach [206, 207], giving a value for how likely a tree is based on the data, while Bayesian phylogenetics uses a probabilistic approach [208, 209], combining a prior distribution with the likelihood to give the posterior distribution that can then be summarized into a tree. Bayesian phylogenetics can also be used with a molecular clock model to estimate split times and effective population sizes in a similar fashion population genetic methods do [210].

5. Research aims

The main focus of this thesis is to study the westward expansions of sheep through Europe since the Neolithic and the population movements and demographic dynamics of the European sheep population before the appearance of modern sheep breeds in the West. This domesticate has played a key role in the history of European populations since the moment farmers arrived to the sub-continent. This does not only highlight the importance of studying its history *per se*, but means that said history is intimately ligated with that of the human populations that exploited them, how they consumed their products and, in some instances, if there was a human demographic change that also affected the livestock of said population.

The demographic history of sheep in Europe is not well described, but shedding light on it could help us understand not only this domesticate better, but also how human farming communities changed from the Neolithic onward. With this in mind, I focused on using publicly available genomic sequences and generating new ones from ancient and modern samples from relevant locations to describe the evolution and demography of domestic sheep in Europe and how human populations have affected these processes over time. I compared modern and ancient novel genomes with publicly available modern samples to describe the genetic diversity of this domesticate and how it has changed over the millennia since they left the Fertile Crescent, and to study how human cultural and demographic changes affected it.

Specific aims included:

- I. Generate whole genome sequencing data of ancient European sheep from key locations (e.g. Iberia, Scandinavia and Sardinia) to characterize the demographic history of these domestic populations.
- II. Improve the understanding of the demographic events that shaped modern European sheep genetic diversity in domestic, feral and wild populations.
- III. Date and quantify the extent and direction of gene flow after the initial expansion of this species into Europe.
- IV. Relate these processes with human demographic changes.
- V. Describe changes in the way humans exploited sheep, and how this shaped sheep's gene pool in Europe.

6. Summary of Results

6.1 Sheep domestication and expansion during the Neolithic (Paper I, II and III)

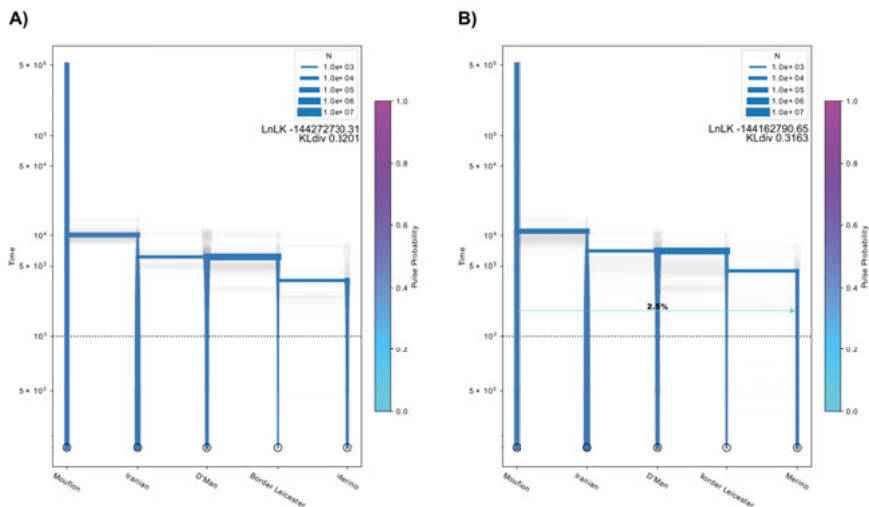


Figure 6.1. Figure 4 of Paper I: Maximum likelihood inference of the demographic history of Western sheep using Momi2. Both models present the same topology, but A) assumes no admixture while B) considers an admixture pulse from an outgroup into Iberian sheep, as reported in previous studies [127, 59].

Even if the origin of domestic sheep has been identified in the Fertile Crescent, the exact location, timing and development of this process are very poorly understood. With several putative regions within this region and up to three independent domestication events suggested in the literature [9, 107, 121], current available data has been insufficient to test either of these hypotheses.

While the specific dynamics during the domestication of sheep in the Fertile Crescent are out of the scope of this dissertation, in **Paper I** we reconstructed the demographic history of modern European sheep and when they did split from their wild counterparts. Our models also included options for multiple domestication events, to test if the "East-West" geographical cline described in previous works [76] and replicated in our own analyses could be better explained by a single or multiple domestication events. Our results consistently

favoured the single domestication event, which our best fitting models dated to 10,114 and 11,007 years ago (see Figure 6.1A and B), agreeing with archaeological estimates [9, 29]. These dates are, however, surprisingly recent if we have in mind that these splits must have happened before the actual domestication, and the fact that the modern Iranian mouflon population used as outgroup may not be the wild source population from which domestic sheep descend. Early gene flow from these or other closely related wild populations after the domestication may help explaining this. We see evidence of this admixture between early domestics and wild mouflons in **Paper II**, where all Neolithic samples share a fraction of the Asiatic mouflon component, including Iberian samples and the European mouflons (Figure 6.2B). This component decreases over time in Iberia, with Roman and modern sheep showing almost none of it. The admixture graph in **Paper II** also inferred small amounts of gene flow both from Anatolian Neolithic and Asiatic mouflon at the base of the branch of Neolithic Iberian and Early Chalcolithic Iberian sheep, and European mouflons (Figure 6.2A).

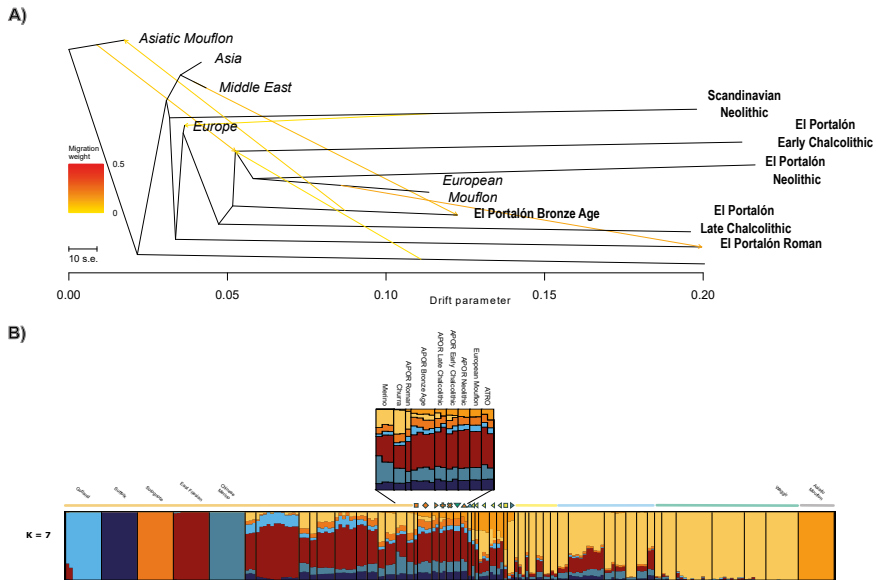


Figure 6.2. Adapted from Figures 1 and 2 of Paper II: A) Maximum likelihood admixture tree using ancient Iberian samples from El Portalón. B) Admixture graph of modern and ancient sheep.

On the other hand, both **Paper I** and **Paper III** agree that, even if we see evidence of recent admixture from domestic sheep into Iranian mouflon populations, this gene flow is not bidirectional.

6.2 Secondary expansion associated with the expansion of archaic long wool (Paper I, II and IV)

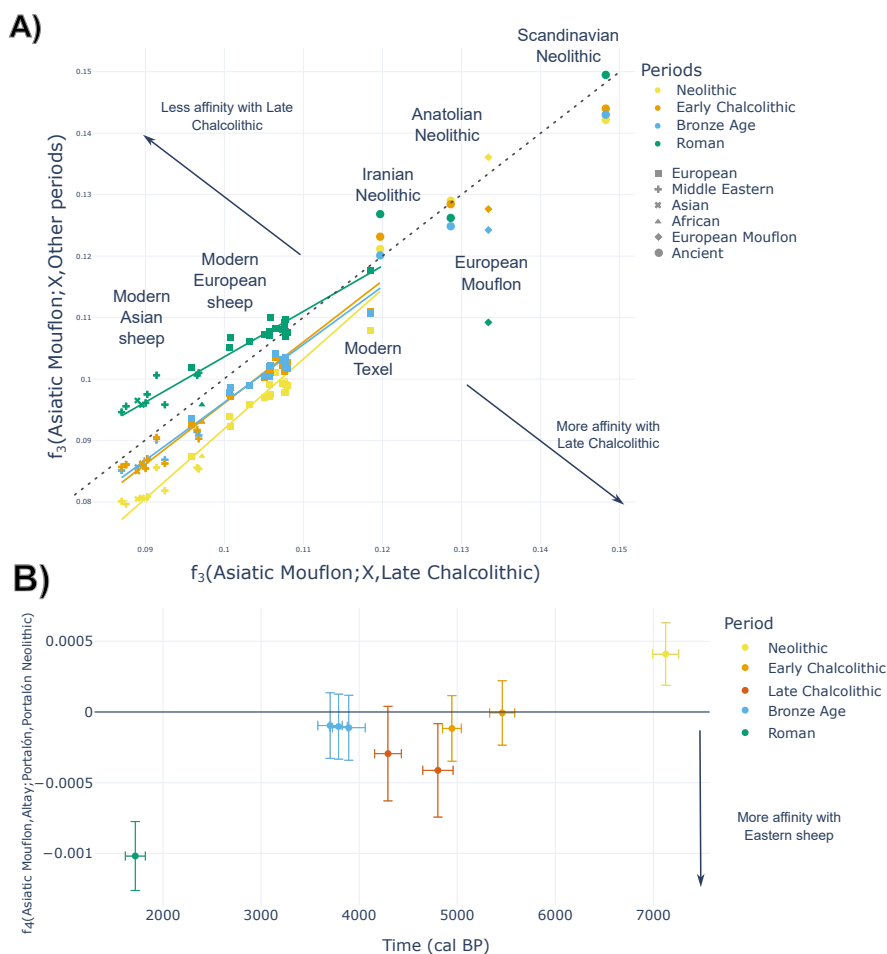


Figure 6.3. Adapted from Figures 2 and 3 of Paper II: A) Comparison of the affinity between the different periods of El Portalón with other ancient and modern sheep using Outgroup F_3 Statistics. B) Affinity to Eastern ancestry using F_4 Statistics for all El Portalón samples, with Altay as the source and the oldest El Portalón Neolithic sample as the baseline.

Both archaeological and genetic studies have pointed out at the possibility of a secondary expansion of sheep from the Middle East or Central Asia related with wool and the development of the Secondary Product Revolution [52, 114, 115, 116, 50, 112, 30]. The demographic reconstruction of **Paper I** likely captured this expansion in a secondary split (see Figure 6.1), dated quite after the initial expansion of domestic sheep through Eurasia, as a fast tri-

furcation between European, Iranian and North African sheep slightly before 5,000 years ago. These slightly predate the estimated time for the start of the Secondary Product Revolution [115], and suggest all modern sheep included are more closely related to each other than with their Neolithic counterparts. This is also what we see in **Paper II**, where all modern sheep share more drift with Late Chalcolithic Iberian sheep than with earlier samples (Figure 6.3). These Late Chalcolithic sheep also seem to have suffered a recent bottleneck, and present a higher amount of shared drift with Eastern sheep than previous Iberian individuals. These sheep with more Eastern ancestry and reduced genetic diversity, which appeared in the same temporal range of the arrival of Steppe ancestry into Iberian humans, probably represent the expansion of woolly sheep to Iberia. The fact that this signal can also be replicated with some of the primitive breeds Chessa et al. [50] aggregated with the Mediterranean mouflons as remnants of Neolithic sheep suggests that they captured a posterior expansion, while these isolated populations retained the archaic woolly phenotype. This is corroborated by the results of **Paper IV**. While the oldest samples are more recent than this secondary expansion, we see long-standing continuity in the Baltic region since the Late Neolithic/Early Bronze Age, supporting the archaic status of NEST breeds. This, in addition to the fact that the Stora Förvar sample included in **Paper II** also shares more drift with the Late Chalcolithic Iberian sheep than with earlier samples suggest these populations represent remnants of the secondary expansion associated with the woolly and short tail phenotypes, while more modern phenotypes present in Europe today may have expanded in a more recent expansion [45].

6.3 Secondary expansion likely associated with the arrival of fine wool to Europe (Paper II)

In **Paper II**, after the initial arrival of Eastern ancestry, we see a reversal of this signal in the El Portalón gene pool during the Bronze Age (Figure 6.3). This can be interpreted as the migrant ancestry being diluted into the local gene pool, by a complete replacement of primitive sheep more focused on meat production or a mix of both. Archaeological studies have pointed out that during this period the North and East of Iberia reduced significantly their secondary exploitation, favouring meat production. This contrast with the Argaric culture in the South, which used their sheep mostly for wool production [211]. They, however, refer to some secondary exploitation on El Portalón and other sites during this period, so we could assume that at least part of the local stock had acquired the woolly phenotype.

As our dataset has a 2,000 year gap between samples, we can't analyze what happened during the Late Bronze Age and Early Iron Age, but by the Roman period we see the arrival of a completely different genetic make-up to Iberia. This individual presents an even higher affinity to Eastern modern

breeds than the Late Chalcolithic (Figure 6.3B), but similar when compared with primitive breeds and the Stora Förvar sample. This suggest a later wave of Eastern ancestry during the Roman empire, matching the pattern described by Chessa et al., 2009 [50]. Regarding the origin of this ancestry, Ryder, 1987 [45] hypothesized, based on Roman historical sources, about the expansion of the fine wool trait associated with Merino during the Roman period from the region of Colchis (modern Georgia) into Greece and Italy, and then into Iberia. Our results suggest this expansion may have had a quite wider effect than that of seeding the origin of fine wool sheep. We also tested if there has been an increase in Eastern ancestry in the European gene pool since the Roman period, and our analysis only found increased affinity for Eastern ancestry in some Northern and Eastern European breeds (Figure 6.4), which suggest that the Roman wave was the last to reach Western Europe. This pattern was also observed in Northern African/Sahelian breeds.

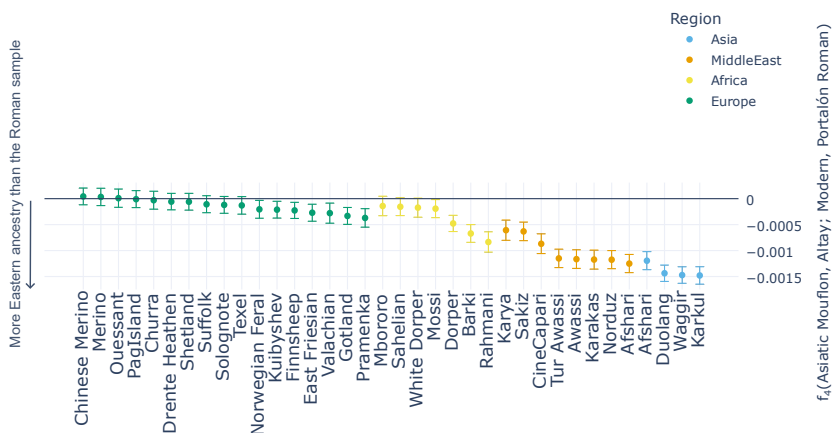


Figure 6.4. Adapted from Figure 3 of Paper II: F_4 Statistics comparing the affinity of modern breeds to the Roman sample and more Eastern related ancestry (using Altay as a reference).

6.4 Loss of genetic diversity in modern sheep breeds (Paper I, II, IV)

The demographic history of domestic species is inextricably linked to bottlenecks and losses of genetic diversity, normally associated with the domestication process and the posterior successive migrations. Comparisons of modern sheep genomes, however, showed that this species has higher levels of genetic diversity than other species such as cattle [76]. This, however, does not mean

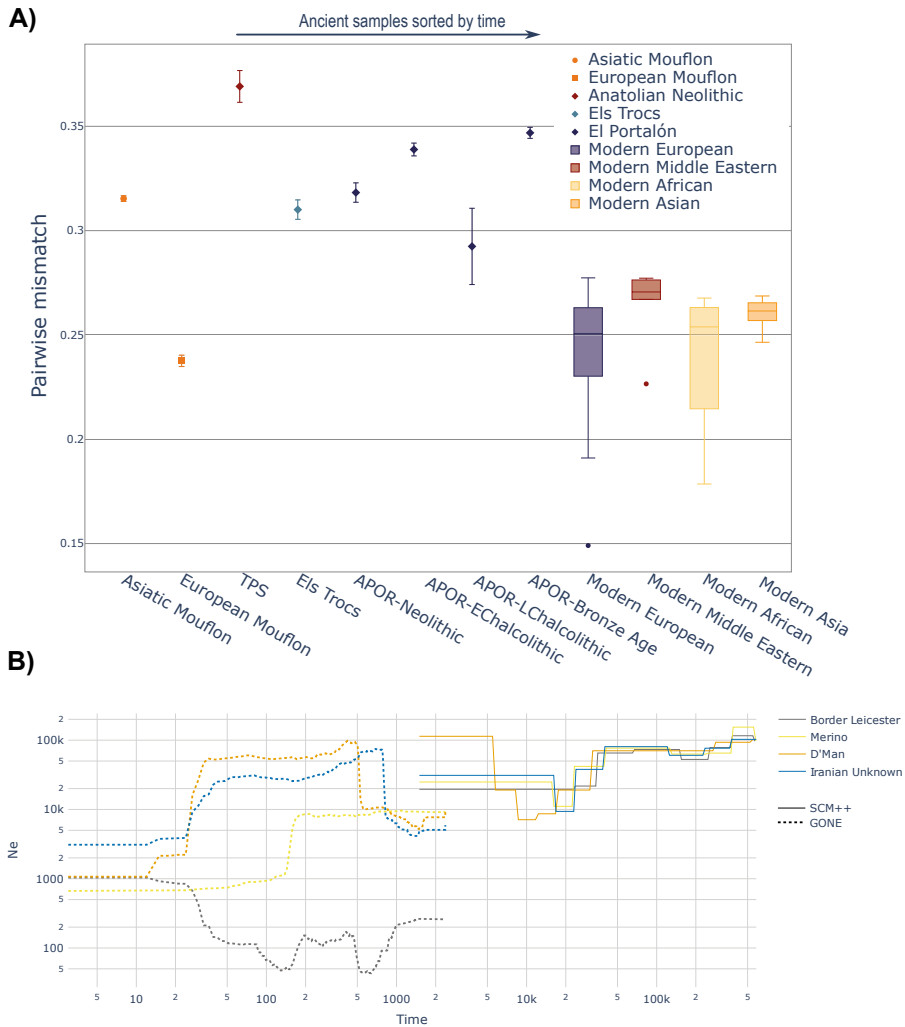


Figure 6.5. Adapted from Figure 2 of Paper II and Figure 5 of Paper I: A) Pairwise conditional molecular diversity. Wild, feral and ancient populations are represented by dots, while modern breeds are aggregated by continental groups. B) N_e change over time for 4 domestic breeds using a generation time of 3 years (both for GONE and SMC++) and a mutation rate of 1×10^{-8} (only for SMC++)

they have not suffered several decreases of genetic diversity, normally associated with bottlenecks and/or migrations. In **Paper II** we see that the Neolithic Anatolian samples have higher diversity levels than modern wild mouflons (Figure 6.5), probably because of the historical decline of population size in wild populations. These Anatolian sheep also have higher levels of genetic diversity than the Iberian Neolithic samples, reflecting the presumed bottle-

neck related with the Neolithic Expansion. We see, however, that the genetic diversity of Iberian sheep starts increasing soon after arrival, with the first El Portalón sheep displaying slightly higher levels of diversity. This trend continues up to the Bronze Age, with the exception of the Late Chalcolithic samples, which reinforce the idea of them belonging to a secondary expansion.

While the Baltic island populations of **Paper IV** have been isolated for a while by geography, we do not see a decrease between the Late Neolithic samples from Stora Förvar and the Medieval ones from Kastelholm. Both populations show a lower level of diversity than the Iberian sheep, with a pairwise mismatch probability of ~ 0.27 in the Baltic populations, and all Iberian samples over 0.30. The only exception is, as said before, the Late Chalcolithic, which show a similar value to the Baltic samples. All ancient samples, however, show higher levels of genetic diversity than modern NEST breeds, which highlights that, even if compared with other species sheep have retained high levels of genetic diversity, migrations and particularly modern breeding practices have reduced this diversity significantly.

The intensity of some of this modern selection practices can be seen in **Paper I** (Figure 6.5B), where the estimation of the N_e over time indicates that Border Leicester suffered at least two strong bottlenecks in the last 500 years to single digit population sizes. All other breeds also suffered recent bottlenecks, but Border Leicester's extreme case can be attributed to its origin as one of the first modern selected breeds, Dishley Leicester, which originated on one farm from a limited stock [212].

6.5 Genetic structure of feral and wild mouflons from the Mediterranean and the Middle East (Papers II and III)

Our results confirm Sardinian and Corsican mouflons as feralized Neolithic sheep. **Paper II** highlights the close relationship between Corsican mouflons and Neolithic Iberian sheep (Figure 6.2). This result is corroborated by the trees in **Paper III**, which place all the mouflons in Corsica as a basal group in Haplogroup B (HPG-B) (Figure 6.6). Mouflons from Sardinia form two geographically distinct clusters, but the South-Western population seems to have received gene flow both from the North-Eastern mouflons and domestic sheep. Both clusters are an outgroup to domestic sheep.

Anatolian mouflons fall within two different haplogroups: three samples form a basal group to all domestic HPG-A sheep, and may represent a remnant of the original wild lineage from which these sheep (associated with the Eastern Neolithic expansion) [112, 30] may have been domesticated. The other two Anatolian mouflons belong to what has been labeled as HPG-X, a haplogroup described in this population [213]. These mouflons form a basal cluster to all

7. Conclusions and future prospects

Prior to starting this dissertation, there was little work done on reconstructing the demographic history of sheep since their domestication from whole genomes. Early genetic analyses focusing on uniparental markers [124, 123, 120, 122], retroviruses [50] and genotyping data [76, 127] had described modern sheep genetic diversity, but there were no broad whole genome studies published yet. In the last 5 years, however, we have seen an explosion of available sheep whole genome data with the publication of several big modern datasets with samples from different breeds from all over the world [130, 131, 132, 214]. These genome-wide data analyses with global datasets have helped to better describe modern genetic diversity in domestic sheep and their relationship with wild relatives. While in other species we have also seen a fast increase in the number of published ancient sequences [86], for sheep only a few, mostly low coverage, samples have become available [30, 139, 140].

The results contained in this dissertation highlight the dynamic and complex history of domestic sheep and the intrinsic limitations of using only modern genomes. Without proper representation of ancient samples from different times and regions, the regional patterns that formed modern breeds will not be properly described, even if later those breeds became extremely popular (e.g. Merino or Romanov). Our results also stress the power of "vertical cuts" on a single or few related sites. Sampling from a single region over a long period of time offers us the chance to study how that population's gene pool changed over time with increased resolution. While it would have been useful to have ancient references from candidate regions for the source of the several expansions described in this thesis, even a few samples over a long time-span were able to pinpoint them and when they happened. This brings to the forefront the need for wide (geographical) and deep (temporal) sampling of ancient samples to be able to better describe these processes.

Our results also highlight the interconnected nature of sheep and human demographic histories. This relationship offers several applications for future studies to gain additional resolution while studying the human past. Domestic species' role within human populations place them as an interesting model organism to study human populations, their movements and economies. This enhances the interdisciplinary nature of archaeogenetics combining genetic analysis with both archaeology and zooarchaeology. Hopefully, in the future, more multi-species comparisons will be used to describe the fine-scale patterns of expansion, trade and cultural evolution of these societies.

Lastly, I would like to point out the importance of fine-scale, local patterns while explaining a continental process. Most of these big population movements have been described as a broad model of unidirectional expansion, but recent analyses are suggesting more complex, "reticulated" processes at a local scale and several smaller waves and back-migrations in some cases [14] and cases of long local isolation from incoming ancestries [215]. These complex demographic events will only get better and better described as more data from modern, ancient and environmental DNA gets generated and new methods to reconstruct more complex and accurate demographic models are developed. Increasing the nuance of the models and narratives around the human and non-human past will help us understand them better, and learning to combine all these kinds of data we are now producing will be fundamental.

8. Svensk smmanfattning

Får har varit en nyckelresurs för mänskligheten ända sedan de för cirka 10 000- 12 000 år sedan domesticerades inom en region i mellanöstern kallad den bördiga halvmånen. Vår kunskap om hur denna domesticering gick till och vad som hände efter deras initiala expansion från domesticeringsområdet till alla hörn av Europa och senare Afrika och Amerika är dock liten. I denna avhandling använder jag toppmoderna populationsgenetiska- och arkeogenetiska metoder för att belysa hur får har utvecklats från denna initiala domesticering till den stora mångfald av moderna raser vi ser idag. Fokus ligger på demografiska händelser som har format den moderna fårpopulationens genetiska landskap i Europa samt hur dessa demografiska förändringar relaterar till mänskliga populationers demografiska historia. Genom att analysera DNA från både antika och moderna får har, utöver en övergripande demografiska historia för får i Europa, tre viktiga Europeiska platser blivit karakteriserade. Dessa är den Iberiska halvön, Östersjöregionen och Medelhavsöarna. Jag har kunnat fastställa att den initiala uppdelningen mellan domesticerade och vilda får skedde för 10 000-11 000 år sedan. Detta datum kan dock vara en underskattning på grund av inblandning mellan tidiga domesticerade populationer och deras vilda förfäder innan de lämnade den bördiga halvmånen. Resultaten bekräftar dock att den initiala neolitiska expansionen till Europa följde två oberoende vägar, genom Donau-Rhen-axeln i Centraleuropa och över Medelhavet. Dagens mufflon från Korsika och Sardinien härstammar från dessa tidiga domesticerade får och har varit isolerade på sina öar ända sedan dess. Även två oberoende expansioner till Europa med östlig härstamning har kunnat identifieras. Den första expansionen inträffade under mitten av senneolitikum (bondestenålderns senare del) och senkalkolitikum (kopparstenåldern), samtidigt med utbredningen av stäpphärstamning i Europa och övergången från användning av domesticerade djur för kött- och läderproduktion till sekundära produkter som inte innebar slakt av djuren, såsom dragkraft, mejeriprodukter eller ull. Denna första expansion av ulliga får till Europa kan kopplas till vissa av de primitiva raser som finns idag, vilket antyder att de är en rest av denna expansion. En senare expansion, associerad med mer moderna fenotyper, ägde rum någon gång under sen bronsålder/tidig järnålder och omformade majoriteten av genpoolen hos de europeiska populationerna. Denna expansion nådde dock inte Östersjöregionen, där fårraserna har upplevt kontinuitet sedan åtminstone senare delen av stenåldern/tidig bronsålder.

Även om moderna får uppvisar en högre genetisk mångfald än andra domesticerade arter, tyder mina analyser av olika antika populationer på att moderna avelspraxis för produktionsfår och isolering av primitiva raser (lantraser)

har reducerat denna mångfald betydligt från förhistoriska nivåer. Slutligen har jag lyckats beskriva fylogenen för moderna vilda och förvildade mufflon från Medelhavet och Mellanöstern. Som tidigare nämnts utgör populationerna på Sardinien och Korsika förvildade rester av domesticerade neolitiska får, medan mufflon på Cypern är närmare släkt med mufflon från Iran och Anatolien. Denna avhandling belyser den dynamiska naturen hos fårens demografiska historia och hur responsiv den har varit gentemot mänskliga demografiska och kulturella förändringar, vilket placerar detta tamdjur inte bara som en intressant art att undersöka för att förstå dess utveckling, utan även som en proxy för att studera mänskliga populationer och deras demografiska och kulturella förändringar över tid.

9. Acknowledgements

I would like to start this section by apologizing, for I'm terrible at this. If my mention to you ends up being too cold, or too cheesy, excuse me. Everybody mentioned here and people that I forgot in the moment of writing it, are, nonetheless, valued coworkers and friends, and my gratitude with everybody that has helped me along this journey is immense. This said, lets get personal.

The first mention has to be, of course, for my supervisor. Torsten, you gave me a chance when I was not sure I even deserved one. You offered me a lifeline when I was in a really bad place, both in the metaphorical and literal sense. Working here have taught me there are better ways of doing research, and that doing good research is not in conflict with being a nice person. You are both an example and an inspiration.

This also goes for my co-supervisor, Mattias. Thanks for checking out from time to time and always have a spot on your busy schedule for checking my work and provide your valuable insight. Thank you, and the other PIs, for creating this nice place for people to do research in. They where not alone on this endeavour, so I cannot forget everybody else that made this program an awesome place to work in.

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Now, unless you speak Spanish, you can stop.

Estas palabras en castellano van para mi familia. A mis padres por el incesante apoyo, a mi hermano por su entusiasmo e interés, y a mi tío por su ejemplo. Tampoco quiero dejar pasar la oportunidad de agradecer el apoyo de Pablo, Alicia y Alba. Muchas gracias a todos por nunca dudar de mí.

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