Comparative phylogeography as an integrative approach to understand human and other mammal distributions in Europe

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Abstract

Phylogeography refers to the phylogenetic analysis of organisms in the context of their geographical distribution. The analytical methods build phylogenetic trees and networks from haplotypes in order to investigate the history of the organisms. Phylogeographic studies have revealed the importance of climatic oscillations and the role of the Last Glacial Maximum (27,500 to 16,000 years ago) with the formation of refugia where distinct haplotypes originate in Europe. The population expansions and contractions into these refugial areas have driven the evolution of different lineages but the similarities and differences between species are still poorly understood.

This thesis aims to gain a better understanding of the phylogeographical processes of different mammals' species in Europe. This was done by collecting published mitochondrial DNA control region sequences of 29 different species and analysing them individually and comparatively. This research presents a standardised way of understanding phylogeography from the mitochondrial DNA perspective to improve the comparison of studies in the field.

The project investigates the patterns of genetic diversity by examining various diversity indices to test for trends and commonalities. To enhance knowledge in phylogeography and the importance of refugia during the Last Glacial Maximum in Europe through a comparative phylogeographic meta-analysis of mammal species. This thesis developed novel insights into the phylogeographic interactions of different mammal species, including modern humans, in the European geographical context. Modern human phylogeography pattern from the short control region has been contextualised in the patterns observed for other mammal species, showing a homogeneous distribution across the continent.

Finally, the commensal species *Mus musculus domesticus* (western house mouse) was investigated in detail from a current and a past phylogeographic perspective in two islands, Cyprus and Britain, using ancient and modern DNA. This was done using this new knowledge as a bioproxy to understand more recent human movements associated with the transport of this species.

This thesis, therefore, provides an integrated study with a new comparative framework and with results on the phylogeographical patterns of humans and other mammals in Europe.

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Evolution. Through this entire PhD journey I have been able to (start to) understand a little bit better the beauty of that central concept in *biology*. But also I have experienced the personal meaning behind it, our own *evolutionary* concept, the one that you have to experience yourself and fulfilled with personal and professional moments. For that reason, during these three years, I have *evolved*. And we do not evolve only by ourselves.

It all started with *migration*, from an island to another. We can define this as an own *founder effect* where a small population (1 individual, in this case) arrive at a new place. Leaving behind many things is not an easy task and *adapting* to a new *environment* takes time, but not that much if people around you make things easy.

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Author's declaration

I confirm that this thesis comprises my original work. Additional datasets and material used in this thesis have been fully referenced and acknowledged throughout.

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Chapter 1. General introduction

1.1 Introduction and literature review

1.1.1 Phylogeography

Biogeography is a subject that it is not difficult to define, it is the study of the geographic distribution of the species – but comprises great complexity. It includes the study of geology, geography and biology and, therefore, two main traditions in biogeographic research have been proposed; ecological and historical biogeography. Historical biogeography has developed different strategies to understand the evolutionary and geographical relationships of species since its inception (De Candolle 1820). During the end of 20th century and the beginning of 21st, new approaches took population genetics with a phylogenetic perspective in the context of biogeography to establish a new approach, called phylogeography.

The main debates in evolutionary biology were based on the understanding of how microevolutionary processes within species can be extrapolated to the differences between species or higher taxa (Avise et al. 1987). Traditionally, microevolution has been related to population genetics and evolutionary processes like mutation, genetic drift and natural selection. However, the phylogeny or the macroevolutionary perspective, especially in palaeontology, often had another vision sometimes separated from this approach. The connection between these different fields was not clear and the historical perspective for population genetic analysis was mostly unknown (Hickerson et al. 2010).

Avise et al. (1987) coined the term phylogeography, to describe a discipline with conceptual and technical roots linked to the emerging field of molecular genetics, but before that, about a decade earlier, mitochondrial DNA (mtDNA) had begun to be used for addressing how individuals are genealogically linked through their shared ancestors (Brown and Wright 1979). The reasons that were traditionally invoked to justify the choice of mtDNA were and still are, its high level of variability, its maternal inheritance, and its supposed neutral mode of evolution (Nabholz et al. 2008). The historical roots of phylogeography are intertwined with mtDNA studies. Major studies in the 1970s and 1980s were based on population surveys of different species in America (Avise et al. 1979; Lansman et al. 1983), which mainly laid the foundations for phylogeographic approaches. This knowledge expanded rapidly with the first

complete mtDNA genomes published soon afterwards for the house mouse (Bibb et al. 1981) and humans (Anderson et al. 1981).

Studies started to connect the phylogenetic approach to mtDNA with a geographical context uncovering different patterns in the spatial arrangements of the mtDNA lineages (Avise and Ayala 2009). Identifying patterns that might help to characterise organisms that occupied diverse habitat has been the main goal for phylogeographers during the last decades. The literal meaning of phylogeography is the phylogenetic analysis of organismal data in the context of the geographic distribution of the organism (Hickerson et al. 2010). In this way, phylogeography deals with historical and phylogenetic components of the spatial distributions of gene lineages (Avise 2000). Through this, the relationship between geographic phenomena and the mechanisms driving speciation can be addressed. The final aim of phylogeography might be understanding microevolution and speciation in its geographic or spatiotemporal context (Kidd and Ritchie 2006).

With this approach, phylogeography becomes an integrative field that lies at the junction between macroevolution and microevolution (Avise 2000). The interpretation of the different lineages' distributions requires a good understanding of many fields to extrapolate microevolutionary processes operating within species to explain differences among them from a macroevolutionary perspective (Figure 1.1). The main challenge for phylogeography is to be able to extract the information that describes the relationship between patterns and processes from complex natural data (Dawson 2014). This is a significant challenge for an observational science if it is compared with experimental scientific approaches and their power to establish cause and effect (Freckleton 2009).

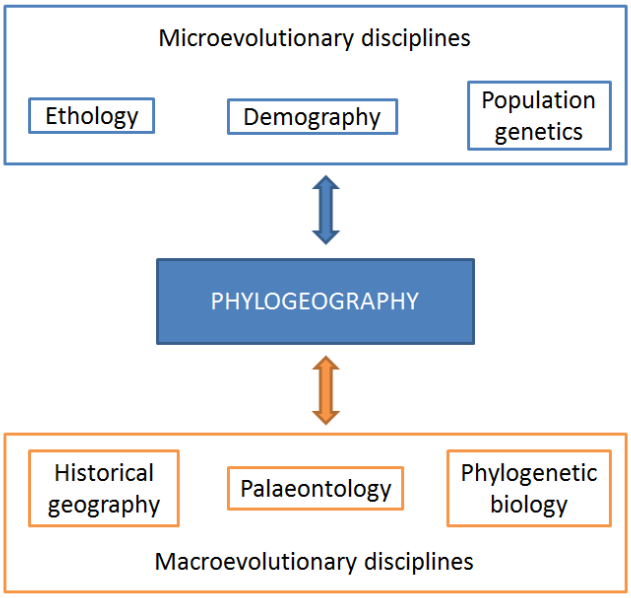

Figure 1.1 The central position between micro and macro evolutionary processes (Adapted from Avise 2000).

Phylogeography adds an essential component to the understanding of population structure. Changes over time in the physical and biotic environment of a population lead to demographic variations that correlate with the structure of population genealogies (Avise 2000). The combination of phylogeographic and population-genetic approaches creates an important new framework for appreciating the processes that have shaped speciation and population distributions (Beheregaray and Caccone 2007). The comparison of phylogeographic data for multiple co-distributed taxa adds a valued extension for this framework.

Avise et al. (1987) added that genetic data from multiple co-distributed taxa could improve the investigation and questions about the geographic or climatological phenomena that generated the observed distribution of different species. In terms of evolutionary biology, phylogeography has become one of the most integrative fields and it can be combined, for example, with ecological models (Peterson 2003), but also with such diverse disciplines including climatology, computer science and geology (Hickerson et al. 2010). The perspective of the phylogeography has transformed aspects of biodiversity conservation, biogeography, ecology, genetics, and population biology (Avise et al. 2016).

1.1.2 Comparative phylogeography

The demographic history of organisms can be tracked by using different genetic markers. Fitting their genealogies to geographical and temporal contexts can provide information about

the history of a particular species (Jones et al. 2013). However, in the case of more than one organism being examined, comparative phylogeography can be used to infer common histories between them (Gutiérrez-García and Vázquez-Domínguez 2011). The development of different molecular markers is allowing the investigation of interspecific phylogeographic patterns.

MtDNA genealogies are traditionally used to infer historical demographies through coalescence theory (Kingman 1982). Statements that some markers are more sensitive to population structure than others have been part of the debate in molecular ecology (Karl et al. 2012). Some studies have suggested that mtDNA has more power to detect population structure than single nuclear loci, but two or more polymorphic nuclear loci are expected to be more sensitive than mtDNA (Larson et al. 2009). For example, mtDNA has been suggested to show population divergence in recently divided populations due to higher levels of genetic drift, or that microsatellites will show divergence due to high mutation rates and heterozygosities (Karl et al. 2012). However, no class of markers is a priori more sensitive, for example better able to detect population differentiation, under every condition. One important caveat is that diversities among markers in these simulations are held to be identical. Species and evolutionary history influence can make it such that polymorphic mtDNA loci have more power than a cluster of microsatellite loci depending on overall diversity in these markers (Karl et al. 2012).

The aim of these studies might be to search for concordant geographical distribution among lineages within different species indicating a possible influence of a common historical factor (Taberlet et al. 1998). This study of geographic variation is the comparison of broadly co-distributed species (Cracraft 1989) or comparative phylogeography.

The historical stability of communities can be measured by the degree of phylogeographic concordance of the analysed species (Zink 2002). Combining the historical biogeography with the comparative phylogeography can reveal the history of the groups of species at different temporal scales. One of the first case studies was made by Avise (1992) who documented a similar phylogeographic pattern in several animal species in North America. Using mtDNA as a marker, a hypothesis was proposed concluding that a common historical event separated the Atlantic and Gulf coasts regarding their ancestral community gene pools for certain North American species.

Through comparative phylogeography, congruent geographical patterns in genetic variation can be tested. A parsimonious explanation for a common pattern would be that historically co-distributed species might respond in analogous ways to specific isolating barriers (Wiley 1988).

This is in accordance with the two ways in which organisms respond to changes in their environment. The first is to move and change their geographical distribution (extinction can also be included), while the second is to evolve (Eldredge 1995). However, the individualistic nature of species' responses to climate change implies that the adaptations of individual species or population can vary depending on the climate (Stewart 2008). Non-analogue ecological communities, also sometimes called disharmonious communities (Graham 1986), are being suggested as one of the most important characteristics to consider in the analysis of the different species histories. This has proved that the reality is much more complex giving more importance to the separate response of the species to environmental changes leading to non-analogue communities (Stewart 2009). Animals and plants could respond to climate change by geographical shifts that contribute to the modification in ecological communities. The individualistic response of species and the important role of the ecology in the process have implications to speciation and evolution. Furthermore, studies of one species by itself would not reveal general patterns.

The genetic data of different co-distributed species has to be analysed carefully, but undoubtedly, it represents an outstanding tool to understand speciation and evolution. Concentrating on the individualistic responses of species to past climate or environmental changes could be a more valuable way to proceed in a similar manner that studies of biological diversity loss should, instead of focusing on the ephemeral associations that communities represent (Graham 1988). Future environmental fluctuations would cause different responses of species so static models for conservation area design would not be realistic (Thomas and Gillingham 2015).

The phylogeographic approach in recent decades has allowed inferences in different aspects of the post-glacial colonisation in different species (Avise 2000). The genetic diversity and lineages have been one of the fundamental bases for these studies that have been focused principally on Europe (Taberlet et al. 1998; Hewitt 1999, 2004). Studies of changes in the biogeography of other species can provide a potential model for human evolution in the context of Europe. These phylogeographic studies are, for example, helping to understand the important role of population contractions into areas, described as refugia, where species survived for an entire glacial or interglacial cycle (Hewitt 1996; Stewart and Stringer 2012).

More recently, domestic animals have also been used as bioproxies given their association with human migration and activities. The spread of the Neolithic to Europe has been inferred by the domestication process of pigs (Larson et al. 2007) and goats (Naderi et al. 2007). Rats

(Matisoo-Smith et al. 2004; Wilmshurst et al. 2008) and flies (Keller 2007) have also been used as commensal bioproxies. Mice, as another commensal species with human, have demonstrated that they can be used as a bioproxy to offer insight into human movements in the past (Förster et al. 2009; Searle et al. 2009; Hardouin et al. 2010; Jones et al. 2012, 2013). The house mouse (*Mus musculus domesticus*) has been a human commensal since the beginning of agriculture and they have spread together for about 12,000 years (Cucchi et al. 2006; Bonhomme and Searle 2012). In this way, the colonisation history of the house mouse is informative about the humans that transported them (Bonhomme and Searle 2012). In the Mediterranean Basin, for example, the distribution of different mitochondrial clades of *Mus musculus domesticus* has revealed Iron Age relationships between central European and Mediterranean civilisations (Bonhomme et al. 2011). In the British Isles, with mitochondrial DNA markers, links between house mouse phylogeographic patterns and human activities have been suggested (Searle et al. 2009).

With such a variety of approaches, comparative phylogeography becomes significant to comprehend human phylogeographic patterns through the understanding of other species' distributional and demographic histories. Phylogeographic comparison among organisms is needed to reveal unavailable insights from individual examples (Bermingham and Moritz 1998). The value of studying co-distributed species has been long appreciated (e.g. Wares et al. 2001; Hickerson and Cunningham 2005; Crandall et al. 2008; Hickerson and Meyer 2008; Costedoat and Gilles 2009; Marko and Moran 2009), however hypothesis testing has been less common in the literature. In this context, the challenge for phylogeography has to focus on extracting information and describing the relationships between processes and patterns.

The investigation of co-distributed species using statistical phylogeography can provide insights into the different responses to climate change affected by their life history and dispersal characteristics (Waltari et al. 2007). One of the main objectives for the future of phylogeography is to understand why co-distributed species show these discrepancies and whether the response to change is a stochastic or a predictable process (Barrow et al. 2017). Testing hypothesis related with the species distributions in Europe will help to enhance knowledge in evolutionary processes as migration and speciation. The geographical trends revealed by comparative phylogeography are the evidence needed to define refugia, diversification and dispersal of populations (Carnaval et al. 2009; Lexer et al. 2013; Avise et al. 2016).

1.1.3 Climate during the last 60 kya in Europe

In order to understand the demographic distributions of different species in Europe, this thesis has a temporal scope from the last part of the Late Quaternary until today. The Quaternary begins around 2.6 million years ago (mya) and continues to the present date. It is a period well characterised by climate oscillations with increasing intensity of glacial periods (Lowe and Walker 1997). Through the Quaternary we can identify two epochs; the Pleistocene (which starts at the same point as the Quaternary, 2.6 mya, and finishes 11,700 years ago and the Holocene (from 11,700 years ago until today).

Around 2.4 mya, the Arctic ice cap became established. From then until 1 mya, the ice sheets advanced and retreated with a cycle's duration of roughly 41,000 years. After this date, the periodicity changed to a 100,000-year cycle and had become increasingly dramatic (Hewitt 2000). These cycles suggest a mechanism, and the Milankovitch theory proposes that regular variations in the Earth's orbit are the pacemakers of the ice-age cycles (Bennett 1997). These changes are caused by different variations in the dominance of three different component cycles (Lowe and Walker 1997). The 100 ky cycle, knows as orbital eccentricity, is a process where the orbit of the earth around the sun changes from circular to elliptical and back (Imbrie et al. 1993). The variation in the Earth's axial tilt has a 41 ky cycle, knows as obliquity cycle, and precession due to the Earth's axial wobble has a 19–23 ky cycle. All these variations modify the insolation of the Earth changing the energy received by the planet. Climate change in those cases is caused by the high quantity of energy transported by the oceanic circulation system (Webb et al. 1997).

The obliquity cycle is dominant during the early Pleistocene (2.6 – 0.78 mya). During the Middle (0.78 – 0.12 mya) and Late Pleistocene (0.12 ma– present), it is the eccentricity cycle that dominates. This has led to long-lasting glacial periods (ca. 100 ky) and much shorter interglacials (ca. 15 ky) (Pisias and Moore 1981; Lowe and Walker 1997). Palaeoclimatic records reveal that two interglacials took place over the last 150 ky. Evidence supports rapid warming and slow cooling through this time. The period identified in Northern Europe as the Weichselian, which occurred from 110,000 to 12,000 years ago, represents the most recent

glacial (Table 1.1).

Table 1.1 Geologic time scale from the Pliocene until Present and Marine Oxygen Isotope Stages (MIS).

ERA	PERIOD/SYSTEM	SERIES/EPOCH	MILLION YEARS
CENOZOIC	QUATERNARY	Holocene	Present-0.00117
		Pleistocene	0.000117-2.58
	NEOGENE	Pliocene	2.58 - 5.3

Years before present	Isotope Stage	Interglacial /Glacial
	1	Holocene
11 500	2	Weichselian
24 000	3	
59 000	4	
74 000	5	

The Weichselian is also characterised by some warmer and colder episodes. The Greenland ice cores where the ratio of ^{16}O and ^{18}O indicates extension or retraction of ice sheets and therefore terrestrial stadials (cooler periods) and interstadials (warmer periods), reflect the temperature changes over this period (Rasmussen et al. 2014). These changes in the ratio ^{16}O:^{18}O are referred to as Marine Isotope Stages (MIS). The MIS 3 starting at 60 kya, followed by MIS 2, with the Last Glacial Maximum (LGM) at 21 kya, ending with the rapid warming of MIS 1, and the Holocene interglacial, from 10 kya, will be the temporal scope of this project.

The Last Glacial Maximum (LGM) represents a cold period during the MIS 2 where global ice cover reached its greatest level during the late Pleistocene. The main ice sheet covered Scandinavia but at its maximum extent reached southwest Germany (Clark et al. 2009). Other major centres were in the Baltic region and the Alps. The sea level dropped and the mean temperature during winter in Central Europe was -20˚C (Barron et al. 2003). Some open grasslands still prevailed in southern areas over Europe with pockets of forest in some areas (Guthrie and Van Kolfschoten 2000).

Between the LGM and the next warmer period is an interval sometimes defined as Late Glacial and is also a cold period although warmer than the LGM. This warming led to the return of some boreal woodland and shrub patches to Northern Europe (Allen et al. 2010). The Bølling/Allerød (circa 14.7–12.6 kya) was a warm phase that was marked by an abrupt rise in

temperature just after this short interval after the LGM. The Younger Dryas (12.6–11.5 kya) marked the last period of the Pleistocene with a dramatic cooling. Replacement of the woodlands with shrub-tundra took place in the north and open steppe vegetation returned in the south together with periglacial environments in Europe (Bell and Walker 2005). Around 11.5 kya a rapid warming of 15˚C over 1,500 years marks the beginning of the Holocene (Bell and Walker 2005). The vanishing of the ice sheets caused sea levels to rise dramatically and the warmer and wetter conditions enabled, for example, tree species to recolonise northern areas of Europe.

The great level of complexity shown here demonstrates the importance of defining a Milankovitch scale of climate change (i.e. the LGM cooling and the Holocene warming) as a context for understanding phylogeography (Brace et al. 2012). The sub-Milankovitch scale for climate change is more difficult to address in phylogeography due to a variety of reasons, including the dating of the fossils analysed and the limits of available ancient DNA data. Therefore, this thesis will concentrate on the importance of the LGM and the Holocene warming as the major climatic driven effects on populations.

1.1.4 Phylogeographic patterns in Europe after the LGM and comparison between modern humans and other mammals

All these climate oscillations during the late Pleistocene have significantly affected the past and modern distributions of species and the impact of the LGM on the present-day distribution of the species has been extensively discussed in the phylogeographic literature (Hewitt 1996; Bennet and Provan 2008). The expansion-contraction cycles have led to the actual genetic diversity where different clades might be attributed to different areas where distinct populations evolved in isolation from which they expanded (Avise et al. 1987). The areas where species persist during a glaciation period have traditionally been described as refugia. The understanding of how species responded to these periods has had a relevant interest in a variety of fields from palaeoecology to phylogeography due to the implications for evolutionary processes.

Quaternary refugia can be defined as the geographical region that a species inhabits during the period of a glacial/interglacial cycle, representing the species' maximum contraction in their geographical ranges (Stewart et al. 2010). This definition allows a more flexible concept for species regarding their adaptations to different climatic conditions. From here on, this is the definition that will be used for this thesis.

A well-defined model has been established for temperate species in Europe (e.g. Hewitt 1996; Taberlet et al. 1998; Lister 2004; Randi 2007; Bennett and Provan 2008; Stewart et al. 2010). The model proposes that temperate species were restricted to southern refugia, principally in the Iberian, Italian and Balkan peninsulas during glaciations (Hewitt 1996, 1999; Taberlet et al. 1998; Hewitt et al. 2004). Understanding a refugium as an area where the biotic and abiotic conditions are adequate for a population to remain stable (Bennett and Provan 2008), cryptic or northern refugia have also been suggested as refugia for temperate-adapted species that can occur at higher latitudes, within regions of unsuitable habitat (Stewart and Lister 2001; Stewart 2003; Bhagwat and Willis 2008; Stewart and Stringer 2012). Phylogeographic studies and palaeontological studies have revealed faunal and floral cryptic northern refugia for temperate species during the last ice age (Kotlík et al. 2006; Bennett and Provan 2008; Tougard et al. 2008; Vialatte et al. 2008; Lagerholm et al. 2014).

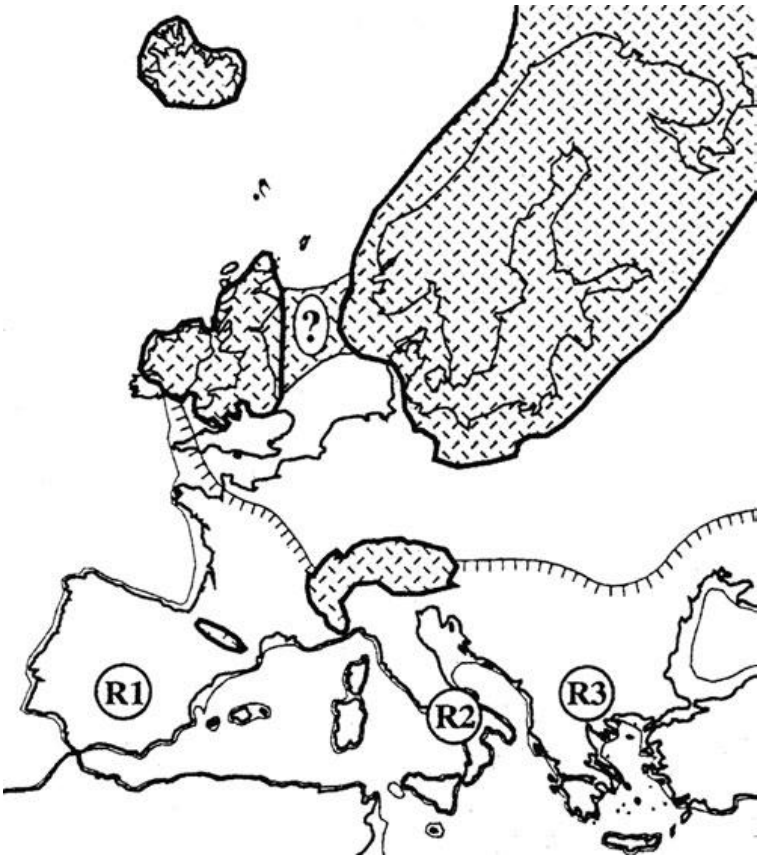

Figure 1.2 Classical southern glacial refugia for temperate species identified by phylogeographical research (source: Taberlet al. 1998). R1: Iberia refugium; R2: Italian refugium; R3: Balkans refugium.

For cold-adapted taxa some efforts have also been made to identify a general model, however the evaluation of how cold-species population expanded and contracted has been complicated based solely on modern phylogeographic studies. Cold-adapted species will retreat into refugia

during warm stages like interglacials (Barnosky and Kraatz 2007; Stewart and Dalén 2008). Polar refugia (in interglacials) have been suggested for some mammal species at high latitude regions (Fedorov et al. 1999; Dalén et al. 2005; Stewart and Dalén 2008). Arctic species such as the collared lemming (*Dicrostonyx groenlandicus*) and the Arctic fox (*Vulpes lagopus*) are in polar refugium now (Fedorov and Stenseth 2001; Dalén et al. 2005). However, cryptic southern refugia have also been suggested for species situated at lower latitudes than their general range during interglacials (Stewart and Lister 2001).

The retreat into refugia has genetic consequences for species, often leading to a decrease of diversity. The reduction in population size between populations creates this overall loss of genetic diversity and gene flow between refugia is not expected to occur. When the conditions improve, populations can spread out of the refugium and extend their range. Species can respond to climate or environmental changes in an individualistic way suggesting that refugia may not coincide in their timing of retreat and expansion implying that refugial areas may change geographically (Stewart 2008; Stewart et al. 2010).

The individualistic response of species to this contraction makes the pattern even more complex from a geographical and temporal perspective. Through the literature, mammal communities, for example, are often stated and regarded as a single unit moving through the landscape (van Kolfschoten and Laban 1995; Stewart et al. 2003). However, even populations may respond in an individualistic way to changes in the environment (Stewart 2008). The principle that modern communities' ranges are equal to past ranges (uniformitarian principle) may not apply and a past species assemblage or community composition may be very different to which species occur together today (Finlayson 2004). This adds another level of complexity to our understanding of biogeographical knowledge of different species.

The effects of the LGM on European mammals have been examined in detail in numerous phylogeographic studies (e.g. Hewitt 1996; Taberlet et al. 1998; Hewitt 2004; Provan and Bennett 2008). However, the influence of this cold Quaternary period on the geographical distribution of genetic diversity is still unclear and further integrative research needs to be done. Understanding these different patterns and responses through comparative phylogeography in a general meta-analysis and discussion seems to be an important approach to bring knowledge into evolutionary processes triggered by climate changes. In the first part of this thesis, an extensive comparison between 29 mammal species with a European range is made based on the mitochondrial DNA control region; testing the main hypotheses suggested for temperate and cold-adapted mammals from a phylogeographic perspective.

Using the different ranges of phylogeographic patterns in species in Europe to identify likely similar and different histories between modern humans and other mammals may help to establish similarities based on ranges, adaptations, habitats and movement. This novel approach will represent a new context for understanding comparative phylogeography including modern humans.

The genetic makeup of current modern human European population and the historical processes which generated these patterns have attracted great interest from population geneticists, anthropologists, historians and archaeologists (Günther and Jakobsson 2016). The study of the human past using the techniques of molecular genetics was defined by Renfrew and Boyle (2000) with the term archaeogenetics. The mtDNA of human cells can give us a lot of information due to the number of copies that can be found in one cell, its high evolutionary rate and non-recombining nature transferring only through the maternal lineage. The mutations acquired over time can be used to subdivide the human population into different clades or haplogroups. The human mitochondrial genome is a small circular DNA molecule that comprises 16,569 base pairs, which form an inner light (L) strand and an outer heavy (H) strand whose names reflect the molecular weight that is affected by the guanine content (Stewart and Chinnery 2015).

One of the first studies of human phylogeography was conducted by Brown (1980) studying humans from different geographic and ethnic backgrounds using restriction-enzyme fragment length polymorphism (RFLP) in the mtDNA in order to trace human history. Later studies were developed focusing on these RFLP (Brown 1980; Johnson et al. 1983). During the 90s a new target appeared: the first hypervariable segment (HSV-I) of the control region. This segment is non-coding and also fast evolving which are important characteristics in phylogenetic studies. However, its high levels of recurrent mutation can blur the structure of the phylogenetic tree (Torroni et al. 2006).

With these studies a new nomenclature was initiated for the mtDNA haplogroups. A group of similar haplotypes that share a common ancestor with a single-nucleotide polymorphism mutation started to be defined as haplogroups (Arora et al. 2015). The first letters of the alphabet represented the first branches of the phylogenies and started to be proposed in studies on the Native Americans (Torroni et al. 1993). During the next years, other haplogroup structures for different continents were also established (Torroni et al. 1994; Richards et al. 2000). The main rules for mtDNA haplogroups nomenclature were first proposed by Richards et al. (1998). The terminology has been followed with the same rules developing a system

respecting the published record and novel data (Torroni et al. 2006). However, sometimes the nomenclature has not been used consistently, for example the same name has been coined for different haplogroups or different names used for the same haplogroups (van Oven and Kayser 2009).

Focusing only on the mtDNA of modern humans and analysing the geographical variation of the lineages in the context of the phylogenetic estimate of the genealogy of this specific marker, a great number of studies have been developed (Richards et al. 1998; Simoni et al. 2000; Richards et al. 2002). However, the main caveat is that through modern DNA we can only infer past events from the perspective of present distribution patterns. The arrival of ancient DNA analyses has the advantage of providing direct genetic evidence at a given point in the context of time. This allows complementing the hypotheses concerning the genetic affinity of ancient populations (Brandt et al. 2015).

The first studies were focused on the short control region as a marker. The outputs of these studies showed a more homogenous pattern across Europe than previously imagined. Even some populations that were considered relatively isolated as the Basques, in southwest Europe, or the Sardinian population in the Mediterranean seemed to be quite similar in terms of genetic frequencies for different haplogroups (at that time called lineage clusters)(Pala et al. 2014). That was not the case for the Saami, an indigenous Finno-Ugric people, which traditionally inhabit the Arctic area. Between 30-50% of lineages in these groups belonged to two subgroups that are extremely rare in Europe (Sajantila et al. 1995). But these analyses were made from summary statistic and their genetic history was then not related with other European populations. However more recent analyses have demonstrated that the Saami shared ancestry with other Europeans rather than from northeast Asia as was previously suggested (Huyghe et al. 2011). This distinctiveness might be due to genetic drift after the resettlement process of Scandinavia from the south around 10,000 ya (Tambets et al. 2004).

The first anatomically modern humans lived in Europe as early as 43 kyr ago (Benazzi et al. 2011). As there is evidence of a genetic turnover of Europeans before the LGM, possibly in relation to climate oscillations (Fu et al. 2016; Nielsen et al. 2017), these early Paleolithic Europeans have probably made little genetic contribution to the current European people (Günther and Jakobsson 2016). However, the precise contributions from early Europeans are still under debate (Gallego-Llorente et al. 2016).

To understand the presence of modern humans in Europe three critical periods need to be considered. The first one is the colonisation of Europe, approximately 45 kya due to the

expansion of modern humans out of Africa. Second, is the LGM between 27 and 16 kya. And third, the spread of Neolithic culture from the Near East and its arrival in Europe around 9 and 5 kya (Pinhasi et al. 2012). These are considered the major demographic events that shaped European modern human phylogeography.

1.1.5 Human-mediated phylogeographic patterns

The relationship between other mammal species and modern humans can also be closer for commensal and domestic animals that are moving with our species. Using certain species as a bioproxy for humans has been developed as a useful research tool to understand more recent human phylogeographical patterns.

For the last millennia, modern humans have been transporting species outside their normal range (Hulme 2009). These movements have caused a clear modification of the phylogeographic patterns of several species that share a close association with humans (e.g. Larson et al. 2007; Naderi et al. 2007). Human-mediated transportations have also shaped current patterns of phylogeography for commensal or domestic species. It is still difficult to distinguish between natural movement and migration during the Late Pleistocene and prehistoric, human-mediated introductions for these species (Zeder 2008), but combining phylogeographic patterns and species life history information is helping to explain much better these patterns. Therefore, those organisms that are transported by people can be used as bioproxies for human movement (Jones et al. 2013), and this can have a profound impact in the understanding of more recent transportation and on our knowledge of more recent human movements.

Several domestic species have already been used as bioproxies for human movement because of their close association with our species in more recent times (Matisoo-Smith and Robins 2004; Naderi et al. 2007; Wilmshurst et al. 2008; Koch et al. 2015). House mice (*Mus musculus domesticus*) represent an invasive species that have accompanied humans since the beginning of agriculture and ocean-going navigation (Cucchi 2008) and have demonstrated their usefulness as a bioproxy to offer insight into human movements of population in the past (Förster et al. 2009; Searle et al. 2009; Hardouin et al. 2010; Jones et al. 2012, 2013). In the second part of this thesis, two case studies are used to address a comparative analysis based on the movement observed in the western house mice in two European islands (Cyprus and Britain) from the modern and the ancient perspective.

The western house mouse is considered a good bioproxy and phylogeographic studies of this species can complement our knowledge of the phylogeography of humans (Jones et al. 2013). In the last decades, several studies have been able to highlight links between the colonization of mice and humans by analysing mitochondrial control region sequences of insular populations of house mice (e.g. Gündüz et al. 2001; Duplantier et al. 2002; van Vuuren and Chown 2007; Förster et al. 2009; Searle et al. 2009; Hardouin et al. 2010; Jones et al. 2010, 2011, 2012; Gabriel et al. 2011; Gabriel et al. 2015; Gray et al. 2014). Specifically, in the Mediterranean Basin, for example, the distribution of different mitochondrial clades of *Mus musculus domesticus* has revealed Iron Age relationships between the central European continent and Mediterranean civilizations (Bonhomme et al. 2011). In the British Isles, with mitochondrial DNA markers, links between house mouse phylogeographic patterns and human activities have also been suggested (Searle et al. 2009).

The house mice expansion patterns in the Mediterranean Basin and the British Isles are an excellent bioproxy to analyse human movement history. As expected for a commensal species, the western house mouse is characterised by a complex history shaped by founder effects, genetic drift and admixture. Two insular areas, such as Cyprus and Britain, might represent important territories of human and mouse migration, where some hypotheses have suggested the connections between house mice introductions and the human transport (Searle et al. 2009; Bonhomme et al. 2011; García-Rodríguez et al. 2018).

Until now, only one study has been able to extract ancient DNA from the house mice (Jones et al. 2012). In the British Isles, the earliest credible records of house mouse in Britain date from the Iron Age (Coy 1984). In this thesis, the first ancient DNA study in *Mus musculus domesticus* in the British Isles is conducted to provide a new approach to test the colonisation of the British Isles of this invasive species by adding the time dimension to the arrival of house mice.

1.2 Research Outline

1.2.1 Research aims and objectives

This thesis investigates different approaches in comparative phylogeography to understand the demographic patterns for mammal species, including modern humans, in Europe and to compare them, searching for similarities and differences. This chapter has outlined several inherent issues related to the comparative phylogeographic approaches that remain unexplored. Thus, the final aim of this research is to overcome these considerable gaps and to

enhance knowledge in evolution by elucidating patterns of population movement in the past that can be associated with several species, and also with their individualistic responses to changes.

In the first part of the thesis (Chapters 2-4), the research investigates patterns of genetic diversity by examining various diversity indices across twenty-nine mammal species to test for trends and commonalities. The overall aim of this research is to enhance knowledge in phylogeography and the importance of refugia during the LGM in Europe through a comparative phylogeographic meta-analysis of mammal species in order to elucidate patterns of population movement in the past. This thesis develops novel insights into the phylogeographic interactions of different mammal species, including modern humans, in the European geographical context. Modern humans are integrated into the meta-analysis trying to find a new comparative approach that helps to understand better the main phylogeographic pattern of our species.

The second part of the thesis (Chapter 5 and Chapter 6) investigates the phylogeographic patterns of the human commensal species, the western house mouse (*Mus musculus domesticus*), in two different European islands, Cyprus and Britain, from the modern and ancient DNA perspective, respectively. The main aim of this part of the thesis is to understand the house mouse phylogeographic patterns in two islands in Europe and to use this new knowledge as a bioproxy to understand more recent human movements associated with the transport of the species.

Correspondingly, this research has five overall objectives (O):

O1. Describe and compare the phylogeography of wild mammal species in Europe in order to identify patterns of distribution change from Late Pleistocene to phylogeographical patterns today.

O2. Use the different ranges of phylogeographic patterns in mammal species in Europe to identify likely similar and different histories and establish similarities based on genetic diversities indexes.

O3. Assess the human phylogeography in Europe through ancient DNA to elucidate patterns of population movement during the Palaeolithic and Mesolithic that may be similar to other mammal species.

O4. Develop a phylogeographic study of the species *Mus musculus domesticus* across the European Island of Cyprus with the aim to investigate mouse expansion patterns in Cyprus and indirectly the movement of human populations.

O5. Obtain the first ancient DNA data for the house mice in Britain and shed light on the colonisation events that shaped the introduction of this species.

The structure of this project will be based on the research aims and objectives outlined above. Therefore, this research is organised to achieve the mentioned objectives. These objectives refer to the four main data chapters and the conclusion chapter (Chapter 7) of the thesis.

1.2.2 Thesis structure

As mentioned above, this thesis is structured into two parts. The first part (Chapters 2-4) addresses the three first objectives (O1-O3) outlined and the second part (Chapter 5 and 6) the last two (O4-O5). This thesis also includes a general introduction (this chapter). A material and methods chapter (Chapter 2) which is followed by two data chapters that addressed the first main research aim (Chapter 3-4). Part two is presented without a material and methods chapter. Each data chapter contains its introduction, methods, results and discussion subdivisions. A conclusion chapter (Chapter 7) describes and links the main findings and conclusion of each of the data chapters. The structure of the thesis is outlined below with a summary of each chapter's content.

Chapter 1: Introduction

This chapter provides a comprehensive review of the significant literature in the field of phylogeography and identifies the knowledge gaps that are addressed in this thesis. The Introduction also gives context and justification for the thesis, presenting the research aims and objectives used to address these knowledge gaps.

Chapter 2: Material and Methods

This chapter introduces the main methods and analyses that represent the core of the first part of this thesis that laid the foundations of the main method of this research. The comparative approach that characterised this thesis is presented here in detail with the aim of helping to understand better the context in which this research has been developed.

Chapter 3: Modern mammalian genetic diversity in Europe

This chapter expands the previous results on the study of genetic diversity in Europe by a combination of twenty-nine mammal species genetic diversity measures and their comparison between geographical areas. This chapter addresses the first aim and objective 1 (O1) and 2 (O2).

Chapter 4: Identifying genetic diversity patterns shaped by the LGM in modern humans and other mammal species

This chapter evaluates the different phylogeographic patterns obtained for each species analysed individually discussing the patterns previously described. It also presents new analyses that are based on the meta-analysis approach. The main phylogeographic pattern obtained for modern humans during the Palaeolithic and Mesolithic in Europe is also presented and considered it in the context of other mammal phylogeographies and genetic diversity indices. This chapter addresses the first aim and objectives 1 (O1) and 3 (O3).

Chapter 5: Cyprus as an ancient hub for house mice and humans

In this chapter, the phylogeography of house mice in Cyprus is investigated using mitochondrial D-loop sequences and microsatellite data from modern samples. The dispersal of mice along with humans may have left a complex footprint on the island and this hypothesis is explored. This chapter addresses the second aim and objective 4 (O4).

Chapter 6: Travellers to the north: ancient DNA from the first house mice in the British Isles

The first ancient DNA study in the western house mouse in Britain is developed in this chapter. Eight house mouse and four field mouse specimens from the Bronze and Iron Age were targeted for the D-loop in order to insight the colonisation of England from these two species. This chapter addresses the second aim and objective 5 (O5).

Chapter 7: Final Discussion

This chapter comprises the concluding remarks and a recapitulation of the results obtained in the previous chapters and the conclusion. It also includes the limitations of this research and recommendations for the direction of future research.

Chapter 2. Material and Methods

2.1 Introduction

The advancements in the field of phylogeography have entailed comparative appraisals (Bermingham and Moritz 1998). Comparative phylogeography emerged as an integrative approach to historical biogeography and offered important insights into the factors that shaped genetic variation, and therefore, evolution (Arbogast and Kenagy 2001; Papadopoulou and Knowles 2016). The availability of genetic data in open access databases has helped to develop new studies, but there is still a lack of analyses and synthesised knowledge that can be obtained from them.

A systematic review is characterised by addressing and collecting multiples studies with the aim to summarise their outcomes. The process includes the use of a methodological guideline for the literature search, study screening and selection, data extraction and discussion (Gurevitch et al. 2018). If this systematic review reveals enough quantitative data from the studies chosen, then a meta-analysis can be conducted using statistical analyses. Meta-analyses are an examination and testing of general interactions that allow questioning paradigms on a larger scale than usually possible at a single case study level (Kaiser et al. 2006). To do so, the combination of the results from different studies to create a single and more realistic estimation of an effect is needed (Ferrer 1998). Standardisation and a well design for the effect sizes are also needed to put the outcomes from different studies combined at the same scale.

Synthesizing results across different studies to reach an understanding of a problem is an essential part of the scientific process. One of the main goals for the use of meta-analyses is to reach generalisations across a large number of studies providing a better understanding than obtained from individual studies (Gurevitch et al. 2018). In this thesis, a meta-analysis is conducted to investigate broad patterns of genetic variation and demographic histories throughout Eurasia in order to elucidate concordant geographical patterns across different mammal species identifying common historical processes. Based on the data obtained from the systematic review approach, a meta-analysis has been designed and conducted. Here, the different steps followed to conduct the review and the meta-analysis are presented (Figure 2.1).

Phylogeography focuses on the phylogenetic analysis of genetic data to test assumptions related to the geographical distribution of the species (Hickerson et al. 2010). Phylogeographic studies have been performed on a significant number of different organisms including from wild animals and plants to bacterial and viral pathogens. Mitochondrial DNA (mtDNA) has been traditionally used as the main genetic marker in phylogeographic research, but many studies address phylogeography based on one species and a limited geographical area. The sequences from most of these genetic studies are deposited in the primary public archive for the deposition of genetic sequences such as GenBank (www.ncbi.nlm.nih.gov/genbank/), an accessible online database. This database comprises publicly available nucleotide sequences for more than 400,000 described species (Benson et al. 2018). The aim of testing phylogeographical hypotheses could be facilitated to a great extent by the data available in this database and this research follows this approach to do a comparative analysis.

Significant efforts have been made using comparative phylogeography to understand European distribution of the species and common phylogeographic patterns (Taberlet et al. 1998; Hewitt 1999; Hewitt et al. 2004). However, these analyses were limited by a low number of species and the small number of DNA sequences available at the early 2000s. Today, the access to much more data allows us to test the same phylogeographic hypotheses but founded in a much larger number of species and sequences.

Twenty-nine mammal species were selected based on the availability of the sequences in GenBank. For analysing such data, a database for each species has been created to investigate the various patterns seen in different mammal species, which can then be grouped by similarity according to geographical and genetic diversity indices. These also include the diversity estimates as well as the species' phylogenetic trees, haplotype network diagrams and population differentiation indexes.

A large section of this Ph.D. thesis is based on creating and using a database for each species with sufficient available data. The database is used to address different analyses to infer phylogeographic patterns. To investigate the phylogeographic patterns in different species across Europe it is necessary to delimit certain aspects of the geographical areas included and the genetic markers available for all the species analysed and they are discussed in the following sections.

2.2 Genetic delimitations

Mitochondrial DNA has been commonly used in phylogeographic studies across a wide range of vertebrate species (see Taberlet et al. 1998; Hewitt 2004; Hickerson et al. 2010 and references therein). Animal mtDNA in general exhibits remarkable conservation of gene content (Harrison 1989). The selection of mtDNA is due in part to its relatively rapid rate of mutation, a high number of copies per cell and its haploid maternal inheritance mechanism which make it useful for the elucidation of demographical changes as well as the population history of each species (Avise et al. 1987, 1995; Moritz 1994). This fast-evolving capacity makes mtDNA a good marker that can be used to follow divergence in closely related taxa and even within species. MtDNA is also characterised by low recombination, so it can be assumed that the genealogical history will be the same for the whole molecule, helping the interpretation of the demographic history. Indeed, this information is critical to interpret landscape-level patterns of genetic diversity in the context of phylogeographical reconstruction (Pavlova et al. 2013). For these reasons, mtDNA sequence data are and will continue to represent an important marker in phylogeography (Garrick et al. 2015).

The molecule itself includes two ribosomal RNA (rRNA) genes, 22 transfer RNA (tRNA) genes and other 13 genes that code for electron transport or ATP synthesis proteins. The mtDNA also includes a non-coding region, which is involved in the regulation and initiation of mtDNA replication and transcription, of approximately 1,200 nucleotides and is known by three different terms: control region, D-loop and hypervariable region. The control region (CR) occurs in a non-coding area of the mtDNA and presents strong rate heterogeneity between sites, a high frequency of events as insertion and deletions and lineage specificity which makes it an excellent genetic marker (Saccone et al. 1991; Pesole et al. 1999). This is the region that has been selected for the analysis and it represents a genetic marker that has been widely used in phylogeographic studies (e.g. Seddon et al. 2001; Troy et al. 2001; Scandura et al. 2008).

Achieving a high genetic resolution from short DNA sequences as the control region can only be based on its high variability due to its non-coding DNA nature with a relatively high mutation rate (Moritz et al. 1987). Some caveats can also be added by choosing small fragments due to homoplasies, or the effect of identical mutations that arise in different lineages, leading to misinterpretations in the reconstruction of species and populations histories. Increasing sequence lengths will provide better resolutions, but the absence of

longer fragments available for most of the species (or the reduced number of them) forced this research to be conducted based on a short fragment which has a large number of sequences to be compared with, helping to compensate for the caveat in resolution due to fragment length.

Control region (CR) mitochondrial DNA sequences are targeted for mammal species within a European range. The selection of this region is also based on the availability of the sequences. The primary public archive for the deposition of genetic sequences, GenBank, was searched for mtDNA fragments that could be potentially used in this analysis. Searching on this database under the keyword "control region", 2,578,227 results appeared and 3,156,225 sequences using "d-loop" (December 2016). Knowing that some entries display these two keywords, does not mean that the sum of both values will represent the total of sequences available. However, the next two most commonly used mtDNA regions, cytochrome B (*cyt B)* or cytochrome c oxidase subunit I (*COI),* yield fewer results (449,239 and 2,218,985 respectively). So clearly the CR or D-loop is the mtDNA fragment with the highest number of entries and that is the main reason why it has been selected. To achieve a reliable study comparing different species, this marker has to be consistent through the different species' analyses.

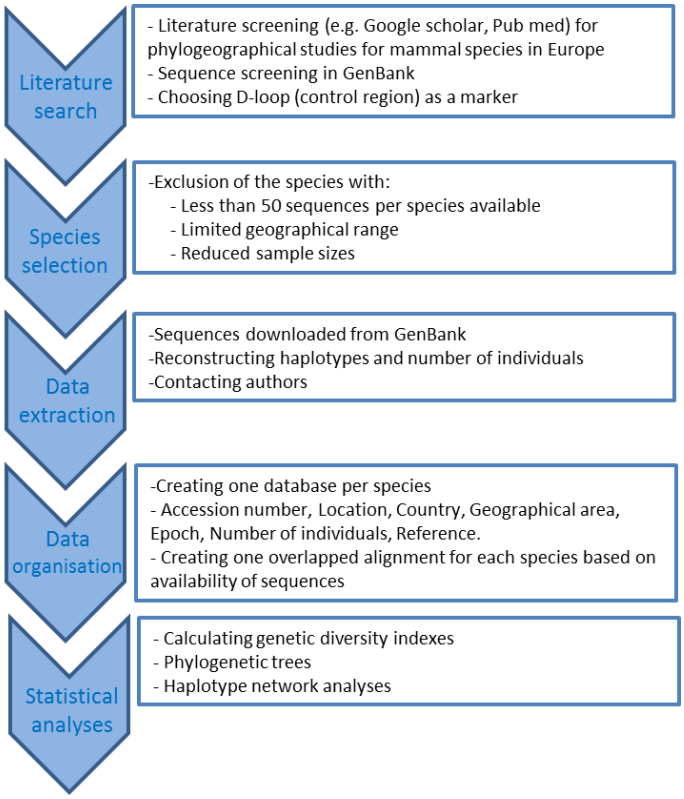

Figure 2.1 Schematic workflow of the review and the meta-analysis followed in this thesis (adapted from Marom et al. 2017).

The sequences have been searched using species names, with “d-loop” or “control region” as keywords on GenBank database. Where sequences were available, the primary literature and papers for each study were found through online data searches (e.g. Google Scholar, PubMed). How sequences’ were submitted onto the database varied widely. Some authors deposited sequences for all the individuals examined in each study, others submitted only each unique haplotype encountered, and others deposited only a single haplotype, and a reconstruction of all the haplotypes from the study is needed.

The use of modern material has not always been sufficient to describe past diversity and resolve historical processes based on current phylogeographic patterns. However, the appearance of ancient DNA (aDNA) has helped understand population dynamics, extinctions and re-colonisations as far back as the Late Pleistocene (Leonard et al. 2000; Shapiro et al. 2004; Thalmann et al. 2013; Horn et al. 2014). Ancient DNA has facilitated connections to be made with possible causal factors behind past shifts in genetic diversity. For this reason, for those species where aDNA is available an effort has been made in order to include the largest number of aDNA sequences available.

The next section outlines the methods applied to the collection, management and analysis of data.

2.3 Species collection

Intense climate changes, such as the LGM, are important for the understanding of evolution and to comprehend how species respond to it. Mammal species have been considered one of the main model systems for palaeontological studies (Raia et al. 2006; Villalobos et al. 2016). Furthermore, mammals have also been important in relation to the study of ice age refugia in Europe enabling the detection of the genetic variation of interest (Bilton et al. 1998; Taberlet et al. 1998). Despite the individualistic responses of mammal species, incorporating phylogeographic information into the evolutionary context has revealed some interesting patterns.

Specific criteria have been followed to address a wider range of mammal species but also to include as much diversity as possible in the analyses. From a body size perspective, small and large (megafauna) mammals have both been targeted, so a minimum of 10 small and 10 large has been established. Carnivores and herbivores were also considered, so a minimum of 10 carnivores and 10 herbivores were set as a minimum. Herbivores are more abundant than

carnivores, but the ecological importance of carnivores make them species that need to be analysed (Peters and Raelson 1984). The different climatic and ecological adaptations to different areas have also to be tested so temperate and cold-adapted species have been considered and a minimum of 5 temperate species and 5 cold-adapted were set. Following these premises, the analyses could be conducted.

All the terrestrial mammal species with a wide range in the European continent have been considered for this study. The IUCN list mammal species was downloaded from http://www.iucnredlist.org/technical-documents/spatial-data, date of download 11/2015). In total 179 terrestrial species were considered. Google Scholar and Web of Science were used as search engines for publications using the keywords "phylogeography Europe" and "control region phylogeography" until December 2017. Only studies where raw data sets in CR mtDNA were searched, to minimise the potential for different signals between genetic markers.

A total of 225 species were investigated for sequences deposited in GenBank (Table A1.1 in Appendix 1). The searching was made using species name, with D-loop or control region as keywords. The data collection was ceased in January 2018 to allow the meta-analysis to proceed.

A total of 69 species were discarded due to a total range of less than 0.5 x 10^6 km^2 not covering an area where a general phylogeographic pattern could be identified. 36 other species were also discarded based on the low number of sequences available in Genbank, representing less than 50 sequences available for the c*yt B* and the D-loop. Therefore, a total of 74 species were examined where 73% (54 species) had more data available for the D-loop than the *cyt B*. Furthermore, from the 20 species that yielded more sequences for the *cyt B*, 6 of them have more than 50 sequences so where also included for the D-loop.

Out of 60 mammal species, 13 were discarded because they represented bats, 9 because the range covered was not enough to conduct the analysis and 6 due to problems with the sequences available, e.g. short fragments, unverified sequences. The data available in Genbank have delimited the analysis but in total 84 species were included in the preliminary search. For those species with less than 50 sequences available the analysis has not been conducted. This leads to a total of 29 species that have been included in the analysis (Table 2.1).

Table 2.1 Mammal species that have been chosen for the meta-analysis. CR and D-loop columns indicate the number of results for each species in GenBank associated with control region and D-loop as keywords.

Species	Common Name	CR	D-loop	Climate adaptation	Size	Diet	Family
Arvicola amphibius	European Water Vole		92	Temperate	Small	Herbivore	Cricetidae
Arvicola sapidus	Southern Water Vole	7	89	Temperate	Small	Herbivore	Cricetidae
Microtus arvalis	Common Vole	287	138	Temperate	Small	Herbivore	Cricetidae
Myodes glareolus	Bank Vole	92	129	Temperate	Small	Herbivore	Cricetidae
Lemmus lemmus	Norway Lemming	42	1	Cold	Small	Herbivore	Cricetidae
Cricetus cricetus	Black-bellied Hamster		119	Temperate	Small	Herbivore	Cricetidae
Sciurus vulgaris	Eurasian Red Squirrel	92	507	Temperate	Small	Herbivore	Sciuridae
Castor fiber	Eurasian Beaver	34	61	Temperate	Small	Herbivore	Castoridae
Lepus europaeus	European Hare	305	563	Temperate	Small	Herbivore	Leporidae
Lepus timidus	Mountain Hare	134	188	Cold	Small	Herbivore	Leporidae
Erinaceus europaeus	Western European Hedgehog	481	128	Temperate	Small	Herbivore	Erinaceidae
Erinaceus concolor	Hedgehog	34		Temperate	Small	Herbivore	Erinaceidae
Sorex minutus	Eurasian Pygmy Shrew	158		Temperate	Small	Herbivore	Soricidae
Canis lupus	Gray Wolf	4968	4301	Temperate	Large	Carnivore	Canidae
Vulpes lagopus	Arctic Fox	80	100	Cold	Small	Carnivore	Canidae
Vulpes vulpes	Red Fox	708	137	Temperate	Small	Carnivore	Canidae
Gulo gulo	Wolverine	271	5	Cold	Small	Carnivore	Mustelidae
Mustela erminea	Stoat	119	220	Cold	Small	Carnivore	Mustelidae
Mustela nivalis	Least Weasel	122	140	Temperate	Small	Carnivore	Mustelidae
Martes martes	Pine Marten	55	153	Temperate	Small	Carnivore	Mustelidae
Lynx lynx	Eurasian Lynx	75	17	Temperate	Large	Carnivore	Felidae
Ursus arctos	Brown Bear	774	415	Temperate	Large	Carnivore	Ursidae
Homo sapiens	Modern Human	-	-	Temperate	Large	Carnivore	Hominidae
Alces alces	Eurasian Elk	308	212	Temperate	Large	Herbivore	Cervidae
Cervus elaphus	Red Deer	846	870	Temperate	Large	Herbivore	Cervidae
Capreolus capreolus	European Roe Deer	122	734	Temperate	Large	Herbivore	Cervidae
Rangifer tarandus	Reindeer	918	1403	Cold	Large	Herbivore	Cervidae
Bison bonasus	European Bison	79	163	Temperate	Large	Herbivore	Bovidae
Sus scrofa	Wild Boar	5138	4909	Temperate	Large	Herbivore	Suidae

The individual information obtained for each of the 29 species (for studies used see Table 2.2) analysed are presented here including their distribution and habitat with a summary of the previous phylogeographic results for the control region. The classification follows the mammal classification based on orders.

RODENTIA

Arvicola amphibius (European Water Vole)

Habitat and distribution: Current taxonomic determinations identify three different species of water voles that are associated with different ranges and areas. The northern water vole (*Arvicola amphibius*) with distribution across Eurasia, the southern common vole (*Arvicola sapidus*) in Iberia and France, and *Arvicola scherman* with a distribution characterised by several European mountain systems such as the Alps, Carpathians, Cantabrian Mountains, Massif Central and Pyrenees (Musser and Carleton 2005). The European water vole survives in a range of habitats around rivers and streams and in the lowlands and the mountains (Harrison and Bates 1991).

Previous phylogeographic studies: Three main studies have been published aimed at resolving the evolution of the different water vole lineages through molecular analysis based on mtDNA (Taberlet et al. 1998; Piertney et al. 2005; Brace et al. 2016). Taberlet et al. (1998) addressed the phylogeography of the water vole identifying one lineage corresponding to *A. sapidus* and three others with *A. amphibius* [*terrestris*]. In Piertney et al. (2005) common voles across Britain were targeted showing two different clades suggesting two possible colonisation events, both during the early Holocene. Brace et al. (2016) added aDNA sequences from the Pleistocene and Holocene confirming the two colonisation events in Britain, one during the Pleistocene and the other during the early Holocene.

Arvicola sapidus (Southern Water Vole)

Habitat and distribution: *Arvicola sapidus*, the southwestern water vole, inhabits in parts of France, Spain and Portugal (Quéré and Le Louarn 2011). The origin of this species has been located in the Iberian Peninsula during the Pleistocene according to the fossil record (Sesé Benito 1994). The water vole is almost always found near water, preferring small freshwater lakes, ponds and rivers (Fedriani 2002).

Previous phylogeographic studies: Not many phylogeographic studies have been done in *Arvicola sapidus* (Centeno-Cuadros et al. 2009; Centeno Cuadros et al. 2011). These studies proved a relatively shallow phylogeographic structure with geographical coherence, however, seven spatially continuous groups inferred (Centeno Cuadros et al. 2009).

Microtus arvalis (Common Vole)

Habitat and distribution: *Microtus arvalis* is widespread in Europe with ranges from France to Central Asia (Amori et al. 2008). Farmland and open grassland are the habitats inhabited by the common vole with a broad range of altitudes occupied (Hausser 1995).

Previous phylogeographic studies: Two different lineages have been identified using mtDNA as a marker and reflect the two main forms of the common vole, the *arvalis* and the *obscurus* subspecies, that occupied the west and east of its range respectively (Haynes et al. 2003; Jaarola et al. 2004). A hybrid zone between these two lineages has been described in the central European part of Russia (Meyer et al. 1997).

The common vole is considered a species that does not conform to the southern refugial hypotheses (Fink et al. 2004; Heckel et al. 2005; Tougard et al. 2008). The study by Tougard et al. (2008) showed a west-central European persistence rather than southern refugia in Italy or Spain. The level of complexity shown by different phylogeographic studies using different markers has described at least five main lineages of *M. arvalis* in the European continent using the cytochrome *b (*cyt *b)* marker (Buzan et al. 2010; Stojak et al. 2015).

Myodes [Clethrionomys] glareolus (Bank Vole)

Habitat and distribution: The bank vole is a species with a wide range in the Palaearctic from the British Isles through continental Europe to Russia. *Myodes glareolus* is primarily a woodland species but can also be found in scrub and hedges (Spitzenberger 1999).

Previous phylogeographic studies: From the phylogeographic perspective, unfortunately, most of the studies that have been carried out for the bank vole used cyt *b* as the genetic marker. From this, a strong complexity has been revealed based on at least seven well-defined lineages identified (Deffontaine et al. 2009). There is much available data for the control region. However, there are important geographical restrictions for these sequences as the most extensive investigation has been done to address Chernobyl radiation and associations between the species and in Puumala virus (e.g. Dekonenko et al. 2003; Meeks et al. 2007).

Therefore, the phylogeographic inferences based on control region are relatively restricted or biased by this oversampling.

Lemmus lemmus (Norwegian lemming)

Habitat and distribution: *Lemmus lemmus* is a species that inhabits mountain tundra of some regions in Scandinavia, Finland and the Kola Peninsula in Russia. It represents the only endemic mammal of the Scandinavian region known as Fennoscandia and the southern border of the species range is unstable due to significant migrations. The Norwegian lemming can also be found in forests and close to rivers and lakes (Hansson 1999).

Previous phylogeographic studies: Fossil records from the Late Pleistocene from the genus *Lemmus* are found in the mid-latitude steppe-tundra in Europe and Asia (Nadachowski 1989). It is considered a cold-adapted species, whose southern range disappeared with the Holocene interglacial, either becoming extinct or changing their distribution to northern areas in Scandinavia. Two main hypotheses suggested a possible origin for the species. The first, from outside the Scandinavian Ice Sheet and from a non-Siberian source (Østbye et al. 2006) and the second, a northern refugium presence during the LGM surviving as a small source population for modern lineages. However, there is no fossil evidence of *Lemmus lemmus* in Scandinavia during the LGM (Ekman 1922; Fedorov and Stenseth 2001; Lagerholm et al. 2014).

Ancient DNA analyses from the Pleistocene have revealed a high genetic diversity in the populations that inhabited the mid-latitude European areas (Lagerholm et al. 2014). This study also suggested an ice-free area in Scandinavia as a refugium due to that the main haplotype found in modern Scandinavia was not observed in any of the glacial populations south and east of the Scandinavian Ice Sheet. The latter indicated probably a non-postglacial colonisation from older southern populations (Lagerholm et al. 2014).

Cricetus cricetus (Common Hamster)

Habitat and distribution: The common hamster is a steppe species, also occupying meadows and steppe-forests, with an extensive range from Asia to Western Europe (Berdyugin and Bolshakov 1998; Nechay 2000). It forms some isolated populations in Belgium, France, the Netherlands and Western Germany (Mitchell-Jones et al. 1999). Common hamsters in western and central Europe are restricted mainly to agricultural sites and suitable microclimates (Nechay et al. 1977).

Previous phylogeographic studies: A steppe belt in Ukraine and Russia has been suggested as the main refugium for *Cricetus cricetus* during the Pleistocene glaciation (Neumann et al. 2005). MtDNA phylogenetic lineage distribution seemed not to correlate with the existence of the two different subspecies, one in the west the other in the east (Mitchell-Jones et al. 1999).

Two main distinct mtDNA lineages have been identified for *C. cricetus* in Europe labelled as 'Northern' and 'Pannonian' (Neumann et al. 2004, 2005). The Northern lineage has been suggested as an expansive population from northern 'cryptic' refugium around Germany as a source for western populations. The 'Pannonian' lineage has been hypothesised to have expanded from the south reaching Czech Republic (Neumann et al. 2004, 2005). A more complex scenario exists in Poland with mixed signals from an eastern influence and the Pannonian area (Banaszek et al. 2009). The distinct north-south distribution in central Europe seems to differ from the phylogeographical structure found for other muroids in Europe (Jaarola and Searle 2002; Michaux et al. 2003).

Sciurus vulgaris (Red squirrel)

Habitat and distribution: The red squirrel is a species characterised by a great phenotypic variation that has led to the description of many different subspecies of *Sciurus vulgaris* (Barrat et al. 1999). It is a ubiquitous species and can be found in many types of coniferous, deciduous and mixed forests across Eurasia representing an extremely arboreal species with a distribution closely linked to the distribution of woodland habitat (Lurz et al. 2005). A classification made by Sidorowicz (1971) describing 17 subspecies has been used in the latest review on the subspecies status (Lurz et al. 2005), but these morphological groupings do not necessarily reveal the different phylogeographical patterns of the red squirrel (Hale et al. 2004; Grill et al. 2009).

Previous phylogeographic studies: Studies using mtDNA D-loop as a marker have shown a lack of phylogeographical structure in Europe with the only exception of individuals from the region of Calabria, in the south of Italy, representing a different phylogroup and all the European individuals clustering together in a unique, distinct phylogroup (Grill et al. 2009). This genetic structure might show the evolutionary history of the species during the LGM because a rapid demographic expansion seems to have occurred (Grill et al. 2009; Dozières et al. 2012). Another explanation suggested for this pattern in some areas, like France, is related to high levels of gene flow leading to a lack of genetical differentiation of the population (Dozières et al. 2012).

Castor fiber (Eurasian Beaver)

Habitat and distribution: The beaver is the largest Eurasian rodent and its habitat is characterised by living along rivers with adaptation for semi-aquatic life but may inhabit agricultural lands or urban areas (Tattersall 1999; Halley and Rosell 2003). Its distribution was wider in the past but over-hunting had reduced the number of individuals and also its range, being only around 1,200 individuals in Europe at the start of the 20th century (Nolet and Rosell 1998).

Previous phylogeographic studies: The first phylogeographical studies based on mtDNA showed non-sharing haplotypes between populations with some described as monomorphic (Ducroz et al. 2005; Durka et al. 2005). The species showed a high level of genetic structure across Europe with a strong differentiation of modern populations (Durka et al. 2005). However, aDNA has introduced a more complex scenario to the demographical pattern of the beavers, but they have not shown any notable degree of divergence between Late Pleistocene and Holocene samples (Horn et al. 2014; Marr et al. 2018).

LAGOMORPHA

Lepus europaeus (Brown Hare)

Habitat and distribution: The brown hare is a widespread and highly adaptable species that inhabits a great variety of environments in Europe. The species is also characterised by an altitude range up to 1500 meters in the Alps.

Previous phylogeographic studies: The presence of fossil records from the late Pleistocene in southern Europe has been suggested as an indicator for refugia there (Corbet 1986). The Balkan Peninsula has been indicated as a possible important refugium for *Lepus europaeus*, even multiple refugia have been indicated (Kasapidis et al. 2005). This has been previously suggested in Djan et al. (2017) as a postglacial expansion. At least four different clades have been identified for the species with a strong genetic structure (Fickel et al. 2008; Stamatis et al. 2009).

Lepus timidus (Mountain Hare)

Habitat and distribution: *Lepus timidus*, or the mountain hare, is an Arctic species which inhabits tundra and taiga but also has an Alpine range where it lives in an isolated glacial relict

population (Bisi et al. 2011). The fossil record shows that *L. timidus* was the most common and widely distributed hare species in Europe during the last glacial period, with fossils being found in Central Europe and southern France (Martínez 1980), northern Spain (Altuna 1970) and also in Ireland (Woodman et al. 1997).

Previous phylogeographic studies: Phylogeographic studies based on mtDNA has demonstrated the introgression of *L. timidus* mtDNA in the Iberian range of *L. europaeus* (Melo-Ferreira et al. 2005). Some populations have been suggested as subspecies; *L. t. varronis* in the Alps, *L. t. hibernicus* in Ireland and *L. t. scoticus* in highland areas of Scotland (Angerbjorn and Flux 1995). The phylogeography of the species seems to be characterised by a strong sub-population division and the presence of distinct clades originating in different refugia or long-term occupations of mountainous areas. Ancient DNA studies (Smith et al. 2017) have confirmed that the mountain hare has shown remarkable resilience throughout the last glacial, likely due to its capacity for occupying diverse habitats.

EULIPOTYPHLA

Erinaceus europaeus (Western European Hedgehog)

Habitat and distribution: According to the classification proposed by Aulagnier et al. (2008) three species of the genus *Erinaceus* were recognised in the western Palearctic; the Western European hedgehog (*E. europaeus*), the Eastern European hedgehog (*E. concolor*) and the Northern white-breasted hedgehog (*E. roumanicus*). Miller (1912) proposed *E. roumanicus* as a separated species from *E. europeaus* for the first time but despite this, the classification was never popular and both continued to be regarded as conspecific (Ellerman and Morrison-Scott 1966).

The western European hedgehog (*E. europaeus*) is distributed across western Europe and its range spreads as far as Scandinavia reaching the Baltic States and northern areas in Russia. Deciduous woodland represents the main habitat of the species although they are also found in pastureland/meadows and grassland. In the fossil record, *E. europaeus* appeared for the first time in the Eemian Interglacial faunas of central Europe, between 133-114 kyr bp (van Kolfschoten et al. 2000).

Previous phylogeographic studies: It represents one of the best genetically characterised species through this area and it was suggested as a principal example of recolonisation of the

north from the classic southern refugial areas (Hewitt 2000). Therefore, hedgehogs played an essential role as a model for revealing significant aspects of the Quaternary phylogeography of Europe.

Three main clades of mitochondrial DNA have been identified for this species. The first one (E1) is a central European clade recolonising from the Apennine Peninsula up into the continent centre, even as far as Scandinavia and Estonia. The second is a group (E2) described from Iberia that recolonised the north through France to the Netherlands and the British Isles; and the third one (E3) is a restricted group from Sicily (Seddon et al. 2001; Bolfíková and Hulva 2012). In central Europe exists a contact zone between *E. europeaus* and *E. roumanicus* (the northern white-breasted hedgehog) but the reproductive isolation between both seems to be maintained (Bolfíková and Hulva 2012).

Erinaceus concolor (Hedgehog)

Habitat and distribution: The range of southern *E. concolor* includes Asia Minor and the Levant, but is isolated from the *E. roumanicus* range by the Bosporus Strait and Caucasus Mountains (Seddon et al. 2002). In the Mediterranean region, the species occurs in Greece, Anatolian Turkey, Israel, Syria and Lebanon. Their habitat is mainly urban, suburban and related to agricultural areas.

Previous phylogeographic studies: Studies on mtDNA sequences (Santucci et al. 1998) provided evidence of further phylogenetic divergence within the Eastern hedgehog, with a clear differentiation between populations from Europe and those from the Near East including a taxonomic distinction (Krystufek 2002). Genetic data showed that *E. roumanicus* is a sister species to *E. concolor* (time of divergence is suggested to 1.7-2.2 Myr; Bannikova et al. 2014) and the sister taxon to this group is *E. europaeus* (time of divergence is suggested to 3.2-4.5 Myr; Seddon et al. 2001).

Sorex minutus (Pygmy shrew)

Habitat and distribution: The species lives in areas with dense vegetation at ground level. Its distribution goes from the British Isles and Iberia through much of continental Europe, European Russia and Siberia to Lake Baikal in the east.

Previous phylogeographic studies: Previous studies on *S. minutus* have resolved a widespread lineage that extends from Britain through central and northern Europe to Siberia, and southern lineages in the three main southern Peninsulas (Mascheretti et al. 2003; McDevitt et

al. 2010). The northern- central European lineage has been suggested to expand from at least one central or eastern European refugium, revealing that the species survived the LGM in northern glacial refugia (Vega et al. 2010). Several studies, using cyt *b*, identified previously northern glacial refugia for the species (Bilton et al. 1998; Mascheretti et al. 2003). Five clades have been identified using the control region, but the support of some of them was low (McDevitt et al. 2010)

CARNIVORES

Canis lupus

Habitat and distribution: *Canis lupus*, the grey wolf, is the largest extant member of the canid family. Originally, it was the world's most widely distributed mammal but it has become extinct in much of western Europe and their present distribution is much more restricted than in the Pleistocene. Currently, the species is spread across the northern hemisphere albeit discontinuously (Nowak 2003). A large number of subspecies have been described based on the considerable variation observed in sizes and coat colours.

Previous phylogeographic studies: MtDNA phylogeographic studies based on modern samples have not revealed a clear geographical structure (Vila et al. 1999; Randi et al. 2000). However, when ancient DNA is added to the equation, two major haplogroups (1 and 2) are resolved showing a discontinuity and population turnover history from the Late Pleistocene to the modern times (Leonard et al. 2007; Pilot et al. 2010). The relationship between wolves and dogs is characterised by hybridisations events that could complicate the phylogeographic resolution of the species (Godinho et al. 2011). Most of the genetic studies have been focusing on short fragments and also in specific geographical regions, so some aspects of the phylogeography of the species are still not well resolved. For now, no strong phylogeographic structure is found for the species (Randi et al. 2000; Pilot et al. 2010)

Vulpes lagopus (Arctic Fox)

Habitat and distribution: The arctic fox is a well-adapted species to arctic conditions (Fuglei and Øritsland 1999). Two different ecotypes of foxes have been identified mainly because of a diet based on lemmings or coastal foxes characterised by eggs and birds (Braestrup 1941). The current habitat of *Vulpes lagopus* is restricted to tundra regions only in the northern hemisphere.

Previous phylogeographic studies: Three main hypotheses have been suggested for the origin of the Scandinavian fox, where Scandinavia was colonised from the south, from the east and surviving the LGM in a local Scandinavian refugium (Frafjord and Hufthammer 1994). The phylogeographic studies have revealed an eastern origin for the postglacial Scandinavian arctic fox population with the central-western European populations being unable to track their habitat responding to climate change (Dalén et al. 2007). The high genetic similarity between the extant populations in Scandinavia and Siberia has been suggested as an eastern origin for the Scandinavian populations (Dalén et al. 2007).

Vulpes vulpes (Red Fox)

Habitat and distribution: The red fox represents the current most widely distributed carnivore in the world with a natural range that extends across the entire Holarctic (Larivière and Pasitschniak-Arts 1996). The habitat of the species ranged from tundra to desserts with a broad spectrum in between.

Previous phylogeographic studies: MtDNA sequences from Europe, northern Asia and North America revealed an ancient intercontinental divergence in the Pleistocene for the species that was followed by secondary contact during the last glaciation (Aubry et al. 2009).The phylogeography of the red fox in Europe is extraordinarily complex. The lack of phylogeographic structure seemed to be the best explanation for the results observed and this uncertainty in Eurasia has already been mentioned in the literature on several occasions (Teacher et al. 2011; Edwards et al. 2012).

Gulo gulo (Wolverine)

Habitat and distribution: The wolverine (*Gulo gulo*) is a species with a circumpolar distribution that corresponds with the Boreal zone of the northern hemisphere (Kvam et al. 1998). In Europe, the modern range of the species includes Scandinavia and Russia, north of 60ºN. It is also a resident species in Mongolia and China in Asia, but also in Alaska and Canada, including some western states in the USA (Whitman 1999). The varieties of habitats that the wolverine inhabits include tundra, taiga, forest and woodlands (Mitchell-Jones et al. 1999).

Previous phylogeographic studies: In the European population five different subpopulations have been identified and its distribution is continuously connected with the eastern Russian population (Walker et al. 2001).

Mustela erminea (Stoat)

Habitat and distribution: *Mustela erminea*, stoat or ermine, inhabits an extensive range of climatic conditions from warm temperate habitats to artic (King 1991). The earliest *M. nivalis* fossils in Eurasia date to the Late Pliocene (Kurten 1968). During the Late Pleistocene, the fossil record reveals the presence of the species in continental Europe during the LGM (Sommer and Benecke 2004) and even around 15,000 years ago in northern Norway, where the ice was still covering significant areas of Fennoscandia (Fjellberg 1978).

Previous phylogeographic studies: The broad distribution of the species has not contributed to a strong regional phylogeographical structure in Eurasia (Dawson et al. 2014). However, four genetically distinct lineages have been identified and corresponded geographically to four probable distinct refugia although including North American samples (Dawson et al. 2014). Despite this, the effects of the LGM and the subsequent postglacial colonisations in Eurasia have yet to be explored. For Ireland, Martínková et al. (2007) concluded a natural colonisation by the stoat probably around the LGM.

Mustela nivalis (Least Weasel)

Habitat and distribution: The weasel is also a species with a wide distribution which includes nearly the entire Holarctic area and inhabits a wide range of habitats. The species has been identified with a broad spectrum of morphological variability which has led to the description of different subspecies (Frank 1985; Meia and Mermod 1992; Abramov and Baryshnikov 2000).

Previous phylogeographic studies: Two main groups have been identified for *M. nivalis* with clade I including individuals from the western-Palaearctic region from Spain to Scandinavia and clade II more represented in eastern Europe and insular weasel populations (Lebarbenchon et al. 2010). In western Europe, two main lineages have been identified; one in the mainland and the other in Corsica (Lebarbenchon et al. 2006).

Martes martes (Pine Marten)

Habitat and distribution: *Martes martes*, commonly known as the European pine marten, is a mustelid with a wide range that inhabits Europe and northern/central Asia. It is a species associated with coniferous and mixed forests (Proulx et al. 2004).

Previous phylogeographic studies: The species seems to be characterised by a mixed pattern of recolonisation after the LGM as previously suggested by Ruiz-González et al. (2013).The fossil

record indicates that *M. martes* could have survived in a cryptic glacial refugium in the Carpathians, as well as in the more traditional Mediterranean refugia (Sommer and Benecke 2004; Sommer and Nadachowski 2006). However, the phylogeographic patterns described for the species are still limited. One of the first studies published suggested that central and northern populations came from different refugia (Davison et al. 2001). The lack of sampling in some areas added some difficulties to the identification of refugia. Ruiz-Gonzalez et al. (2013), added an important specimens number, as well as new locations to previous studies.

Lynx (Eurasian Lynx)

Habitat and distribution: *Lynx lynx* is a felid species that is widespread in Eurasia, from central Eastern Europe to Eastern Asia, but its range has been reduced in modern times (Nowell and Jackson 1996). It is a well-adapted species to different environments and has been considered a polymorphic species regarding its morphology.

Previous phylogeographic studies: From the genetic perspective the Eurasian Lynx has been characterised by profound differences in genetic variability between lynx populations (Hellborg et al. 2002; Gugolz et al. 2008; Schmidt et al. 2011). At least two different refugia, in the Balkans and the Carpathian region, during the LGM are suggested for the Eurasian lynx (Gugolz et al. 2008). This is reinforced by the fossil record of the lynx during the LGM in the Balkan and Carpathian refugia (Sommer and Nadachowski 2006).

Ursus arctos (Brown Bear)

Habitat and distribution: The brown bear is the largest carnivore in Europe. Its habitat has a wide distribution, however it was even more extensive in the past, and has been gradually reduced by human expansion and hunting (Servheen et al. 1990). The species occupies a great variety of habitats from dry steppes in Asia to Arctic shrublands and temperate rain forests. During the Late Pleistocene, the range of *Ursus arctos* overlapped with that of the cave bear, *Ursus spalaeus*, in Europe and western Eurasia. The most recent split between *U. arctos* and another ursid species is with the polar bear (*Ursus maitimus*) estimated at 150 kyr ago based on mtDNA (Lindqvist et al. 2010). However, introgression of mtDNA from polar bears has been detected in modern and also ancient *U. arctos* populations (Edwards et al. 2011; Cahill et al. 2013, 2015).

Previous phylogeographic studies: Brown bear phylogeographic studies have shown a strong geographical structure in terms of the mtDNA variation (Taberlet and Bouvet 1994; Miller et al.

2006; Hirata et al. 2013). However, a lack of phylogeographic structure has been proposed for brown bears during the Late Pleistocene in Europe (Hofreiter et al. 2004). In current populations, two main clades are found representing the south-west and northeast (Leonard et al. 2000). The western clade has been divided into at least two subclades that might represent two separated populations that survived in different refugia during the LGM, Iberia and Italy (Taberlet et al. 1994; Davison et al. 2011). This current phylogeographical distribution is consistent with origins in the three major European southern refugia, so the species has served as one of the model species supporting a scenario of glacial refugia and postglacial recolonisation of central and northern Europe (Taberlet and Bouvet 1994; Taberlet et al. 1998; Hewitt 1999, 2000, 2004). However, Valdiosera et al. (2007) showed an alternative scenario where brown bears were not restricted to Mediterranean peninsulas during the LGM but also survived in mainland Europe.

Homo sapiens (Modern Humans)

Distribution and previous phylogeographic studies: Trying to follow a timeline, modern humans seem likely to arrive in Europe around 45,000 ya at the beginning of the Upper Palaeolithic (50,000-10,000 ya). The first archaeological record in this continent is dated around that time in a wide distribution across Europe with fossils found at Pestera cu Oase in Romania (Trinkaus et al. 2003), at Kent's cavern in United Kingdom (Highman et al. 2011) and at Grotta di Fumane in Italy (Benazzi et al. 2015). The oldest dated modern human in Europe from which mtDNA has been retrieved and assigned to a specific haplogroup are the dental remains found at Grotta di Fumane (Benazzi et al. 2015) and belongs to haplogroup R. The individual at Pestera cu Oase carried haplogroup N (Fu et al. 2015). An individual from Ust'Ishim in western Siberia, dated earlier than these two individuals, has been assigned to haplogroup R as well. This reflects the first roots of the principal haplogroups N and R from where the main European haplogroups arose.

The next two individuals that still belong to the Early Upper Paleolithic in Europe (>33,000 years ago) are from Troisième cavern (Goyet) in Belgium dated around 35,000 ya. Both of them are clustered in haplogroup M, a lineage which is absent in Europeans today (Posth et al. 2016). However, this haplogroup is found at a relatively high frequency in modern Asians, Australasians, and Native Americans. Another individual from Grotta Paglicci (Italy), dated to around the same period as those from Goyet, carries haplogroup U8c (Posth et al. 2016). Haplogroup U8c is a rare clade that is extinct in modern populations and was also described in an individual from Dolni Vestonice in the Czech Republic dated around 30,000 ya (Fu et al.

2013). Two Romanian samples completed the early upper Paleolithic aDNA dataset. The first one is a female from Pestera Muierilor dated around 35,000 ya and belongs to a basal haplogroup U6* that is not present in any extant or ancient humans (Hervella et al. 2016). However, derived U6 haplotypes are found in present North-Western African populations suggesting a possible origin of the lineage in Eurasia and a posterior back-migration to North Africa (Hervella et al. 2016). The other individual, a 33,000-year-old from Romania (Pestera Cioclovina) is assigned to a basal U lineage that had no derived position leading to known subhaplogroups (Posth et al. 2016). Another individual from Russia, Kostenki 14, is clustered on the same haplogroup U2 as the individual Kostenki 12 (Fu et al. 2016).

Continuing the timeline, more individuals from Middle-Upper Palaeolithic (33,000-24,000 ya) have been analysed. From the Czech Republic, six individuals around 30 kya have been examined. Five of these individuals came from Dolni Vestonice and suggest three of them belong to haplogroup U5, one is haplogroup U and the other individual carries haplogroup U8c (Fu et al. 2013, Posth et al. 2016). U5 is also representative of the individual at Pavlov, also in the Czech Republic, and another individual in Austria (Krems-Wachtberg) (Fu et al. 2016). From Italy and Belgium, some individuals from this time belong to haplogroups U2, U5 and M (Posth et al. 2016). The detection of this novel branch of haplogroup M, in three Early Upper Palaeolithic individuals, is surprising because most M branches are found in the Indian Subcontinent and Southeast Asia as well as being widespread in the Pacific and the Americas. The period of the Late Upper Palaeolithic (19,000-10,000 ya) is marked by the rise of new subhaplogroups like U5b1, U5b2, U5b2a and U8a. The individuals came from Germany, Italy, Belgium, France and Spain.

The first industry in Europe produced by modern humans is the Aurignacian (appeared around 42 cal. ka before present (bp)). It is characterised by prismatic blade production with retouched blades, carinated and nose-end scrapers (Klein 2008) and was made by hunter-gatherers until about 30 cal. ka bp. The wider technocomplex includes ornaments such as beads, bone and antler implements such as needles and awls (Klein 2008). New technical innovations such as projectile hunting gear, bows and arrows appeared around 28 cal. ka bp following the Aurignacian. This new industry is named the Gravettian and occurs until around 23 cal. ka bp at the beginning of the cooling into the LGM. More cultural complexity lead to new behaviours such as the construction of dwellings of mammoth bones and the transportation of raw material over longer distances (Nalawade-Chawan et al. 2014).

In western and central Europe, after an improvement of the climate conditions around 19 cal. ka bp, a new culture that represents the culmination of Upper Palaeolithic cultural development appeared. Small geometrically shaped implements, stone tools as triangles, conical points or semilunar blades were starting to be used. Bone was used extensively to make wedges, adzes, hammers, barbed points and harpoons, eyed needles and jewellery. This culture is known as the Magdalenian and it spread rapidly over Europe.

As the ice sheets melted around northern Europe, modern humans were recolonising the north with similar stone tools to before the LGM although adding tiny bladelets that were set into composite tools as harpoons. These characteristic tools enable us to recognise what is known as the Mesolithic. Regarding the mtDNA haplogroups, the U clade is dominant in the European Mesolithic with almost all the aDNA samples from this period belonging to this haplogroup branch. U5 provides the most common branch found but U2 or U4 have also been found. However new haplogroups arrive in Europe such as haplogroup C and have been suggested as a possible arrival from eastern refugia (Derenko et al. 2010).

ARTIODACTYLA

Alces alces (Eurasian Elk)

Habitat and distribution: The main habitats of *Alces alces* are the coniferous forests and bogs in northern latitudes. They especially favour river valleys and lakes. The modern range comprises northern Eurasia although they are also present in northern America.

Previous phylogeographic studies: The moose is one of the first large mammal species that recolonised areas in Europe that were covered by glaciers after the LGM (Schmölcke and Zachos 2005). Previous studies suggested three main mtDNA lineages of moose well characterised by continent, with Asian, European and American clades identified (Hundermark et al. 2002). A contact zone between the Asian and European lineages occurs around Western Siberia (Moskvitina et al. 2011). The European lineage has been divided into three different sub-clades that were also suggested as possible LGM refugia for the species (Niedzialkowska et al. 2014). These are known as western, central and eastern clades (W, Ce and E, respectively). The western clade (W) is identified in northern and central Europe, the central (Ce) covers the western part of the species' range and the eastern clade inhabits almost the whole range of the species in Europe, except for Scandinavia (Niedzialkowska et al. 2014). This phylogeographic pattern has probably been shaped by Late Pleistocene as well as the recent

human impacts on the species, such as overhunting and reintroductions (Niedziałkowska et al. 2014; Świsłocka et al. 2015).

Capreolus capreolus (Roe deer)

Habitat and distribution: The roe deer, *Capreolus capreolus*, is a widespread species that has an extensive range in the Palaearctic, being found in most parts of continental Europe (Stubbe 1999). It occupies different habitats from forest to semi-desert environments and is also well adapted to modern agricultural landscapes (Andersen et al. 1998).

Previous phylogeographic studies: Despite the fact that *C. capreolus* is one of the genetically best-studied species, roe deer mtDNA studies have shown a complex pattern with difficulties in the identification of refugia and postglacial colonisations. Substantial studies have pointed to three main clades in western, eastern and central-northern areas in Europe (Vernesi et al. 2002; Randi et al. 2004; Sommer et al. 2008). The western and the eastern clades are confined to Iberia and south-eastern Europe respectively, probably the Balkans, while the origin of the central-northern clade is still under debate (Sommer et al. 2008; McDevitt and Zachos 2014). In Italy, also the appearance of several genetic groups has been proposed (Lorenzini and Lovari 2006).

Cervus elaphus (Red deer)

Habitat and distribution: The red deer is the most widespread deer species in the world. There are 22 different subspecies described in the Holarctic (Trense 1989; Geist and McShea 1999). Its habitat is characterised by great diversity but generally occupies woodland and feeds in (or at the edge) grasslands.

Previous phylogeographic studies: The first phylogeographical study of this species was made by Ludt et al. (2004) and they concluded that a large number of subspecies has to be reconceived due to their results. Four different subgroups of red deer were identified in Europe, however, more sampling was required to better understand the possible reasons for this subdivision (Ludt et al. 2004).

Skog *et al.*'s (2009) results across the entire European range of red deer found three major clades, called haplogroups A, B and C, with different geographical distributions. The genetic analysis of both studies exhibited a large-scale structuring with differentiation between western Europe (Hg A), eastern-central Europe (Hg C) and Mediterranean region (Hg B). The three clades showed a similar phylogeographical pattern to many other European mammals

(Hewitt 2004; Skog et al. 2009). Clades A and C can be identified as descended from glacial refugial populations in the Iberian Peninsula and the Balkans, respectively (Skog et al. 2009; Niedzialkowska et al. 2011). The fossil record of this species seems to be consistent with this phylogeographical data (Sommer and Nadachowski 2006).

Red deer has been translocated in different areas by humans for more than a millennium and this has had a substantial impact on the current phylogeographic patterns (Hartl et al. 2003). Studies in Ireland, for example, have been able to detect translocation from Scotland (McDevitt et al. 2009c; Carden et al. 2012). This has to be taken into account when phylogeographical patterns are described.

Rangifer tarandus (Reindeer)

Habitat and distribution: The reindeer is a relatively widespread species around the northern Holarctic from the northwest USA to Norway. The habitat range of this herbivore species is also wide from continental coastal plains to mountain ranges but also spanning the high Arctic to Boreal forests. It has been classified into three different ecological groups; woodland, tundra and arctic islands forms (Banfield 1961). In North America, *Rangifer tarandus* is also known as caribou, but the European range (and therefore the classical reindeer designation) will be analysed here.

Banfield (1961) described the distribution of the species during the Pleistocene based on the fossil records and the presence of the species south of the ice sheet in Eurasia is confirmed, helping him to suggest three different ecotypes originated in three or more isolated refugia during the last glacial.

Previous phylogeographic studies: The first phylogeographic studies based on the control region resolved three main clusters, with two of them, found in Eurasia (but also one of them in North America with a probable Beringian origin) and probably originated in separate glacial populations (Flagstad and Røed 2003). Some more subdivisions have been added for two of these three clusters, also changing the nomenclature, not making easy the designation of them (Kvie et al. 2016).

Bison bonasus (European Bison)

Habitat and distribution: *Bison bonasus* is found now in Europe and the Caucasus, where it has been reintroduced. The habitat of the species is characterised by deciduous forest with scattered open glades and woodlands.

Previous phylogeographic studies: The European bison or wisent is one of the species (and genera) whose evolutionary history in Eurasia is still not well resolved despite its current endangered status and having a particularly rich fossil record (Kowalski 1967; Groves 1981). The species has no distinguishable identified fossils in the Pleistocene and seems to appear during the early Holocene (Benecke 2005). However, a recent study found that the ancestors of modern wisent were also present in Europe through the Late Pleistocene, with hybridisation processes between wisent and aurochs (Soubrier et al. 2016).

The mtDNA analyses have revealed two different clades, including Clade X that is related to modern and historical wisent, but divergent from a modern wisent lineage probably due to a severe bottleneck that led to modern wisent (Soubrier et al. 2016).

Sus scrofa (Wild Boar)

Habitat and distribution: South-East Asia seems to be the area where the wild boar (*Sus scrofa*) was originated after the differentiation of the genus *Sus* about 3 million years ago (Lucchini et al. 2005). It is a species with one of the widest geographical ranges of all terrestrial mammals being native to Asia, Europe and North Africa but presents as an introduced species in all the continents, except Antarctica (Scandura et al. 2011).

Previous phylogeographic studies: The oldest record of *Sus scrofa* in Europe are dated from the Early Pleistocene around 1.5-1.0 Mya and belonged to two archaeological sites, one in Germany and the other one in Spain (Rook and Martínez-Navarro 2010). In relation to the mtDNA estimation for the most recent common ancestor in Eurasia, the values changed and are closer to a more recent differentiation between 0.8 and 0.4 Mya (Mona et al. 2007).

Quaternary contraction and expansion events due to climate fluctuation may explain the actual genetic variation in the wild boar across Europe, as can be described for other temperate mammals (Hewitt 2004). The current distribution of the wild boar was shaped by the glaciations of the late Pleistocene forcing the species to take southern areas as refugia and re-colonising the continent from there (Scandura et al. 2011).

Studies of mtDNA have contributed to the understanding of the phylogeographic pattern of *Sus scrofa* in Europe. Based on the control region, two main European lineages or haplogroups have been identified sharing similar distributions. The first one is widespread over the continent from the west in Portugal to eastern Poland and is known as E1. This lineage can be divided in two main clades, A-side and C-side, described by Larson et al. (2005). The second

main lineage is E2 has been found in Italy and Sardinia today and in Croatia before the Neolithic based on an aDNA study (Larson et al. 2007).

A Near Eastern haplogroup has also been identified in Europe but only in individuals from the Neolithic in France and Germany in the west (Larson et al. 2007). In the actual distribution of wild boar, the Near Eastern (NE) haplogroup is only found in eastern Greece and Turkey. Also found in Europe is the Asian (A) clade. Individuals from the Iberian and Italian Peninsulas and one individual from Belgium are clustered in this clade that is today native to Asia. Domestic pigs also carried this haplogroup across Europe and this might be a consequence of extensive cross-breeding performed mainly between the 18th to the early 19th century in Britain (Jones 1998).

2.4 Geographical delimitations

From the geographical perspective of this project, Europe has been defined following specific borders based on the extent of political Europe. The northern border is represented by the Arctic Ocean, the western one by the Atlantic Ocean, and on the southern one by the Mediterranean Sea and the Black Sea. The continent's eastern boundary runs along the Ural Mountains. For some species, areas that can be easily recognised as the Caucasus, Northern Africa and the Near East have been included if data were available.

Given the variability of areas sampled and also based on the scope of this research, specific areas have been defined within Europe in order to test the central hypothesis. Europe has been divided into ten regions based on the significant biogeographic subdivision that were identified from previous phylogeographic studies (Petit et al. 2003; Lumibao et al. 2017). These areas are represented by the Iberian Peninsula, Western Europe, Central Europe, Apennine Peninsula, British Isles, Balkans, Eastern Europe, Scandinavia, Caucasus and the Near East (Figure 2.2). The definition of these areas could be altered based on more accurate available geographical information for species where a large area of the continent was not sampled. Through this delimitation, the understanding and identification of refugial areas can be addressed with confidence. This is because the main hypotheses suggested for most of the species previously analysed were southern and northern refugia.

The three main traditional refugia that have been suggested for the southern refugia paradigm are Iberia, Italy and the Balkans (Hewitt 2000). Therefore, these areas have been included in the analysis but also some others that could represent northern refugia as have been

previously suggested (Stewart et al. 2010). The areas chosen also reflect the main barriers that might influence the migration of different species in the Late Pleistocene and Holocene.

Figure 2.2 Map representing the geographical regions considered for the analysis. Each colour represents one area.

2.5 Database

For each analysed species in Europe, one database was created using Microsoft™ Excel. The purpose of the database was to create a Europe-wide record of the information available for the different species regarding mtDNA CR. This includes the lab code of the sample, the GenBank accession number, the site, the country, the area, the date (in case of ancient DNA sample), references (Table 2.2) and haplotype assigned to the sample (after analysis). The classification of "area" is divided by main geographical zones across Eurasia (discussed above) and is the principal distinction that is taken into account for the analysis of the general patterns. Not assigning a coordinate for each sample is because the insufficient available information (see Gratton et al. 2016) hence; countries are defined and selected as the minimum unit to take account in the main analysis.

Table 2.2 Mammal species that have been chosen for the meta-analysis and studies which sequences were included in the analysis.

Species	References
Arvicola amphibius	Piertney et al. (2005), Brace et al. (2016)
Arvicola sapidus	Centeno-Cuadros et al. (2009), Centeno-Cuadros and Godoy (2010), Alasaad et al. (2011)
Microtus arvalis	Haring et al.(2000), Fink et al. (2004), Heckel et al. (2005), Borkowska et al. (2010), Borkowska (2011)
Myodes glareolus	Stacy et al. (1997), Matson et al. (2000), Matson and Baker (2001), Spitzenberger et al. (2000), Dekonenko et al. (2003), Dunina-Barkovskaya (2004), Yashina et al. (2005 *Unpublished*), Wickliffe et al. (2006), Meeks et al. (2007, 2009), Johansson et al.(2008), Razzauti et al. (2012), Çolak et al. (2016)
Lemmus lemmus	Stacy and Ehrich (1998 *Unpublished*), Fedorov and Stenseth (2001), Lagerholm et al. (2014)
Cricetus cricetus	Neumann et al. (2004), Banaszek et al. (2009), Banaszek and Ziomek (2011), Schroder et al. (2014), Hegyeli et al. (2015), Feoktistova et al. (2016)
Sciurus vulgaris	Barratt et al. (1999), Reyes et al. (2000), Hale et al. (2004), Tamura and Hayashi (2007), Finnegan et al. (2008), Grill et al.(2009), Dozieres et al. (2012), Simpson et al. (2013), Liu et al. (2014), Rezouki et al. (2014), Madsen et al. (2015), Lucas et al. (2015)
Castor fiber	Durka et al. (2005), Horn et al. (2011, 2014), Kropf et al. (2013), Biedrzycka et al. (2014), Frosch et al. (2014), Senn et al. (2014)
Erinaceus europaeus	Seddon et al. (2001), Bolfíková and Hulva (2012)
Erinaceus concolor	Seddon et al. (2001, 2002), Bolfíková and Hulva (2012)
Sorex minutus	McDevitt et al. (2009, 2010, 2011)
Lepus europaeus	Thulin et al. (1997), Pierpaoli et al. (1999), Arnason et al. (2002), Kasapidis et al. (2005), Fickel et al. (2005, 2008), Schmidt and Fickel (2005 *Unpublished*), Fredsted et al. (2006), Melo-Ferreira et al. (2007, 2011), Sert et al. (2009), Stamatis et al. (2009), Menzies et al. (2010 *Unpublished*), Pietri et al. (2011), Antoniou et al. (2013), Canu et al. (2013), Sanz-Martín et al. (2014), Mengoni et al. (2015), Vernesi et al. (2016), Giannoulis et al. (2018)

Table 2.2 Mammal species that have been chosen for the meta-analysis and studies which sequences were included in the analysis.

Lepus timidus	Thulin et al. (1997), Pierpaoli et al. (1999), Wu and Zhang et al. (2000 *Unpublished*), Waltari et al. (2004), Waltari and Cook (2005), Fredsted et al. (2006), Melo-Ferreira et al. (2007, 2014), Stamatis et al. (2008), Prost et al. (2010), Vernesi et al. (2010 *Unpublished*), Zachos et al. (2010), Liu et al. (2011), Fu (2015 *Unpublished*), Mengoni et al. (2015)
Canis lupus	Tsuda et al. (1997), Vila et al. (1997, 1999), Randi et al. (2000), Valière et al. (2003), Verginelli et al. (2005), Björnerfeldt et al. (2006), Gomercic et al. (2010), Pilot et al. (2006, 2010, 2014), Baltrunaite et al. (2013), Boggiano et al. (2013), Druzhkova et al. (2013), Thalmann et al. (2013), Jansson et al. (2014), Ersmark et al. (2016), Koblmüller et al. (2016), Montana et al. (2017)
Vulpes lagopus	Maldonado et al (1997), Strand et al. (2000 *Unpublished*), Dalen et al. (2002, 2004, 2007), Nyström et al. (2006), Dzhikiya et al. (2007), Mellows et al. (2012), Ploshnitsa et al. (2013), Koepfli et al. (2015), Yan et al. (2016)
Vulpes vulpes	Koop et al. (1998), Okumura et al. (1996), Valiere et al. (2003), Statham et al. (2005, 2012, 2014), Arnason et al. (2006), Inoue et al. (2007), Kirschning et al. (2007), Berry (2008), Zhong et al. (2010), Teacher et al. (2011), Edwards et al. (2012), Kutschera et al. (2013), Galov et al. (2014), Koepfli et al. (2015), Leite et al. (2015), Sun et al. (2015)
Gulo gulo	Walker et al. (2001), Tomasik and Cook (2005), Zigouris et al. (2013).
Mustela erminea	Kurose et al. (1999, 2005), Martinkova et al. (2007), Dawson et al. (2014), Emami Khoyi et al. (2016)
Mustela nivalis	Kurose et al. (1999, 2005), Lebarbenchon et al. (2006, 2010), Yu et al. (2011), Emami-Khoyi et al. (2016), Rodrigues et al. (2016)
Martes martes	Davison et al. (2001), Statham et al. (2005), Pertoldi et al. (2008, 2014), Ruiz-Gonzalez et al. (2008, 2013), Rozhnov et al. (2010), Hosoda et al. (2011), Nagai et al. (2012), Sindičić (2015 *Unpublished*), Korablev et al. (2017)
Lynx lynx	Hellborg et al. (2002), Gugolz et al. (2008), Sindičić et al. (2012), Ratkiewicz et al. (2014), Rueness et al. (2014), Rodríguez-Varela et al. (2015, 2016), Li et al. (2016), Paijmans et al. (2016)
Ursus arctos	Taberlet and Bouvet (1994), Leonard et al. (2000), Masuda et al. (2001), Barnes et al. (2002), Hofreiter et al. (2004), Valdiosera et al. (2007, 2008), Bon et al. (2008), Calvignac et al. (2008, 2009), García et al. (2009 *Unpublished*), Korsten et al. (2009), Murtskhvaladze et al. (2010), Edwards et al. (2011, 2014), Kocijan et al. (2011), Hailer et al. (2012), Bray et al. (2013), Frosch et al. (2014b), Salomashkina et al. (2014, 2017), Baca et al. (2014), Xenikoudakis et al. (2015), Ashrafzadeh et al. (2016), Çilingir et al. (2016), Fortes et al. (2016)

Table 2.2 Mammal species that have been chosen for the meta-analysis and studies which sequences were included in the analysis.

Homo sapiens	*Palaeolithic: Bramanti et al. (2009), Krause et al. (2010), Hervella et al. (2012), Brandt et al. (2013), Raghavan et al. (2014), Seguin-Orlando et al. (2014), Benazzi et al. (2015), Fu et al. (2015, 2016), Posth et al. (2016) *Mesolithic: Bramanti et al. (2009), Delsate et al. (2009), Malmström et al. (2009, 2015), Der Sarkissian et al. (2011, 2013, 2014), Sanchez-Quinto et al. (2012), Skoglund et al. (2012, 2014), Bollongino et al. (2013), Brandt et al. (2013), Lazaridis et al. (2014, 2016), Olalde et al. (2014), Haak et al. (2015), Hofmanová et al. (2015), Mathieson et al. (2015), Fu et al. (2016), Posth et al. (2016)
Alces alces	Polziehn and Strobeck (1997), Hundertmark et al. (2002), Swislocka et al. (2008, 2013), Moskvitina et al. (2011), Hassanin et al. (2012), Kholodova et al. (2014), Niedziałkowska et al. (2014), Kangas et al. (2015), Nemoikina et al. (2016), Wennerström et al. (2016)
Capreolus capreolus	Douzery and Randi (1997), Wiehler and Tiedemann (1998), Vernesi et al. (2002, 2016), Randi et al. (2004), Fajardo et al. (2007), Royo et al. (2007), Gentile et al. (2009), Hassanin et al. (2011), Zvychainaya et al. (2011), Fickel et al. (2012, Unpublished), Mucci et al. (2012), Baker and Hoezel (2013, 2014), Lorenzini et al. (2014), Matosiuk et al. (2014), Olano-Marin et al. (2014), Puraite et al. (2014), Biosa et al. (2015), Nemeth et al. (2015 Unpublished)
Cervus elaphus	Hmwe et al. (2006), Nussey et al. (2006), Egyed et al. (2008 *Unpublished*), Nielsen et al. (2008), Perez-Espona et al. (2009), Skog et al. (2009), Haanes et al. (2010), Niedziałkowska et al. (2011, 2012), Biedrzycka et al. (2012), Carden et al. (2012), Rosvold et al. (2012), Meiri et al. (2013), Krojerova-Prokesova et al. (2015), Borowski et al. (2016), Carranza et al. (2016), Frank et al. (2017)
Rangifer tarandus	Dueck (1998), Gravlund et al. (1998), Hundertmark et al. (2002), Flagstad and Røed (2003), Røed et al. (2008, 2011, 2014), Eger et al. (2009), McDevitt et al. (2009b), Bjornstad and Røed (2010), Kholodova et al. (2011), Lorenzen et al. (2011), Baranova et al. (2012), Bjornstad et al. (2012), Carden et al. (2012), Letts et al. (2012), Baranova et al. (2016), Kvie et al. (2016a, 2016b), Korolev et al. (2017)
Bison bonasus	Bork et al. (1991), Ward et al. (1999), Verkaar et al. (2004), Anderung et al. (2006), Wójcik et al. (2009), Zeyland et al. (2012), Yudin et al. (2012), Massilani et al. (2016), Soubrier et al. (2016), Wecek et al. (2016)
Sus scrofa	Okumura et al. (1996), Giuffra et al. (2000), Alves et al. (2003), Larson et al. (2005, 2007), Fang et al. (2006), Scandura et al. (2008), Hajji and Zachos (2011), Kim et al. (2011), Alexandri et al. (2012), van Asch et al. (2012), Ottoni et al. (2013), Kusza et al. (2014), Vilaça et al. (2014), Velickovic et al. (2015), Menendez et al. (2016)

All this information is retrieved from GenBank entries and directly from the publications (or supplementary materials). From the papers, the number of individuals (or frequencies) for each haplotype retrieved were obtained enabling a full reconstruction of all the original studies included in the database. These reconstructed data sets were combined for each species to create species-level diversity estimates across the sampled range. As mentioned before, one of the main difficulties is based on reconstructing the haplotypes. A high number of authors submitted only the haplotype sequences to GenBank, so it is essential to reconstruct and to know how many individuals are represented by each haplotype. From these papers, numbers of individuals for each haplotype are obtained (where published), enabling the full reconstruction of the original study data set through manual re-assembly using FASTA/Geneious files downloaded from GenBank. Some of the sequences have been impossible to attribute to a specific number of individuals, but sequences are still added to the analysis. After the creation of the database, the analysis will be the same for each species.

2.6 Data analysis

All sequences obtained were aligned and edited using the software BioEdit 7.2.3 (Hall 1999) (http://www.mbio.ncsu.edu/BioEdit/bioedit.html) and Geneious 9.1.4 (Kearse et al. 2012). Due to the variation in overlap and length of the currently available CR sequences from Genbank some adjustments have to be made. Within each species, sequences were standardised to the minimum overlapping sequence length available for each species. The alignment which allows the comparison with as many aDNA sequences as possible (where published) will be the one selected for the analysis. Ancient DNA typically presents shorter fragments due to a lack of preservation over time. As a result of these shorter alignments, the number of haplotypes might be reduced due to collapsing into larger ones. This will represent a caveat that needs consideration because it might represent a reduction of the resolution. However, for the majority of the species, the main genetic clades are not lost. If there was not aDNA data available, then the longest fragments had priority. Therefore, some sequences were not included in the analysis because of short length.

The most common measures of genetic diversity in population studies are haplotype and nucleotide diversity (Egeland and Salas 2008, Goodall-Copestake et al. 2012). To calculate those values, a full reconstruction of the data sets (including all individuals) is required. That is why it is so important that what is mentioned in the last section is considered. The number of haplotypes, haplotype (hd) and nucleotide (π) diversity are calculated using DNAsp v.5.10.01

(Librado and Rozas 2009). During the analysis, considerable confusion on each haplotype designation has been revealed. This is due to the variation in the sequence length and lack of common designation for new and already described haplotypes in different studies. This is the main reason to recalculate the number of haplotypes for the meta-analysis and then numbering them (this will vary regarding the numbers of haplotypes described per species).

The number of individuals sampled for each species and the sample sizes per population varied among species and studies. Samples were grouped by the different regions described in section 2.4 ensuring a common within-region samples size that comprises a higher minimum number of samples. To understand what proportion of the population diversity (genetic diversity) was represented by the different sample sizes, haplotype sampling coverage was estimated following the methods of Dixon (2006). These are based on the number of haplotypes and individuals sampled using the Stirling probability distribution and Bayes theorem to obtain a posterior distribution of the total number of haplotypes in the population, including those that are not yet observed due to sampling constraints.

Under-sampling can influence the diversity indexes (Goodall-Copestake et al. 2012) with, for example, haplotype diversity generally being increased with sample sizes (Pereira et al. 2004). Haplotype sampling coverage estimates indicate the proportion of the population genetic diversity that is represented by that specific sample size, so high level of sampling completeness is a requirement to address the meta-analysis. Following Pedreschi et al. (2018) a minimum of 75% completeness was established. An extra effort to standardise across differences in the geographical distribution of sampling was made by using rarefraction (Heck et al. 1975). Considering the effect of different sample sizes on genetic diversity estimations a rarefraction method implemented in HP- RARE (Kalinowski 2005) was used to calculate haplotype richness and the richness of private alleles. The minimum sample size between species and regions was established as the number of haplotypes rarefied following Lumibao et al. (2017).

For all the 30 species analysed, and in addition to this interspecific study, an intraspecific analysis was conducted. This analysis enables a comparison of the effects and includes inferences on the location of refugia for differently adapted mammal taxa and the resultant patterns from different phylogeographical studies.

Knowing the different haplotypes, a better phylogenetic analysis has been done through a phylogenetic tree for each species in order to identify the main mtDNA haplogroups. For the selection of the best model of nucleotide substitution JModelTest (Posada 2008) has been

used under the BIC criterion. The Bayesian phylogenetic method was implemented using MrBayes (Ronquist et al. 2012). The phylogenetic trees are represented using FigTree (http://tree.bio.ed.ac.uk/software/figtree/).

In many cases, phylogenetic trees might not accurately mirror the reticulated relationship among haplotypes (Posada and Crandall 2001). Networks can reflect these connections with more details, so network analysis is carried out through a median-joining networks algorithm using Network (Fluxus Technology Ltd) and PopART 1.0 (Leigh et al. 2015). Furthermore, temporal networks are also created using a statistical parsimony network using the script TempNet (Prost and Anderson 2011) in R (R Core Team 2013). This is useful for heterochronous DNA data (sequences of different ages) and to display information from more than one geographical group, fitting perfectly for the analysis.

Through all these analyses, this thesis addresses fundamental questions in phylogeography and with a novelty of approach and develops a useful method that could also be implemented for other genetic markers in future research. The methods and the materials presented above represent the core of this research and lay the foundations for the next chapters. The comparative approach that characterised this research is presented here in detail with the aim to help to understand better the context in which this thesis has been developed.

Chapter 3. Modern mammalian genetic diversity in Europe

3.1 Introduction

Genetic diversity has been traditionally considered one of the most fundamental dimensions of biodiversity (May 1994). The amount of genetic diversity within a species provides the potential for evolutionary change (Lewontin 1974). However, the general patterns of diversity are not always evident when the approach is focused on the individual taxa and their phylogeographic and phylogenetic relationships (Taberlet et al. 1998). Knowledge of the current European distribution of genetic diversity across different species is an important task to be addressed in order to understand the legacy of the Late Pleistocene glaciation in the evolution of the species.

The comparative analysis of the spatial distribution of genetic diversity of species can answer many questions about the different demographic and regional trends (Bermingham and Moritz 1998; Arbogast and Kenagy, 2001; Hewitt 2004; Hickerson et al. 2010; Gratton et al. 2017; Lumibao et al. 2017; Pedreschi et al. 2018). Current geographical patterns of biodiversity in Europe are shaped by significant climatic fluctuations during the Quaternary (Hewitt 2000). Genetic data have emerged as the most important source of information about demographic histories of species. Their spatial patterns, based on genetic diversity, can infer population range dynamics (Hewitt 2000; Drummond et al. 2005; Gratton et al. 2017). Traditionally, phylogeographic studies have suggested strong latitudinal patterns of genetic diversity due to repeated population expansions and contractions across glacial/interglacial periods including a loss of diversity from southern to northern Europe (Taberlet et al. 1998; Hewitt 1999, 2000, 2004).

The last glaciation in Europe, especially the Last Glacial Maximum (LGM), has been conventionally suggested as the period where many temperate species retreated to southern areas, recolonising central and northern Europe after the glaciation (Taberlet et al. 1998; Hewitt 1999, 2000, 2004). At least three main glacial refugia were identified for temperate species in southern Europe; Iberian, Italian and Balkan peninsulas (Hewitt 1999). Prolonged isolation in refugia is likely to have had an effect on the diversity and divergence of the populations. Therefore, these areas have been suggested as concentrating the highest genetic diversity in the European continent. As a consequence, the intraspecific diversity should

decline away from refugia, due to successive founder events during postglacial colonisation (Hewitt 1996, 2000; Petit et al. 2003). However, the presence of northern refugia probably has an impact on the genetic diversity patterns in Europe (Stewart et al. 2010). Refugia can also be identified based on the endemic haplotypes found in those areas in addition to higher genetic diversity values (Maggs et al. 2008).

The phylogeographic patterns found in Europe have also been used to understand the genetic implications of current climate change (Petit et al. 2003; Hampe and Petit 2005; Linares and Tiscar 2010). The analysis of genetic data using trees suggested that southern refugia contributed to the post-glacial migration (Petit et al. 2002). This pattern was also supported in Petit et al. (2003), indicating a relatively common pattern for different trees and shrubs species in Europe using chloroplast DNA. Recent studies (Lumibao et al. 2017) have confirmed the classic southern richness and northern purity for woody taxa of the continent. However, the individualistic response of species makes it necessary to test this model for animal species (Stewart et al. 2010; Pedreschi et al. 2018).

For animals, more descriptive interspecific analyses have been done with some reviews pointing to traditional patterns of diversity (Taberlet et al. 1998; Hewitt 2000). However, these studies did not reflect a definitive pattern of diversity due to a low number of comparison studies between species and a reduced number of species and individuals analysed at the start of the 2000s (Taberlet et al. 1998; Hewitt 2000). The most recent study of this nature (Pedreschi et al. 2018) including small mammals, established a complex scenario where no general patterns were found.

The present study investigates general patterns of genetic diversity by examining the mitochondrial DNA (mtDNA) control region for a range of mammal species testing for congruence in genetic diversity patterns among them. The traditional pattern of southern richness and northern purity is tested and this analysis will provide a better understanding of the genetic diversity patterns in Europe and to identify possible refugia.

3.2 Materials and Methods

3.2.1 Data collection

All terrestrial mammal species with a broad geographical range (0.5×10^6 km^2) in the European continent have been considered. In total 181 terrestrial species were considered to be included in the analysis. However, due to small sample size, peculiarities in the sequence

availability and small sample ranges covered for the species a total of 84 species were selected, of these, 54 species were discarded as sample size availability was less than 50 individuals. In total, this resulted in a sample size of 29 species.

The main methods that defined how the sequences were obtained are described in Chapter 2. MtDNA sequences were targeted for mammal species within a European range. The selection of mtDNA is due in part to its relatively rapid rate of mutation, a high number of copies per cell and its haploid maternal inheritance mechanism which make it useful for the elucidation of demographical changes as well as the population history of each species (Avise 1987, 1995; Moritz 1994). For these reasons, mtDNA sequence data are and will continue to represent an important marker in phylogeography (Garrick et al. 2015). As different genetic markers could potentially distort the comparison based on diversity across taxa, the same mtDNA fragment has been chosen across all species. The region selected for the analysis (D-loop) is also widely used in phylogeographic studies (e.g. Seddon et al. 2001; Troy et al. 2001; Scandura et al. 2008). The D-loop occurs in a non-coding area of the mtDNA. It presents a strong rate of heterogeneity between sites, a high frequency of events (i.e., insertion and deletions and lineage specificity) which makes it a good genetic marker for phylogeographic purposes (Saccone et al. 1991; Pesole et al. 1999).

Phylogeographic studies of mammals in Europe were surveyed in the literature and for sequence availability. Publications with the keywords “phylogeography” “Europe” “mtDNA” were searched in Google Scholar and Web of Science. Furthermore, exhaustive research for data availability was done through GenBank where sequences have been searched using species names, with “d-loop” or “control region” as keywords in this database. This search was conducted until January 2018.

The total number of individuals included for each taxon and the number of individuals per population varied among the studies considered for the meta-analysis. To test the main hypothesis and to consider the inconsistency of regions sampled, specific areas have been defined within Europe. The continent has been divided into ten regions based on significant biogeographic subdivisions or discontinuities identified from previous phylogeographic and palaeoecological studies. This ensured a minimum sample size across each region of more than 10 individuals for the species analysed (see Chapter 2). These regions are represented by the Iberian Peninsula, Western Europe, Central Europe, Apennine Peninsula, British Isles, Balkans, Eastern Europe, Fennoscandia, Caucasus and the Near East (see Chapter 2).

An effort to standardise for differences in the size and distribution of sampling has been made. Rarefraction (Heck et al. 1975) was used to standardise across uneven sample size between species. Haplotype sampling coverage (i.e., what proportion of the population/genetic diversity is represented by our samples) was estimated using the methods of Dixon (2006), based on the number of haplotypes and individuals sampled. The Stirling probability distribution and the Bayes theorem were used to obtain a posterior distribution of the total number of haplotypes, in the population including those not yet observed.

3.2.2 Data analysis

All sequences obtained were aligned and edited manually using the software BioEdit 7.2.3 (Hall 1999) (http://www.mbio.ncsu.edu/BioEdit/bioedit.html) and Geneious 9.1.4 (Kearse et al. 2012). Due to the variation in overlap and length of the current control region (CR) sequences available from Genbank, some adjustments have to be made. Within each species, sequences were standardised to the minimum overlapping sequence length available for each species. The alignment which allows the comparison with as many ancient DNA sequences as possible (where published) will be the one selected for the analysis. If there was no ancient DNA data available, then the longest fragments had priority. Therefore, some sequences were not included in the analysis because of short lengths.

The most common measures of genetic diversity in population studies are haplotype and nucleotide diversity (Egeland and Salas 2008, Goodall-Copestake et al. 2012). To calculate those values, a full reconstruction of the data sets was required. The number of haplotypes, haplotype (*h*d) and nucleotide (π) diversity was calculated using DNAsp v.5.10.01 (Librado and Rozas 2009). The variation in the sequence length and lack of common designation for new and already described haplotypes in different studies, is the main reason to recalculate the number of haplotypes and numbered them according to the number of new haplotypes identified per species.

A commonly used simple estimation for genetic diversity is the raw number of haplotypes. Haplotype uniqueness has also been suggested as a parameter to identify refugial populations (Petit et al. 2002; Maggs et al. 2008). High numbers of private haplotypes are associated with refugial areas, as well as areas of high allelic richness which would be indicative of refugia if the haplotype frequencies are higher than the genetic distance between haplotypes (Petit et al. 2002; Petit et al. 2003; Provan and Bennett 2008). For standardisation of the private haplotypes richness, a rarefraction method was set to a standard sample size of 5 and 10 using

HP-Rare v1 (Kalinowski 2004). The mean across all species was calculated for each of the regions to examine general trends for diversity and identify patterns of diversity in the continent.

3.3 Results

A total of 29 mammal species were investigated for genetic diversity measures across the European continent (Table 3.1). For 14 species ancient DNA (aDNA) sequences were available and then added to the comparative analysis for the temporal periods. For *Homo sapiens*, the Mesolithic samples were used as modern samples to avoid the complexity of the current diversity in Europe (Soares et al. 2010) and understand better the implications of the LGM. The minimum number of individuals per species included in the analysis was 60 for *Erinaceus concolor* and the maximum number of individuals included for one species was 4077 for *Cervus elaphus*. In total, between 8 and 247 different haplotypes were obtained for the species analysed. The sequence lengths, as well as the numbers of haplotypes observed, the completeness and the most likely number of haplotypes reported are presented in Table 3.1 for each species.

Table 3.1 Species that were included in the analysis and for which genetic diversity measures were calculated. Number of individuals, sequence length, number of haplotypes observed and the most likely number of haplotypes in population and the percentage for completeness of sampling (Dixon 2006).

Family	Species	Common Name	Individuals included	Sequence length	Number of haplotypes	Most likely No. of haplotypes (Range)	Completeness (%)	Ancient DNA
Cricetidae	*Arvicola amphibius*	European Water Vole	90	643	58	93(77-184)	62	✓
Cricetidae	*Arvicola sapidus*	Southern Water Vole	276	204	76	78 (76-81)	97	
Cricetidae	*Microtus arvalis*	Common Vole	683	274	73	73 (73-73)	100	
Cricetidae	*Myodes glareolus*	Bank Vole	1110	250	126	126 (126-126)	100	
Cricetidae	*Lemmus lemmus*	Norway Lemming	105	98	19	19 (19-20)	100	✓
Cricetidae	*Cricetus cricetus*	Black-bellied Hamster	561	210	44	44 (44-44)	100	
Sciuridae	*Sciurus vulgaris*	Eurasian Red Squirrel	1050	249	214	215 (214-218)	100	
Castoridae	*Castor fiber*	Eurasian Beaver	633	487	36	36 (36-36)	100	✓
Leporidae	*Lepus europaeus*	European Hare	2177	225	247	247 (247-247)	100	
Leporidae	*Lepus timidus*	Mountain Hare	454	266	200	233 (220-247)	86	✓
Erinaceidae	*Erinaceus europaeus*	Western European Hedgehog	387	405	56	56 (56-57)	100	
Erinaceidae	*Erinaceus concolor*	Hedgehog	62	388	20	21 (20-24)	95	
Soricidae	*Sorex minutus*	Eurasian Pygmy Shrew	280	290	138	171 (158-187)	81	
Canidae	*Canis lupus*	Gray Wolf	1613	235	35	35 (35-35)	100	✓
Canidae	*Vulpes lagopus*	Arctic Fox	351	278	35	35 (35-35)	100	✓

Table 3.2 Species that were included in the analysis and for which genetic diversity measures were calculated. Number of individuals, sequence length, number of haplotypes observed and the most likely number of haplotypes in population and the percentage for completeness of sampling (Dixon 2006).

Canidae	*Vulpes vulpes*	Red Fox	983	219	146	146 (146-147)	100	✓
Mustelidae	*Gulo gulo*	Wolverine	237	317	8	8 (8-8)	100	
Mustelidae	*Mustela erminea*	Stoat	207	502	66	69 (66-74)	96	
Mustelidae	*Mustela nivalis*	Least Weasel	192	514	82	94 (87-103)	87	
Mustelidae	*Martes martes*	Pine Marten	705	217	77	77 (77-77)	100	
Felidae	*Lynx lynx*	Eurasian Lynx	810	498	50	50 (50-50)	100	✓
Ursidae	*Ursus arctos*	Brown Bear	849	122	141	141 (141-143)	100	✓
Hominidae	*Homo sapiens*	Modern Human	86	325	35	39 (36-45)	90	✓
Cervidae	*Alces alces*	Eurasian Elk	1586	465	74	74(74-74)	100	
Cervidae	*Capreolus capreolus*	European Roe Deer	2839	293	181	181 (181-181)	100	
Cervidae	*Cervus elaphus*	Red Deer	4077	180	46	46(46-46)	100	✓
Cervidae	*Rangifer tarandus*	Reindeer	1607	117	236	236 (236-237)	100	✓
Bovidae	*Bison bonasus*	European Bison	172	225	25	25 (25-25)	100	✓
Suidae	*Sus scrofa*	Wild Boar	1220	73	39	39 (39-39)	100	✓

The haplotype (*h*d) and nucleotide (π) diversity values for each species were calculated without including aDNA sequences (Figure 3.1). Haplotype diversity measures ranged from 0.4611 to 0.9863 and nucleotide diversity values ranged from 0.0055 to 0.067. The lowest values for haplotype diversity were found for *Bison bison*, *Gulo gulo* and *Sus scrofa* while for nucleotide diversity they were found for *Gulo gulo*, *Mustela erminea* and *Lynx lynx* (Figure 3.1). The highest values of diversity were identified in *Arvicola amphibius*, *Lepus timidus* and *Mustela nivalis*.

a)

b)

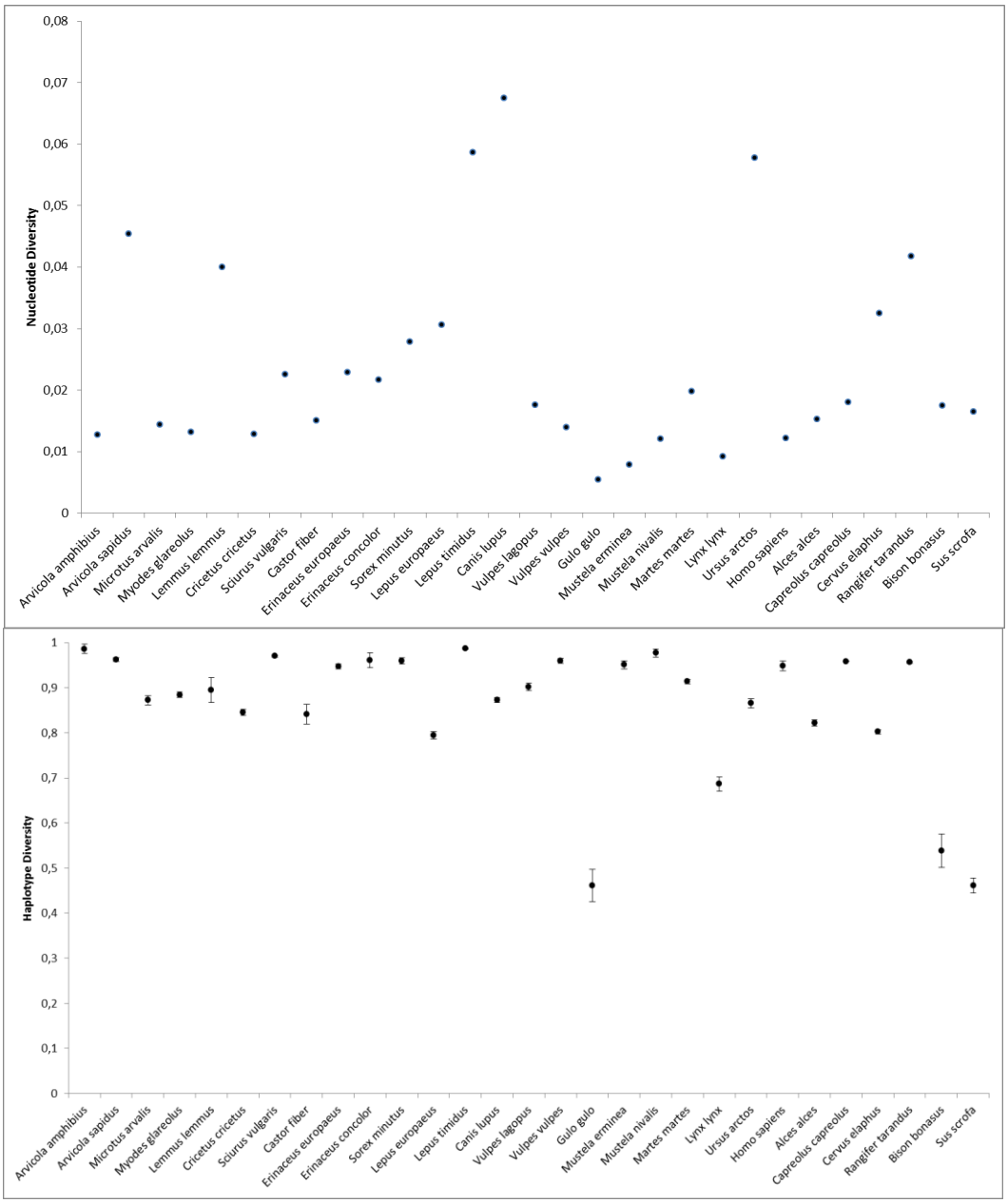

Figure 3.1 a) Nucleotide diversity values for each of the 29 different species analysed. b) Haplotype diversity values.

For rodents, eulipotyphla, carnivores and arctiodactyla different groups were analysed (Figure 3.2). Rodents and Eulipotyphla show relatively constant high values for haplotype and nucleotide diversity. This is in accordance with Pedreschi et al. 2018, including the high diversity values for small mammals. For carnivores and artiodactyla the diversity values are more variable, finding species with relatively low haplotype diversity (*Gulo gulo, Lynx lynx, Bison bonasus* and *Sus scrofa*). For larger mammals, the constant diversity values found for small mammals are not identified for large mammals. The highest values of diversity were identified in *Arvicola amphibius, Lepus timidus* and *Mustela nivalis*. The small mammals (0.94; σ= 0.04) displayed higher average haplotype diversity than the large mammals (0.78; σ= 0.17).

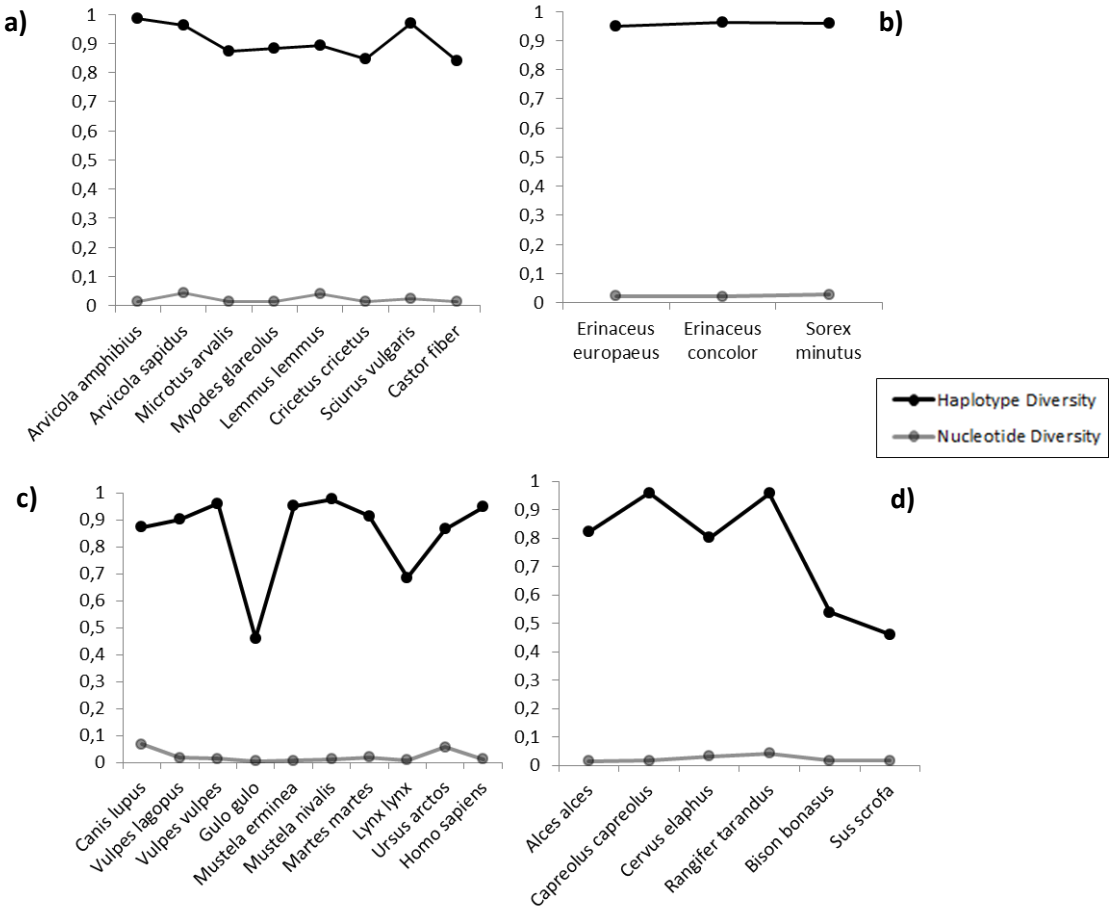

Figure 3.2 Nucleotide diversity and haplotype diversity values for each of the 4 different groups defined by orders. a) Rodents; b) Eulypotyphla; c) Carnivores; d) Artiodactyla

The haplotype diversity values were also calculated for different geographical regions of the European continent. Consistent with previous studies (Hewitt 1999; Petit et al. 2003) the averaged genetic diversity across the 29 different European species showed significant regional differentiation (Figure 3.4). Surprisingly, Iberia presents the lowest value of haplotype diversity (*h*d= 0.64) in the continent with Eastern Europe presenting the highest (*h*d=0.783).

The number of private haplotypes and allelic richness for each species were calculated after rarefraction (Heck et al. 1975) to a sample size of S=5 and S=10. High allele endemism is generally predicted to be an indicator of persistent isolation of populations in refugial areas, and therefore can be used as a proxy to identify refugia (Petit et al. 2002; Maggs et al. 2008). Table 3.2 shows the different values obtained for private alleles per region and allelic richness based on rarefraction to S=5 and S=10. The private allelic richness does not decline significantly with latitude from south to north (slope of the linear regression P>0.05) (Figure A2.1 in Appendix 2).

Table 3.3 Allelic richness (S=5 and S=10), private allelic richness (S=5 and S=10) values calculated for the eleven different regions identified in Europe for this study and averaged across all taxa.

Region	Allelic richness (S=5)	Allelic richness (S=10)	Private Allelic Richness (S=5)	Private Allelic Richness (S=10)
Iberia	2.76	3.89	2.27	2.96
Apennine	2.84	4.26	1.89	2.20
Balkans	3.01	4.53	2.08	2.71
Western	3.03	4.43	2.01	2.80
Central	3.41	5.02	2.19	3.04
Eastern	3.42	5.26	2.29	3.16
Scandinavia	2.95	3.98	1.84	2.16
British Isles	3.38	4.42	2.59	2.98
Caucasus	3.31	4.59	2.35	3.20
Near East	3.62	5.38	2.68	4.21

The genetic diversity through different temporal periods was also calculated for 12 species that have sufficient ancient sequences available (*Arvicola amphibius, Bison bonasus, Canis lupus, Castor fiber, Cervus elaphus, Homo sapiens, Lemmus lemmus, Lynx lynx, Rangifer tarandus, Ursus arctos, Vulpes lagopus* and *Vulpes vulpes*). The Pleistocene represents the period with higher diversity compared with the Holocene and modern diversity for seven species (Figure 3.3). Four species showed no significant change in haplotype diversity over time (*Arvicola amphibius*, *Vulpes lagopus*, *Vulpes vulpes* and *Rangifer tarandus*). Only one species, *Homo sapiens*, showed higher haplotype diversity in the Holocene than in the Pleistocene.

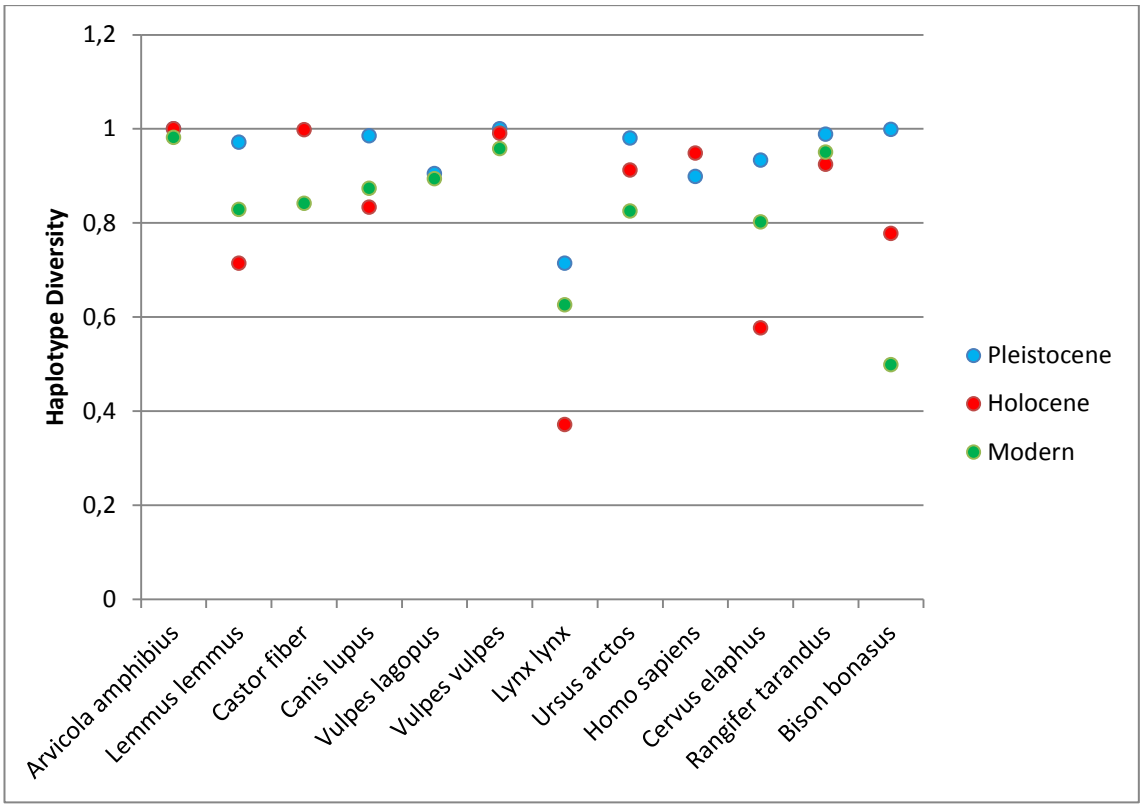

Figure 3.3 Haplotype diversity values for those species with different temporal sequences including Pleistocene (Blue), Holocene (Red) and Modern (Green).

Species diversity indices for mtDNA were not found to consistently correlate with the area occupied (range) of the species analysed, so no relationship was evident between the area and any of these measures for genetic diversity (Figure A2.2 in Appendix 2).

3.4 Discussion

In the northern hemisphere, the well-known pattern of southern richness and northern purity was explained by repeated range contraction and possible northern extinction during the Ice Age (Hewitt 2000). The extent of the expansions and their directions can be inferred by genetic diversity (Ibrahim et al. 1996). It has been hypothesized that for temperate species, southern populations survived in glacial refugia preserving genetic diversity and regions in the north were colonised during the Holocene shaped by founder effects that decreased genetic variability with increasing distance from refugia (Hewitt 1996). The decrease in species richness has also been identified from east to west explained by east-west colonisation throughout the Quaternary, also known as the oceanic-continental gradient (Stewart et al. 2010). The present study indicates that the genetic landscape of Europe is not as clear as

previously thought and the main genetic signals previously identified are blurred due to the high variability of diversities found across species.

This chapter represents an updated and expanded study in relation to Pedreschi et al. (2018), where only small mammals were considered. Furthermore, the methods presented in Petit et al. (2003) and Lumibao et al. (2017) are also used and applied to animals. The results here indicate that the species-specific response found for small mammals is also confirmed in the context of large mammals. The species investigated in this chapter are all the Eurasian terrestrial mammal species that presented sufficient mtDNA control region sequences available to draw conclusions about their genetic diversity indices. The different patterns of genetic diversity examined here, show a species-specific response based on the individualism of each species analysed with different responses to climate oscillations in agreement with Pedreschi et al. (2018). For each glaciation that has occurred in Europe, genetic lineages are likely to be lost, complicating the interpretation of colonisation patterns. Climate oscillations have led to the replacement of important genetic lineages with new ones (Searle et al. 2009; Brace et al. 2012, 2016; Martínková et al. 2013), indicating that modern diversity alone cannot explain historical patterns (Hofreiter and Stewart 2009; Searle et al. 2009; Pedreschi et al. 2018).

The south-north paradigm for genetic diversity based on southern richness and northern purity does not correspond with the mtDNA genetic diversity found for 29 mammal species across the European range studied here. The haplotype and nucleotide diversity do not seem to be particularly high in southern regions (Iberia, Apennines and Balkans) compared to the mid-latitudes or even the northern latitudes of the European continent (Figure 3.4). Particularly interesting is the Iberian case, that shows the lowest haplotype diversity of all the regions analysed. Iberia has been considered one of the most important refugial areas during the LGM and in many cases has been attributed to high diversity values (Hewitt 2004). Also, Italy does not show higher haplotype diversity than northern areas in the continent.

The lower haplotype diversity displayed by southern peninsula might be reflecting the importance of calculating diversity indexes for many species. Including traditionally considering cold-adapted species in this analysis have contributed to re-shape the patterns of diversity in Europe. This can help to explain why the lower diversity found in southern areas is not in agreement with previous general hypothesis suggested (Hewit 1999; Petit et al. 2003).

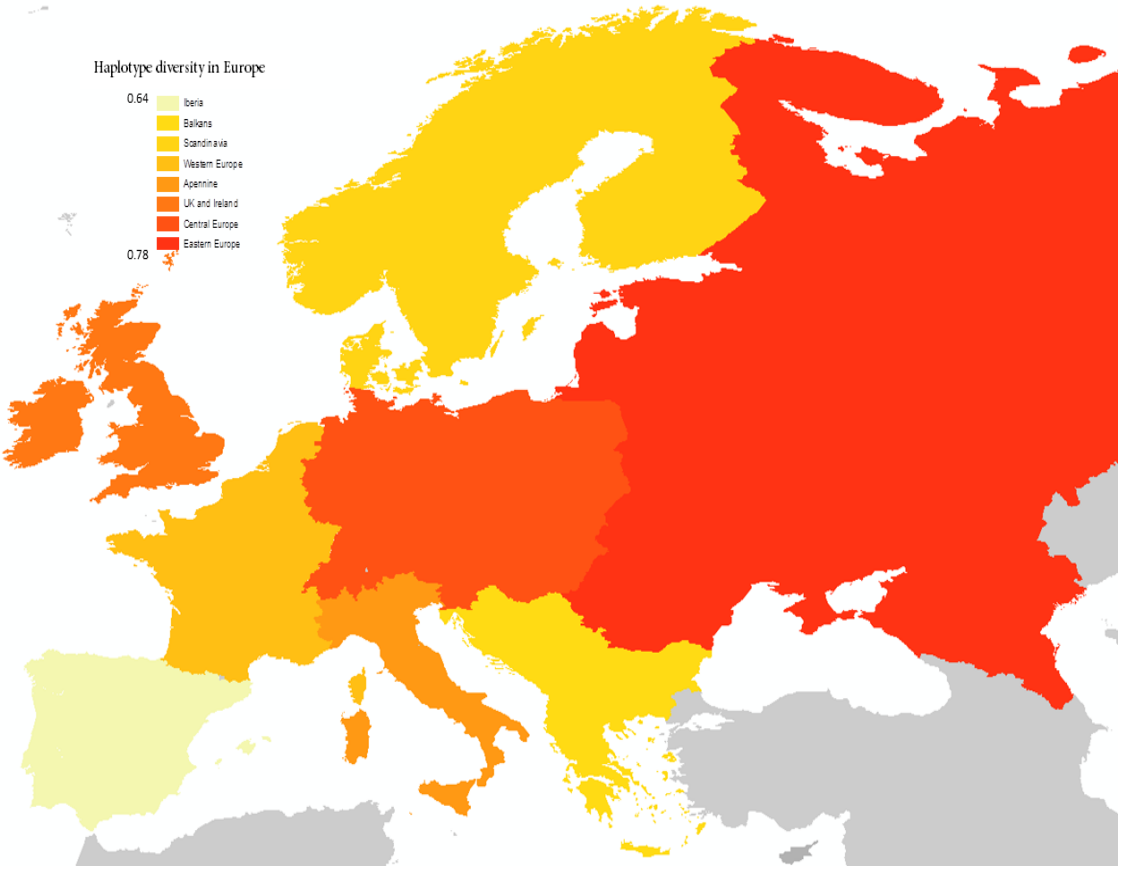

Figure 3.4 Map showing the haplotype diversity values per geographical region included in the analysis. The darker red colour represents the highest values, the lighter the lower.

The two different explanations that were suggested for the southern richness and northern purity were based, first, on the number of species and allelic diversity related to the loss of alleles due to population bottlenecking during expansion, preserving higher diversity in stable populations (Hewitt 1996, 2000, 2004). The second explanation is related to the more prolonged survival of the populations by moving up and down mountains (Tribsch and Schönswetter 2003). Testing the allelic richness of the species in Europe, the southern areas do not show higher values on average than the north (Table 3.2). This result can be explained due to the comparative approach of this research including a higher number of studies in the analysis. Furthermore, the inclusion of temperate and cold-adapted species might help to change the paradigm by having a more complex genetic diversity landscape in Europe.

The high diversity, including private haplotypes (or alleles), expected when populations have contracted into refugia is not identified in this analysis for southern areas. Allelic diversity and heterozygosity are predicted to have higher values in populations that were/are stable (refugia) and to decrease in the direction of the expansion due to founder effects (Maggs et al.

2008; Grassi et al. 2009; Jezkova et al. 2011). The presence of haplotypes that are not found in other populations has been traditionally related with a refugium. Expanding populations can also show high diversity, but it is expected to have a low proportion of private haplotypes (Maggs et al. 2008). The higher frequencies of private alleles have also been used to infer population persistence (Hewitt 1996; Excoffier et al. 2008; White et al. 2013). The results presented in this chapter do not show a higher presence of private haplotypes in southern areas than northern areas (Table 3.2) and this assumption will need to be reconsidered, at least as a common or general pattern for species diversity.

The results presented here have shown that genetic diversity in the mtDNA reflects a more profound complexity that should be taken into consideration for identification of glacial refugia in mammals. These results indicate that common genetic signals are not as easy to detect and instead it is species-specific responses that are of primary importance to reconstruct post-glacial recolonisation patterns. Despite using a more restricted taxonomic group (only mammals) than in previous comparative phylogeographic studies (Taberlet et al. 1998; Hewitt 2000), the number of species included here and the large sample sizes, allowed this analysis to be robust enough to address this important phylogeographic question. The identification of refugia based only on genetic diversity can present serious problems and caveats, as the ones here presented, and have to be taken into account in the future.

The understanding of southern richness based only on the southern refugial paradigm (Hewitt 1996, 1999), could indicate a more simplistic implication and might reflect a 'hotspot' of endemism rather than the source populations that contributed to the post-glacial recolonisation of the north (Bilton et al. 1998; Tougard et al. 2008; Stewart et al. 2010; Pedreschi et al. 2018). If this is the case, the allelic richness shown by mid-latitudinal areas could help us to understand the importance of western and central European areas as a "hub for diversity" rather than simply one of contact and hybridisation zones.

Studies focused on plants have found a wide range of species in more northern latitudes than expected during the ice ages highlighting the possible role of central Europe as an area much more habitable than previously suggested (Petit et al. 2003; Lumibao et al. 2017). In agreement with Petit et al. (2003) the genetically most diverse populations were not located in the southern areas of the continent but at intermediate latitudes. This was suggested as a likely consequence of the admixture of divergent lineages colonising the northern regions from separate refugia that have inflated measures of diversity, but this pattern, as indicated, could also highlight the importance of an east-west mid-latitudinal belt as a possible area for refugia.

The phylogeographic patterns have been suggested to be inversely correlated with dispersal rates (Hofreiter et al. 2004). However, no correlation between genetic diversity and the range of species was found (Figure A2.2 in Appendix 2), also suggesting a more complex scenario regarding the dispersal of species and their phylogeographic patterns, at least based on diversity. The analysis of mtDNA, which is transmitted by the maternal lineage, forms an important caveat in this assertion, as the different dispersal behaviours between male and females could reflect different phylogeographic patterns based on the marker analysed (e.g. brown bear, Valdiosera et al. 2007). However, it still represents the most common genetic marker used in phylogeographic studies, so a better understanding of its patterns will always be valuable (Hung et al. 2016).

Including aDNA in this chapter has helped to answer new questions about the diversity in different temporal periods. This is an improvement from previous comparative approaches and follows the approach from Lorenzen et al. (2011) where different mammal species were targeted during different temporal periods. The extinction and reduction in diversity have been recorded in many mammal species (Barnosky et al. 2004; Hofreiter 2007). For example, *Bison bonasus* is showing a clear drop in diversity from Peistocene to Holocene, but also from Holocene to modern times. Understanding if these extinctions were caused by climate change, human hunting and activities, or a combination of the two, is difficult to discern within the scope of the present work. However, the results here proved the important reduction in genetic diversity through the Late Pleistocene-Holocene transition.

The analysis of haplotype diversity through different temporal periods has demonstrated that the highest diversities are found in the aDNA samples from the Pleistocene/Late Pleistocene (Figure 3.3). Holocene and modern sequences do display lower diversity than Pleistocene samples, in agreement with the pattern described for many mammal species (Lorenzen et al. 2011). Only for modern humans there is a higher diversity in Mesolithic samples than in Palaeolithic samples. The explanation for this result might be related with the more recent expansion of the species during the beginning of the Holocene in the European continent, probably with a reduction of population during the LGM and explained by a scenario of turnovers and movement (Yang and Fu 2018). Furthermore, the relatively recent colonisation of Europe by modern humans, in comparison with other mammals that have resisted in the continent previous glacial and interglacial cycles, may contribute to the genetic diversity pattern found for our species.

3.5 Conclusion

This research provides a new comparative approach to estimate genetic diversity in Europe and reveals a complex scenario that is not characterised by a ”southern richness northern purity” pattern. The importance of mid-latitude areas of Europe as a possible refugial region instead of merely one of the contact zones is reflected in this chapter. Furthermore, with this analysis, the caveat of using only genetic diversity as a marker for identifying refugia has been demonstrated due to the complexity found in the European genetic landscape.

The temporal analysis has shown the importance of the Late Pleistocene as a reservoir for diversity and the loss of diversity through the Holocene, except for modern humans.

Chapter 4. Identifying genetic diversity patterns shaped by the LGM in modern humans and other mammal species

4.1 Introduction

In the last two decades, phylogeography has become a major component of biogeography, with phylogeographic methods used to identify and address fundamental questions in evolution. One of the most important, ongoing challenges in phylogeography is the understanding of how the contemporary genetic patterns of many different mammals in Europe are shaped by climate change during the Late Pleistocene. During glacial periods the ranges of temperate and cold-adapted species contracted or expanded due to their climate adaptations (Hewitt 2000; Stewart and Lister 2001; Lister 2004; Stewart et al. 2010; Morales-Barbero et al. 2017). Those areas representing the species' maximum contraction in their geographical range are called refugia (Provan and Bennet 2008; Stewart et al. 2010). The importance of the Last Glacial Maximum (LGM), 24,000 to 15,000 years ago, in shaping the genetic landscape of many species has been demonstrated (Hofreiter and Barnes 2010) but there is still a lack of understanding about how and where species survived during this period.

The data presented in the first phylogeographic studies of Europe suggested that the vast majority of the temperate species analysed responded with a post-glacial colonisation of central and northern Europe from southern refugia (Hewitt 1999, 2004: Seddon et al. 2001). These southern refugia have been traditionally identified on the southern peninsulas (Iberia, Italy and the Balkans) with at least three main latitudinal expansion routes (Hewitt 1999; 2000). In addition to the traditional southern European refugial paradigm (Hewitt 2000), several studies also indicate that this model is probably too simplistic and does not fit as a general pattern for many temperate species (Taberlet et al. 1998; Valdiosera et al. 2007; Bhagwat and Willis 2008; Schmitt and Varga 2012; Stewart et al. 2010; Pedreschi et al. 2018). Therefore, many concepts have also been developed to explain the disparities in the phylogeographic histories including the existence of cryptic northern refugia (Stewart and Lister 2001), microrefugia (Rull et al. 1988, Rull 2009) or refugia within refugia (Gómez and Lunt 2007).

Understanding the effects of the last glacial and post-glacial period in cold-adapted species is more complex and has been more difficult to suggest a general model. Stewart et al. (2010)

suggested that the range of cold-adapted species is at its minimum in the current interglacial period and therefore such species are in refugia now. However, the evaluation of how cold-species' populations expand and contract is complicated as they are based mostly on modern phylogeographic studies and the identification of survival by habitat tracking or local extinctions is complicated (Lagerholm et al. 2017). Ancient DNA (aDNA) has given an insight into a more common pattern for cold-adapted taxa characterised mainly by extinctions and population turnovers rather than survival by population contractions during the post-glacial period (Dalén et al. 2007; Lagerholm et al. 2014; Palkopoulou et al. 2016). Range shifts and habitat tracking have however also been identified in other species (Leonard et al. 2007; Hofreiter et al. 2007; Lagerholm et al. 2017).

The majority of the literature regarding phylogeographic studies is based on local populations and, in many cases, there is a lack of a more general context of the species history itself. Due to the different natures of the studies, it is not an easy task to compare analyses due to discrepancies in genetic markers, geographical areas sampled and theoretical approaches. Recently, some efforts have been made to present reviews or meta-analyses of the data available (Lenstra et al. 2014; Niedziałkowska et al. 2017; Pedreschi et al. 2018). Mitochondrial DNA (mtDNA) has become the preferable option for phylogeographic studies, due to its relatively rapid rate of mutation, a high number of copies per cell and its haploid maternal inheritance (Avise 1987, 1995; Moritz 1994). Here, the mitochondrial control region (CR or D-loop) has been chosen to address the analysis as a standard genetic marker, as it represents the most commonly used genetic marker in phylogeographic studies (see Chapter 2). Following this approach, a better understanding of the different phylogeographic models proposed is expected based on intraspecific analyses.

The geographical distributions of the species are influenced by ecological and historical parameters. By comparing different species, it is possible to identify similar or dissimilar patterns of movements in the past that have shaped the current distribution and the impact of climate on them (Avise 2000). The application of molecular markers has helped to compare the phylogeographic patterns of several species that shared a common area (Taberlet et al. 1998; Hewitt 1999; Hewitt 2000; Petit et al. 2003; Maggs et al. 2008). However, this has proved as a difficult task as most of the taxa analysed show no evidence of common phylogeographies, although some general trends have been identified (Hewitt 2000; 2004).

Some species have been proposed as a model for different expansion and contraction routes aiming to simplify the complexity of the phylogeographic patterns (Hewitt 2004). The brown

bear (*Ursus arctos*), the European hedgehog (*Erinaceus* spp.) and the meadow grasshopper (*Chorthippus parallelus*) were suggested as paradigm species with three different routes representing southern refugia based on mitochondrial DNA (mtDNA) data. However, species-specific studies have at times contradicted or supported these assumptions (e.g. Valdiosera et al. 2007; Stojak et al. 2016), and no larger comparative analyses have been done to test them.

Refugial populations have been traditionally inferred by diversity indices, but endemic or private alleles could contribute to a better level of resolution as it makes possible the distinction between refugial populations and more recently recolonised areas (Maggs et al. 2008). Combining these two approaches has proved insightful as to common phylogeographic patterns (Petit et al. 2003; Maggs et al. 2008; Lumibao et al. 2017).

Modern humans have sometimes been considered as a different species in terms of their response to climatic oscillations and environmental changes. However, the context of human evolution has demonstrated that our species was subjected to ecological constraints similar to those of other species despite high adaptability to different environments (Willis and Whittaker 2000; Stewart and Stringer 2012). Genomic data from modern and ancient humans have helped to identify migration routes, diversification events and genetic admixture (Nielsen et al. 2017). The last decade has been particularly important to understand past migrations in Europe, thanks to ancient DNA (aDNA) and in particular mtDNA sequences. The hypervariable segment I (HVS-I) is a fragment in the control region of the mtDNA that represent a similar size segment that the sequences that have been traditionally used for other mammal species (e.g. Seddon et al. 2001; Troy et al. 2001; Scandura et al. 2008), that have mainly contributed to the most important phylogeographic studies in Europe (Taberlet et a. 1998; Hewitt 2000, 2004).

A great number of studies have been developed focusing only on the mtDNA of modern humans and analysing the geographical variation of the lineages in the context of the genealogy of this specific marker (Richards et al. 1998; Simoni et al. 2000; Richards et al. 2002). The majority of research on mtDNA in anthropological studies has used HVS-I to reconstruct the population history of our species. However, the main caveat is that through modern DNA past events can only be inferred from the perspective of present distribution patterns. The arrival of aDNA analyses has the advantage of providing direct genetic evidence at a given point in the context of time. Understanding the importance of the LGM in human populations can be a difficult task due to population movements after the Mesolithic and the genetic signals from the Neolithic (Richards 2003). In order to exclude the complexity brought by the Neolithic expansions to Europe and blurring the postglacial recolonisations movements,

Palaeolithic and Mesolithic (that are treated as “modern” population) are analysed in detail in this chapter to understand the species-specific phylogeographic pattern for our species.

This chapter aims to determine the main phylogeographic patterns of 29 different mammal species, including modern humans, by combining all available sequences of a fragment of the control region of the mtDNA for species within the European range. This intraspecific approach enables a better comparison of the effect of geography on genetic diversity at an individual species level. A comparative genealogical meta-analysis study is also presented, containing data from previously published studies, reanalysed in a common framework. This chapter is also trying to elucidate patterns of biodiversity and colonisations based on genetic signatures, such as haplotype diversity and private haplotypes richness, for the detection of potential refugia and possible common patterns of phylogeography between species. Modern humans are considered within this broad-based comparison to establish where they fit within the patterns seen in other mammals in Europe.

4.2 Methods

The main methods that defined how the sequences were obtained are described in Chapter 2. The total number of individuals included for each taxon and the number of individuals per population varied among the studies considered for the meta-analysis. To test the main hypothesis and to consider the inconsistency of regions sampled, specific areas have been defined within Europe. The continent has been divided into ten regions based on significant biogeographic subdivisions or discontinuities identified from previous phylogeographic and palaeoecological studies. This ensured a minimum sample size across each region of more than five individuals for the species analysed. These regions are represented by the Iberian Peninsula, Western Europe, Central Europe, Apennine Peninsula, British Isles, Balkans, Eastern Europe, Fennoscandia, Caucasus and the Near East (see Chapter 2 for more details).

For those species with aDNA data different temporal periods were defined in this chapter. Pleistocene samples represent specimens >30.000 years ago (the Late Pleistocene is defined as the period between 30.000 and 12.000 years ago). Holocene samples represent sequences between 12.000 and 2.000 years ago. Historical samples from 2.000 years ago until 1900 and modern samples from 1900 until current times.

For modern humans, a more detailed analysis was carried. The HVS-I region for all the sequences available for the Palaeolithic and Mesolithic in Europe were retrieved from

GenBank. Reconstructions of the sequences were needed for some individuals and some sequences were discarded due to their poor quality. One of the main caveats of the analysis is that the HVS-I region does not define all the main haplogroups for human mtDNA. For example, haplogroup U8 is defined by some mutations outside this fragment. This reduces the resolution of this study, but the justification for using this region is due to the higher number of sequences that can be included in the analysis. Furthermore, the main aim of this chapter is developing a method suitable for all the different species that are analysed, as complete mtDNA sequences are not so common in the literature to allow their use. The fragment analysed corresponds to the interval 16056-16380 (325 bp).

The phylogenetic trees calculated for all the species followed the methods presented in Chapter 2. For each species, one phylogenetic tree based on the control region sequences was calculated in MrBayes (Ronquist et al. 2012) after the selection of the best fit model chosen in Jmodeltest (Posada 2008) under the BIC criterion and were visualised in FigTree (http://tree.bio.ed.ac.uk/software/figtree/).

In many cases, phylogenetic trees might not accurately mirror the reticulated relationship among haplotypes (Posada and Crandall 2001). Networks can reflect these connections with more details, so network analysis is carried out through a median-joining networks algorithm using Network (Fluxus Technology Ltd) and PopART 1.0 (Leigh et al. 2015). Furthermore, temporal networks are also created using a statistical parsimony network using the script TempNet (Prost and Anderson 2011) in R (R Core Team 2013). This is useful for heterochronous DNA data (sequences of different ages) and to display information from more than one geographical group, fitting perfectly for the analysis.

The most common measures of genetic diversity in population studies are haplotype and nucleotide diversity (Egeland and Salas 2008; Goodall-Copestake et al. 2012). To calculate those values, a full reconstruction of the data sets was required. The number of haplotypes and haplotype (*h*d) diversity was calculated using DNAsp v.5.10.01 (Librado and Rozas 2009). In order to compare haplotype diversity between species and regions, a statistical test was performed. Since the distribution of the differences between the various haplotype diversities is not known, a Wilcoxon Signed Rank Test, a non-parametric test, was chosen (see, for example, Hollander and Wolfe (1973).

Another commonly used estimation for genetic diversity is the raw number of haplotypes. Haplotype uniqueness has also been suggested as a parameter to identify refugial populations (Petit et al. 2002; Maggs et al. 2008). High numbers of private haplotypes are associated with

refugial areas, as well as areas of high allelic richness which would be indicative of refugia if the haplotype frequencies are higher than the genetic distance between haplotypes (Petit et al. 2002; Petit et al. 2003; Provan and Bennett 2008). For standardisation of the private allelic richness, a rarefraction method was set to a standard sample size of 10 using HP-Rare v1 (Kalinowsky 2004). These values were calculated for each species and per region (where sufficient sequences were available) with the aim to determinate similar patterns between species.

4.3 Results

4.3.1 Species by species

Hereunder, the individual results obtained for each of the 29 species analysed are presented including a discussion of the phylogeographic patterns found. The classification follows the mammal classification based on orders.

RODENTIA

Arvicola amphibius (European Water Vole)

A total of 119 sequences were included in the analysis for *A. amphibius*. Some areas did not have high sample sizes, so results should be taken cautiously. The genetic diversity of the species seemed to be high across all the temporal stages analysed from the Pleistocene to the present time (Table 4.1a). However, the temporal network helped to identify a certain lack of genetic continuity since the Holocene into modern times (Figure 4.1a). The phylogenetic tree (Figure 4.2) also resolved the three main clades previously identified for the species (Piertney et al. 2005; Brace et al. 2016).

Table 4.1 *Arvicola amphibius* D-loop fragment sequences retrieved and analysed by temporal episodes (a) and geographical regions (b). n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

a)

Time	n	BP	Haplotypes	*h*d	π
Pleistocene	9	643	9	1	0.01735
Younger Dryas	9	643	8	0.9722	0.00912
Holocene	7	643	7	1	0.01361

Bronze Age/Roman	5	643	4	0.9	0.00222
Historical/Modern	89	643	58	0.9815	0.01931
Total	119	643	83	0.9863	0.01269

b)

Region	n	BP	Haplotypes	Hd	π
Apennine	2	643	2	1	0.01899
Balkans	2	643	2	1	0.00791
Central Europe	2	643	2	1	-
Eastern Europe	7	643	7	1	0.0106
Iberia	2	643	1	0	0
Scandinavia	5	643	5	1	0.00696
Scotland	35	643	16	0.916	0.00503
Uk (Eng-Wales)	33	643	23	0.9697	0.00968
Western Europe	2	643	2	1	-
Total	90	643	58	0.9815	0.01931

The number of individuals sampled across different areas varies considerably and for some of them the sample size is too low (n<5) to infer any phylogeographic pattern based on genetic diversity (Table 4.1b). However, it is relevant to indicate the low diversity found in the main southern refugia peninsulas (<0.02 for haplotype diversity).

Three main clades can be identified for the species (Clade I, II and III in Figure 4.2). Clade I is found in continental Europe and the British Isles from the Late Pleistocene until today (especially in Scotland). Clade II is more restricted and more common in Holocene samples than Clade I. Clade III has a much more restricted distribution as it is only found in historical samples from Italy (and southern Switzerland) and shows no evidence for post-glacial colonisation of the north.

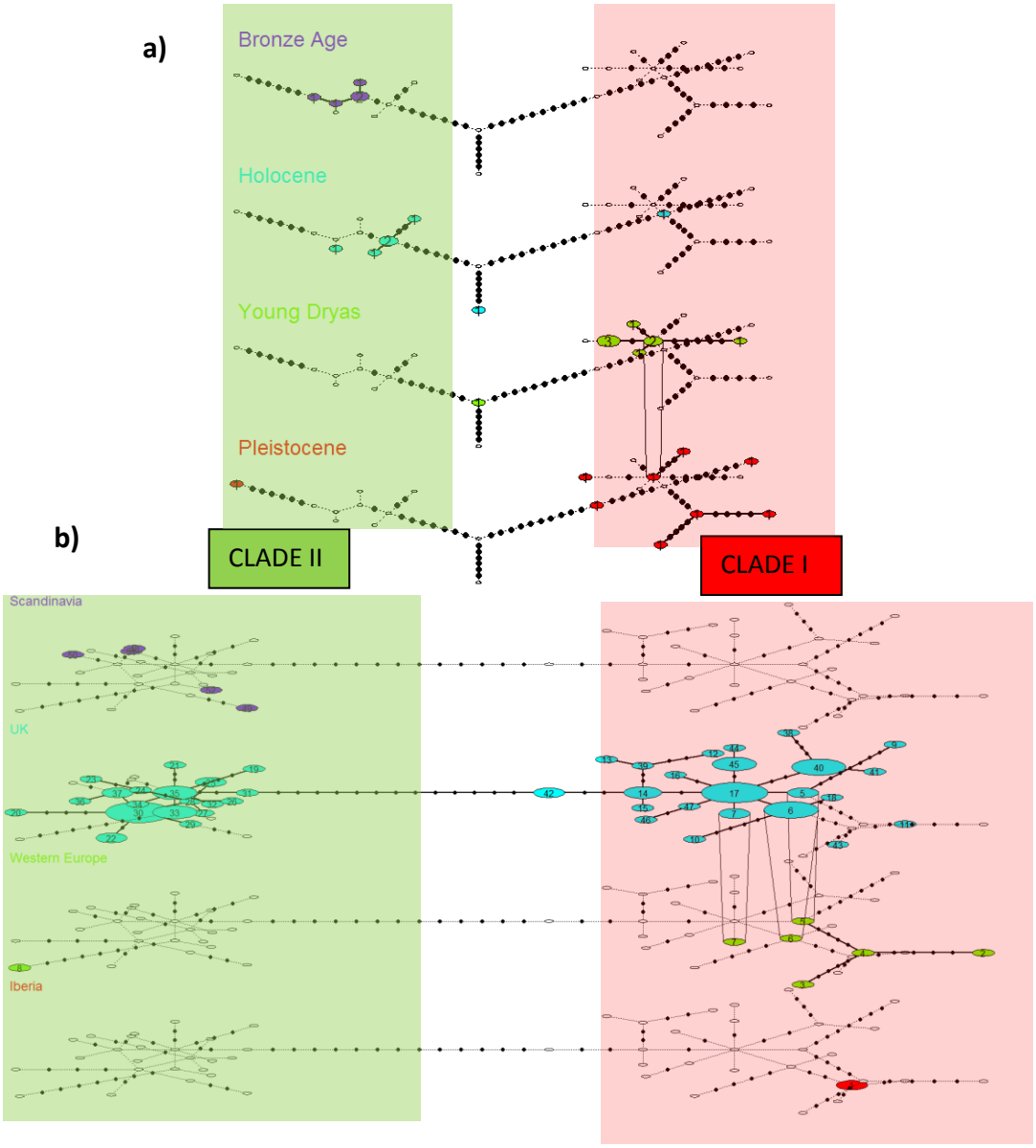

Figure 4.1 a) *Arvicola amphibius* D-loop temporal network showing the presence of the different haplotypes in the four periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given period. b) *Arvicola amphibius* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

A population replacement seemed to occur in Europe, probably after the Younger Dryas, as the Pleistocene samples across continental Europe seemed to be part of Clade I and Holocene samples from Belgium and Germany fall within Clade II. However, Clade I is found in the unique historical sample available from Belgium, indicating a likely survival of these clades even if it is not present in the Holocene samples (Brace et al. 2016). In Figure 4.1a, the shift from Clade I to Clade II is evident and is a full turnover by the Bronze Age/Roman period. The expansion is more likely to have occurred from a northern/eastern refugium rather than a

more traditional southern peninsula refugium as is clear from the lack of genetic legacy from the Apennine Peninsula.

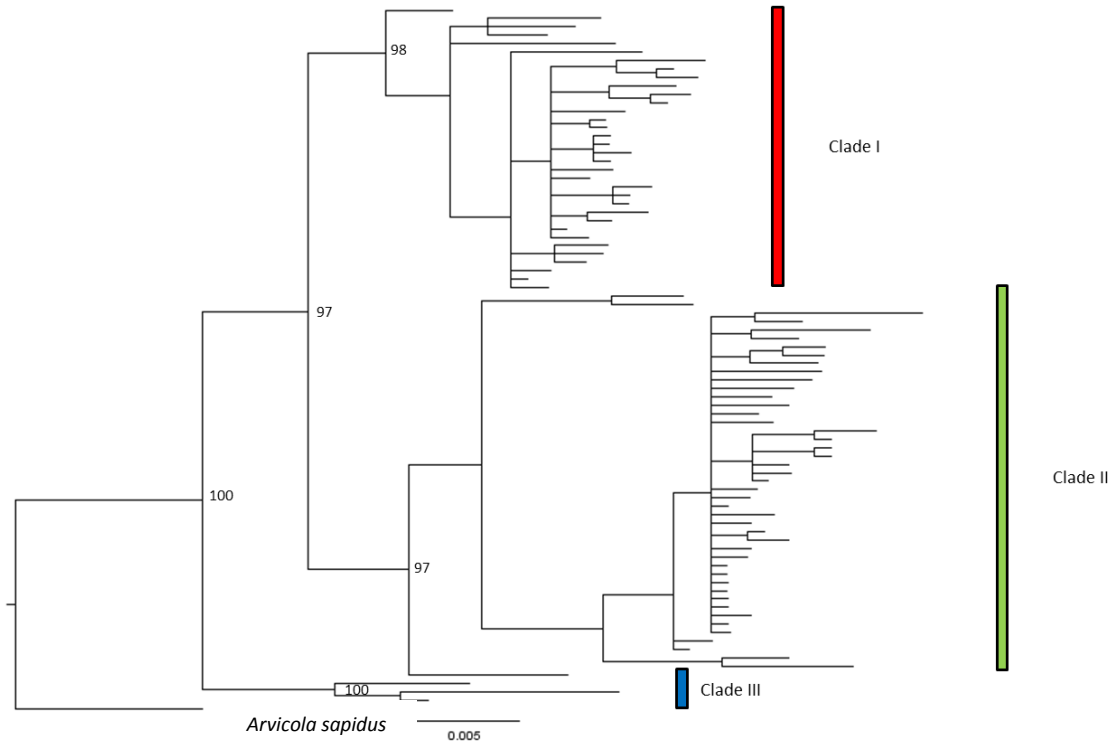

Figure 4.2 *Arvicola amphibius* D-loop Bayesian phylogenetic tree with the three main clades previously identified in Brace et al. (2016).

Clade I is particularly important as it is found in Iberia, Western Europe and the British Isles (Figure 4.1b). The presence of this clade in Iberia may indicate that this area acted as a refugium for the whole clade. However, the limitation in sample size (1 sample) is not strong evidence and so opens the possibility that other refugia existed in western Europe/British Isles for Clade I, especially as Pleistocene samples from Marine Isotope Stage 3 (MIS3) of this clade have been found in the England (Figure 4.3).

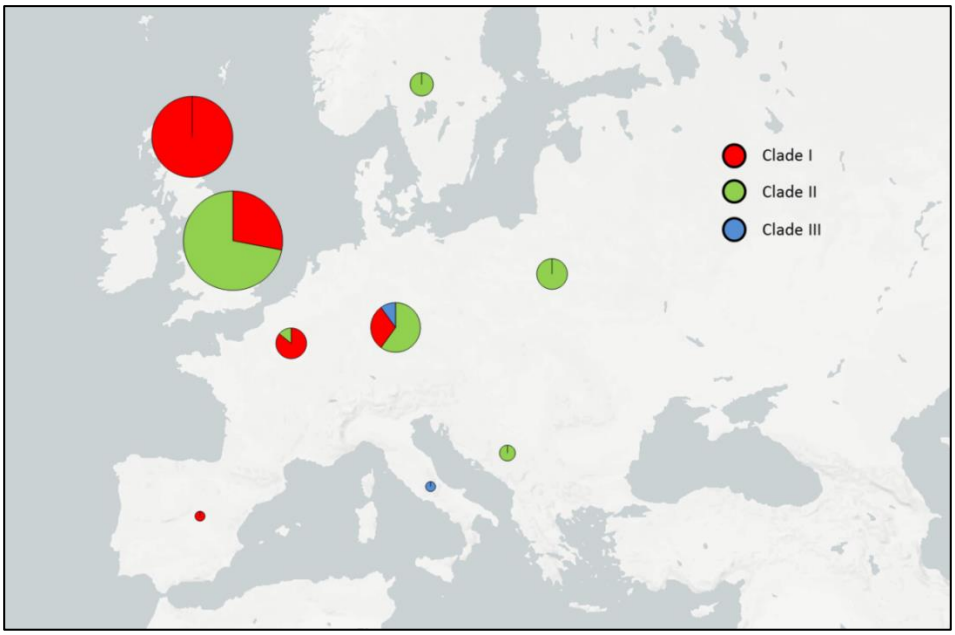

Figure 4.3 Map of the distribution of the main clades identified in the phylogenetic tree for *Arvicola amphibius*.

The importance of aDNA to identify the population history of the species is proved by the British and Scottish sequences in Brace et al. (2016). The more comprehensive scheme developed by this study needs to be a stepping stone for future research for *A. amphibius*.

Arvicola sapidus (Southern Water Vole)

In the present analysis, 276 individuals were included and 76 different haplotypes were identified (Table 4.2). The species revealed a high overall genetic diversity (π=0.04542; *h*=0.9626). The Iberian Peninsula and southern France were the areas sampled, reflecting high diversity for most of the areas described (except for eastern Iberia). The phylogenetic tree (Figure 4.4) showed the clades delimited by previous studies and confirmed the presence of at least six different clades in Iberia (Centeno-Cuadros et al. 2009; Centeno Cuadros et al. 2011).

Table 4.2 *Arvicola sapidus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
France	54	204	17	0.914	0.02479
NorthEast Iberia	35	204	12	0.672	0.03128
NorthWestIberia	14	204	10	0.945	0.04249
North Iberia	33	204	21	0.953	0.04109
SouthEast Iberia	3	204	3	1	0.01307
SouthWest Iberia	60	204	13	0.819	0.04297
South Iberia	69	204	12	0.8218	0.02643
East Iberia	8	204	2	0.25	0.01103
Total	276	204	76	0.9626	0.04542

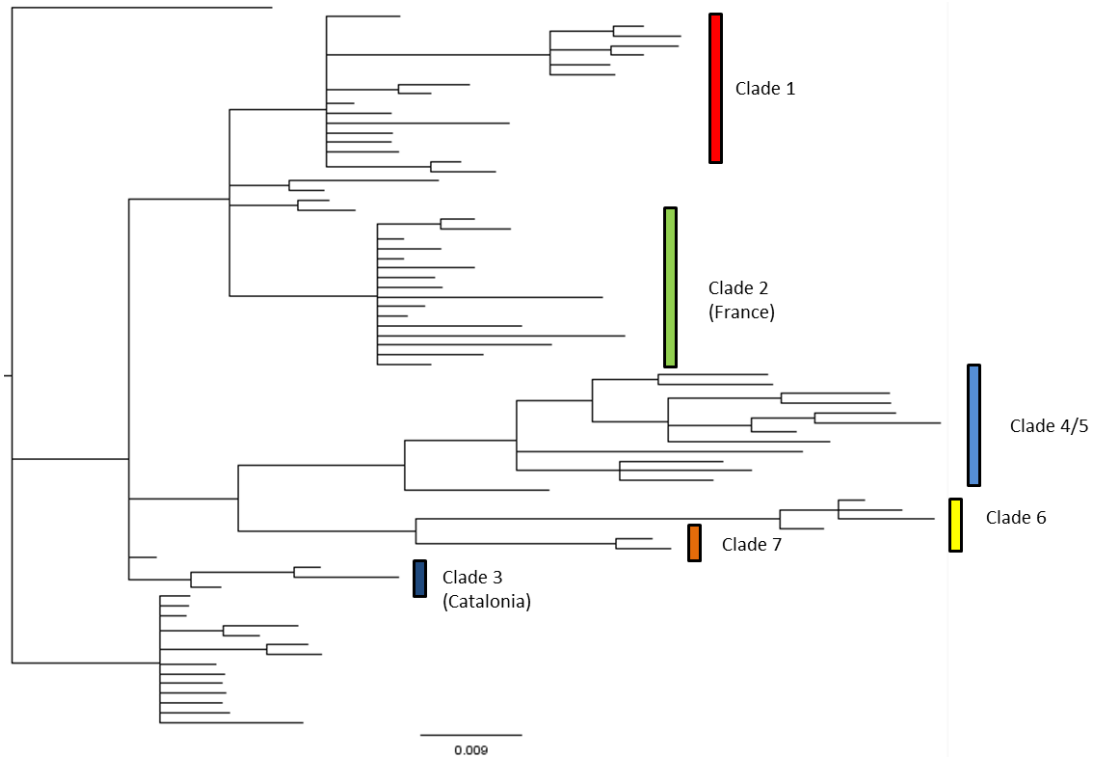

Figure 4.4 *Arvicola sapidus* D-loop Bayesian phylogenetic tree with the seven main clades.

The possibility of refugia-within-refugia seemed to be supported for this species based on the variability found in Iberia. However, the evidence for recolonisation of northern latitudes from the Iberian Peninsula could not be confirmed as the genetic diversity for the French samples does not seem to be reduced (Table 4.2). Furthermore, the distinct clade that French haplotypes formed (clade 2) has been suggested to colonise France before the LGM (Centeno-

Cuadros et al. 2009) so will not represent a post-glacial colonisation, questioning the refugia-within-refugia hypothesis for the species.

Microtus arvalis (Common Vole)

A total of 683 individuals were analysed and 73 different haplotypes were reported (Table 4.3). This analysis covered all the areas analysed by different studies using the D-loop. The genetic diversity may be biased by the small samples for western Europe and Iberia.

Table 4.3 *Microtus arvalis* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Iberia	47	274	2	0.3164	0.00117
Western Europe	48	274	10	0.789	0.01704
Central Europe	588	274	62	0.8334	0.01234
Total	683	274	73	0.8724	0.01443

The phylogenetic tree resolved three main clades that can be assigned or related to different geographical areas (Figure 4.5). The genetic structure of the tree is in agreement with the limited dispersal ability of small rodents over large distances (van de Zande et al. 2000). Hamilton et al. (2005) pointed that effective dispersal rates between male and female present lower values for females and higher for males and this can be explained by the strong geographical structure in Europe for mtDNA.

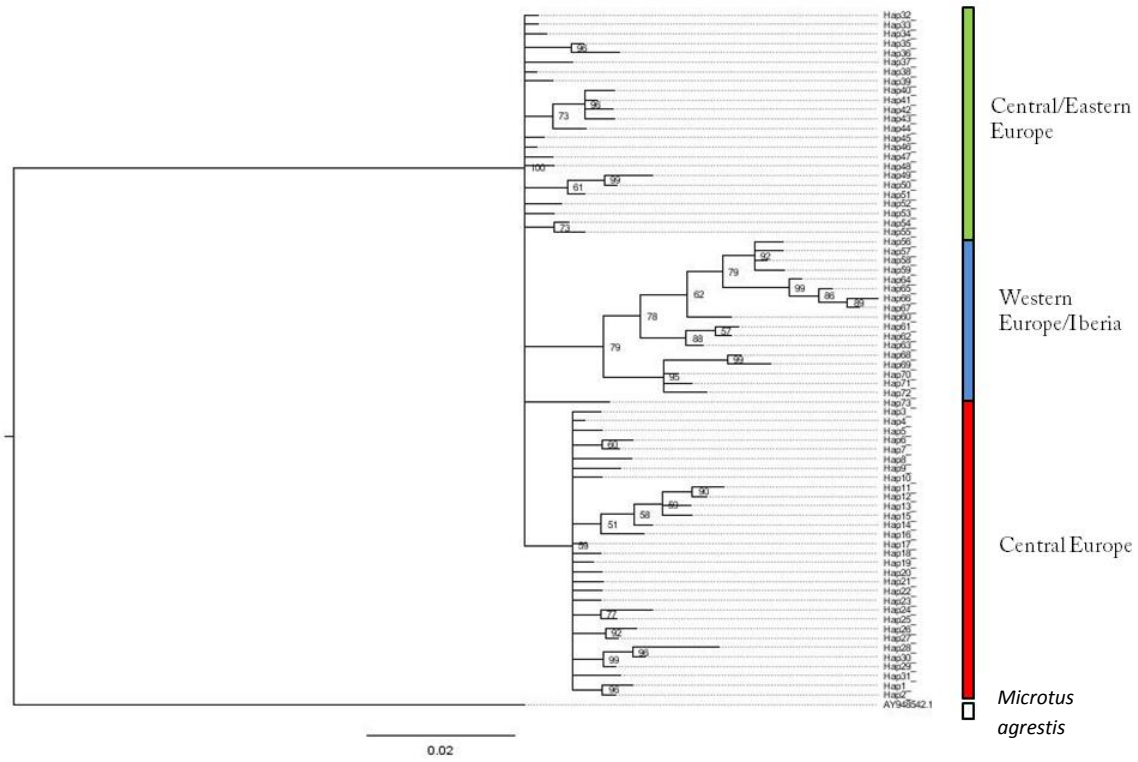

Figure 4.5 *Microtus arvalis* D-loop Bayesian phylogenetic tree with the main clades identified.

The geographical network (Figure 4.6) showed no continuity through the different geographical areas with a higher number of haplotypes (this can be due to a higher samples size) in central Europe. Iberia does not seem to represent a refugium as it has low diversity, but this might reflect the small samples size, and more sampling might be needed to confirm the hypothesis of Iberia as a refugium for the species. Central Europe seems to have much more variability. Unfortunately, the east of Europe is not well represented in the database for the D-loop making impossible the detection of the suggested northern refugium in the Carpathians (Stojak et al. 2015).

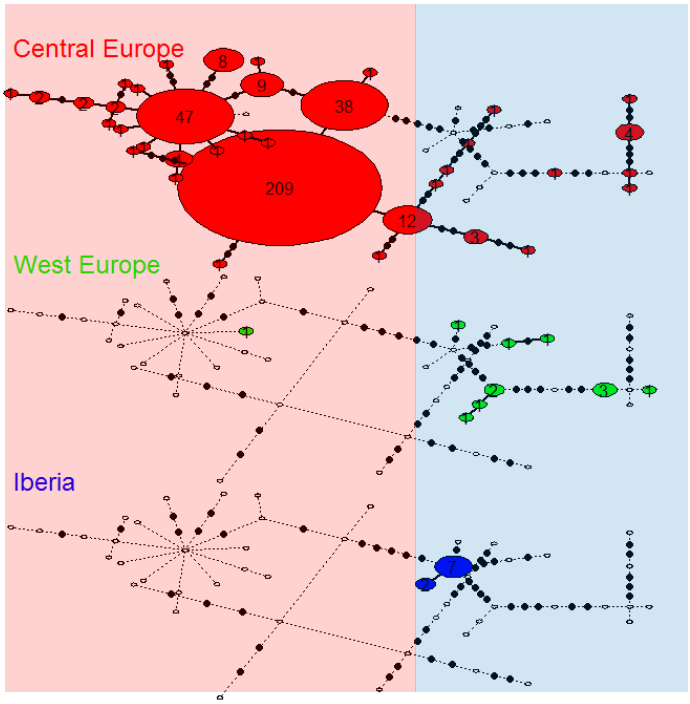

Figure 4.6 *Microtus arvalis* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

Myodes [Clethrionomys] glareolus (Bank Vole)

The levels of haplotype diversity show specific variability and high values in northern areas (but noting that there is a lack of sampling in southern areas). The high diversity found across different regions might indicate the complexity below the colonisation patterns of the species (Table 4.4).

Table 4.4 *Myodes glareolus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Eastern Europe	807	250	38	0.7969	0.00654
Central Europe	67	250	24	0.8345	0.01105
UK	2	250	2	1	0.004
Scandinavia	198	250	52	0.8923	0.02463
Near East (Turkey)	36	250	17	0.9286	0.00879
Total	1110	250	126	0.8842	0.0132

The phylogenetic tree (Figure 4.7) resolved two main clades but with a high number of subclades within them following the results for the cyt *b* (Deffontaine et al. 2009). No strong

geographical pattern seems to be causing this result, as the two main clades are formed by samples from diverse locations across the continent.

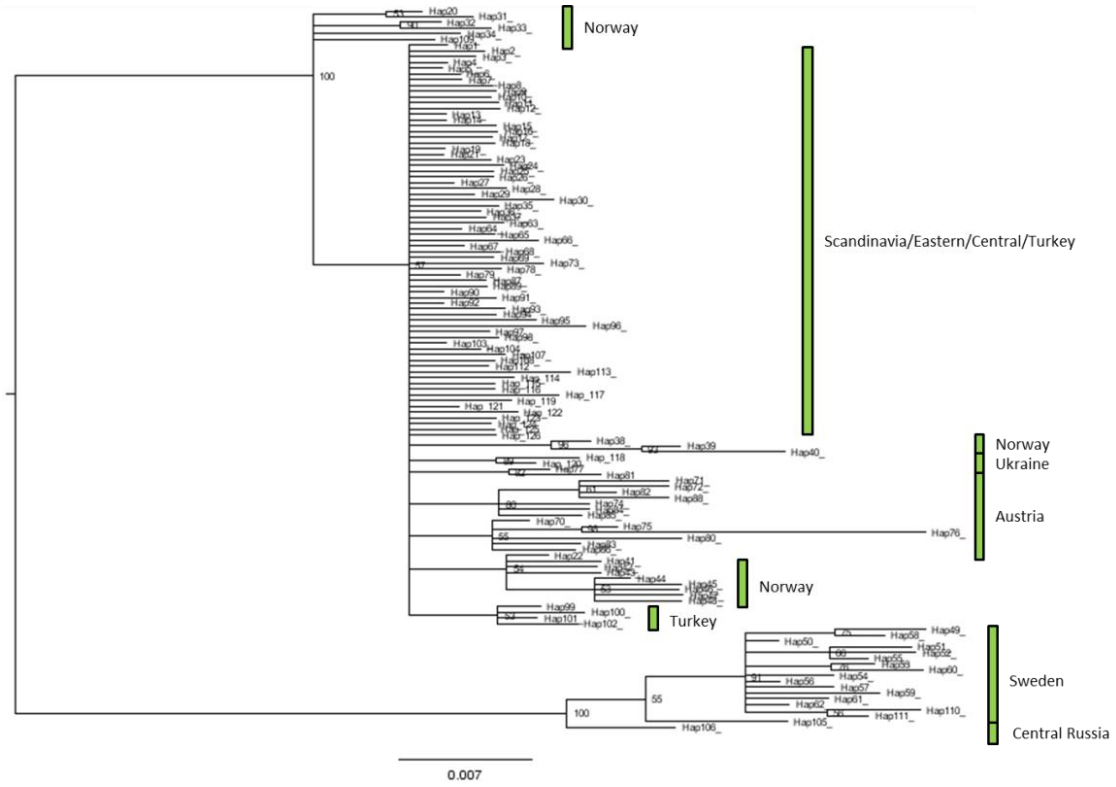

Figure 4.7 *Myodes glareolus* D-loop Bayesian phylogenetic tree with the main clades identified.

The network analysis displayed an interesting difference between some individuals from Scandinavia and the rest of the populations (Figure 4.8). This is also shown in the phylogenetic tree for the main clade with Swedish and Russian samples. Despite this clade, and due to the lack of sampling in western and southern areas, no more subclades where characterised through the phylogenetic tree and the network produced. In this case, cyt *b* seems a much better option to infer the phylogeographic pattern of the species and new studies have contributed to understanding better the demographic history in many areas of Europe (Filipi et al. 2015). It appears that the postglacial expansion was likely from multiple refugia and via different routes, with the traditional southern peninsular refugia maintaining populations throughout the Pleistocene but without contributing to the recolonisation of mainland Europe (Deffontaine et al. 2005).

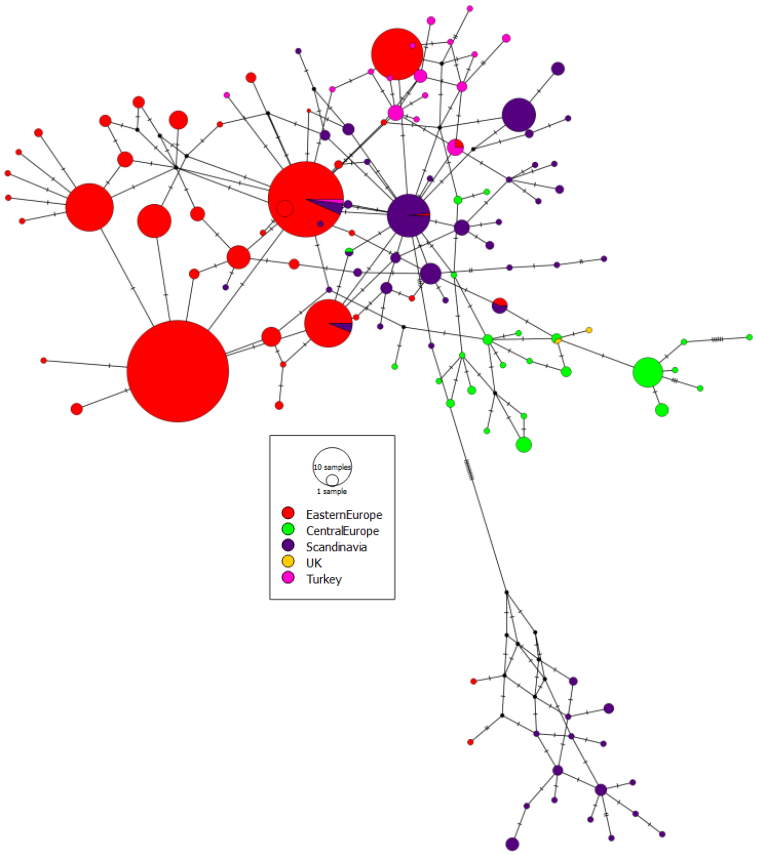

Figure 4.8 Median-Joining network of all the D-loop sequences available for *Myodes glareolus*.

Lemmus lemmus (Norwegian lemming)

A total of 135 individuals have been included in the analysis (Table 4.5). The Pleistocene samples have the higher nucleotide and haplotype diversity values in agreement with Lagerholm et al. (2014) and related to the reduction of the genetic diversity in current times. The number of haplotypes found for the Pleistocene (12) almost matches the number amongst the modern samples (19), even if the number of sequences available for the Pleistocene is less (Table 4.5).

Table 4.5 *Lemmus lemmus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Time	n	BP	Haplotypes	*h*d	π
Pleistocene	15	98	12	0.9714	0.0863
Late Pleistocene	8	98	5	0.7857	0.06259
Holocene	7	98	4	0.7143	0.01504
Modern	105	98	19	0.8284	0.01207
Total	135	98	40	0.8947	0.04

In the phylogenetic tree (Figure 4.9), the three main clades previously identified are well resolved apart from some uncertainty between Clade A and B that has already been reported (see Lagerholm et al. 2014). In all the clades there are Pleistocene samples from western, central and eastern Europe, but the modern Scandinavian samples are only present in Clade B. This suggests that the extinction of Clades A and C across the Pleistocene-Holocene transition had a main role in the loss of genetic diversity of the species observed (Table 4.5).

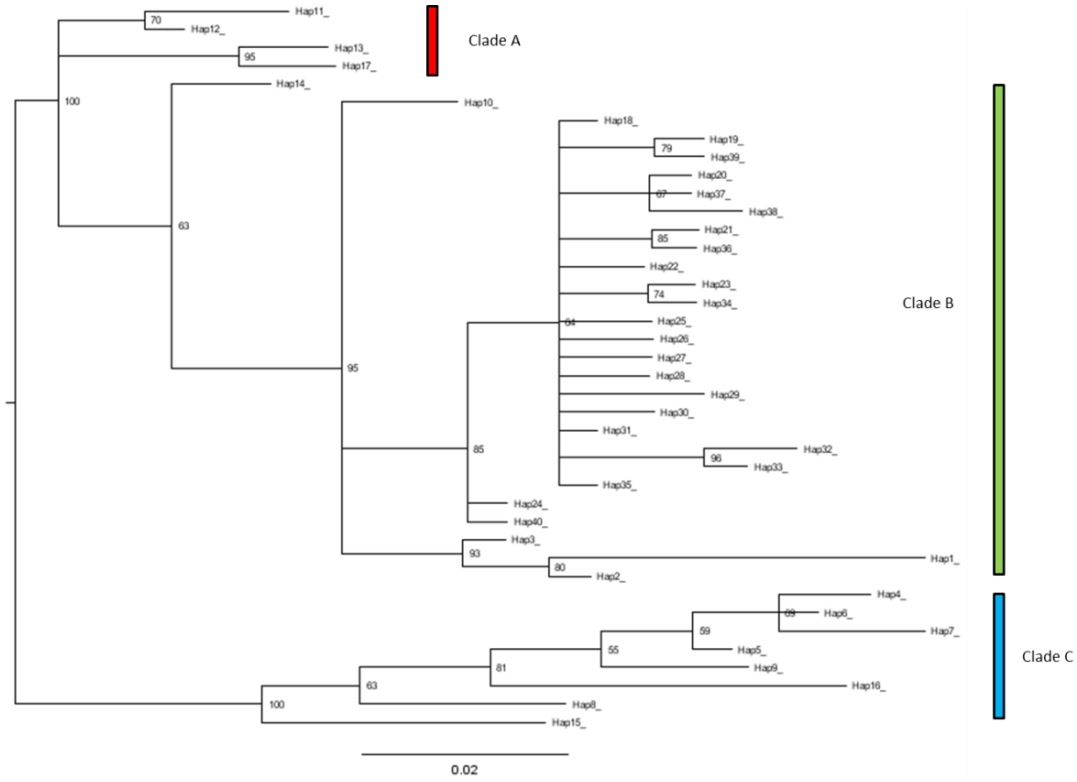

Figure 4.9 *Lemmus lemmus* D-loop Bayesian phylogenetic tree with the main clades identified.

The modern population displayed the lowest nucleotide diversity and the star-shape haplotype network (Figure 4.10) might indicate a reduction in population size followed by a more recent expansion, which was previously described by Fedorov and Stenseth (2001). This could reflect a bottleneck during the LGM or a postglacial recolonisation founder effect in the region. The Holocene samples from Sirijorda Cave in Norway also supported the continuity between this period and modern time making it less likely for the hypothesis of a more recent colonisation due to a lack of continuity between Pleistocene/Late Pleistocene and the present (Figure 4.10) (Lagerholm et al. 2014).

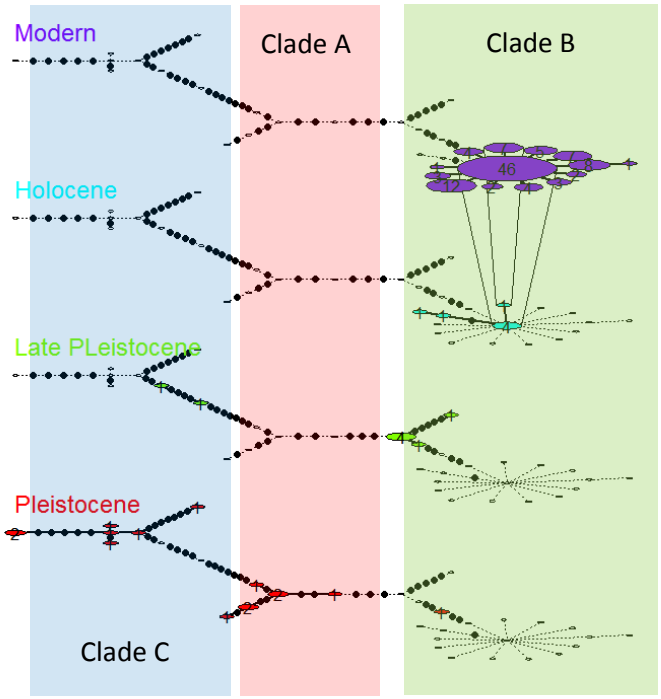

Figure 4.10 *Lemmus lemmus* D-loop temporal network showing the presence of the different haplotypes in the four periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given time period. Haplotypes found in multiple periods are connected by vertical lines. Within each layer, black dots represent one mutation.

The loss of clade C is highlighted in the temporal network (Figure 4.10), where the biggest bottleneck is identified during the Late Pleistocene/Holocene transition. The Holocene and modern samples display the same pattern for clade B, indicating a possible colonisation of Scandinavia or the bottleneck caused by this transition. Clade A loss could be a consequence of LGM, but the small sample size does not allow better testing of this. However, the likely presence of boreal trees in the area during the LGM (Parducci et al. 2012) has contributed to support the presence of a local northern refugium.

Cricetus cricetus (Common Hamster)

A total of 561 sequences were included in the analysis of the species (Table 4.6). Unfortunately, the majority of the samples are concentrated in Central Europe. However, the samples sizes in western and eastern Europe are high enough to be considered for detecting any phylogeographic pattern based on diversity (>50).

Table 4.6 *Cricetus cricetus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	N	BP	Haplotypes	*h*d	π
Western Europe	84	210	3	0.047	0.00023
Central Europe	420	210	23	0.805	0.01171
Eastern Europe	57	210	22	0.906	0.01289
Total	561	210	44	0.845	0.0129

The phylogenetic tree is not well resolved and it did not show the two main clades previously described (Figure 4.11). However, Neumann et al. (2005) identified those using combined haplotypes from three different partial mtDNA genes and only using the D-loop does not seem enough to reveal those differences. The north-south division previously found for the species could not be confirmed with this analysis.

The genetic data suggest that *C. cricetus* could cope well with cold climates and hence the LGM caused a retreat but without significantly affecting the population size of the initially expanding populations (Neumman et al. 2005). The networks (Figure 4.12) showed that western Europe is characterised by a main haplotype in agreement with the low haplotype diversity found in this area (Table 4.6). The difference between the individuals from the west is seen in the networks, with only three haplotypes represented its diversity. However, there is only one major phylogroup that includes the majority of the haplotypes except for one haplotype in the phylogenetic tree, indicating no strong differentiation of populations (Figure 4.11).

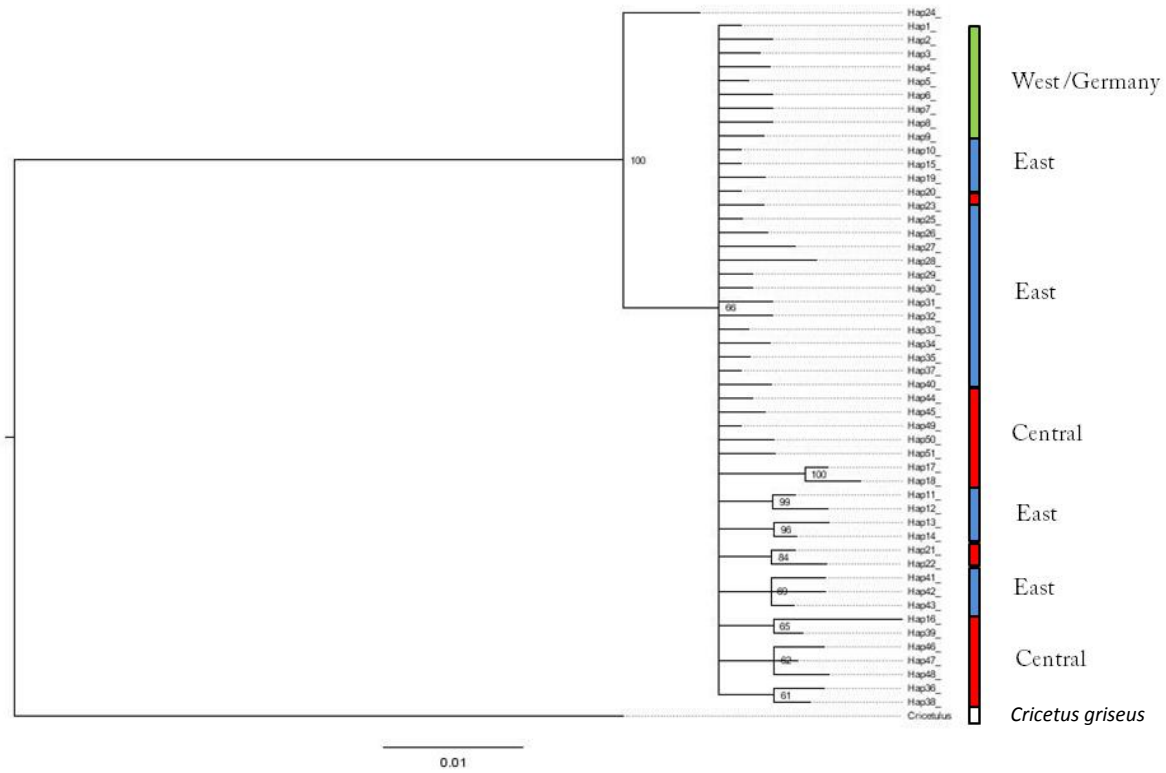

Figure 4.11 *Cricetus cricetus* D-loop Bayesian phylogenetic tree with the main geographical regions identified.

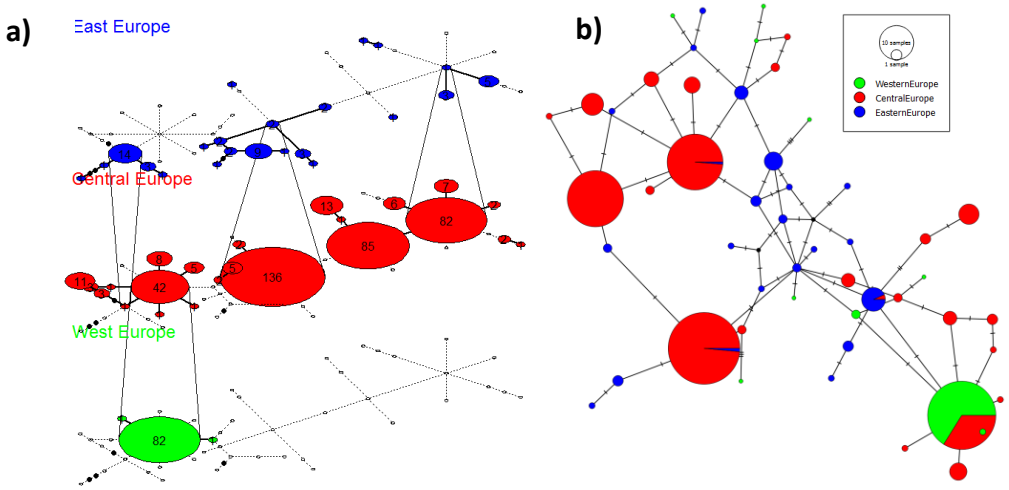

Figure 4.12 a) *Cricetus cricetus* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation. b) Median-Joining network of all the D-loop sequences available for *Cricetus cricetus*.

Eastern Europe showed the highest diversity suggesting a main refugium in the east for this species during the last glaciation as has been suggested by Neumann et al. (2005). The phylogenetic structure of *C. cricetus* in Europe can be explained as a result of expansion from an eastern refugium covering the area of Russia and Ukraine. This is in concordance with the

fact that common hamsters are typical continental steppe animals that are adapted to open landscapes. Regarding the viability of the species during the LGM in northern latitudes, Grulich (1987) proposed that *C. cricetus* could not have survived through this period in Europe, but Jánossy (1986) and Hír (1997) showed an almost uninterrupted record of the species in Hungary from 40 kya onwards and it is well documented in western Europe in Late Pleistocene deposits (Cordy 1991).

Sciurus vulgaris (Red squirrel)

For this analysis, a total of 1050 individuals have been used, resolving 214 distinct haplotypes with high values for haplotype and nucleotide diversity (Table 4.7). The total length of the fragment analysed is 249 bp.

Table 4.7 *Sciurus vulgaris* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	N	BP	Haplotypes	*h*d	π
Iberia	131	249	10	0.762	0.00986
Apennine	79	249	28	0.912	0.03061
Balkans	4	249	4	1	0.03024
West Europe	222	249	67	0.934	0.02182
UK	442	249	50	0.906	0.01853
Scandinavia	95	249	16	0.779	0.01706
Central Europe	29	249	19	0.906	0.00235
East Europe	2	249	2	1	0.04839
Asia	46	249	41	0.9942	0.02836
Total	1050	249	214	0.9699	0.02255

The haplotype and nucleotide diversities of the species are relatively high and particularly in Western European countries. The high diversity in the Alps and central Europe is common for other rodents and has been previously discussed in the literature (Barrat et al. 1999; Trizio et al. 2005; Grill et al. 2009). This might reflect the low mobility of the species and sensitivity to barriers (Grill et al. 2009). Surprisingly, the genetic diversity in Iberia and the Apennines is not higher than in other areas and this might be due to recent bottlenecks (Grill et al. 2009).

The phylogenetic analysis (Figure 4.13) did not resolve geographical patterns for the main branch of the phylogenetic tree. One haplotype from the UK seems to form a different phylogroup than the continental sequences, although this is probably due to a considerable

number of non-identified nucleotides (Ns) in the sequence. Some lineages appeared with a better geographical resolution.

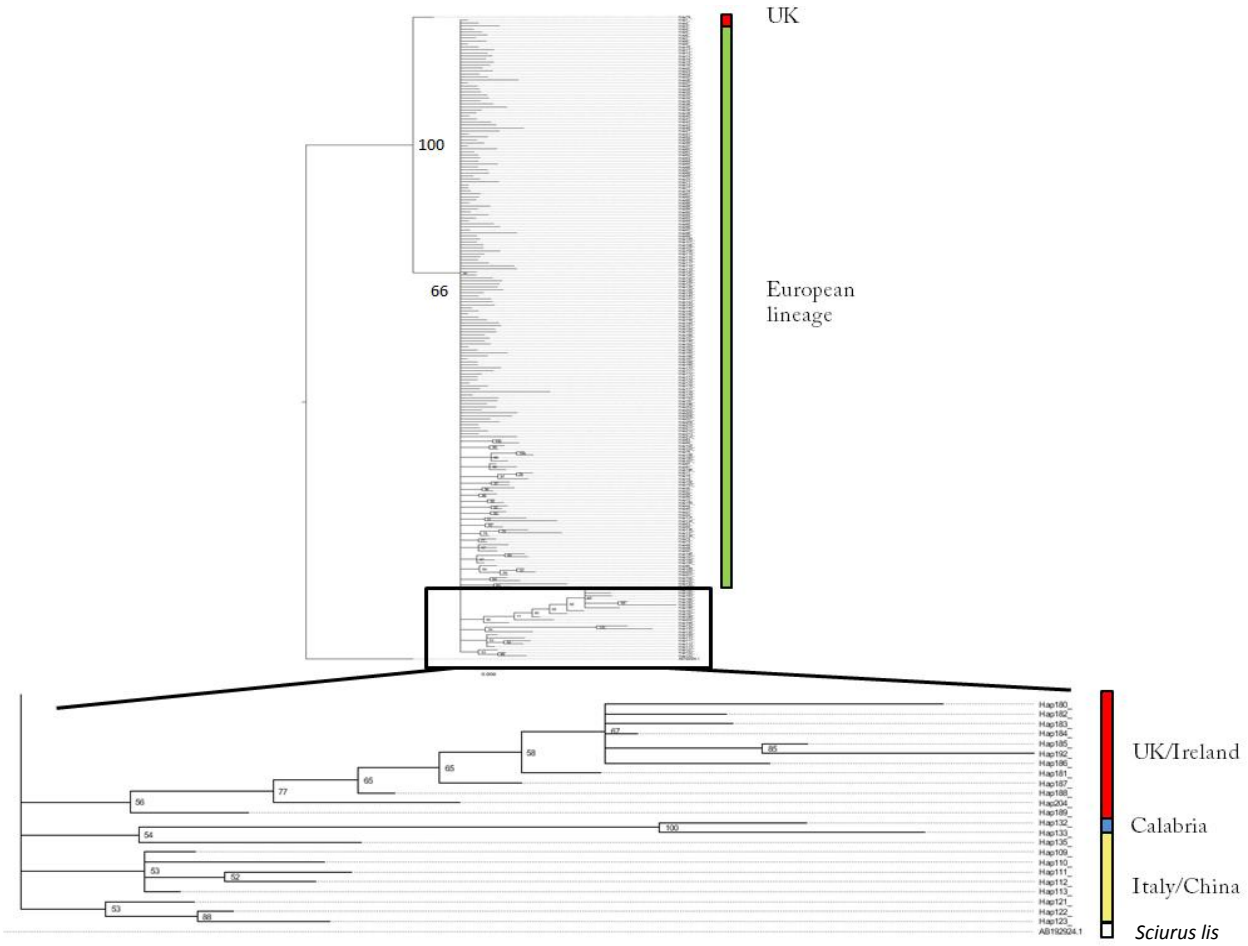

Figure 4.13 *Sciurus vulgaris* D-loop Bayesian phylogenetic tree with the main clades identified.

As previously reported (Grill et al. 2009) the Calabrian group forms a clade, but individuals from the British Isles also configured as a relatively separate clade. The relationship between haplotypes found in China and Italy is also seen here (Liu et al. 2014). However, no significant phylogroup clustering for the individuals from Calabria is reported in agreement with Lucas et al. (2015). In summary, mtDNA genealogies are not structured following a geographical provenance from the three main possible southern refugia.

In the geographical network, only the Calabrian cluster appeared to be far from the main haplotypes (Figure 4.14). However, it showed continuity between the main haplotypes described for the Apennine Peninsula, central and western Europe. Western Europe seems to have the higher haplotype diversity and is characterised by at least five main haplotypes. This could also suggest that a band from western to eastern Europe acted as a genetic reservoir

during the LGM with some population expansion to the south and/or north with changes in the climate conditions.

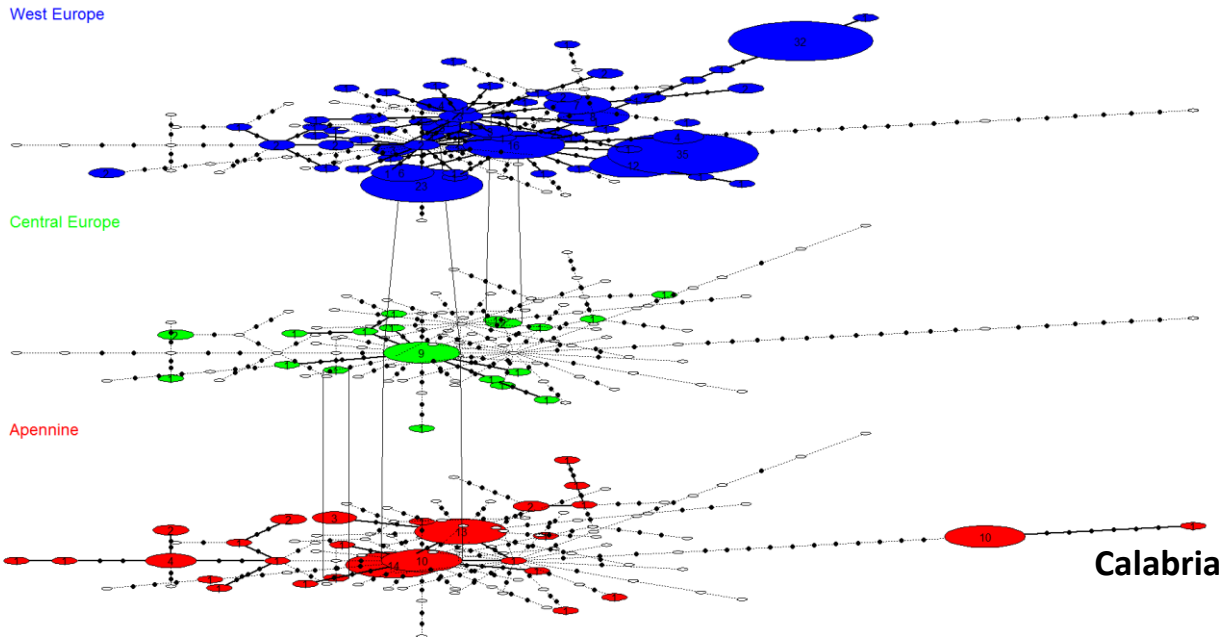

Figure 4.14 *Sciurus vulgaris* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

Other species associated with pine trees (whether as obligate pine associated species or one strongly associated with pine), such as forest-dwelling beetles (*Pytho sp*.), have been proposed as not having been restricted to refugial areas during glacial periods (Painter et al. 2007). This might be in concordance with the wide range of pine trees (Grichuk 1984; Alfano et al. 2003). Red squirrels feed preferably on pine cones, so they live in association with pine trees and our analysis has indicated a similar pattern rather that southern refugia for this species which may have been more widespread during glacial maxima.

Castor fiber (Eurasian Beaver)

The analysis included 681 sequences and the alignment was based in a 487 bp fragment. The identification of southern refugia for the species is complicated due to the lack of sampling in southern areas of Europe. However, the presence of beaver fossils during the Late Pleistocene in Italy and the ecological preference of the species open the possibility of refugia in southern Europe (Legge and Rowley-Conwy 1986; Barisone et al. 2006). The western clade refugium has been suggested in Iberia given the ecological preferences of beavers (Horn et al. 2014), but this is not inferred by phylogeographical data. In the analysis, and with the genetic data available, Iberia cannot be confirmed as a refugium for the western or central clade. The western

samples seemed not contribute to the Scandinavian populations. However, the haplotype found in higher frequency in Scandinavia is also found in central European samples opening the possibility of northern refugia for the species rather than an Iberian refugium, due to the absence of evidence of this from the genetic data (Table 4.8).

Table 4.8 *Castor fiber* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Apennine	1	487	1	-	-
Balkans	1	487	1	-	-
Mongolia	12	487	1	-	-
Western Europe	18	487	2	0.1111	0.00412
Central Europe	445	487	41	0.7755	0.00711
Eastern Europe	173	487	27	0.8598	0.02323
North Sea	3	487	2	0.6667	0.00137
Scandinavia	28	487	10	0.5476	0.01402
Total	681	487	82	0.863	0.01502

In the phylogenetic tree, the eastern and the western clades are well defined (Figure 4.15) and probably represent at least two main refugial populations. This indicates a strong west-east differentiation in central Europe, with the western clade found in eastern areas of Poland probably representing a contact zone of the two clades. This has also been documented for other species such as *Ursus arctos* and *Erinaceus europaeus* (Hewitt 2004).

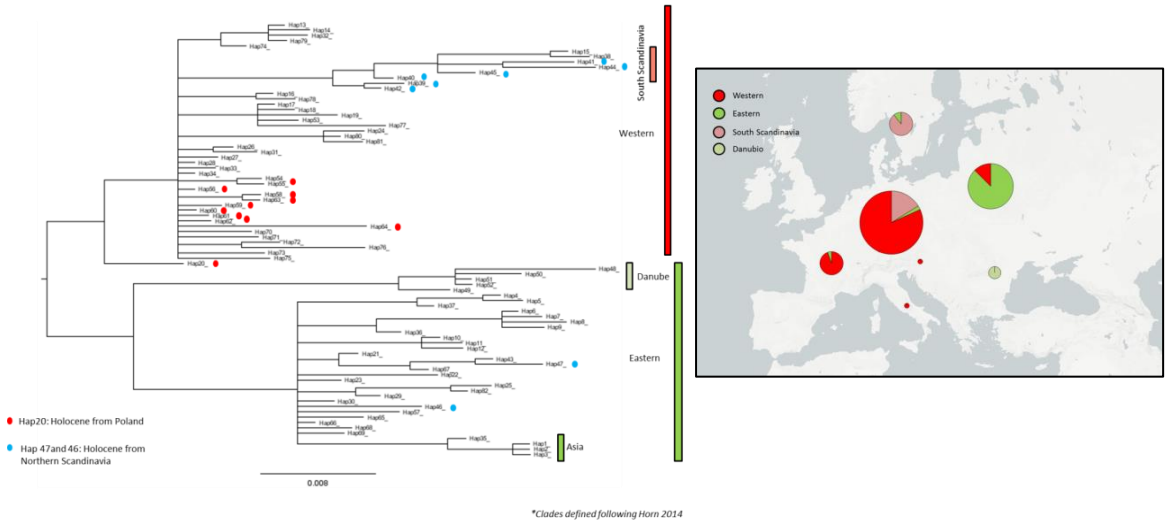

Figure 4.15 *Castor fiber* D-loop Bayesian phylogenetic tree and map of the distribution of the main clades identified.

The western clade includes the southern Scandinavian subclade reflecting the connection between the central European populations (western clade) and Scandinavia (Figure 4.15). This opens the possibility for northern refugia in Central Europe that contributed at least to southern Scandinavian areas. The beaver has been compared with the brown-bear pattern of postglacial recolonisation from Iberia (Hewitt 2000) despite the lack of evidence from the phylogeographical data. The low diversity found in Western Europe (the closest area to Iberia) does not suggest strong evidence of this pattern for the beaver.

The Holocene samples showed higher diversity than modern samples and the decrease in genetic diversity is most likely caused by anthropogenic influences (Horn et al. 2014). In the temporal network (Figure 4.16) the reduction in the number of haplotypes is manifested. It also shows how the modern samples showed a much more structured phylogeographic pattern. The low sample sizes in Italy and the Balkans (n=2) does not allow the confirmation of these peninsulas as refugia for *Castor fiber*.

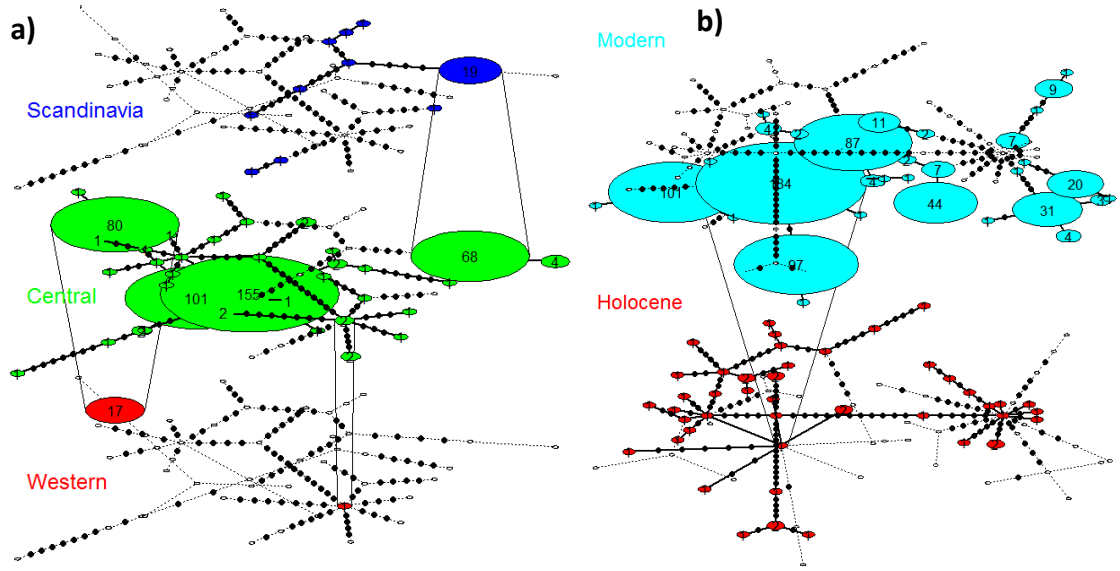

Figure 4.16 a) *Castor fiber* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation. b) *Castor fiber* D-loop temporal network showing the presence of the different haplotypes in the Holocene (in red) and in modern samples (in blue).

The phylogeographic pattern for the species is shaped by complex transitions from the Pleistocene until now, with the anthropogenic influences clearly affecting and probably blurring patterns. Pleistocene aDNA samples from before the LGM would help to better resolve this structure, as Marr et al. (2018) presented in their new study, but they have not shown any notable degree of divergence between Late Pleistocene and Holocene samples (sequences not included in this analysis).

LAGOMORPHA

Lepus europaeus (Brown Hare)

A total of 2171 sequences were used in the analysis (Table 4.9). The highest diversity indices were found in Anatolia, British Isles and the Balkans (Table 4.9). The lowest was found in Scandinavia and the Mediterranean islands (except the Greek islands). In agreement with previous studies (Kasapidis et al. 2005; Fickel et al. 2008; Stamatis et al. 2009), the Balkans and Anatolian regions seemed to be particularly important for the genetic variability of the species, and probably contributed as refugia for the species during the LGM explaining the high haplotype and nucleotide diversity values found in both areas. The British Isles high diversity is more complex to explain as most of the samples collected are from an unpublished study (Menzies et al. unpublished) whose sequences were available on Genbank. The previous study (Stamatis et al. 2009) suggested the opposite, with the British Isles representing an area with low diversity, although it is based only in two individuals, so more research need to be done in the region.

Table 4.9 *Lepus europaeus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Alps	113	225	11	0.7555	0.03942
Anatolia	73	225	59	0.9909	0.05004
Apennine	230	225	28	0.7972	0.03323
Balkans	171	225	55	0.9546	0.02858
Central Europe	900	225	37	0.5985	0.01285
Corsica	16	225	5	0.5333	0.03128
Crete	12	225	3	0.3182	0.00677
Cyprus	6	225	1	-	-
Eastern Europe	14	225	10	0.9451	0.03646
Greek Islands	17	225	9	0.9191	0.0471
Iberia	220	225	20	0.8149	0.04743
Scandinavia	375	225	5	0.2958	0.00594
UK	13	225	12	0.9872	0.04136
Western Europe	11	225	9	0.9636	0.01721
Total	2177	225	247	0.7945	0.03058

The phylogenetic tree (Figure 4.17) resolved five main clades that corresponded with previous results (Stamatis et al. 2009). Clade SEE (south-eastern European type) is mostly related with samples from the Balkans. Clade M is related with the possible existence of the subspecies *L.e. meridiei* in Italy, but the differences found here and also with microsatellite data (Canu et al. 2013), do not support the subspecies level of this population. Clade EuH(A) (European type haplogroup, subgroup A) is the main lineage that encompassed haplotypes from various regions of central/western Europe and the British Isles.

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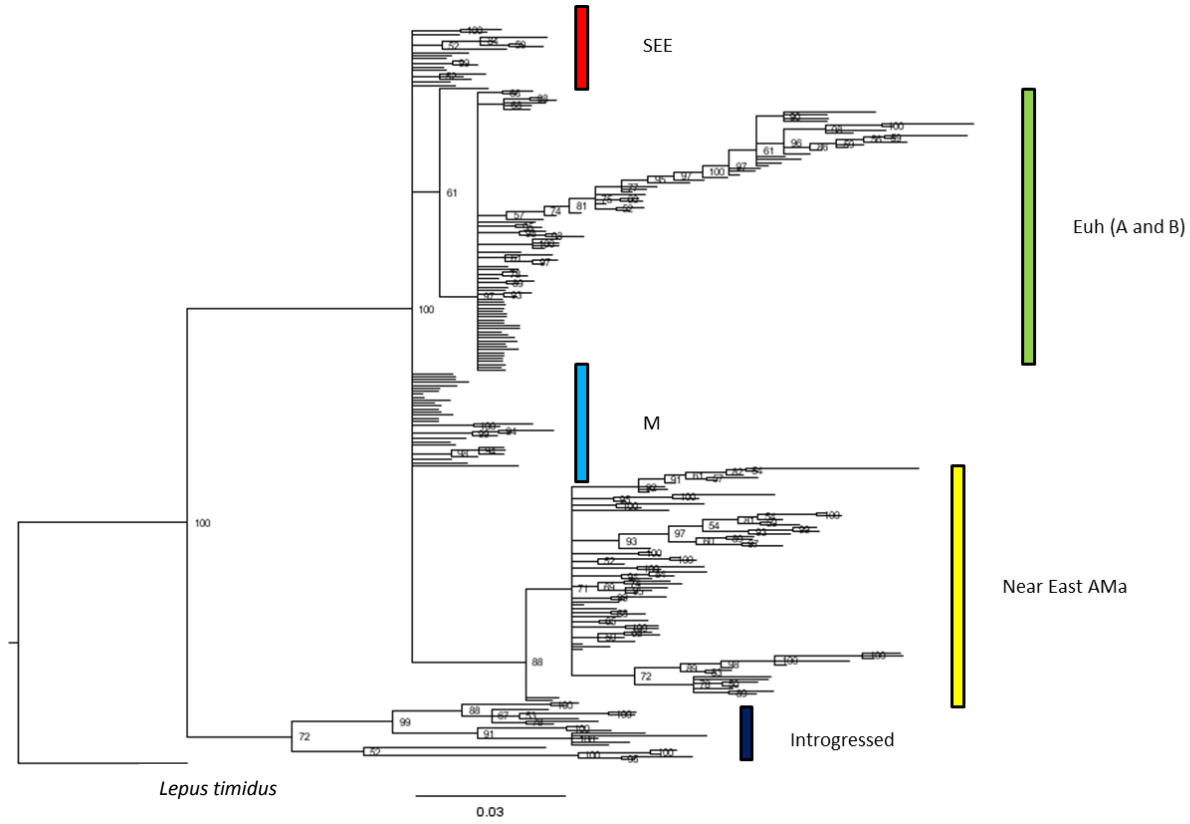

Figure 4.17 *Lepus europaeus* D-loop Bayesian phylogenetic tree with the main clades identified. Clade SEE (south-eastern European type), EuH (European type haplogroup), AMa (Anatolian/Middle Eastern type haplogroup), Clade M (*L.e. meridiei).*

The Median-Joining network has confirmed the distribution of the clades (Figure 4.18). Clade EuH is particularly interesting as two main haplotypes comprised most of the samples and they are shared by different regions but predominantly from Scandinavia and Central Europe. This could reflect the existence of two different refugia for this clade, but the location of them is indeterminate, as the wider geographical area where this clade is present complicates the identification.

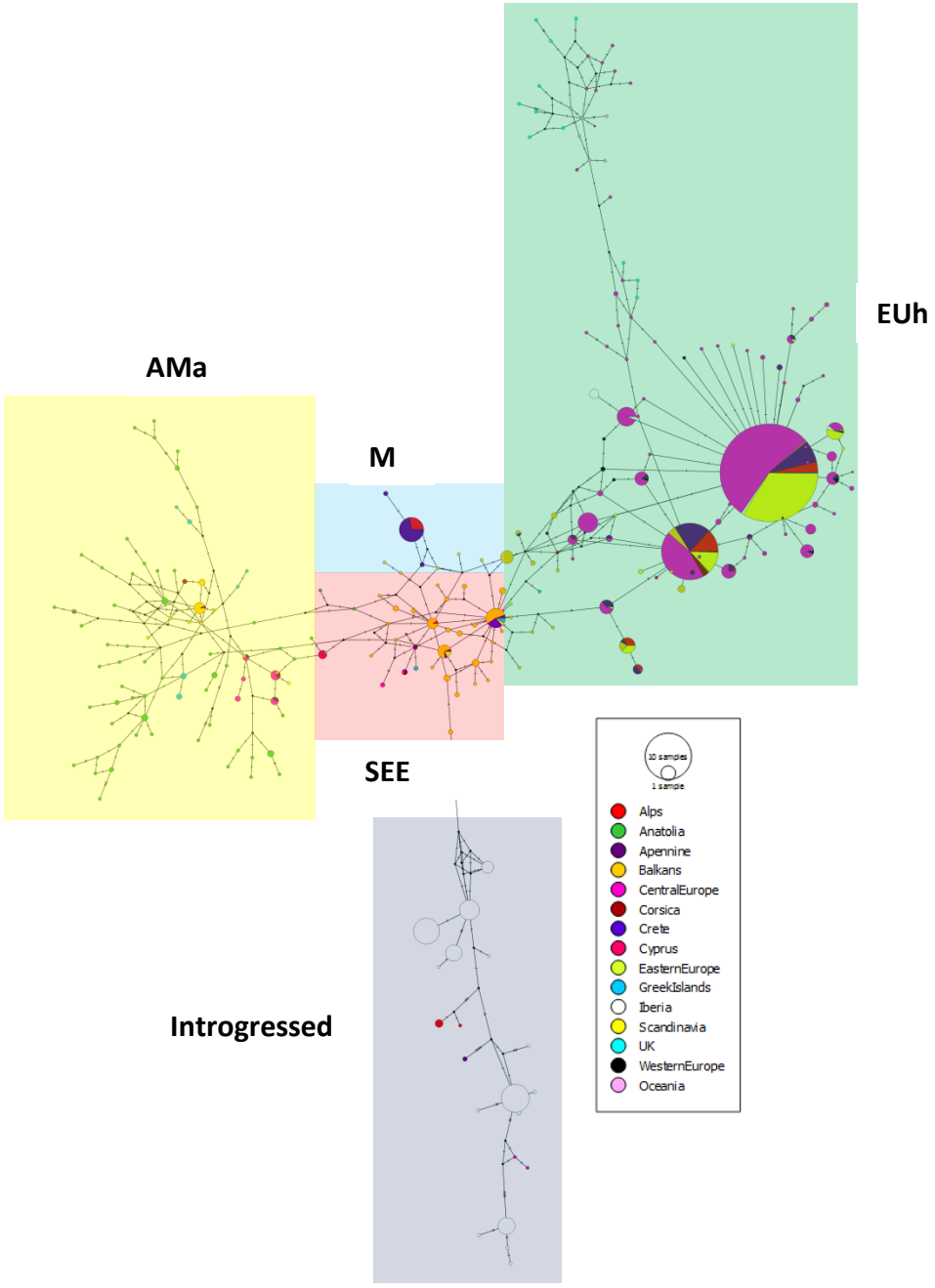

Figure 4.18 Median-Joining network of all the D-loop sequences available for *Lepus europaeus*.

It seems plausible from these results that the central European populations derived from a Balkan (probably the northern part) refugium or refugia. This has been previously suggested in Djan et al. (2017) as a postglacial expansion. Furthermore, the shared haplotypes found in Scandinavia and Central Europe, as well as the low diversity found in this areas make this route likely as a postglacial expansion. However, the role of other possible refugial areas needs to be explored in more detail probably through aDNA if possible.

Lepus timidus (Mountain Hare)

A total of 454 sequences were collected for the analysis (Table 4.10). The genetic diversity of the species is very high across regions with the lowest being found for the population in western Europe. This high diversity might be explained due to the occupation of vast areas of the central European plain during glacial periods by arctic–boreal species (Hewitt 2004).

Table 4.10 *Lepus timidus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	Hd	π
Apennine	76	266	20	0.9165	0.04581
Central Europe	115	266	20	0.8918	0.01474
Eastern Europe	98	266	78	0.9952	0.05817
Western Europe	7	266	4	0.8095	0.04123
Scandinavia	64	266	37	0.9335	0.04786
UK	44	266	19	0.9123	0.04197
Asia	25	266	17	0.9667	0.06389
Non geographical area	25	266	-	-	-
Total	454	266	200	0.987	0.05864

The phylogenetic tree (Figure 4.19) showed well-resolved branches that have been suggested to indicate the subspecies level of some of these populations (Hamill et al. 2006). However, for example, the previously suggested subspecies, like *L. t. hibernicus* in Ireland does not represent a deep lineage that supported this level. The Alpine population, in contrast, represented a well-supported clade that is more in agreement with the possible subspecies level of this population, *L. t. varronis*.

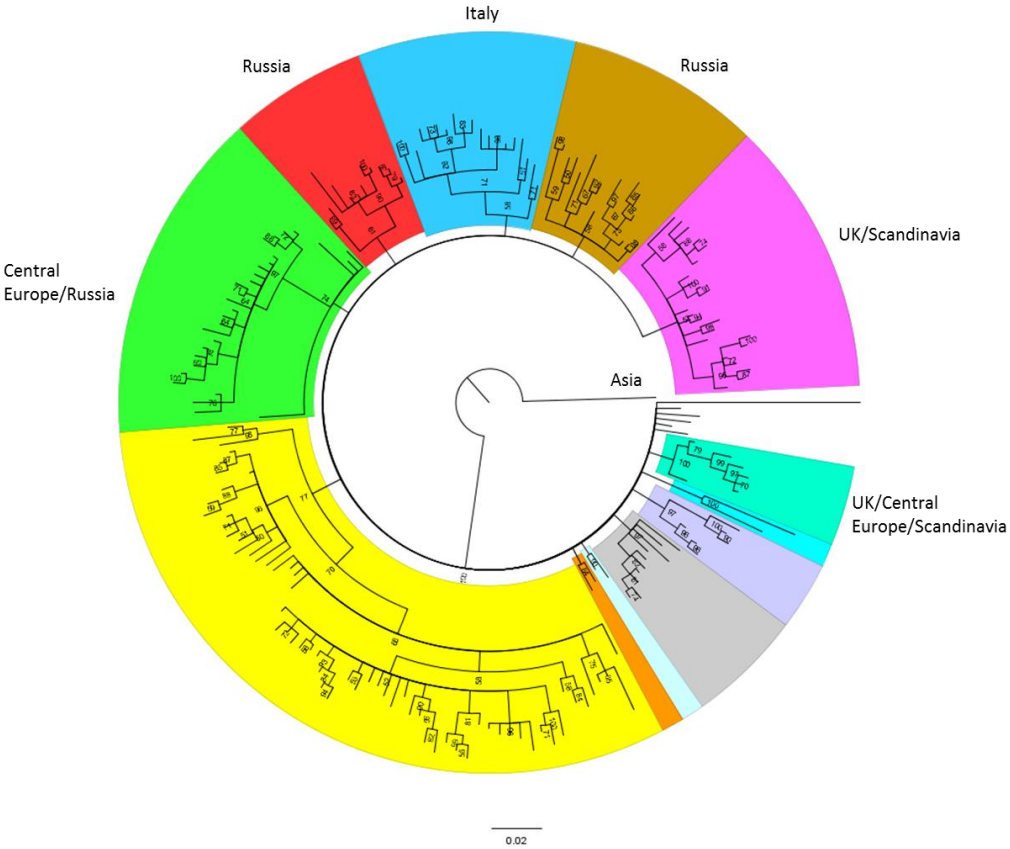

Figure 4.19 *Lepus timidus* D-loop Bayesian phylogenetic tree with the main clades identified.

The species seems to be characterised by high variability even if some of the population seemed to be in isolation. The subspecies level may need further exploration to clarify the status, as some of the populations are divergent enough to be under the subspecies consideration as previously suggested (Hamill et al. 2006). The Median-joining network (Figure 4.20) showed high variability regarding the high number of haplotypes identified that are clustering based on geographical areas. To infer any phylogeographic pattern for this species is challenging but this high diversity could reflect multiple refugia across Europe (Waltari and Cook 2005) or none. The high nucleotide diversity found (Table 4.10) probably indicates that the species did not undergo population decrease in recent times. This might be related with the persistence of suitable habitats for many populations during glacial cycles (Waltari and Cook 2005).

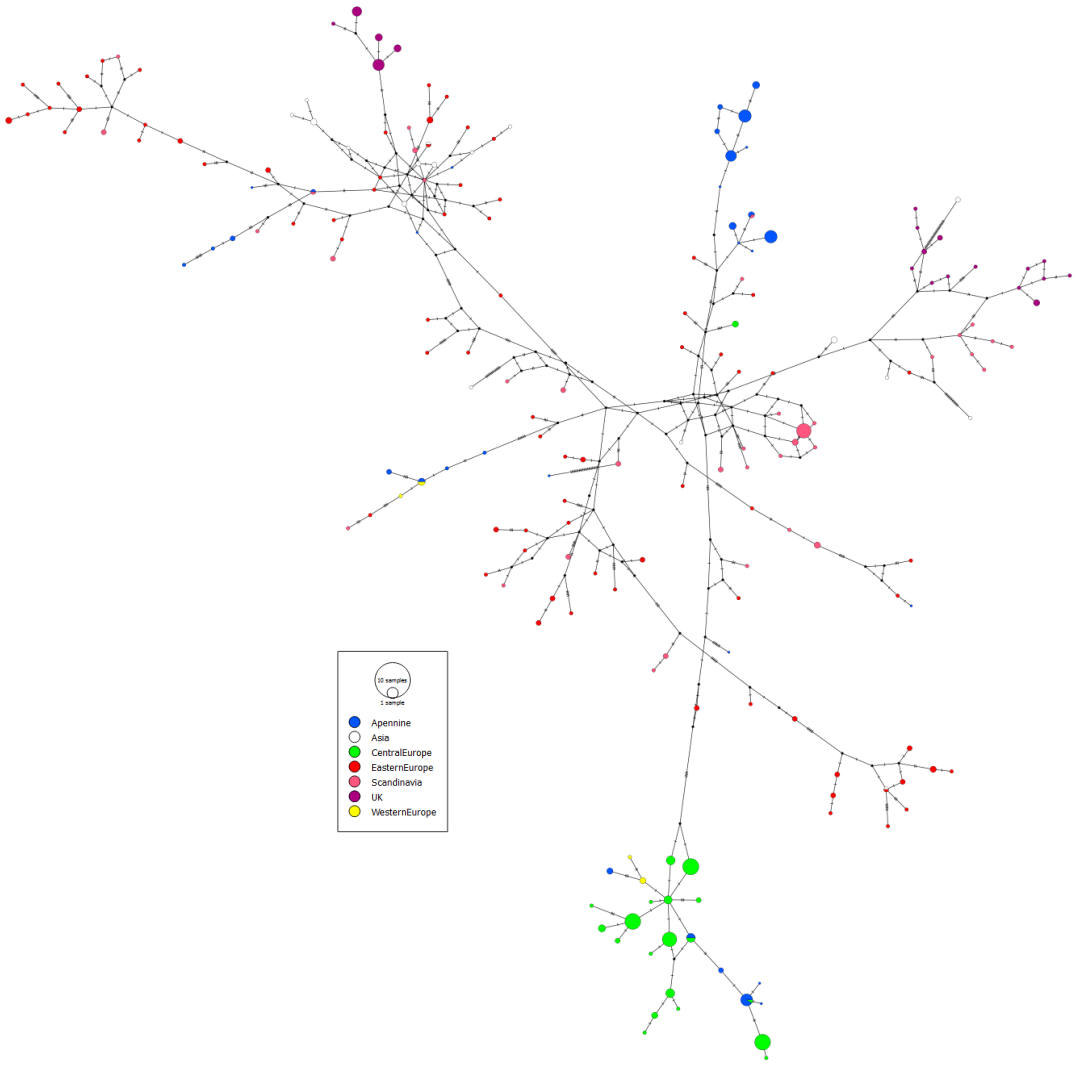

Figure 4.20 Median-Joining network of all the D-loop sequences available for *Lepus timidus*.

The high diversity displayed by the species can be consistent with the different species and subspecies that have been described in the literature. However, the taxonomy needs to be revised as there is not fully agreement on the designation at species and subspecies level.

L. timidus appears to have occupied different geographical areas across their European distribution with a demographic history that is not characterised by population extinctions. These results corroborate the hypothesis that diversification of high-latitude organisms was affected by Late Pleistocene climate fluctuations (Weir and Schluter 2004; Waltari and Cook 2005). Unfortunately, the ancient DNA sequences from Smith et al. (2017) were not added to this analysis due to availability. However, their results suggest that there is no apparent decrease in the genetic variation of the species after the Pleistocene/Holocene transition (Smith et al. 2017), which is in accordance with the results presented here.

EULIPOTYPHLA

Erinaceus europaeus (Western European Hedgehog)

The analysis included 387 individuals and 56 haplotypes have been reported (Table 4.11). Through the phylogenetic analysis, three main clades are identified with the main branches being well supported (Figure 4.21).

Table 4.11 *Erinaceus europaeus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	N	BP	Haplotypes	*h*d	π
Iberia	16	405	3	0.658	0.00307
Apennine	29	405	6	0.768	0.01496
Western Europe	76	405	16	0.913	0.02395
UK	41	405	2	0.18	0.00089
Scandinavia	20	405	4	0.595	0.00194
Central Europe	196	405	24	0.896	0.01084
Eastern Europe	9	405	6	0.833	0.00578
Total	387	405	56	0.947	0.02295

The haplotype diversity revealed that the highest variability is not in areas that have been considered as refugia such as the Apennine Peninsula and Iberia. Diversity does not appear to be lower in northern areas and the highest is reported in western Europe, 0.913 (Table 4.11). The areas identified as southern refugia for *E. europaeus* showed lower values and fewer numbers of haplotypes. This might suggest the possibility of northern refugia for this species (Stewart and Lister 2001) or a secondary contact between the main clades E1 and E2 in Western/Central Europe. Bhagwat and Willis (2008) also suggested that the southern refugia pattern for this species did not match with their analysis and the biogeographical traits of this species could suggest persistence also in northern refugia. The fact that this species presents low mobility might suggest that the phylogeographical pattern described might be shaped by northern refugia.

The phylogenetic tree revealed the three main clades that have been already reported (Seddon et al. 2001; Bolfíková and Hulva 2012). The E3 clade seemed to be more related with the eastern clade (E1) which is the main clade present in the Apennine Peninsula.

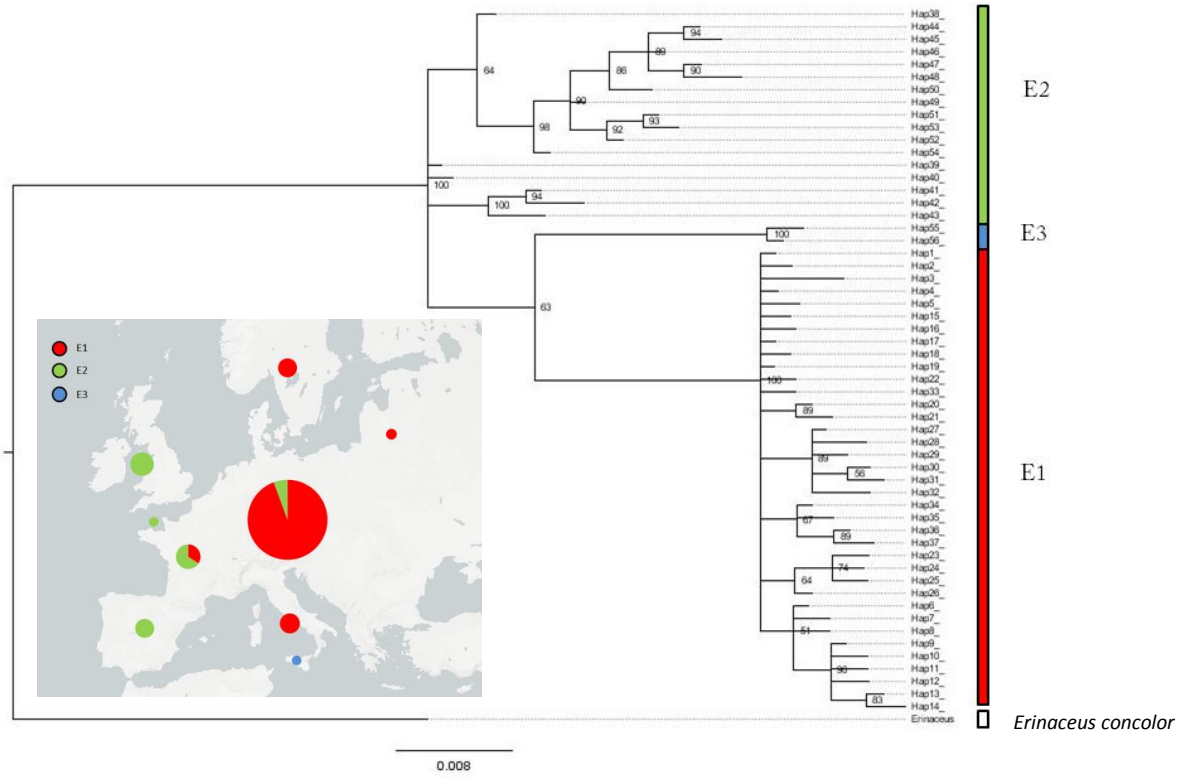

Figure 4.21 *Erinaceus europaeus* D-loop Bayesian phylogenetic tree and map of the distribution of the main clades identified.

To interpret these results, a geographical network has been made (Figure 4.22). Looking at the haplotypes reported in this analysis and separating them by geographical areas a better understanding of the data can be achieved. E2 is the main clade in western Europe, so an analysis of this area has been done. Iberia has been suggested as the refugium for this clade during the LGM, but with the present network, the major haplotypes are in western countries sharing a main haplotype with the individuals in the British Isles and without sharing any haplotype with Iberia. However, the Iberian haplotypes are only a few mutations steps from the main cluster of haplotypes found in the West. This might suggest that Iberia has contributed extensively to the post-glacial colonisation of northern areas or that those areas in the west (France and Belgium) were the core populations for refugia and is where Iberia was colonised from.

Regarding the haplotypes reported in Iberia and the structure of the network (Figure 4.22), the possibility of northern refugia cannot be excluded. The same analysis for central Europe, clade E1, showed a similar pattern. Clade E3 is restricted to Sicily and is the one that appeared to be separated from but close to clade E1.

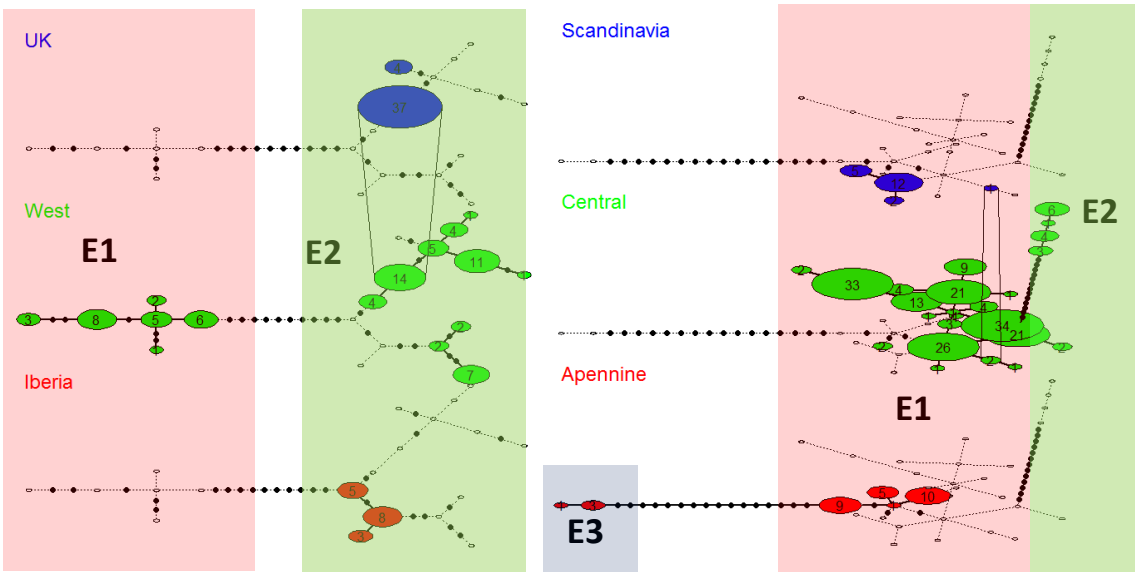

Figure 4.22 *Erinaceus europaeus* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

This analysis suggests that the evidence of southern refugia from the mtDNA perspective for *E. europeaus* is not clear, especially form the diversity perspective, and the pattern might suggest northern refugia due to the genetic diversity observed and the structure of the network analysis.

Erinaceus concolor (Hedgehog)

A total of 62 sequences have been analysed and comprise 20 different haplotypes. The number of individuals per area is not high but may give an idea of the genetic diversity identified in the Near East (Turkey, Lebanon and Israel) which is the area with higher haplotype and nucleotide diversity (Table 4.12).

Table 4.12 *Erinaceus concolor* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	N	BP	Haplotypes	*h*d	π
Apennine	4	388	1	-	-
Balkans	5	388	3	0.7	0.00364
Central Europe	14	388	4	0.78	0.0044
East Europe	16	388	6	0.733	0.0081
Near East	17	388	8	0.882	0.01963
Causcasus	6	388	2	0.533	0.00138
Total	62	388	20	0.926	0.02014

The phylogenetic tree showed a well-supported clade that differentiates the Near East from the rest indicating the differentiation between populations from Europe and those from the Near East as has been previously reported (Krystufek 2002). Some clades corresponded with a geographical area but the yellow clade, in Figure 4.23, may correspond with a hybrid zone making a geographical resolution more complicated.

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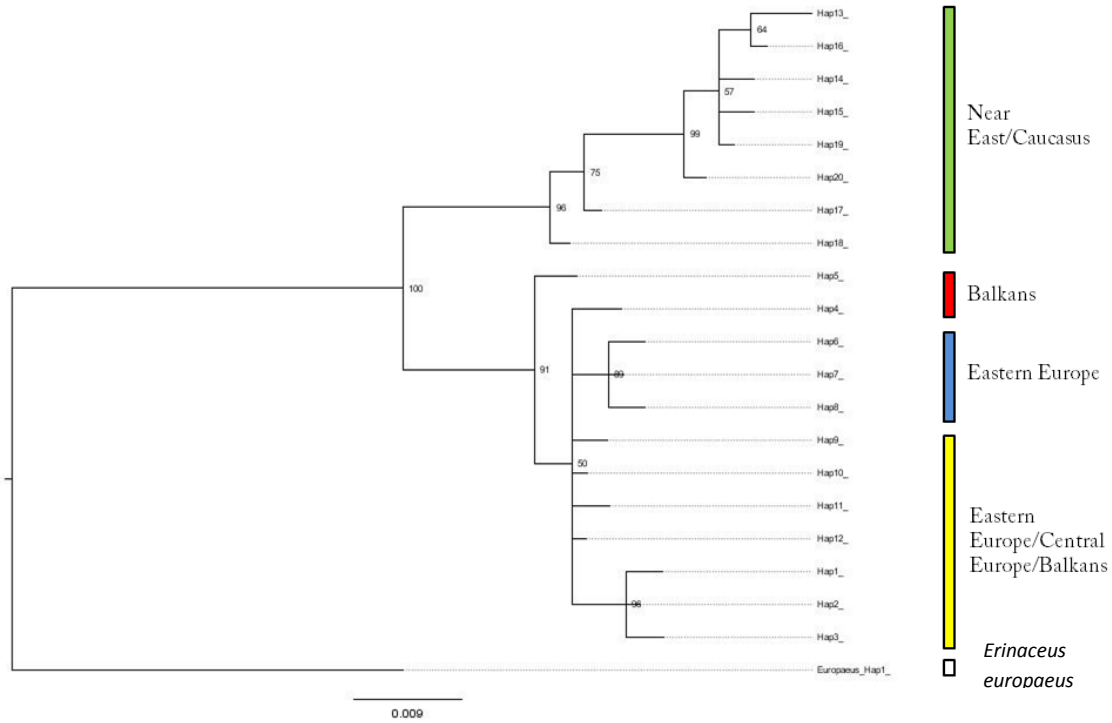


Figure 4.23 *Erinaceus concolor* D-loop Bayesian phylogenetic tree with the main clades identified.

Sorex minutus (Pygmy shrew)

A total of 280 sequences were included in the analysis of *Sorex minutus* (Table 4.13). Unfortunately, some of the locations included displayed low samples sizes, making it unlikely to find a general phylogeographic pattern for the species. The well-studied British Isles has contributed to the knowledge of the colonisation of this area for the species (McDevitt et al. 2009), but not many other areas have been explored in similar numbers.

Table 4.13 *Sorex minutus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Anatolia	2	290	2	-	-
Apennine	8	290	8	1	0.039
Balkans	1	290	1	-	-
CentralEurope	14	290	12	0.978	0.03712
EasternEurope	5	290	4	0.9	0.02226
WesternEurope	23	290	13	0.9407	0.0423
Iberia	5	290	4	0.9	0.05035
Scandinavia	9	290	8	0.9722	0.02969
Siberia	1	290	1	-	-
UK	81	290	57	0.9895	0.03957
Ireland	131	290	28	0.8217	0.013
Total	280	290	138	0.9598	0.02785

From the phylogenetic tree, two main clades can be inferred (Figure 4.24). No geographical pattern seems to be the cause of this differentiation as both clades have broad distributions across Europe. However, one clade seems to be more related to western regions as previously suggested (McDevitt et al. 2010). Some subclades are also indicated in the phylogenetic tree, but the geographical variability does not make an easy resolution of them. The distinctiveness of Iberia and Italy make them unlikely to have contributed to the postglacial colonisation. However, this is not the case for the Balkans and Slovakian samples. As previously suggested, this region may have represented the unique southern refugia for the species as predicted by species distribution modelling (Vega et al. 2010). Further sampling across southern Europe could contribute to understanding the role of possible refugia there and where the Western clade populations have been in refugia. Some areas in southern France have been suggested (McDevitt et al. 2010) but this cannot be reinforced by this analysis.

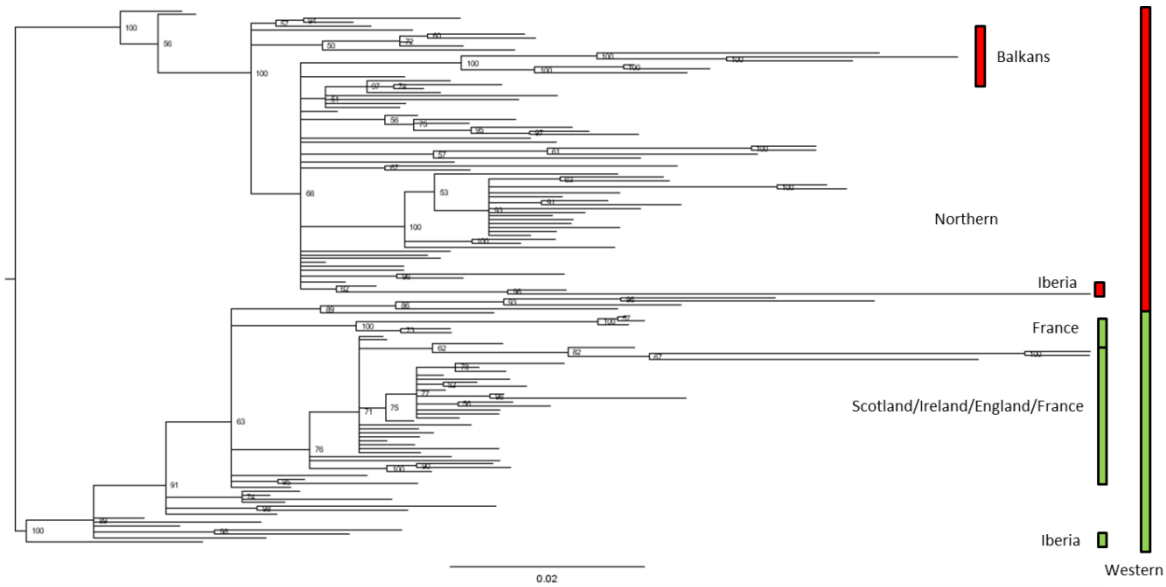


Figure 4.24 *Sorex minutus* D-loop Bayesian phylogenetic tree with the main clades identified.

In the network analysis (Figure 4.25) the two main star-shaped haplotypes found for Irish samples agree with a more plausible recent colonisation during the Holocene transported there by humans (Mascheretti et al. 2003; McDevitt et al. 2009; McDevitt et al. 2010). The French population that has been indicated as a possible refugium for the Western clade does not have a central position in the network that will allow confirmation of this. However, more sampling is needed in the area to be able to solve this question. Although as the British and Irish samples seem unlikely to have contributed to the main variability of this clade, even this option could not be discarded. The Eastern clade is much more complex based on the network shape making any identification of phylogeographic patterns difficult, as many of the haplotypes are uniques for certain localities.

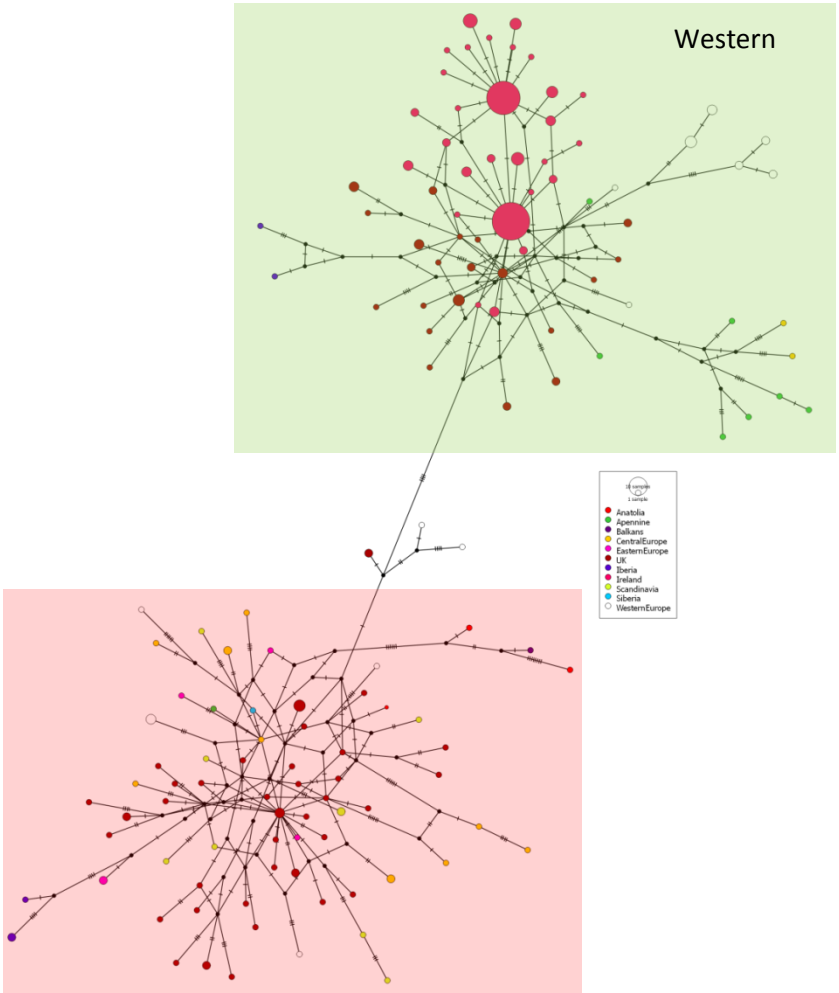


Figure 4.25 Median-Joining network of all the D-loop sequences available for *Sorex minutus*.

Ancient DNA will contribute to insight and confirm the suggested refugial areas and the different routes of colonisations, as the current diversity of the species seems complex enough to be problematic to infer them in more detail.

CARNIVORES

Canis lupus

Two different alignments were constructed in order to include the highest number of ancient DNA sequences as possible. For the longest alignment (235 bp), 1627 sequences were used (Table 4.14). For the shortest (53bp), 1723 sequences were taken into consideration.

Table 4.14 *Canis lupus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Apennine	262	235	7	0.0965	0.00177
Balkans	211	235	12	0.8286	0.02139
Caucasus	16	235	5	0.775	0.02298
Central Europe	39	235	9	0.7018	0.01788
Eastern Europe	770	235	21	0.8112	0.0153
Eastern Russia	11	235	1	-	-
Greenland	6	235	1	-	-
Iberia	81	235	4	0.5194	0.00552
Near East	9	235	5	0.8611	0.01345
Scandinavia	101	235	7	0.5798	0.01303
Siberia	10	235	7	0.9111	0.01792
Urals	20	235	4	0.5	0.00935
Western Europe	91	235	4	0.107	0.00206
Total	1627	235	45	0.8761	0.02213

The genetic diversity values for the species are variable with the highest diversity found in Siberia and the Near East and the lowest in the Apennine Peninsula and Western Europe (Table 4.14). The wide range of diversity probably reflects different demographic histories of the population. However, the high haplotype diversity (0.876) and relatively low nucleotide diversity (0.022) of the species might be consistent with a more recent demographic expansion.

The uniqueness of the Italian wolf is not well identified in the phylogenetic analysis (Figure 4.26). The main haplotype in Italy, w14, (Randi et al. 2000) is also found in the Balkans. However, this is due to a reduction on the fragment length to 235 bp instead of the 543 bp fragment from the original paper. This is a definite caveat of reducing the length of the fragment analysed and has to be considered carefully.

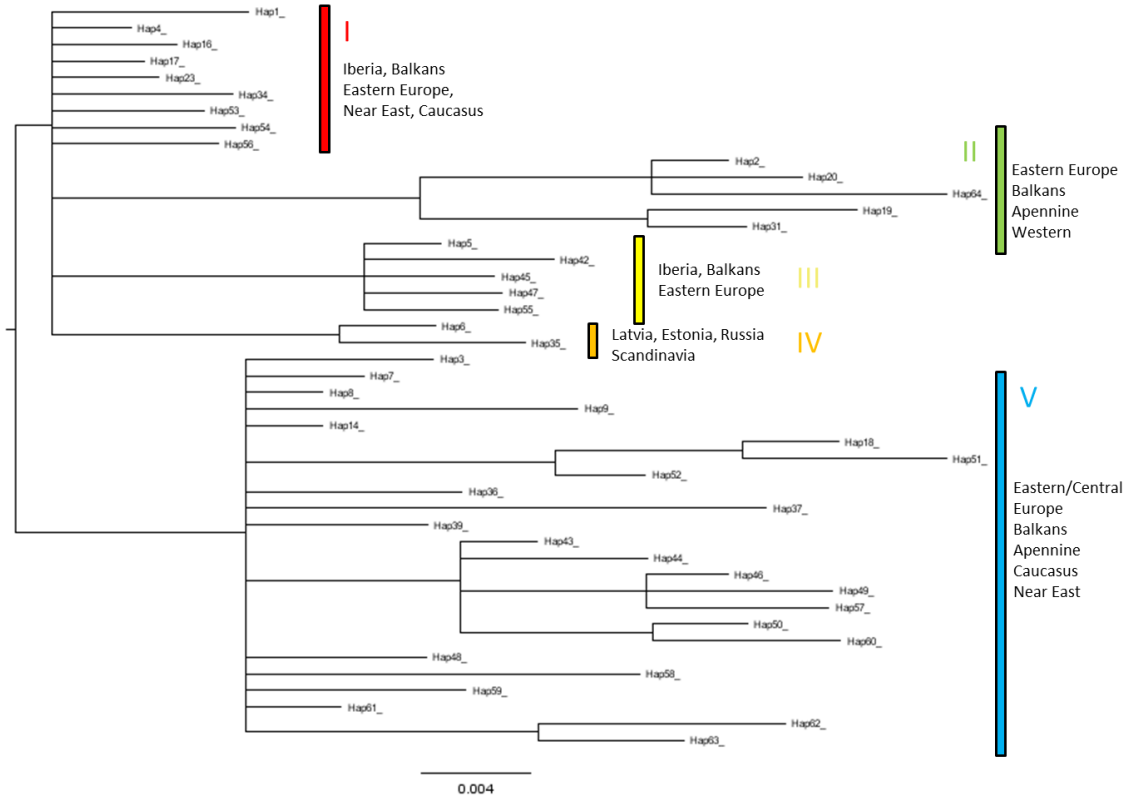


Figure 4.26 *Canis lupus* D-loop Bayesian phylogenetic tree with the main clades identified.

No obvious strong associations between haplogroups and their geographic locations were found (Figure 4.27). Clade I is a good example of this situation. It is present in Iberia in high frequencies, but its presence in eastern Europe complicates the identification of this clade as a possible lineage related with an Iberian refugium population. Clade V is widely distributed and is present in all the regions analysed, except Iberia. In order to shed more light on the genetic singularity and importance of these southern populations as possible refugia, additional aDNA sequences would be needed. With the present analysis, no strong phylogeographic structure is found for the species in agreement with previous important studies on the species (Randi et al. 2000; Pilot et al. 2010; Ersmark et al. 2016)

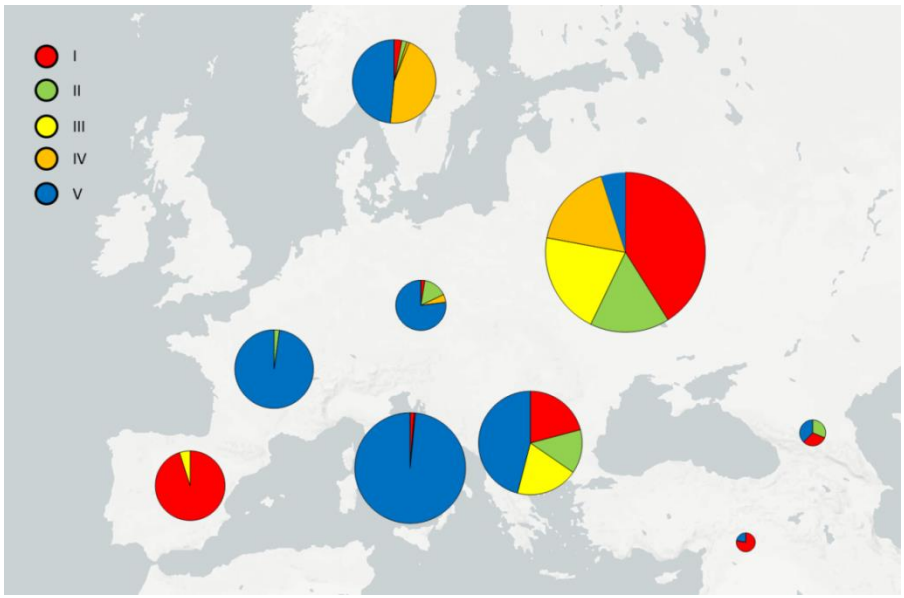
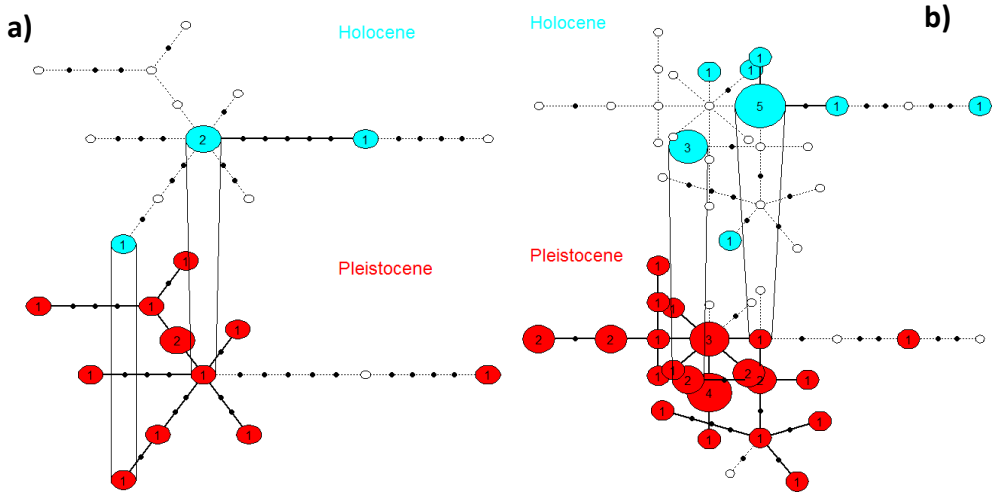


Figure 4.27 Map of the distribution of the main clades identified in the phylogenetic tree for *Canis lupus*.

The temporal networks produced for the two alignments showed certain continuity between Pleistocene and Holocene samples but with a significant reduction in haplotyped diversity (Figure 4.28). However, the previously described division of both contemporary and ancient wolves into two distinct clades is not found (Leonard et al. 2007; Pilot et al. 2010). However, all the Pleistocene and Holocene specimens clustered in clade V, indicating a certain level of division even if modern samples also belong to this clade, but in fewer frequencies (Figure 4.28c). Although the species had an extensive distribution in northern Eurasia during the late Pleistocene (Hofreiter 2007), expansion from several refugia and replacement appear to have played an important role in structuring wolf phylogeography in Europe.



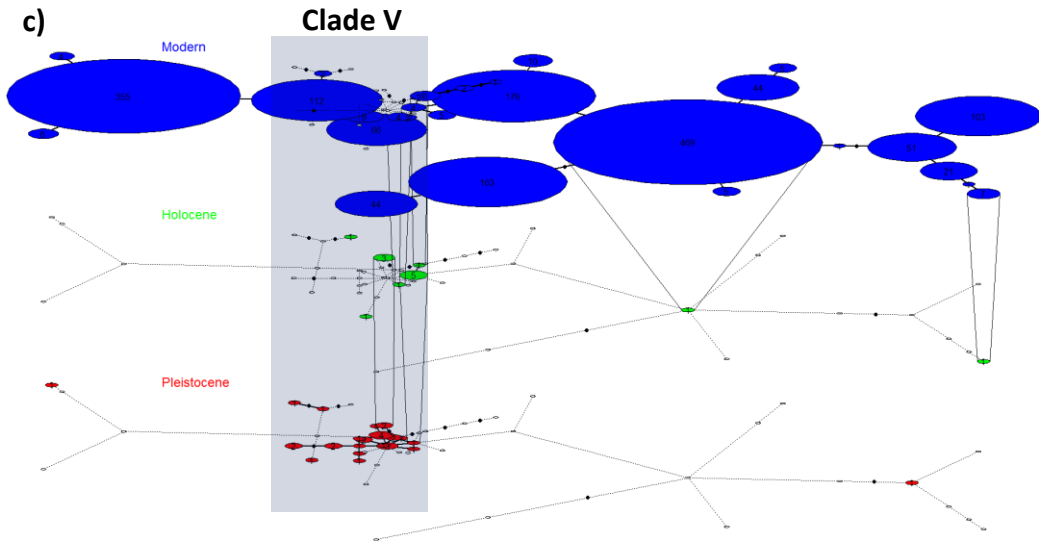


Figure 4.28 a) *Canis lupus* D-loop temporal network (using the 235 bp alignment) showing the presence of the different haplotypes in the two periods analysed. Each layer represents a different temporal period; b) *Canis lupus* D-loop temporal network (using the 53 bp alignment) showing the presence of the different haplotypes in the two periods analysed; c) *Canis lupus* D-loop temporal network (using the 235 bp alignment) showing the presence of the different haplotypes in the three periods analysed. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

Vulpes lagopus (Arctic Fox)

A total of 351 sequences were analysed for *Vulpes lagopus* (Table 4.15). The highest diversity values were found in the European Pleistocene samples and modern Alaskan population. The diversity of the species is relatively high in most of the areas analysed, except for some populations in islands and remote regions such as Iceland and Svalbard.

Table 4.15 *Vulpes lagopus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	Hd	π
Alaska	18	278	8	0.889	0.01238
Artic	81	278	2	0.458	0.00167
Bering	92	278	7	0.542	0.00462
Canadian Archipielago	18	278	9	0.882	0.00929
Svalbard	11	278	2	0.545	0.00999
Siberia	27	278	8	0.803	0.01102
Iceland	38	278	4	0.329	0.00335
Greenland	24	278	9	0.873	0.01314
Scandinavia	18	278	4	0.699	0.01149
Fennoscandia	16	278	3	0.492	0.00918
Europe (Pleistocene)	7	278	5	0.929	0.00939
Total	350	278	35	0.902	0.01758

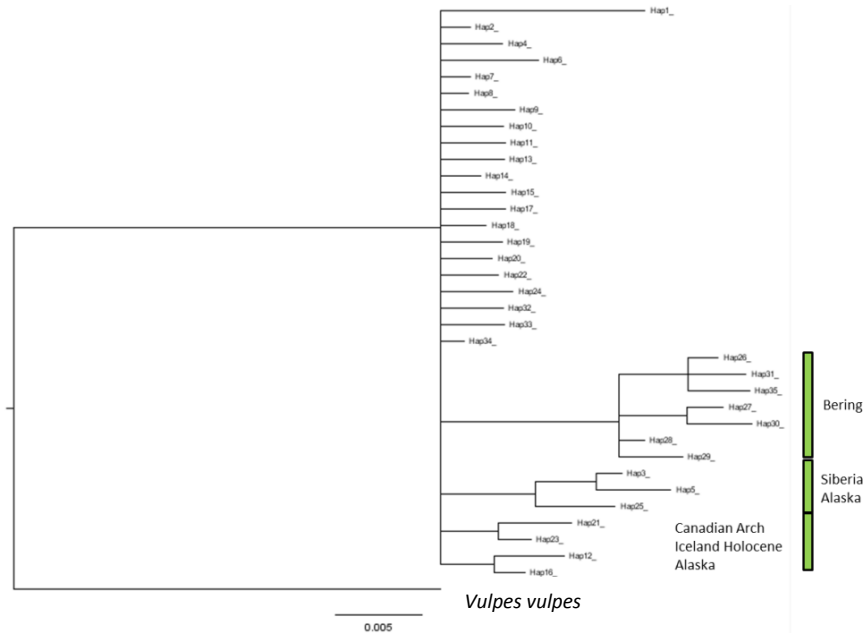


Figure 4.29 *Vulpes lagopus* D-loop Bayesian phylogenetic tree with the main clades identified.

In the phylogenetic tree only the samples from Bering, Siberia, Alaska and Holocene samples from Iceland formed small clades (Figure 4.29). Two haplotypes found from samples from central/western Europe, during the Late Pleistocene, are shared with some modern samples (Figure 4.30), unexpectedly and not in agreement with the analysis from Dalén et al. (2007). This is due to a reduction of 14 bp from Dalén et al. (2007) study, but is something that needs to be further explored as these closer haplotypes could represent a degree of continuity between Late Pleistocene Europe and current Siberian/Alaskan populations.

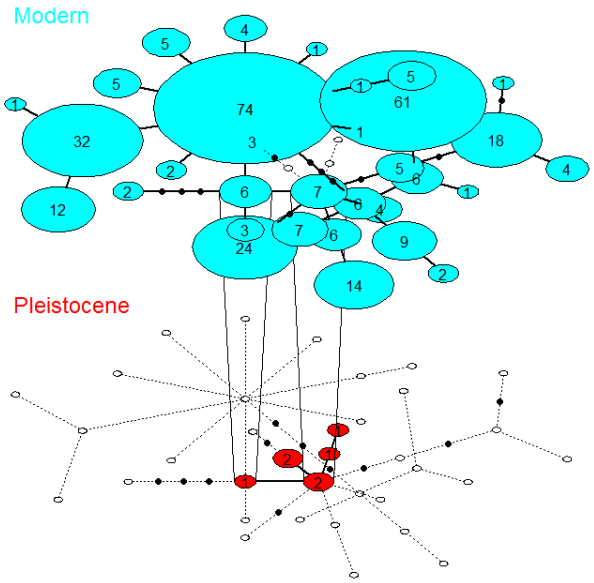


Figure 4.30 *Vulpes lagopus* D-loop sequences temporal network showing the presence of the different haplotypes in the Late Pleistocene and modern time. Each layer represents a different temporal period.

Vulpes vulpes (Red Fox)

A total of 983 sequences were collected for 11 different regions (Table 4.16). The diversity of the species is relatively high in most of the areas sampled. The high diversity found for the red fox is in agreement with a constant occupation of the European continent through different temporal periods and even during the LGM. The temporal network (Figure 4.31a) showed a continuity between the Pleistocene and the Holocene samples where the loss of diversity that has characterised other mammal species (Lorenzen et al. 2011) have not occurred with strength for *V. vulpes*. Except for Scandinavia, the high haplotype and nucleotide diversity found for the species across all the geographical areas analysed may be related to a constant occupation of the territory and stable population over the last 40,000 years (Teacher et al. 2011).

Table 4.16 *Vulpes vulpes* D-loop fragment sequences retrieved and analysed by geographical (a) areas and time periods (b). n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

a)

Region	n	BP	Haplotypes	*h*d	π
Apennine	21	219	5	0.7524	0.00355
Asia	10	219	7	0.8667	0.02558
Balkans	367	219	38	0.9253	0.01431
Central Europe	119	219	34	0.897	0.01255
Eastern Europe	24	219	15	0.9565	0.01604
Iberia	39	219	10	0.8812	0.01372
Near East	5	219	5	1	0.01315
North Africa	11	219	9	0.9636	0.03312
Scandinavia	70	219	11	0.5048	0.00773
UK	231	219	38	0.7816	0.01382
Western Europe	86	219	30	0.9209	0.0163
Total	983	219	146	0.9596	0.01398

b)

Time	n	BP	Haplotypes	*h*d	π
Pleistocene	14	219	14	1	0.01963
Holocene	15	219	14	0.9905	0.0186
Historical/Modern	967	219	126	0.9575	0.0139
Total	996	219	146	0.9596	0.01398

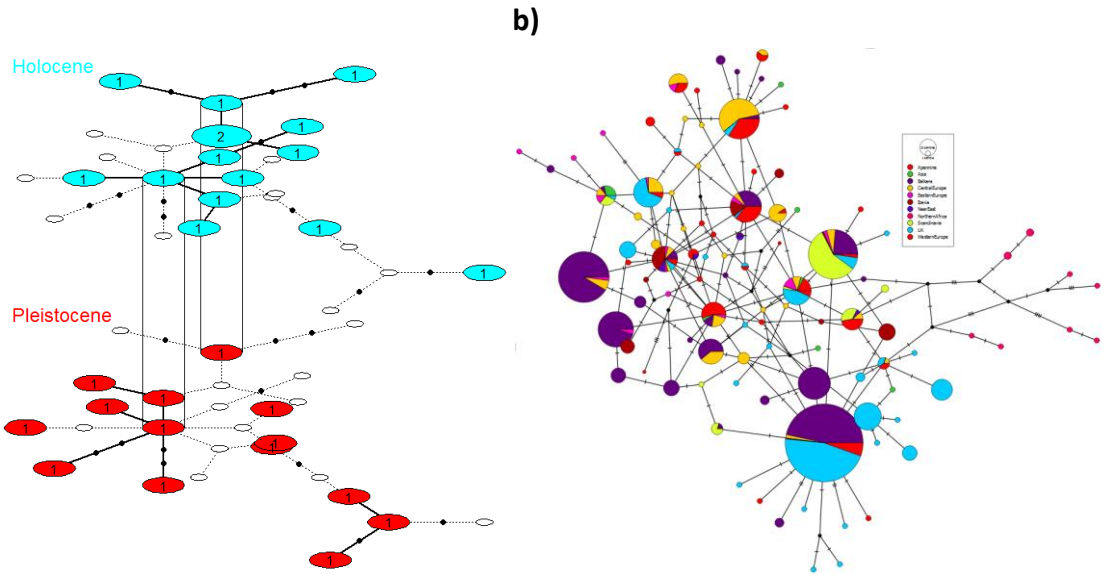


Figure 4.31 a) *Vulpes vulpes* D-loop temporal network showing the presence of the different haplotypes in the two periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent. b) Median-Joining network of all the D-loop sequences available for *Vulpes vulpes*.

Unfortunately, the phylogenetic tree does not solve any of the big phylogeographical questions about the red fox. Only the samples from northern Africa seem to be significantly different from the rest of the Eurasian samples (Figure 4.32). This uncertainty in Eurasia has already been mentioned in the literature on several occasions (Teacher et al. 2011; Edwards et al. 2012).

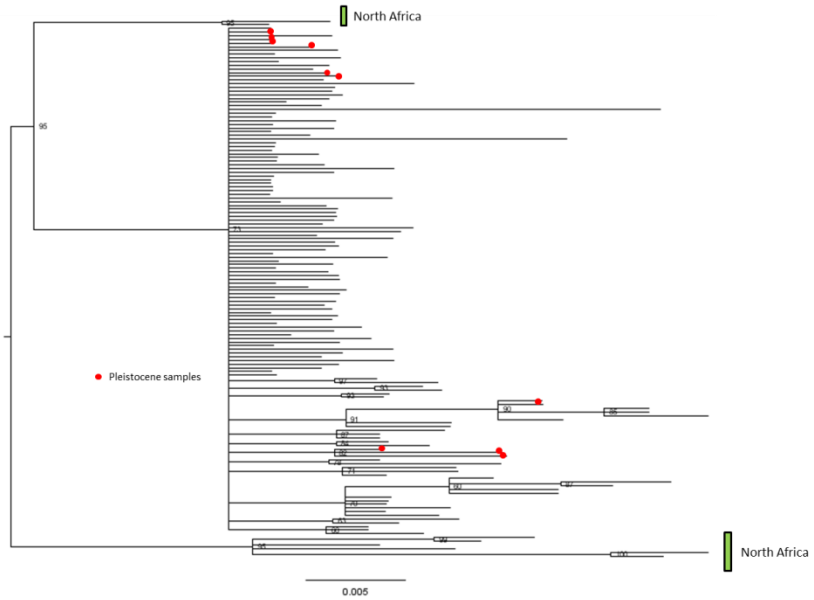


Figure 4.32 *Vulpes vulpes* D-loop Bayesian phylogenetic tree with the main clades identified.

The Median-joining network produced for the 983 sequences collected did not show much more information than the one obtained from the phylogenetic tree. In the network (Figure

4.31b), apart from the mentioned Northern African samples, no other big clusters of sequences are shown. The British samples that comprised a different group from the main European populations (Edwards et al. 2012) did not seem to be much different from other European areas, such as the Balkans, where many haplotypes are shared between these two areas. This is contradictory to the previous results observed (Teacher et al. 2011; Edwards et al. 2012) but it can be explained, again, by the sequence length caveat for the modern samples included. Although, this result may reflect that the lack of phylogeographic structure for the species extended to the British samples, as Pleistocene samples showed, with close haplotype sharing between Britain and Central Europe (Teacher et al. 2011).

The short fragment used for this species (219 bp) does not seem enough to capture the genetic structure of the species and an increment on the length could contribute to improving the resolution of the shallow structure found here. However, species that are considered ecologically adaptable have been suggested to be able to exhibit high diversity and lack of population structure (as found here) related with a constant occupation of Europe (Edwards et al. 2012). The great mobility of the species and the high dispersal abilities have led to the lack of observable phylogeographic pattern in the red fox, probably reinforced by the adaptability of the species to a wide habitat range (Teacher et al. 2011). Red foxes do not seem to fit any of the classic models of postglacial colonisation which makes difficult to identify their former refugial areas (if they were any), indicating that the pattern observed is different.

Gulo gulo (Wolverine)

The sampling across Eurasia is restricted to Scandinavia and Russia so for this reason, Scandinavia has been divided by country. Sweden and Russia have similar genetic diversity (Table 4.17), but in Norway, all the 108 individuals analysed comprise the same haplotype. This represents an extremely low diverse population and needs also to be considered for conservational purposes.

Table 4.17 *Gulo gulo* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Norway	108	317	1	-	-
Sweden	63	317	2	0.0625	0.0004
Russia	59	317	7	0.6184	0.00351
Mongolia	7	317	2	0.4762	0.00302
Total	237	317	8	0.4615	0.00551

The haplotype network (Figure 4.33) showed that the European distribution is connected with the eastern Russian population and therefore with the Mongolian populations. They formed a relatively continuous distribution from east to west suggesting movement across the whole Eurasian range, as previously suggested (Walker et al. 2001; Tomasik and Cook 2005; Zigouris et al. 2013).

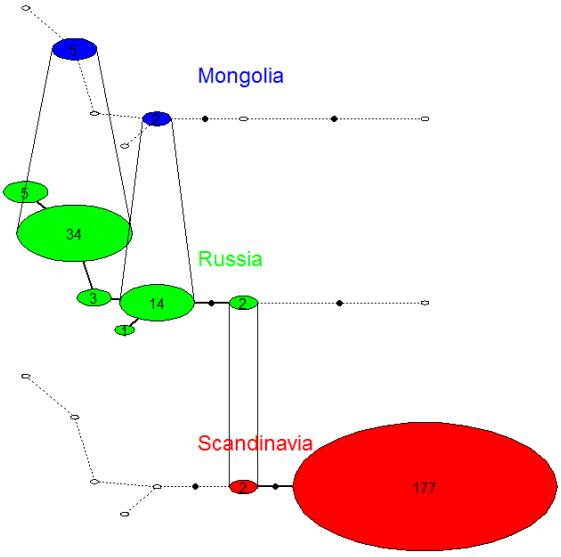


Figure 4.33 *Gulo gulo* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

Mustela erminea (Stoat)

A total of 205 sequences were added to the analysis. Some of the geographical areas have a low sample size, so the phylogeographic pattern inferred is shaped by this caveat and the identification of possible refugia based on diversity is complicated (Table 4.18). However, the highest haplotype diversity is found in eastern Europe while western Europe displayed the highest nucleotide diversity.

Table 4.18 *Mustela erminea* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Apennine	3	502	2	0.6667	0.00402
Asia	7	502	7	1	0.00553
Central Europe	18	502	9	0.8889	0.00383
Eastern Europe	27	502	21	0.963	0.00653
Iberia	1	502	1	-	-
Greenland	1	502	1	-	-
Scandinavia	22	502	6	0.7489	0.00301
UK/Ireland	104	502	21	0.8641	0.00673
Western Europe	19	502	5	0.7661	0.00748
Total	202	502	66	0.9508	0.00792

The phylogenetic tree shows some shallow clades that can be identified with some geographical regions (Figure 4.34). The Irish population seemed to form several distinct clades, as previously suggested, probably representing a natural colonisation of the island possibly at the time of the LGM (Martínková et al. 2007). The small sample sizes for some of the regions do not allow a robust comparison based on genetic diversity. However, the highest diversity that is found in eastern Europe can help to identify where the species may have been in refugia during the LGM contributing, at least partially, to the recolonisation of certain areas of Scandinavia and Central Europe (Figure 4.35a).

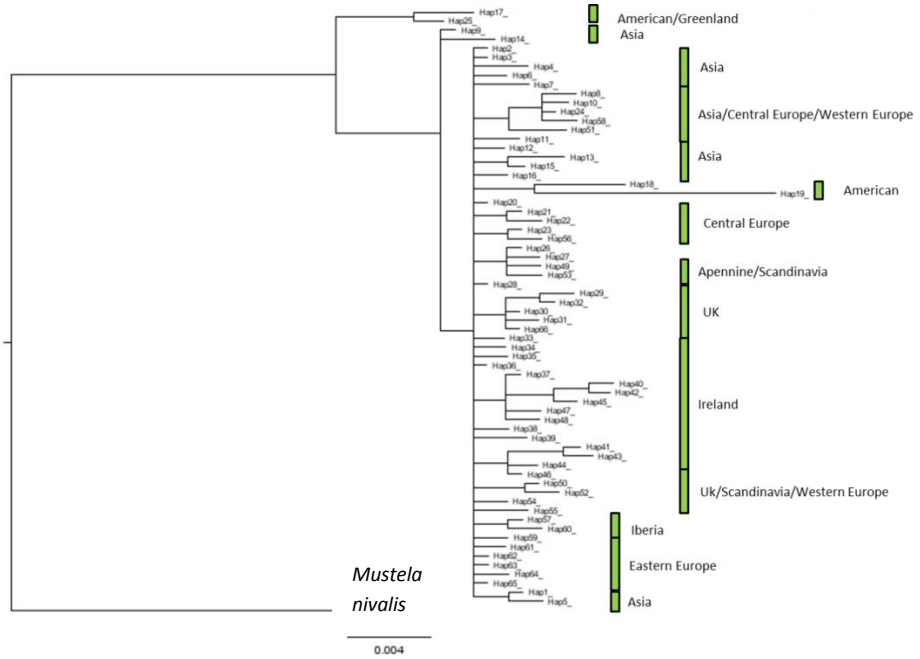


Figure 4.34 *Mustela erminea* D-loop Bayesian phylogenetic tree with the main clades identified.

The continuity found between different areas is consistent with the broad distribution of the species but also reflecting the importance of the east as a possible source of diversity. The high number of haplotypes found in eastern Europe in comparison with the rest of the areas analysed and the presence of some of them, or closely related ones, in central Europe and Scandinavia, makes it possible that the east was a possible reservoir for the genetic variability of the species (Figure 4.35b).

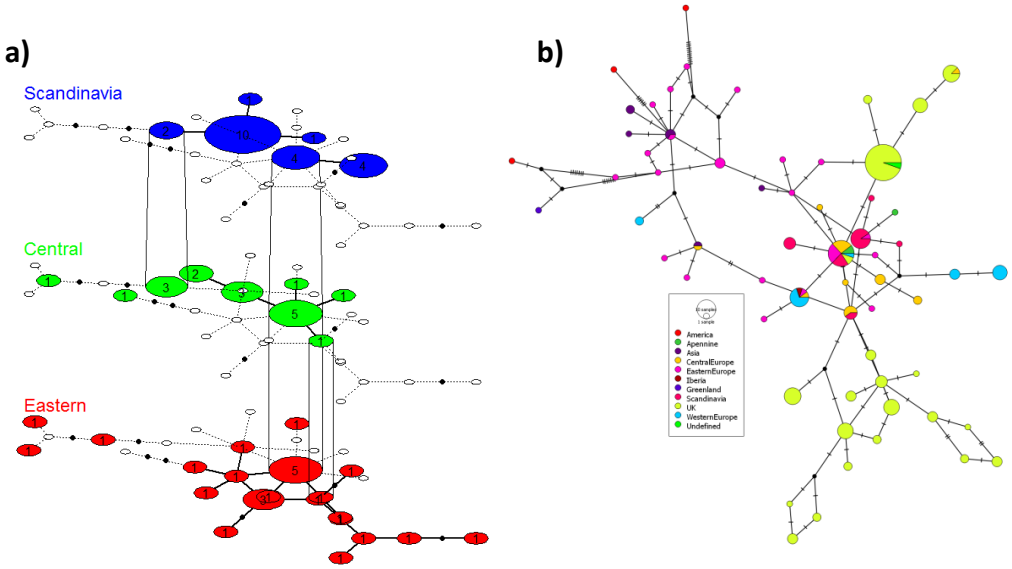


Figure 4.35 a) *Mustela erminea* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation. b) Median-Joining network of all the D-loop sequences available for *Mustela erminea*.

The lack of studies that examined the phylogeography of the species in Europe makes it difficult to identify the source of diversity and the possible refugia of *M. ermine*a. The high diversity found in Eastern Europe might be a consequence of refugia in the area or alternative it is a contact zone with the Asian populations. The presence of a stoat vertebra around 15 kya in Norway opens the possibility of the long-term presence of the species in Scandinavia (Fjellberg 1978). More studies in western and central Europe will contribute to understanding the connection between the east and the west.

Mustela nivalis (Least Weasel)

A total of 192 samples have been considered in the analysis. Unfortunately, the samples sizes of many regions are quite low and inferring phylogeographic patterns from diversity is complicated (Table 4.19). However, the species shows high haplotype diversity in most of the areas analysed, except Iberia.

Table 4.19 *Mustela nivalis* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Iberia	4	514	2	0.5	0.00297
Baleares	3	514	1	-	-
Balkans	7	514	6	0.9524	0.00472
Apennine	11	514	7	0.8909	0.00685
Corsica	8	514	7	0.9643	0.00135
Crete	24	514	3	0.6703	0.00265
Sicily	7	514	3	0.5238	0.00113
Sardinia	2	514	2	1	0.00198
Malta	8	514	1	-	-
Near East	15	514	9	0.8857	0.00376
Caucasus	3	514	3	1	0.04026
Sandinavia	7	514	6	0.9524	0.00547
UK	2	514	2	1	0.00594
North Africa	11	514	5	0.7636	0.00267
West Europe	14	514	7	0.8022	0.00429
Central Europe	7	514	6	0.9524	0.00548
East Europe	19	514	12	0.9357	0.01257
Asia	37	514	18	0.9444	0.01848
Oceania	1	514	1	-	-
Total	190	514	80	0.9769	0.01211

The phylogenetic tree (Figure 4.36) resolved more than the previously identified two clades due to the incorporation of a broader geographical range and Asian haplotypes were included in the analysis. Asian, Eastern European (Ukraine) and Georgian individuals appeared to form separate lineages from the main one that included the two main clades previously described for the species (Lebarbenchon et al. 2010). Clade I includes individuals sampled in the western-Palaearctic region covering the whole range from south to north, from Spain to Finland. Clade II is a more geographically mixed lineage as includes individuals from Eastern Europe and most of the insular *M. nivalis* including in the analysis. The population from Japan formed a different cluster.

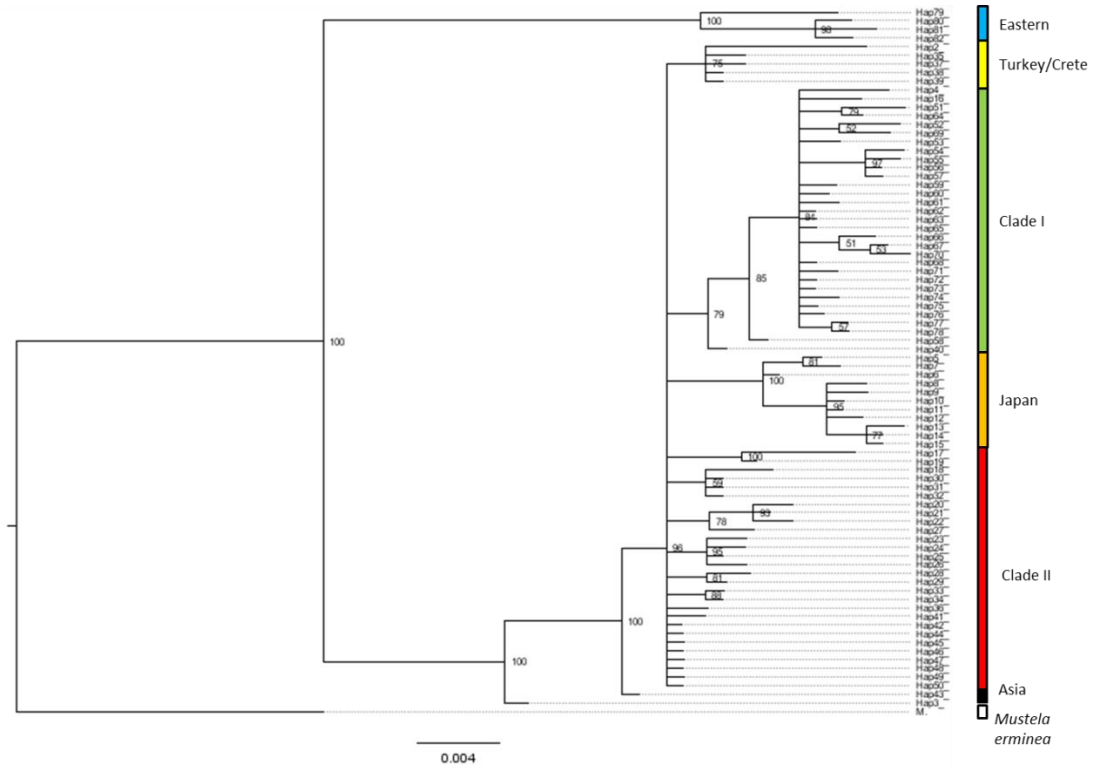


Figure 4.36 *Mustela nivalis* D-loop Bayesian phylogenetic tree with the main clades identified.

From the network analysis (Figure 4.37), the main two clades are also identified. The wide range of geographical areas identified within each clade complicates the identification of refugia for each clade. However, the areas close to the Carpathians and the Balkans displayed the highest diversity and may indicate a refugial area as previously suggested for the *cyt b* (McDevitt et al. 2012). Unfortunately, the control region is not as well sampled as the *cyt b* in important areas in central and eastern Europe such as Poland, where a contact zone has also been described (McDevitt et al. 2012).

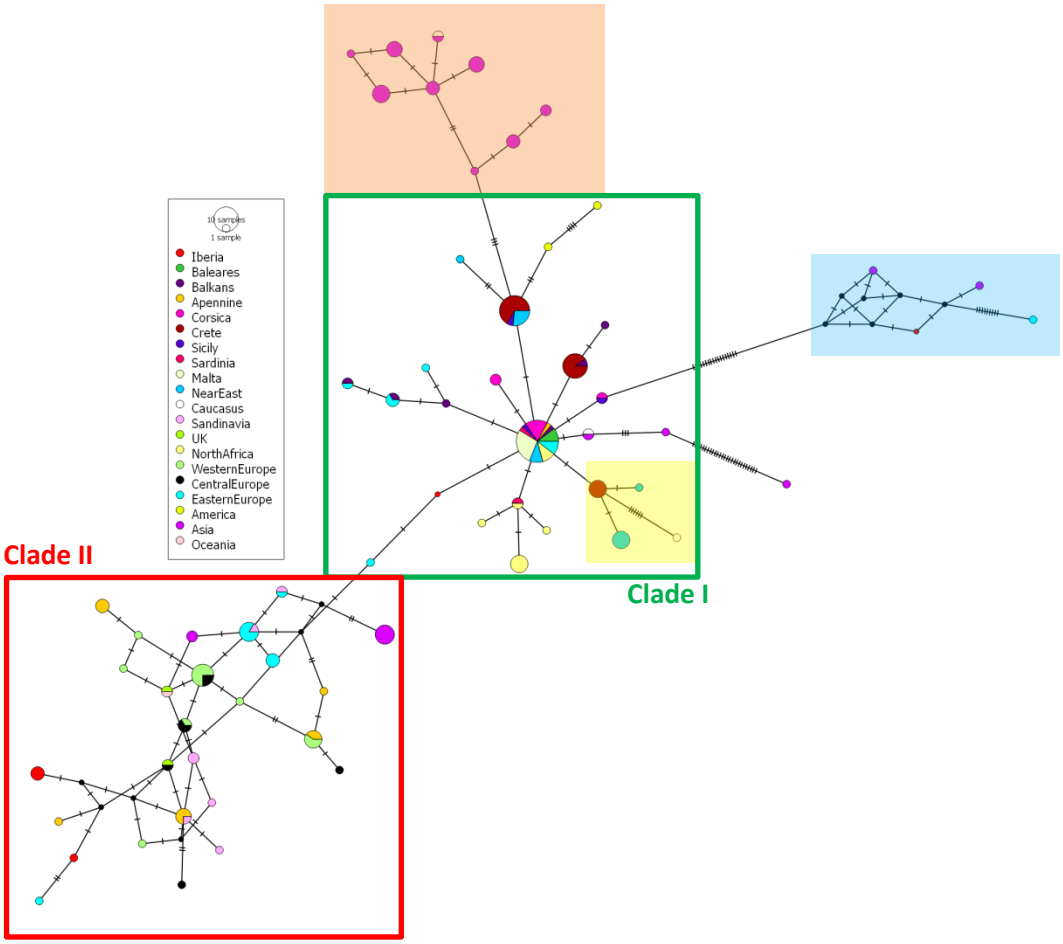


Figure 4.37 Median-Joining network of all the D-loop sequences available for *Mustela nivalis*.

Martes martes (Pine Marten)

A total of 705 individuals were included in the analysis. The highest haplotype diversity is found in the Apennine peninsula (0.8775) and the lowest in Iberia (0.6475) (Table 4.20). The phylogenetic tree has resolved four main clades that have also been previously described (Figure 4.38). The presence of three of these four groups (Mediterranean, Central Europe and Fennoscandian) has been related with the different biogeographic regions: Alpine–Atlantic, Continental, and Boreal, respectively (Roekaerts 2002; Ruiz-González et al. 2013). In this analysis, one more clade is identified for samples from the British Isles (UK, in Figure 4.38), but these samples have previously attributed to the Fennoscandian clade.

Table 4.20 *Martes martes* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Iberia	68	217	7	0.6475	0.00383
Apennine	27	217	10	0.8775	0.00946
Balkans	25	217	7	0.78	0.01101
Western Europe	119	217	14	0.71	0.01026
Scandinavia	168	217	14	0.83	0.02415
UK	97	217	4	0.4263	0.01293
Central Europe	91	217	17	0.8288	0.00855
Eastern Europe	96	217	32	0.87	0.02612
Sardinia	14	217	3	0.7143	0.00434
Total	705	217	77	0.9138	0.01967

The results presented here indicated a complex and mixed pattern of recolonisation of northern Europe from different refugia. The widespread presence of the Central group across central and northern Europe (Figure 4.39), which is barely represented in the three main southern peninsulas, suggested that the source of this lineage is related with a northern refugium as has been previously hypothesised from genetic and palaeontological data (Sommer and Benecke 2004; Sommer and Nadachowski 2006; Ruiz-González et al. 2013). Central and eastern Europe are the areas displaying high genetic diversity (Table 4.20) and makes these regions strong candidates for the location of refugia during the last glaciation.

The Fennoscandian–Russian clade does not seem to have any relationship with the southern clades, as it is not found in any other regions. The demographic history of this clade might be related with the process of speciation of *Martes zibellina* (Ruiz-González et al. 2013). The surprising result of the Mediterranean clade fitting in between variability of the Central and the Fennoscandian clades it is hard to interpret. More sampling in western Europe and the Mediterranean coast might help to clarify these results.

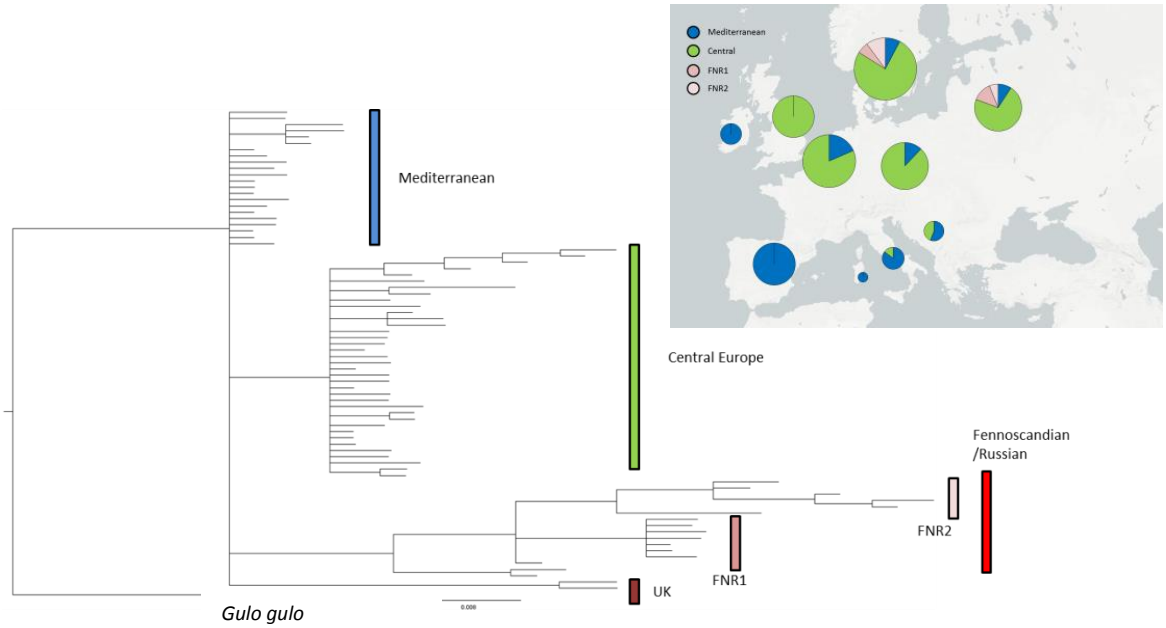


Figure 4.38 *Martes martes* D-loop Bayesian phylogenetic tree and map of the distribution of the main clades identified.

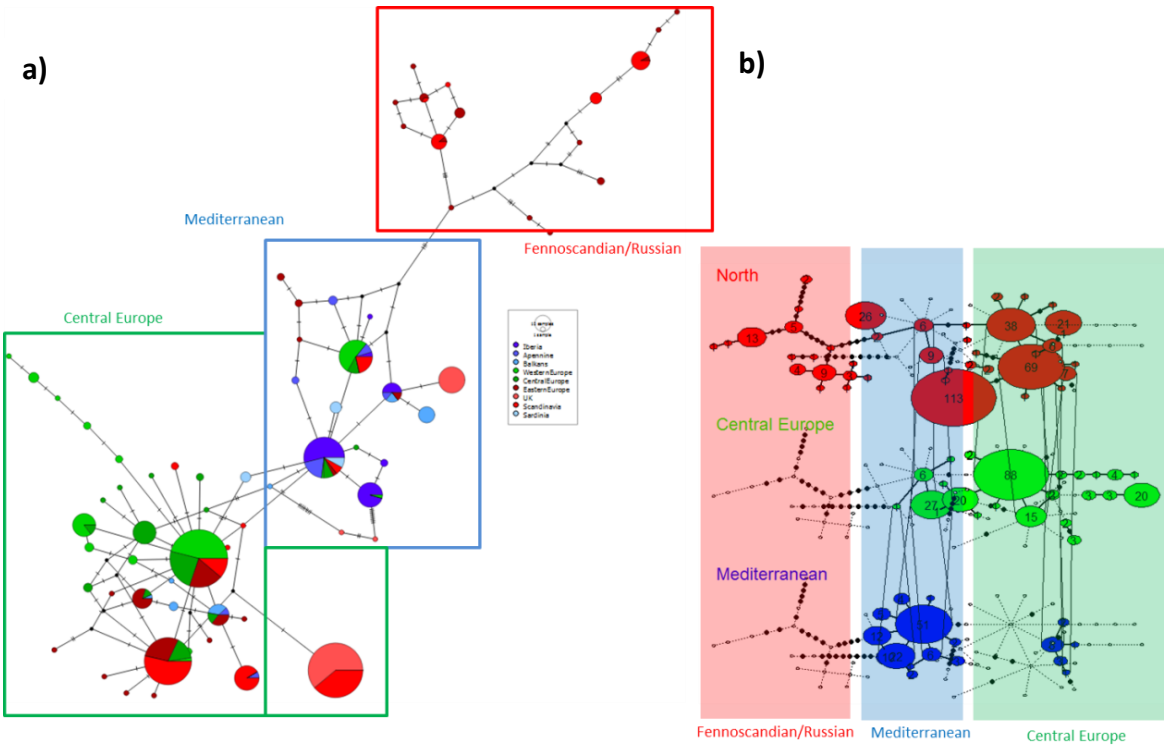


Figure 4.39 a) Median-Joining network of all the D-loop sequences available for *Martes martes*. b) *Martes martes* D-loop geographical network. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

The evidence that cryptic northern refugia existed in central Europe during the LGM does not exclude that southern refugia had an essential role in the postglacial colonisation of the species from the south. Therefore, the species seems to be characterised by a mixed pattern of recolonisation after the LGM as previously suggested by Ruiz-González et al. (2013).

Lynx (Eurasian Lynx)

A total of 832 sequences were included in the analysis (Table 4.21). A total of 56 haplotypes were identified across the four temporal periods identified using the available aDNA. The historical samples displayed the highest diversity (both haplotype and nucleotide), and the Pleistocene is not the period with the highest diversity as suggested for many mammal species (Barnett et al. 2009; Lorenzen et al. 2011).

Table 4.21 *Lynx lynx* D-loop sequences retrieved and analysed by temporal periods. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Time	n	BP	Haplotypes	*h*d	π
Pleistocene	7	498	3	0.7143	0.00479
Holocene	15	498	4	0.3714	0.00436
Historical	135	498	40	0.8734	0.01052
Modern	675	498	22	0.6256	0.00858
Total	832	498	56	0.703	0.00946

The phylogenetic tree resolved at least six clades (IN1-IN5, IN8) that have been previously suggested in the literature (Figure 4.40). The distribution map of the haplogroups (Figure 4.40) helps to identify the possible locations that may represent refugia. Unfortunately, the small sample size in some essential southern areas such as Iberia and Italy is an important caveat to infer the phylogeographic pattern of the species. The main pattern identified is the possibility of an eastern refugium for the species, due to the highest number of haplogroups found in that geographical region. However, through the temporal network (Figure 4.41), the continuity between Pleistocene-Holocene-Modern samples can be appreciated for three of the main clades described (IN3, IN4 and IN8) belonging to southern areas like Iberia, France and Italy, also indicating the possibility of southern refugia s for this species.

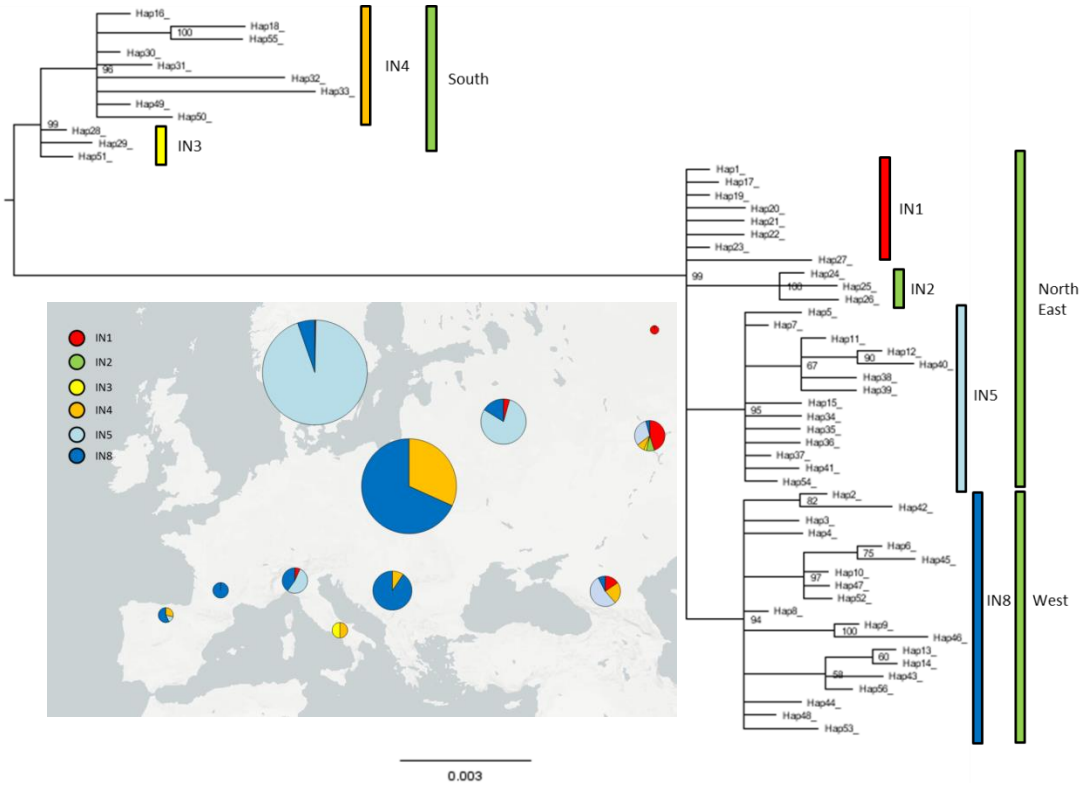


Figure 4.40 *Lynx lynx* D-loop Bayesian phylogenetic tree and map of the distribution of the main clades identified.

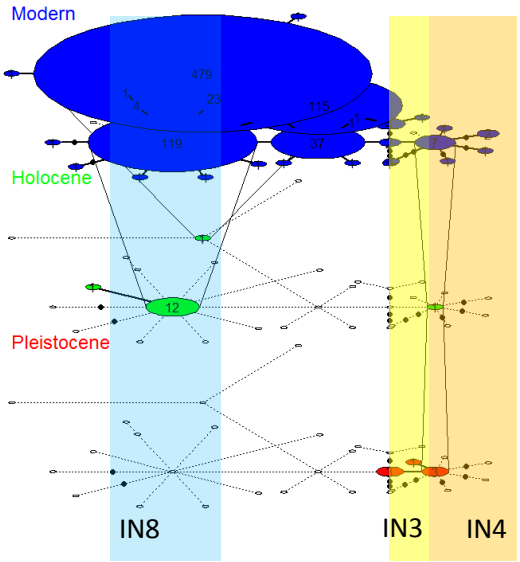


Figure 4.41 *Lynx lynx* D-loop temporal network showing the presence of the different haplotypes in the three periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given time period. Haplotypes found in multiple periods are connected by vertical lines. Within each layer, black dots represent one mutation.

The overall phylogeographic pattern of *Lynx lynx* is complex, but the existence of eastern refugia for the species seems clear from the mtDNA data available. Several refugia in the south

(but also in the north) cannot be discarded and more aDNA studies will probably confirm this helping to understand better the pattern found today and the complexity in the past.

Ursus arctos (Brown Bear)

Here, 826 samples were used to infer the phylogeographic patterns of the species (Table 4. 22). The highest haplotype diversity was found in the Caucasus. Iberia also displayed the highest diversity for the southern peninsulas and it probably reflects the important role that has been already suggested as a source of populations (Taberlet and Bouvet 1994; Davison et al. 2011).

Table 4.22 *Ursus arctos* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	Hd	π
Apennine	6	122	3	0.6	0.0153
Balkans	199	122	13	0.7716	0.04009
Bering	39	122	24	0.8745	0.05214
Caucasus	72	122	17	0.9049	0.04276
Central Europe	10	122	5	0.8222	0.05118
Eastern Europe	181	122	12	0.2273	0.00499
Iberia	61	122	20	0.8186	0.02009
Near/Middle East	60	122	16	0.774	0.0487
North Africa	7	122	3	0.6667	0.05621
Scandinavia	90	122	13	0.7446	0.0476
UK	24	122	8	0.721	0.03647
Western Europe	12	122	7	0.7727	0.02732
Eastern Russia	53	122	6	0.3396	0.00445
Total	814	122	135	0.8456	0.05772

The phylogenetic tree (Figure 4.42) resolved the two main clades that differentiated between the west and the east (clade 1 and 3, respectively) reported firstly by Taberlet and Bouvet (1994). The complexity of the species is based on the number of subclades that have been described in the literature. The presence in Iberia of the two main clades (clade 3 is found in Pleistocene samples from Spain) means that it remains poorly understood although the variety of haplotypes found there indicates a complicated story in the peninsula with turnovers and population migrations.

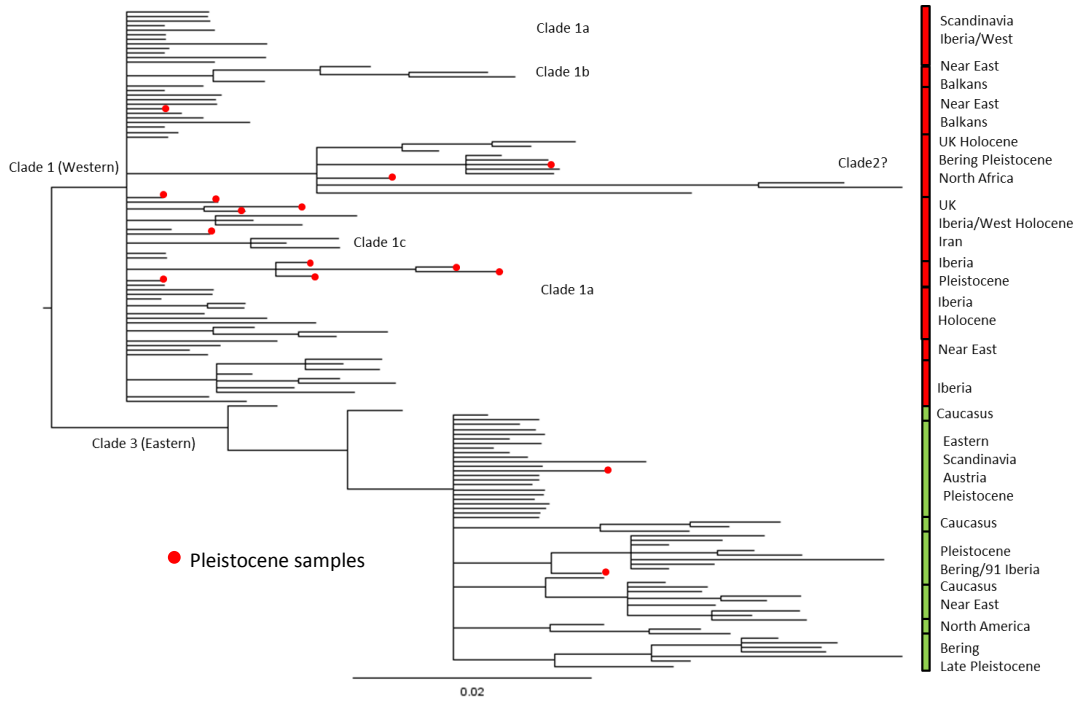


Figure 4.42 *Ursus arctos* D-loop Bayesian phylogenetic tree with the main clades identified. The nomenclature of the subclades is only indicated based on previous studies designation as the resolution of the phylogenetic tree is not as well resolved.

From the temporal network (Figure 4.43), a loss of diversity seems to occur from the Pleistocene to the Late Pleistocene (probably due the LGM). However, there is a recovery in diversity at the beginning of the Holocene until a new decline in brown bear diversity that can be linked to an intense human impact (Kirby and Watkins 2015; but see also Barnes et al. 2002).

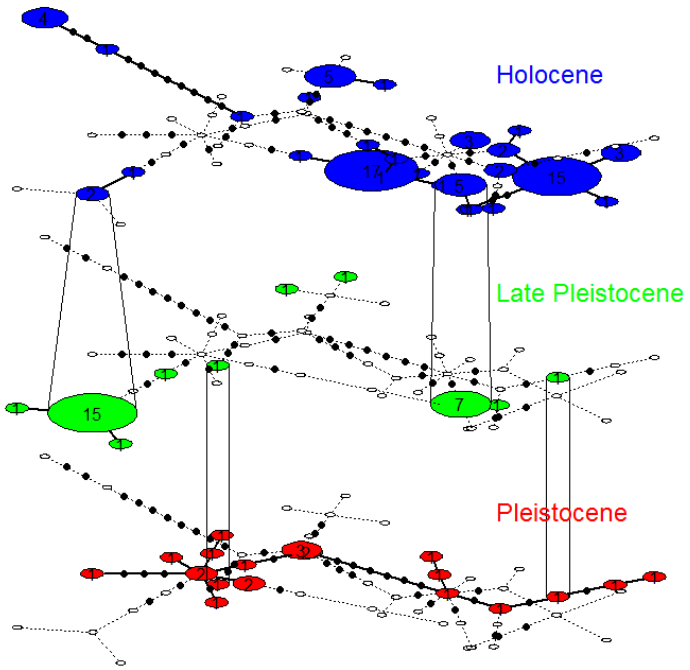


Figure 4.43 *Ursus arctos* D-loop sequences temporal network showing the presence of the different haplotypes in the three periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given period. Haplotypes found in multiple temporal periods are connected by vertical lines. Within each layer, black dots represent one mutation.

The geographical network (Figure 4.44) helped to identify the contact zone in Scandinavia where the two main clades (1 and 3) met. Furthermore, the presence in Scandinavia of the western clade (1) associated traditionally with the Iberian Peninsula as the source for colonisation (Taberlet and Bouvet 1994; Davison et al. 2011) cannot be confirmed with this analysis. The western haplotypes that contributed to the Scandinavian landscape may have arrived from Iberia, but the possibility of northern refugia somewhere in France and Belgium have to be considered as some and close related haplotypes are shared between regions for Holocene samples. This will be in accordance with Valdiosera et al. (2007). A new study, as yet unpublished at the time this thesis was completed (Ersmark et al. *in prep*) has also shown that brown bear was in Belgium during the LGM (16,000 y.a) suggesting that southern Europe was not the area from where the species colonised northern areas in Europe.

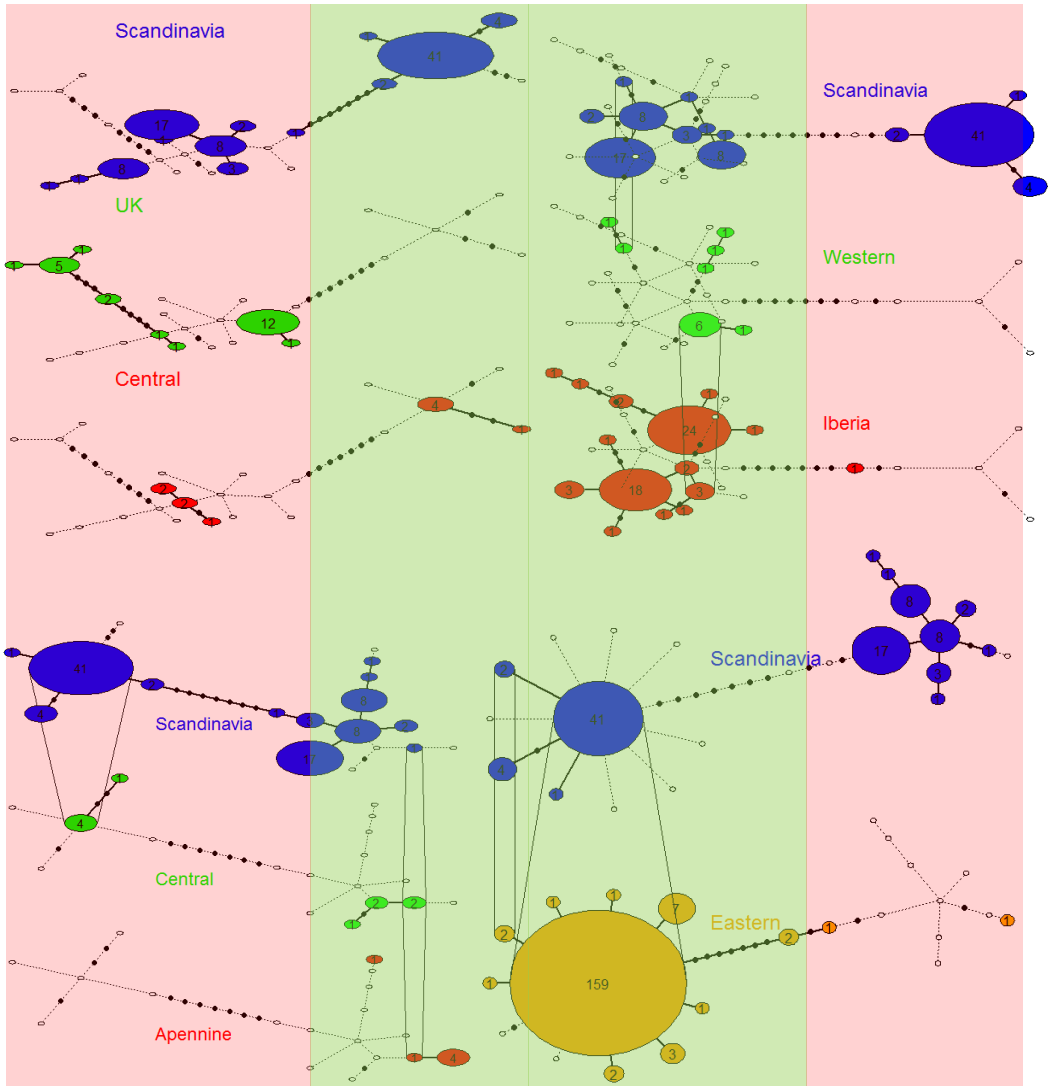


Figure 4.44 Ursus arctos D-loop sequences geographical network showing the presence of the different haplotypes in the different regions analysed. Each layer represents a different geographical area. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given area. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

Subclade 1a in Iberia and 1b in Italy-Balkans have been identified as possible refugia for the species in southern Peninsula (Davison et al. 2011). However, the resolution of the phylogenetic tree and the networks did not allow further exploration of these clades as the reduced short fragment analysed is a limiting factor for understanding the presence of these subclades.

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Alces alces (Eurasian Elk)

In total, 1586 individuals were included in the analysis (Table 4.23). The highest genetic diversity was found in Siberia, where haplotype diversity (*h*) is 0.8517 and nucleotide diversity (π) is 0.01698. This is in accordance with the previously suggested contact zone between the European and the Asian clades (Moskvitina et al. 2011). Central Europe represents the area with less diversity and even if it is the least sampled area, the sample size is high enough (n=52) to be confident about this result.

Table 4.23 *Alces alces* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Central Europe	52	465	6	0.629	0.01138
Eastern Europe	958	465	32	0.7303	0.01274
Scandinavia	246	465	9	0.6585	0.01061
Lapland	81	465	4	0.5886	0.00982
Urals	96	465	16	0.7846	0.00613
Siberia	153	465	23	0.8517	0.01698
Total	1586	465	74	0.8215	0.01524

The phylogenetic analysis including Asian and European samples resolved two main lineages (Figure 4.45). The resolution within the European clade (E, Ce and W) is not particularly well resolved, especially the central-western (Ce and W) difference from the eastern haplogroup (E1-E4). This is reflected in some uncertainty for the assignment of the clades as previously reported (Niedziałkowska et al. 2017).

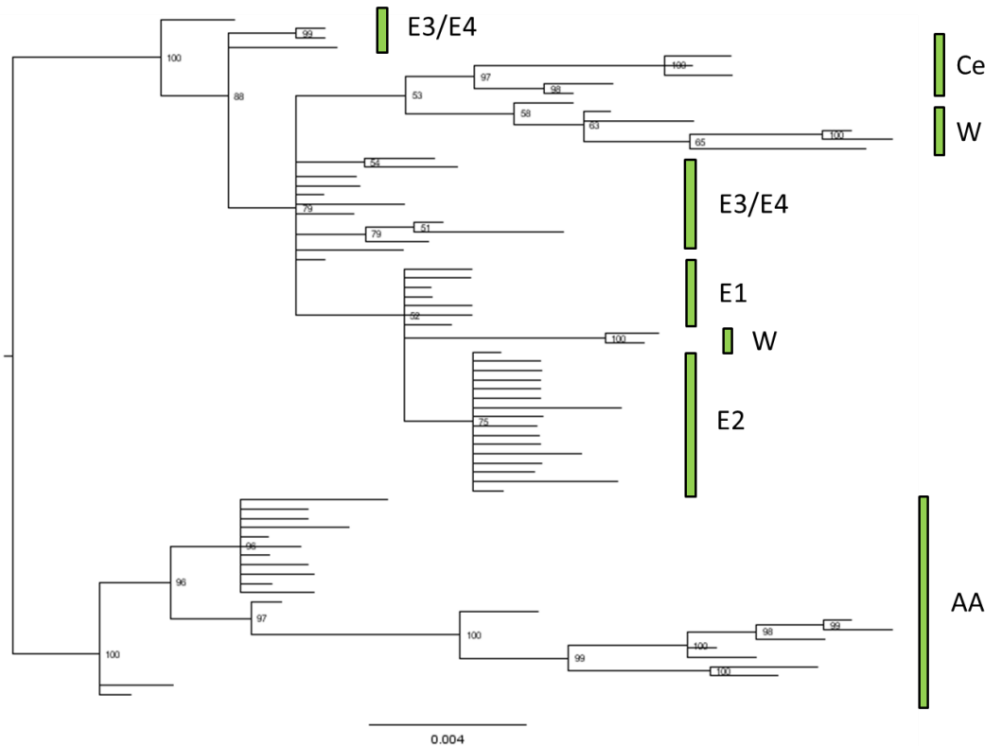

Figure 4.45 *Alces alces* D-loop Bayesian phylogenetic tree with the main clades identified.

The haplotype geographical network showed a relative sharing of haplotypes between different locations (Figure 4.46). Eastern Europe is much better sampled than central Europe, but there is still a certain degree of continuity between these two areas. The presence of moose remains during the LGM in western areas of Siberia (Markova et al. 1995) with the high diversity found in this area and the high number of haplotypes identified (Table 4.23), makes Siberia a possible refugium for the species. All the major central haplotypes seemed to be present in the three main western areas analysed. The eastern populations (even from western Asia) seem to have contributed to the genetic landscape of central Europe.

In Scandinavia, the two main haplotypes identified formed part of the genetic landscape of eastern European diversity. It has been suggested that *A. alces* colonised Scandinavia from the south and the north of Europe with phylogeographic studies supporting this colonisation scenario (Hundertmark et al. 2002; Niedziałkowska et al. 2014). The western clade has also contributed to the current genetic scenario of Scandinavia, possibly after surviving during the LGM in western Europe (Björck 1995). The distribution of the Eastern and Central clades seemed to overlap, as all the haplotypes found in central Europe are found in the east, probably due to mixing after the LGM (Niedziałkowska et al. 2014).

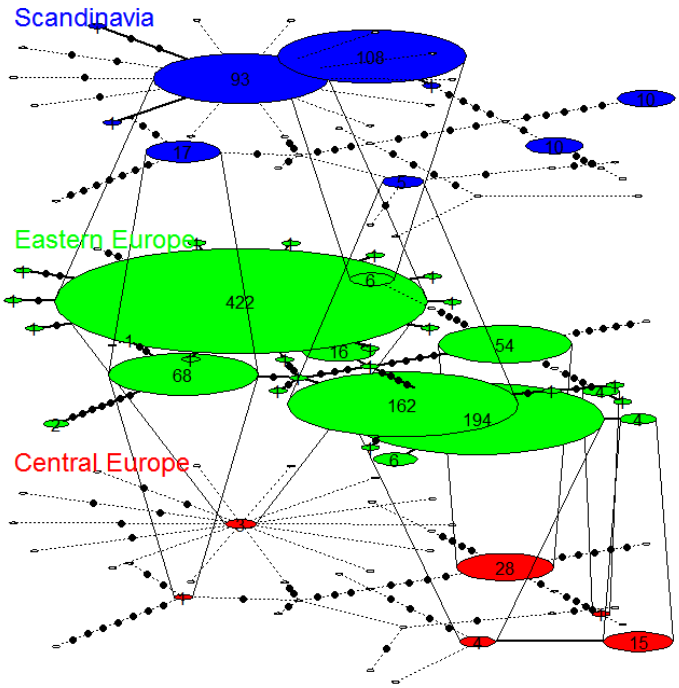

Figure 4.46 *Alces alces* D-loop geographical network. Each layer represents a different geographical area. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given area. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

The genetic structure of the European lineage of *Alces alces* seems to be more complex than previously thought. The high diversity found in Siberia is probably related with a contact zone between different clades, but it cannot be discarded as a possible consequence of a refugium contributing to recolonisation in western and eastern Eurasia. It is likely that the range of central and western haplotypes was broader in the past, with a higher genetic diversity that cannot be seen in the current populations. Ancient DNA studies will help to shed light on the distribution of the species' genetic diversity before, during and after the LGM.

Capreolus capreolus (Roe deer)

Here, a total of 2691 sequences were analysed for the whole range of the species (Table 4.24). The genetic diversity is relatively high for most of the populations (except for Scandinavian and Russian samples). The sample sizes across regions are high (>40), so allowed a confident analysis for understanding the phylogeography of the species. However, the high diversity shown by the species makes it complicated to identify possible refugia based on diversity.

Table 4.14 *Capreolus capreolus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Apennine	1090	293	52	0.8722	0.01102
Balkans	189	293	22	0.9268	0.01422
Central Europe	480	293	62	0.9055	0.01296
Eastern Europe	65	293	21	0.8793	0.02126
Iberia	291	293	22	0.8892	0.01372
Russia	86	293	13	0.6996	0.01912
Scandinavia	43	293	5	0.5504	0.0056
UK	398	293	21	0.7981	0.00761
Western Europe	49	293	14	0.8801	0.00887
Total	2691	293	181	0.9588	0.01801

The phylogenetic tree is not as well resolved as expected probably due to the reduction of the control region fragment (Figure 4.47). However, some distinct clades can be observed and described based on their geographical origins. The gene flow between populations is shown by the high number of haplotypes shared between most of the regions compared especially with connections between the south and the north as well as the east and the west (Figure 4.48). Iberia and western Europe are connected, sharing three main haplotypes between them, similar to the central European samples and Scandinavia (Figure 4.48).

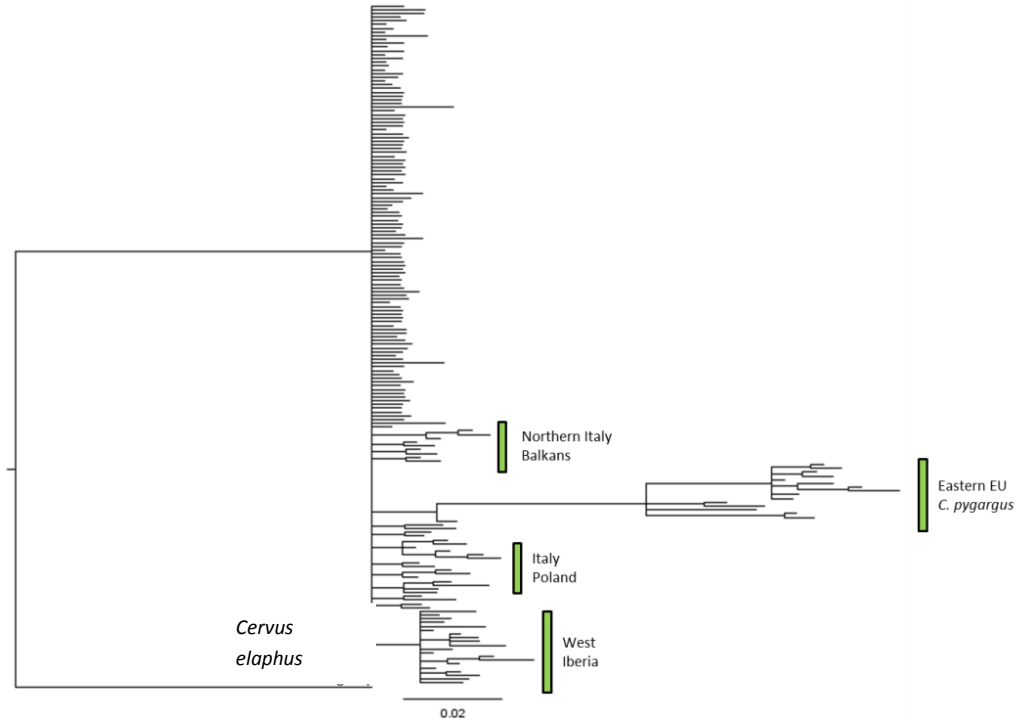

Figure 4.47 *Capreolus capreolus* D-loop Bayesian phylogenetic tree with the main clades identified.

The high diversity across regions for the species is also highlighted through the geographical networks (Figure 4.48). There is haplotype continuity between the most important regions

analysed. The western and Iberian clades previously suggested, seem to be more diverse in Iberia and might reflect a possible southern refugium in the area. The distinctiveness of the Italian clades (Lorenzini and Lovari 2006) is not well supported in this analysis as most of the haplotypes are shared with Central Europe, not indicating a clear refugium in the Apennine peninsula, as the continuity also extends to Scandinavia.

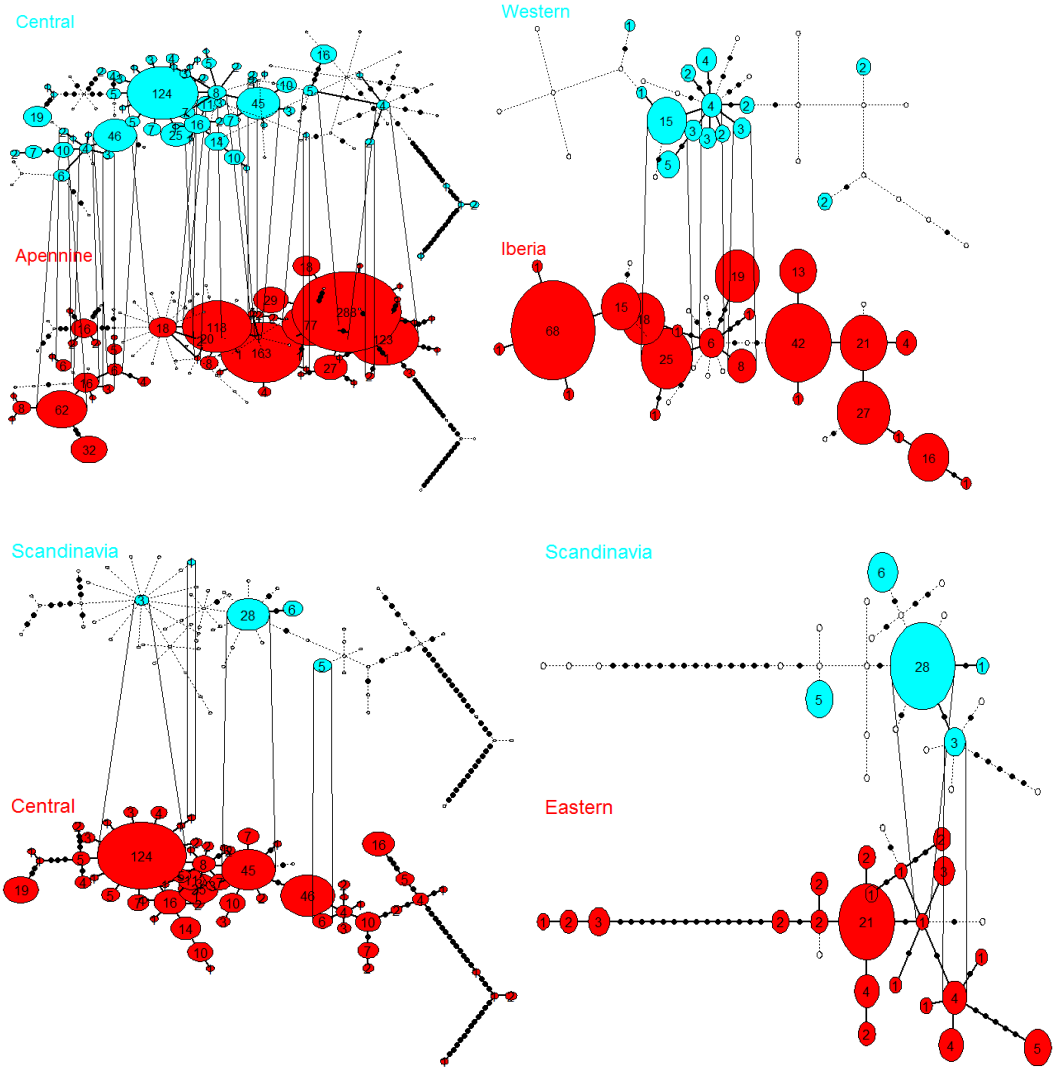

Figure 4.48 *Capreolus capreolus* D-loop sequences geographical network showing the presence of the different haplotypes in the different regions analysed. Each layer represents a different geographical area. Circles represent haplotypes and numbers represent sample sizes. Empty circles represent absent haplotypes for a given area. Haplotypes found in multiple geographical areas are connected by vertical lines. Within each layer, black dots represent one mutation.

The complexity of the phylogeography of *C. capreolus* makes it challenging to identify refugia and possible postglacial colonisation routes in Europe. The appearance of aDNA studies for this species in the upcoming years will undoubtedly contribute to the better understanding of the roe deer phylogeographic patterns.

Cervus elaphus (Red deer)

A total of 60 haplotypes has been identified for 4087 samples analysed. The highest haplotype diversity is found in Iberia and the Caucasus and the lowest in Scandinavia, Balkan and Italian Peninsulas (Table 4.25). The high diversity expected in southern regions for the species is not seen in these results. Surprisingly, the Balkans showed the lowest values of haplotype and nucleotide diversity and is not in accordance with a possible southern based on diversity.

Table 4.25 *Cervus elaphus* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	n	BP	Haplotypes	*h*d	π
Apennine	92	180	5	0.5934	0.02095
Balkans	53	180	3	0.1103	0.0041
Caucasus	6	180	4	0.8	0.03617
Central Europe	1336	180	24	0.7006	0.02688
Eastern Europe	116	180	10	0.6852	0.03313
Iberia	660	180	18	0.7908	0.02307
Scandinavia	341	180	6	0.5459	0.0134
UK/Ireland	1409	180	13	0.7584	0.03004
Near East	3	180	3	1	0.0307
Western Europe	71	180	5	0.6918	0.02697
Total	4087	180	60	0.8022	0.02578

The phylogenetic tree resolved two main clades (Figure 4.49). The first one comprised clade A and the second one presented clade B and C samples but it is not well resolved (clade B is only indicated based on the previous study from Skog et al. 2009).

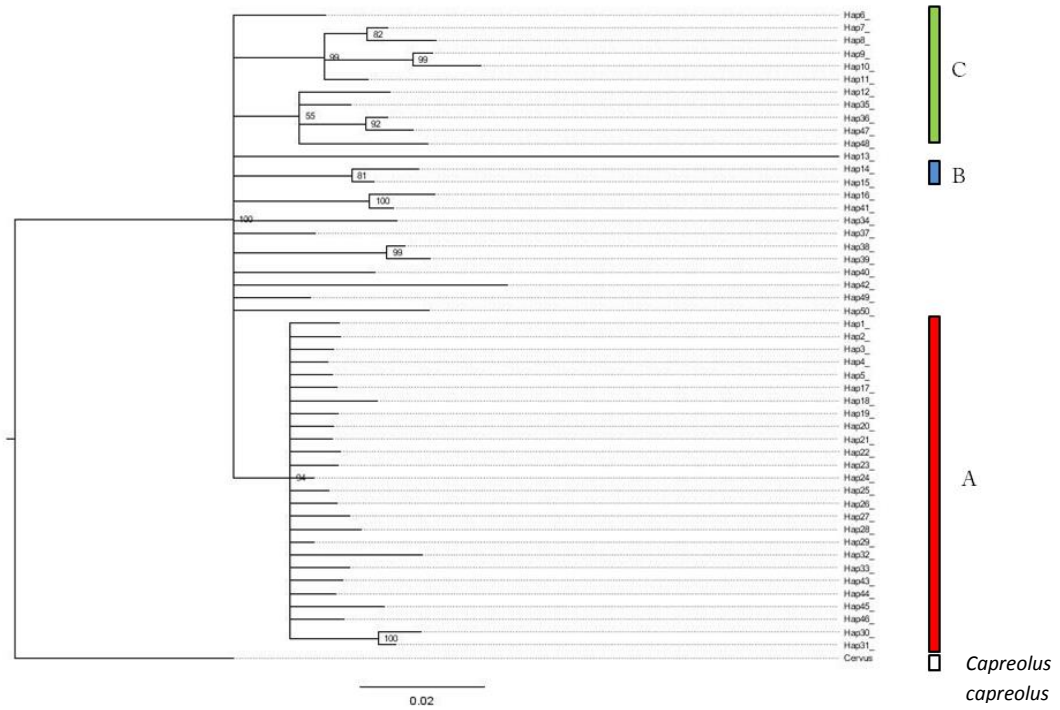

Figure 4.49 *Cervus elaphus* D-loop Bayesian phylogenetic tree with the main clades identified.

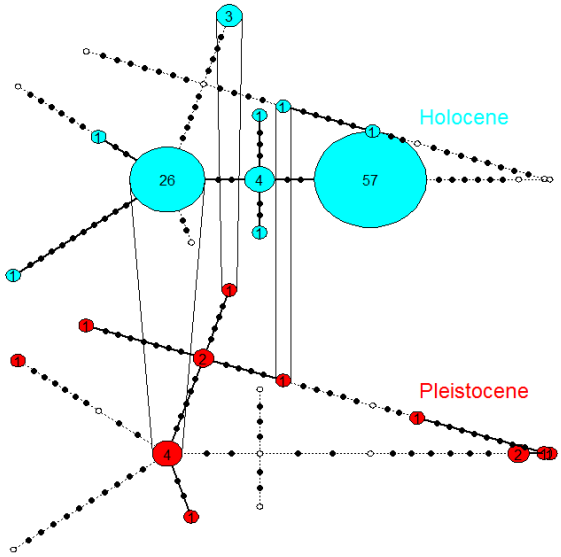

Figure 4.50 *Cervus elaphus* D-loop temporal network showing the presence of the different haplotypes in the two periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent.

In the temporal network (Figure 4.50), the Pleistocene samples are more diverse than the Holocene ones, even if the sample size is higher for this period, reporting a loss of diversity for the species since the Pleistocene. The possibility of the species having a northern refugium

cannot be discarded based on the high diversity found in the north, especially in Central Europe, in accordance with the results presented by Meiri et al. (2013).

Rangifer tarandus (Reindeer)

1609 sequences were collected and analysed for *R. tarandus*. The Pleistocene samples displayed higher haplotype diversity than the modern ones. However, the genetic diversity of the species has been kept in similar values since the Pleistocene and through different periods (Table 4.26). The well sampled Russia and Siberia displayed the highest diversity, but this has to be treated cautiously as the extensive area covered by the species in this country is an essential caveat for understanding diversity in the region. However, comparing it with the Scandinavian samples, the values are higher for the haplotype and nucleotide diversities.

Table 4.26 *Rangifer tarandus* D-loop fragment sequences retrieved and analysed by geographical areas (a) and temporal periods (b). n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

a)

Region	n	BP	Haplotypes	*h*d	π
Alaska	30	117	19	0.9655	0.03649
Asia	4	117	3	0.8333	0.09402
Canada	135	117	57	0.9619	0.04067
Central Europe	5	117	4	0.9	0.04103
Greenland	24	117	2	0.3442	0.00294
Russia	625	117	117	0.967	0.03855
Scandinavia	779	117	61	0.8808	0.03814
Siberia	6	117	6	1	0.04672
UK	1	117	1	-	-
Total	1609	117	236	0.9565	0.04179

b)

Time	n	BP	Haplotypes	*h*d	π
Modern	1199	117	169	0.9503	0.04277
Historical	270	117	52	0.9221	0.03715
Holocene	66	117	28	0.9245	0.03377
Pleistocene	72	117	54	0.9887	0.03514
Total	1607	117	236	0.9565	0.04179

The phylogenetic tree is not well resolved (Figure 4.51). The short fragment analysed (117 bp), in order to include the most aDNA sequences as possible, might be an important caveat to finding the subclades previously identified for the control region (Kvie et al. 2016). However,

some subclades were identified based on the previous nomenclature (Haplogroup I). The low support values identified in some of the branches are in accordance with Kvie et al. (2016) and the uncertainty introduced by using more, but shorter, sequences have not helped for a better resolution of the phylogenetic tree.

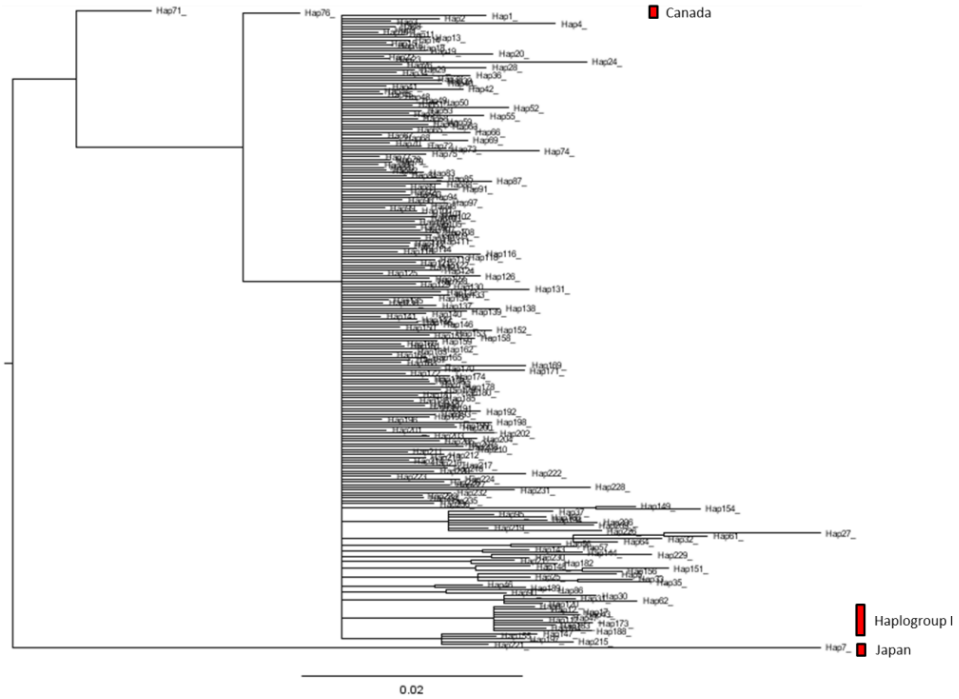

Figure 4.51 *Rangifer tarandus* D-loop Bayesian phylogenetic tree with the main clade (Haplogroup I) identified.

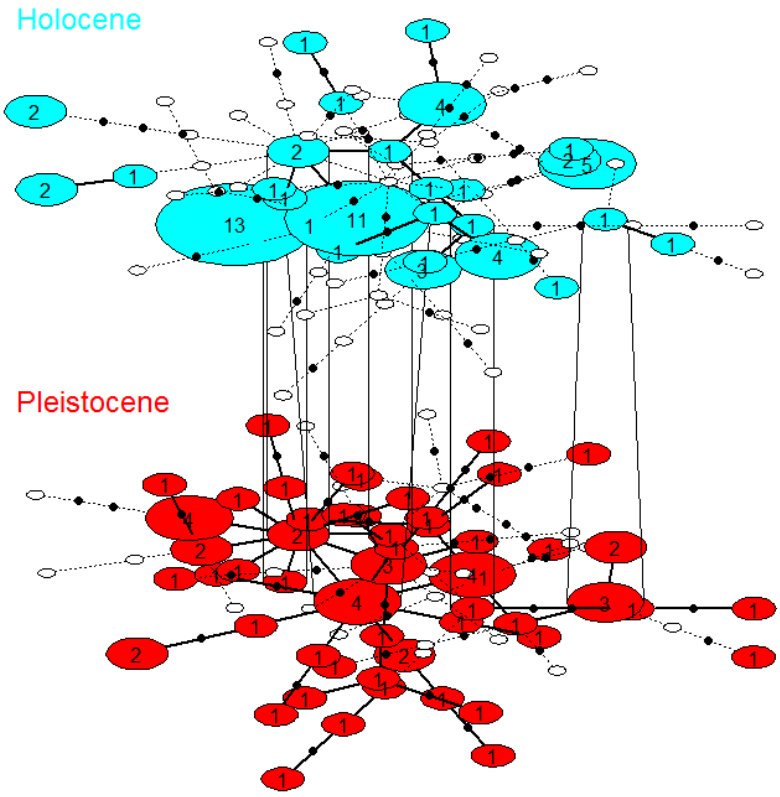

Figure 4.52 *Rangifer tarandus* D-loop temporal network showing the presence of the different haplotypes in the two periods analysed. Each layer represents a different temporal period. Circles represent haplotypes and numbers represent.

One of the analyses that could be done, regarding the lack of clades resolution, is based on a temporal comparison. The temporal network (Figure 4.52) showed an important continuity between the Pleistocene and the Holocene samples included in the analysis without identifying a significant loss of haplotype diversity over time. This is consistent with the demographic estimations previously made for the species (Lorenzen et al. 2011).

With this analysis, the confirmation that *R. tarandus* populations remained relatively panmictic over time has been made. Unfortunately, the short fragment used here did not allow a good resolution of the clades/haplogroups previously identified and inferring possible refugia for the species has been limited.

Bison bonasus (European Bison)

The availability for D-loop sequences varied to a great extent, both in overlap and length, so two different alignments were constructed. The first one covered the entire stretch of 225 bp (n=217) (Table 4.27) and a second alignment with a length of 79 bp (n=267). The second

alignment was made in order to allow the comparison with as many ancient bison sequences as possible.

Table 4.27 *Bison bonasus* D-loop fragment sequences retrieved and analysed by temporal period. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Time	n	BP	Haplotypes	*h*d	π
Pleistocene	36	225	35	0.9984	0.10872
Holocene	9	225	4	0.7778	0.01645
Historical/Modern	172	225	25	0.4985	0.03384
Total	217	225	65	0.7	0.05426

The shortest alignment (79 bp) was used to infer a temporal network (Figure 4.53a). Pleistocene samples present a clear star shape with a central haplotype that is also found in historical and modern samples. During the Holocene, the species seemed to have reduced its genetic variability and this has continued until the current time. The presence of 7 samples from a distinct haplotype in the modern range is probably due to introgression from domestic cattle in European bison from samples coming from Russia (Ward et al. 1999; Yudin et al. 2012).

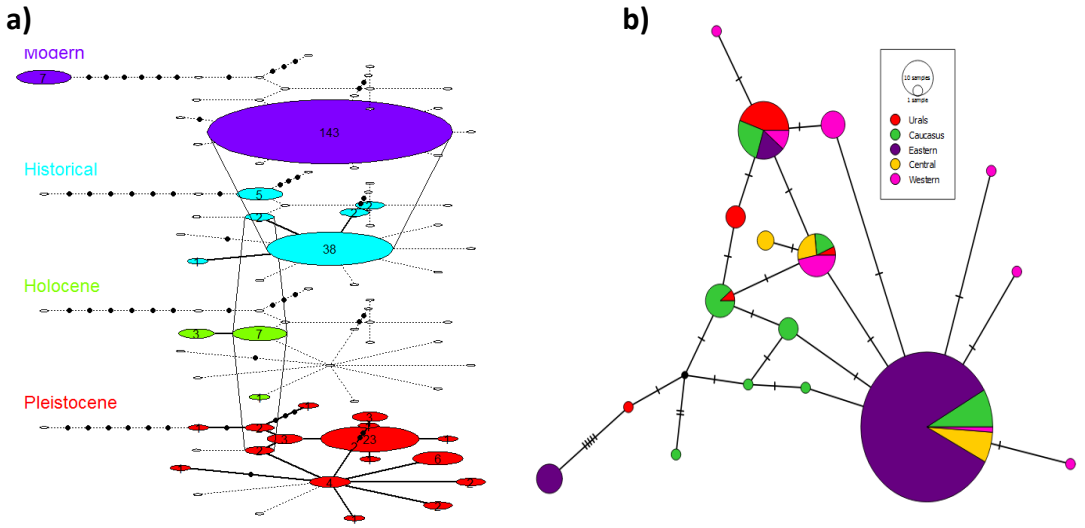

Figure 4.53 a) *Bison bonasus* D-loop temporal network. Haplotypes found in different periods are connected by vertical lines. Within each layer, black dots represent one mutation. b) Median-Joining network of all the D-loop sequences available for *Bison bonasus*.

The extreme reduction of variability in modern samples has been well described and has an essential role in the conservation of the species. The phylogenetic tree based on the longest fragment (225 bp) resolved the two main haplogroups that have been previously described

(Figure 4.54) and that delimited Clade X and the European Bison. Eastern European samples (including Poland), where the species is best represented, showed a star-shaped that probably is reflecting the main haplotype (Clade X) that included almost all modern and historical samples.

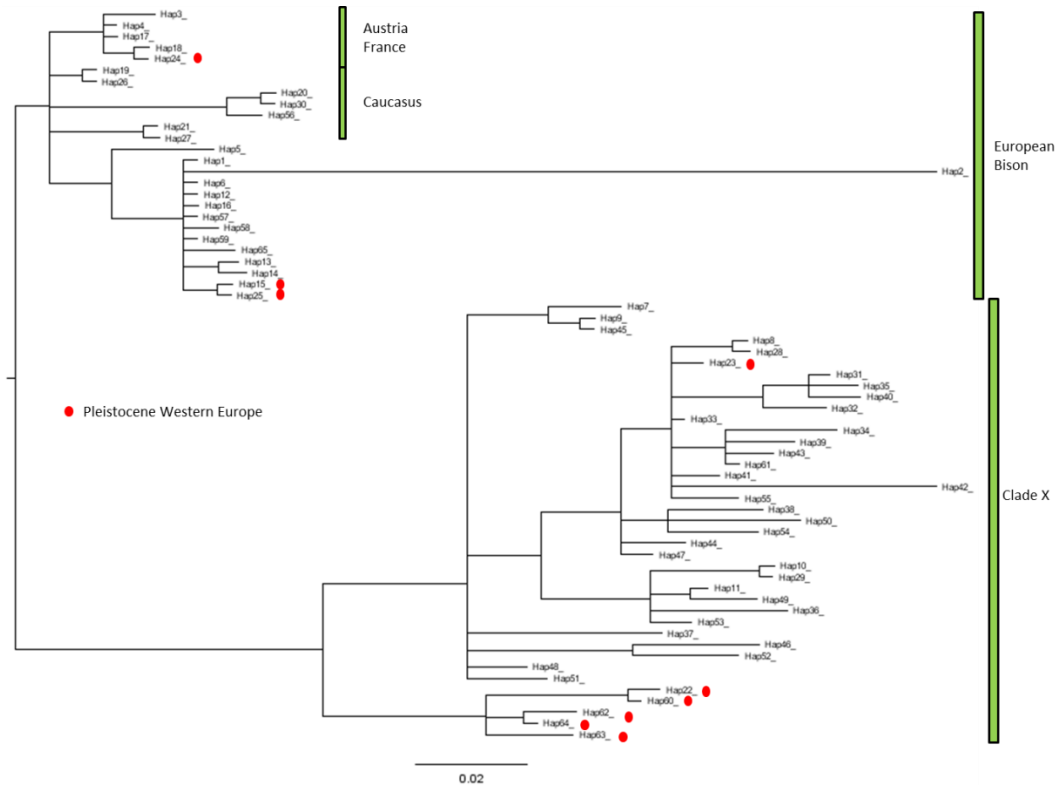

Figure 4.54 *Bison bonasus* D-loop Bayesian phylogenetic tree with the main clades identified.

The other main haplogroup previously described in Soubrier et al. (2016) is not well resolved in the temporal network (Figure 4.53a) due to the short length of the fragment analysed. However, there is some genetic distance between some Pleistocene and Holocene samples to the main modern haplotype. This is reflected in a bottleneck in modern samples and also possibly the extinction of some populations during the beginning of the Holocene and modern times (Lorenzen et al. 2011; Tokarska et al. 2011).

The geographical distribution of the haplotypes found is well represented by the main haplotype that is mostly found in modern samples in Eastern Europe (Figure 4.53b). The European range of the species is restricted today to Białowieża Forest in Poland so the modern diversity and genetic landscape it is limited to infer phylogeographic patterns of the past. The new studies, which mainly incorporated aDNA, have opened a whole new understanding of the evolution of the species.

Sus scrofa (Wild Boar)

The principal analysis that has been done is on those individuals indicated as wild boars in the literature. A total of 1220 individuals were analysed using this short fragment of the control region (73 bp). The representation of wild boar across Europe was such that data from a great variety of areas was included with only a low number of samples from the British Isles and the Caucasus (Table 4.28).

Table 4.28 *Sus scrofa* D-loop fragment sequences retrieved and analysed by geographical areas. n=samples size; BP= length in base pairs of the fragment analysed; Haplotypes= number of haplotypes found; *h*d = haplotype diversity; π= nucleotide diversity.

Region	N	BP	Haplotypes	*h*d	π
Iberia	139	73	4	0.2123	0.01
Apennine	128	73	5	0.7287	0.03981
Balkans	446	73	10	0.34	0.00634
Sardinia	37	73	5	0.779	0.03169
West Europe	50	73	4	0.558	0.0107
UK	7	73	2	0.467	0.0063
Central Europe	60	73	3	0.352	0.00485
East Europe	273	73	7	0.417	0.00754
Near East	50	73	5	0.599	0.02168
Asia	8	73	1	-	-
North Africa	15	73	4	0.629	0.03148
Caucasus	7	73	6	0.952	0.03783
Total	1220	73	39	0.4611	0.01647

The phylogenetic tree showed the main clades described already for the wild boar, so no loss of resolution occurred due to the shorter fragment used (Figure 4.55). Through the map (Figure 4.56) the distribution of the different clades across Europe is represented. The areas that present higher diversity are the Caucasus, Apennine Peninsula and Sardinia, however, the first one might be overestimated due to the short sample size (n=7). The existence of higher genetic diversity at lower latitudes in the Apennine Peninsula might suggest that this southern area had a significant role during the last glaciation as a genetic reservoir.

The two longitudinal extremes across the continent from the west (Iberia) to the east (Eastern Europe) share a similar haplogroups distribution and this is in agreement with previously published studies (Scandura et al. 2008; Alexandri et al. 2012; Vilaça et al. 2014). This supports the genetic proximity of two eastern and western areas increasing the complexity of the pattern expected by isolation by distance (Vilaça et al. 2014). Furthermore, recent

translocation seems to have only affected the local scale (Vernesi et al. 2003) suggesting that postglacial colonisation processes may have shaped the dominant phylogeographical pattern.

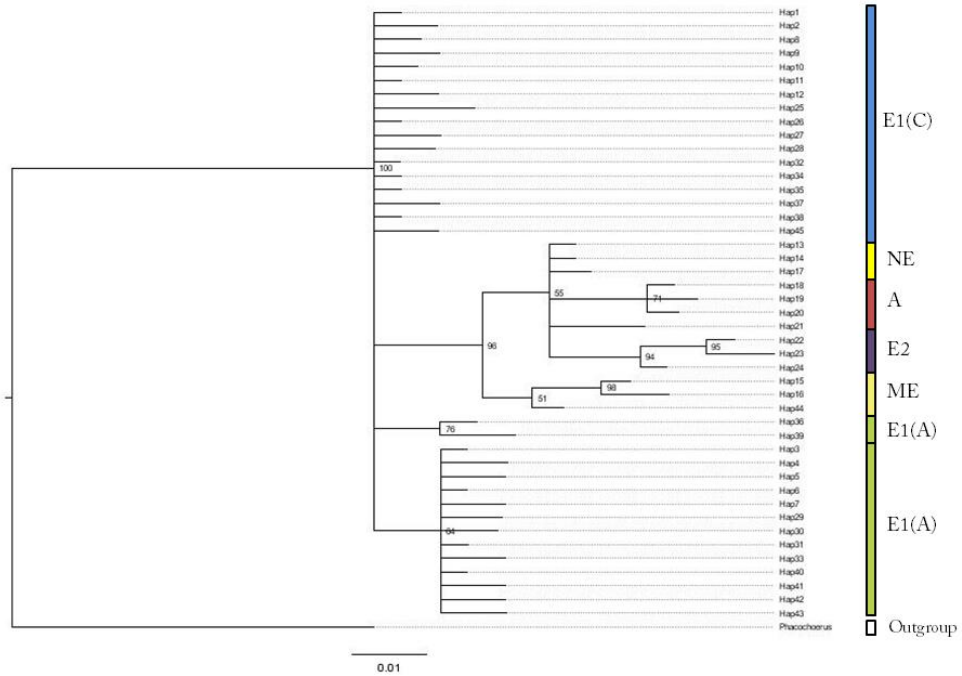

Figure 4.55 *Sus scrofa* D-loop Bayesian phylogenetic tree with the main clades identified.

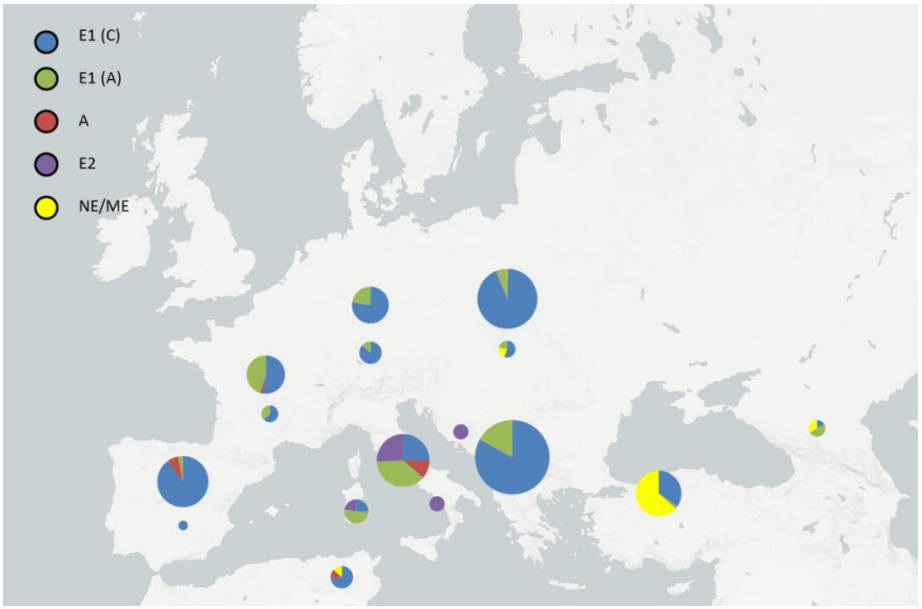

Figure 4.56 Map of the distribution of the main clades identified in the phylogenetic tree for *Sus scrofa*. The smaller pie charts represent the ancient DNA samples.

Through a network between the main southern refugial areas (Figure 4.57), haplotypes are seemed to be shared between them. This may indicate possible gene flow between them but the possibility of modern reintroduction may also be taking account considering the significant

population reduction that the species went through during the last three or four centuries (Danilkin 2001; Apollonio et al. 2010).

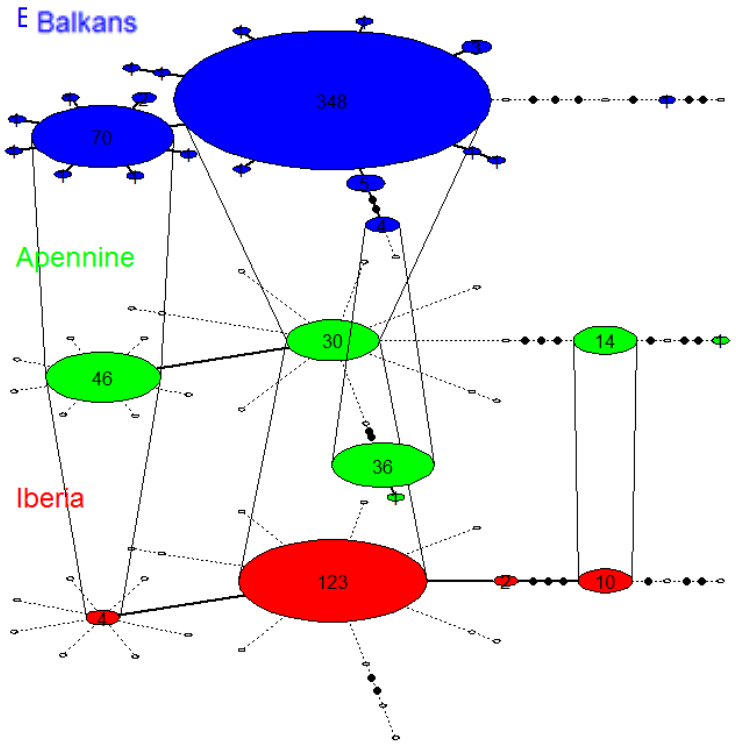

Figure 4.57 Network showing the presence of the different haplotypes in the three main traditional refugia.

A south-north differentiation may not take place in the wild boar as there are some main important haplogroups shared between southern and northern areas (Figure 4.58). The similarity observed between Eastern Europe and Iberia could reflect a distribution where a single group formed a belt from the East to the West. This has been suggested as a pre-LGM distribution (Vilaça et al. 2014), but the present analysis does not show a clear continuity between the east and west to suggest that.

The rare haplogroup E2 found in Sicily and southern Italy is also found in individuals from Croatia in the Mesolithic. This indicates a possible continuity or gene flow between the two areas and this is in agreement with the pattern seen in Figure 4.58, where the main haplotypes are shared between the southern areas.

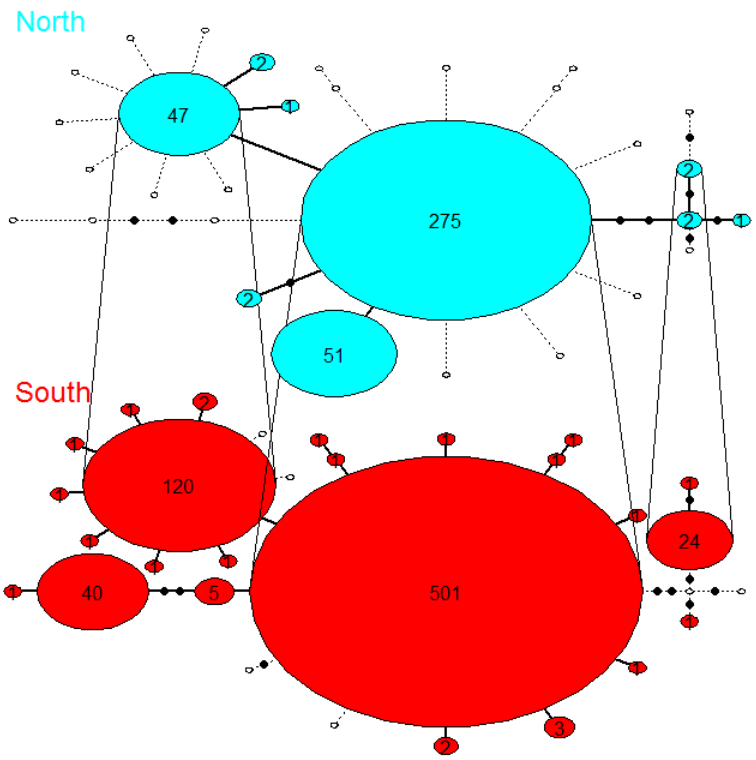

Figure 4.58 Geographical network showing the continuity of the main haplogroups between southern and northern Europe for *Sus scrofa* D-loop.

Regarding clade E1, the A-side group are more common in Central Europe and Italy while the C-side group is mostly represented in Iberia and Eastern Europe (Scandura et al. 2011). The complexity of identifying phylogeographic patterns for the wild boar is augmented by the hybridisation between local wild boars and domesticated pigs blurring the signal for the wild populations (Larson et al. 2007).

Homo sapiens (Modern Humans)

For this chapter, a total of 39 individuals were analysed for the Palaeolithic and 86 individuals have been analysed for the Mesolithic. A total of 19 haplotypes were resolved for the first period and 35 different haplotypes have been resolved for the Mesolithic. The genetic diversity in the Palaeolithic seems to be high across the continent despite the fact that the sample sizes are relatively low (Table 4.29a). The Apennine region (Italy) is the area presenting the highest values for haplotype and nucleotide diversity. However, the genetic variability during the Mesolithic seems to be higher than in the Palaeolithic and especially in the East (Table 4.29). There is a reduction in the number of samples available in western Europe and in the traditional refugial areas that can lead to misinterpretation of the results.

Table 4.29 Individuals from the Palaeolithic (a) and the Mesolithic (b) analysed for the HVS-I fragment. N=number of individuals; BP= base pairs analysed; Haplotypes=number of haplotypes identified; Hd=haplotype diversity; π=nucleotide diversity.

a)

Region	N	BP	Haplotypes	Hd	π
Iberia	3	325	2	0.667	0.0041
Apennine	6	325	5	0.933	0.0072
West Europe	14	325	8	0.89	0.00739
Central Europe	10	325	4	0.711	0.00514
East Europe	6	325	4	0.8	0.00308

b)

Region	N	BP	Haplotypes	Hd	π
Iberia	1	325	1	-	-
Scandinavia	21	325	10	0.867	0.00861
West Europe	5	325	5	1	0.01118
Central Europe	17	325	11	0.926	0.00868
East Europe	40	325	16	0.932	0.01641
Balkans	2	325	2	1	0.00309

The phylogenetic tree for the individuals from Palaeolithic and Mesolithic resolved a pattern difficult to interpret (Figure 4.59). No clear geographical pattern can be seen with the phylogenetic tree analysis.

The Palaeolithic data has been subdivided in order to improve the resolution of the analysis and to distinguish possible signals of the different archaeological cultures present in Europe at that time. The following figure represents a network of all the available HVS-I (mtDNA) sequences for modern humans in the Palaeolithic that were able to be fully reconstructed (Figure 4.60).

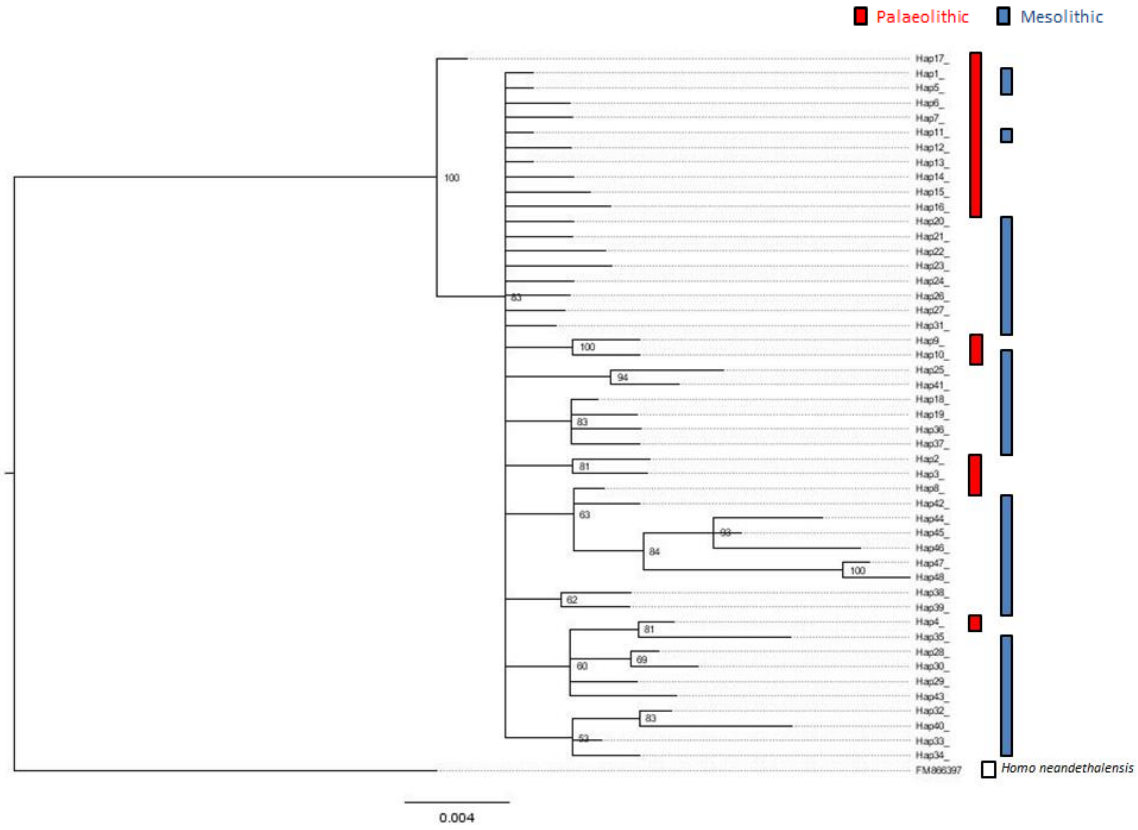

Figure 4.59 Phylogenetic tree for the HSV-I fragment of modern humans in the Palaeolithic and the Mesolithic.

A clear continuity is shown in the temporal network with a main star-shape haplotype from the Early Upper Palaeolithic from which at least four different haplotypes derived (Figure 4.60). During the Middle-Upper Palaeolithic new branches seems to arise and this might be in consensus with the appearance of new haplogroups such as U5 (Lell et al. 2000; Otte et al. 2007). Haplogroups U2 and U8 remained prominent after the LGM in the late Upper Palaeolithic. Intriguingly, these two haplogroups seem to become less frequent after 15 kya and could suggest small cryptic refugia in central Europe (Richards et al. 2016).

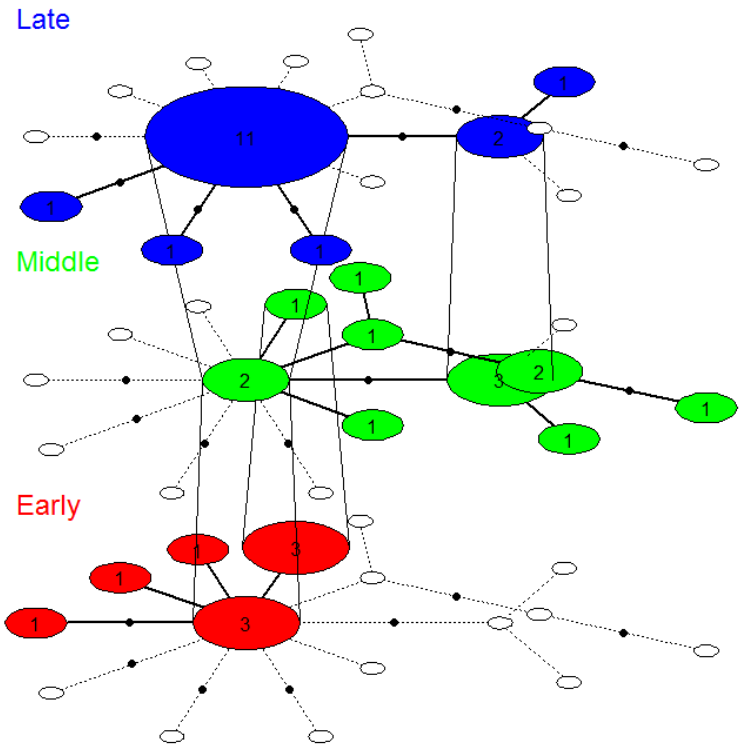

Figure 4.60 Temporal network from Early Upper Palaeolithic to Late Upper Palaeolithic haplotypes.

The comparison between the Palaeolithic and Mesolithic is critical in order to understand the post-glacial recolonisation. A temporal network (Figure 4.61a) shows the continuity between the two periods as well as the arrival of new haplotypes. The central haplotype described for the Palaeolithic is less represented in the Mesolithic and shows more ramifications. This indicates the basal haplotypes present in the Palaeolithic and the new haplogroups arrivals during this transition.

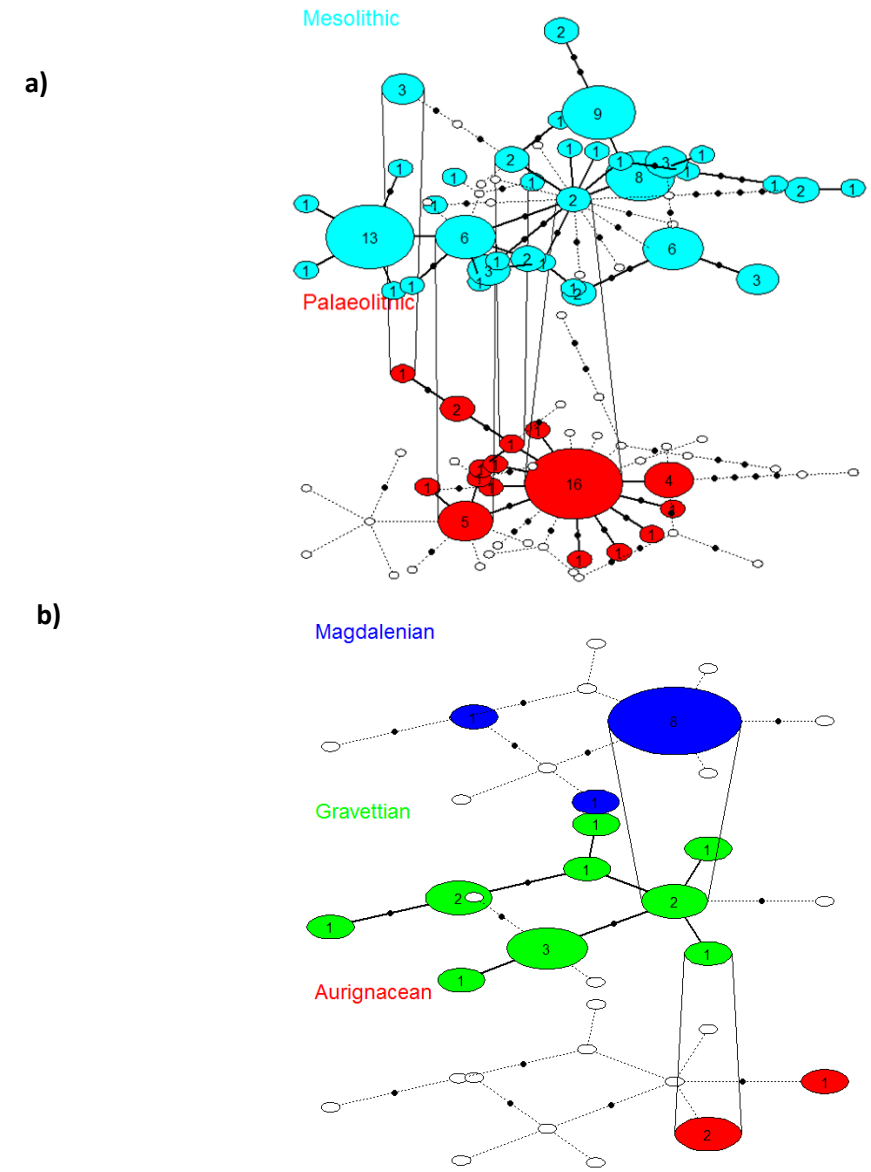

Figure 4.61 a) Temporal network between the Palaeolithic and Mesolithic haplotypes for the HVS-1 region. b) Temporal network to show the different haplotypes related to the main lithic cultures described for AHM.

The analysis through the different lithic cultures shows an evident diversification of the haplotype branches with the arrival of the Gravettian when more variability is seen (Figure 4.61b). However, the Magdalenian showed even less genetic variability with 8 out of 10 individuals clustering on the same haplotype for the HVS-I fragment. New haplogroups, such as U5 and U8, seemed to appear with the Gravettian lithic culture and had not been identified before.

4.3.2 Phylogeographic patterns based on diversity indices for mammals in Europe

Topological congruence of phylogenetic trees occurs when the phylogeographical patterns detected are similar between species that responded to the same historical event (Sullivan et al. 2000). However, tree topologies are insufficient to test the phylogeographical hypothesis and need to be complemented with other approaches, although they represent an excellent starting point for other analyses (Cartens et al. 2005). In this context, two different main topologies were found for all the phylogenetic trees produced for twenty-nine species (Figure 4.62). First, there are nineteen species that have a phylogeny characterised by at least two main clades that are well supported (Figure 4.62a). Second, there are nine species displaying a phylogeny where more than 80% of the haplotype sequences cluster in a well-supported clade without a strong internal structure (Figure 4.62b). MtDNA sequences fail to support topological congruence between all the species, as expected, but these two main topologies define the general patterns.

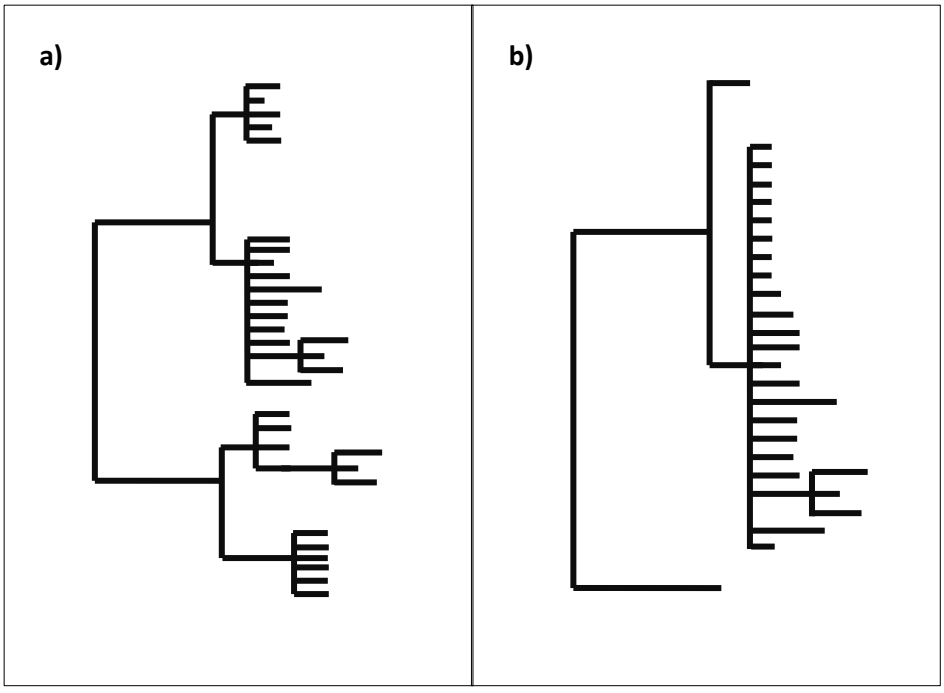

Figure 4.62 Schematic figures of the two main topologies of phylogenetic trees identified for the thirty species analysed. Topology a) is found for *Arvicola amphibius*, *Arvicola sapidus*, *Microtus arvalis*, *Lemmus lemmus*, *Castor fiber*, *Erinaceus euroapeus*, *Erinaceus concolor*, *Sorex minutus*, *Lepus europaeus*, *Lepus timidus*, *Canis lupus*, *Lynx lynx*, *Martes martes*, *Mustela nivalis*, *Ursus arctos*, *Alces alces*, *Cervus elaphus*, *Bison bonasus* and *Sus scrofa*. Topology b) is found for *Cricetus cricetus*, *Myodes glareolus*, *Sciurus vulgaris*, *Mustela erminea*, *Vulpes lagopus*, *Vulpes vulpes*, *Capreolus capreolus*, *Rangifer tarandus* and *Homo sapiens*.

To complement this first approach analysis, haplotype diversity values were calculated for each species and each region analysed. The values are displayed in Figure 4.63, where species are grouped by taxonomic similarities. The results show considerable variability in the diversity displayed by species and regions analysed. To determine the differences between species a Wilcoxon Signed Rank Test was performed between pairs of species. The results show that certain species can only be considered significantly different from the haplotype diversity displayed by each species by region analysed (Table A3.1 in Appendix 3). The species that is more significantly different from the other species is *Vulpes vulpes*, being significantly different to five species, followed by *Capreolus capreolus*, *Sus scrofa*, *Canis lupus*, *Martes martes* and *Cervus elaphus*, which are significantly different to four and three species. For seventeen species non-significant differences were found between pairs of species.

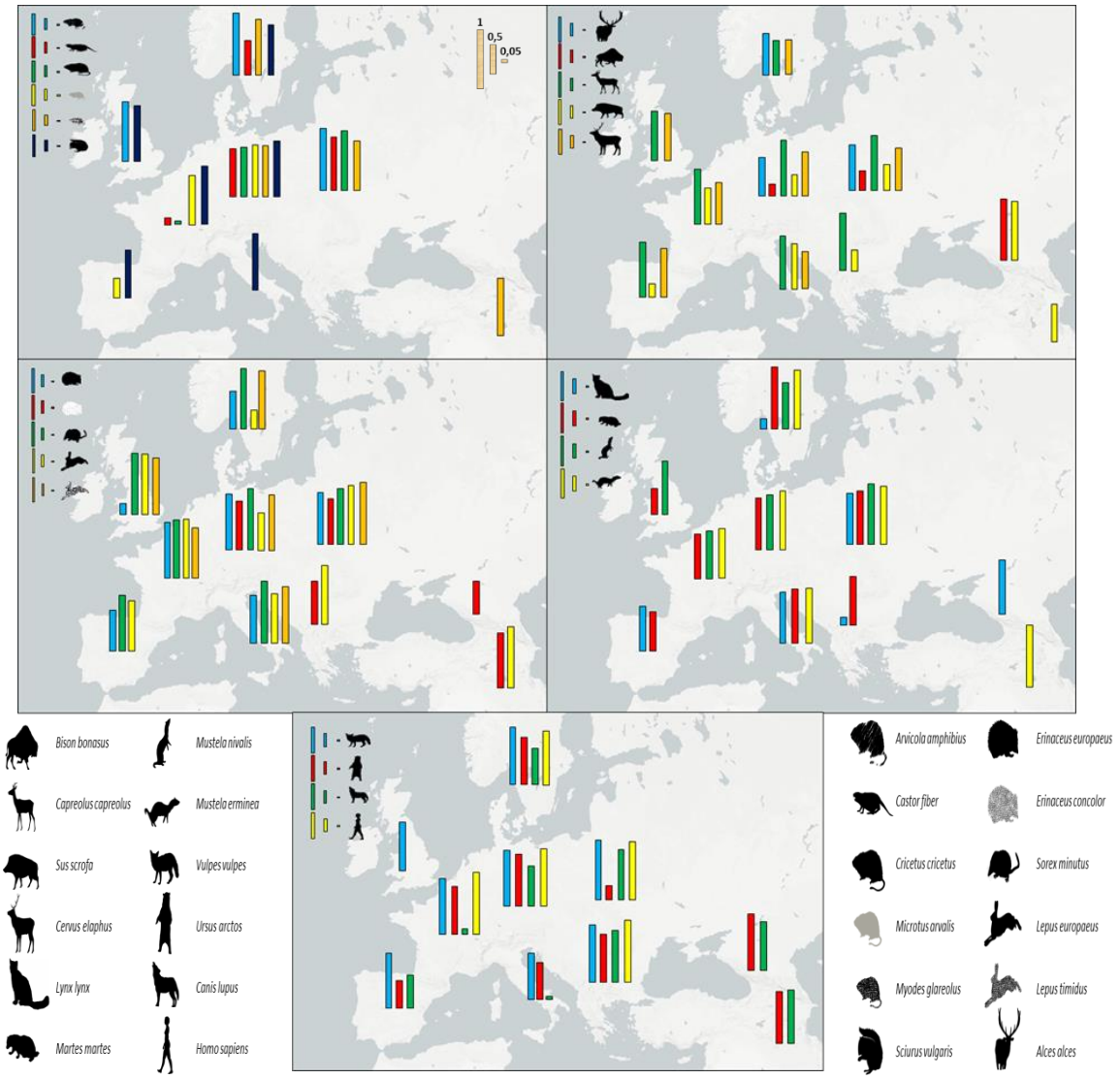

Figure 4.63 Maps displaying the haplotype diversity values for each species per region analysed. Bars represent haplotype diversity values and each colour matches with the species that are classified by orders: Rodents, Artiodactyla, Lagomorpha/Eulipotyphla and Carnivores.

Haplotypes that are not found in other populations and are exclusive to certain regions, defined here as private alleles, can provide evidence of a refugium if they are in low values. As recolonised regions, on the other hand, can display high diversity but it is expected to have a low proportion of private haplotypes (Maggs et al. 2008). Following this approach and the calculation of private allelic richness, after rarefraction to S=10, the values for each species per region are plotted in Figure 4.64.

Four different phylogeographic patterns can be inferred based on the private allelic richness values for some species and complemented by the haplotype diversity (Figure 4.63 and Figure 4.64). The first one is represented by an east-west longitudinal gradient for diversity and it can be seen for *Castor fiber*, *Cricetus cricetus*, *Alces alces*, *Mustela nivalis, Mustela erminea* (except the British Isles) and *Erinaceus concolor*. This pattern is also reinforced by the genetic diversity found for *Castor fiber*, *Cricetus cricetus*, *Alces alces* and *Mustela nivalis* but not for *Mustela erminea* and *Erinaceus concolor*, where the haplotype diversity values seem more homogeneous through the geographical range of the species. The second pattern is a more central (Western-Central belt) distribution of private allelic richness, which was found for *Erinaceus europaeus, Sciurus vulgaris, Sorex minutus,* and *Microtus arvalis.* The haplotype diversity displayed a similar pattern for *Erinaceus europaeus* and *Microtus arvalis*, but it is not appreciated for *Sciurus vulgaris* and *Sorex minutus*, indicating the complexity for the species in diversity terms. For some species a third pattern of distribution for the private allelic richness shows southern areas with more private haplotypes than northern areas. These species are *Capreolus capreolus*, *Sus scrofa*, and *Martes martes*. The rest of the species analysed (eight more species from which enough data was available to infer diversity patterns) displayed and homogeneous pattern where no specific areas show much higher or lower private allelic richness than others. Modern humans from the Palaeolithic and the Mesolithic show this pattern.

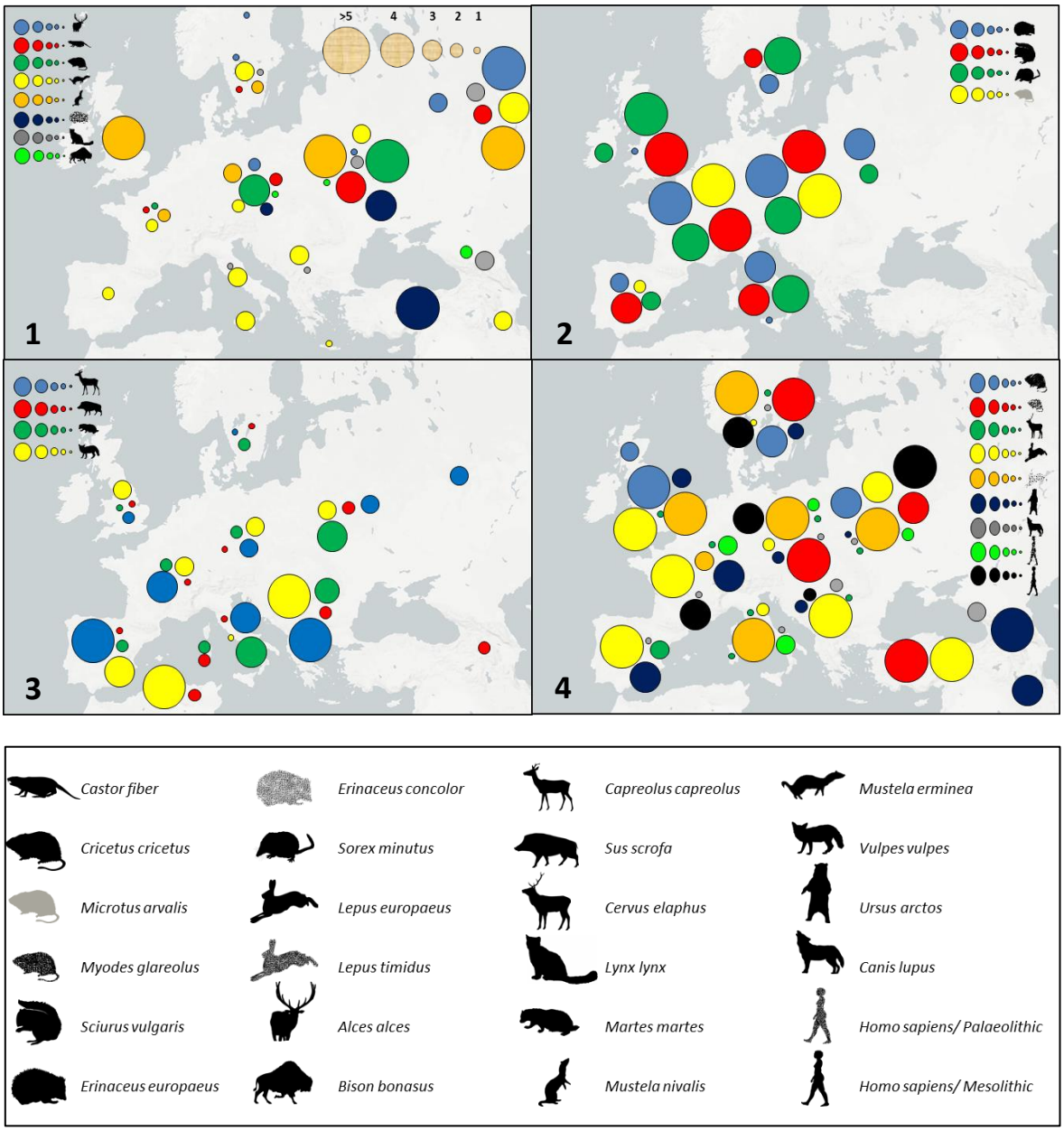

Figure 4.64 Maps displaying the four main patterns of distribution identified for private allelic richness identified. 1. East-West cline; 2. Western-Central Belt; 3. Southern richness; 4. Homogeneous. Circles represent private allelic richness values and each colour matches with the species.

4.4 Discussion

Understanding the phylogeographic pattern of modern humans in Europe is a question that will undoubtedly receive continued attention in the upcoming years. The new methods, such as aDNA, are contributing insights into the main events of European modern humans migration during the Pleistocene (Posth et al. 2016; Fu et al. 2016). MtDNA still represents an important marker for understanding these events, however, it has important limitations

(Rubinoff and Holland 2005). In this chapter, the phylogeographic patterns of modern humans in the European continent during the Palaeolithic and Mesolithic have been addressed from the perspective of a short control region mtDNA sequence, although this has allowed an unexplored comparison with other mammals. The resolution of these results for moderns human is similar to the results obtained for most of the other mammal species in the continent, where the control region have been used extensively. Therefore, the comparison at this low scale of resolution has implied caveats, but also the benefit of a more integrative and comparative analysis between species.

The genetic landscape and the diversity of the current modern human populations in Europe seem to be shaped mainly by the Upper Palaeolithic, specifically the middle and late rather than the early Upper Palaeolithic (Figure 3.58). This is consistent with previous studies based on longer fragments of the mtDNA, where the Upper Palaeolithic populations already represented the major genetic component of modern European populations (Fu et al. 2015, et al. 2016; Posth et al. 2016). The LGM had a tremendous impact on modern humans probably causing a severe bottleneck (Li and Durbin 2011; Posth et al. 2016) due to northern areas becoming uninhabitable and likely those remaining areas were fragmented (Stewart and Stringer 2012). The reduction in mitochondrial diversity found in Posth et al. (2016) is also seen here, even with a lower resolution, and is likely indicating the movement to refugia of hunter-gatherer groups. Limited numbers of geographical areas have been studied, so the location of these refugia is still under debate. Although the reappearance of migrants from southeastern areas in Central Europe mixed with a local postglacial population has been interpreted as a possibility of a certain stability and uniform population during the late Upper Paleolithic and possibly even into the Mesolithic in some areas (Sánchez-Quinto et al. 2012; Lazaridis et al. 2014; Fu et al. 2016; Günther and Jakobsson 2016).

The analysis through the different lithic cultures shows a clear diversification of the haplotype branches with the arrival of the Gravettian when more variability is seen. However, the Magdalenian shows less genetic variability with eight individuals sharing the same haplotype for the HVS-I fragment, even if they are geographically dispersed (Germany, France and Spain) (Figure 3.59b). The haplogroups U5 and U8 seemed to appear with the Gravettian lithic culture and had not been identified before in Aurignacean populations, indicating a possible turnover previously identified in Posth et al. (2016). Higher diversity for the Mesolithic populations than for the Palaeolithic ones is also found. The arrival of new haplogroups has contributed to increasing the diversity of the Mesolithic genetic landscape (see also Chapter 3).

The species-specific analysis of the 29 species examined in this chapter has shown the difficulty of identifying common patterns. The analysis of each species individually has proved the individualistic response of the species previously suggested (Stewart 2009; Stewart et al. 2010; Pedreschi et al. 2018). Identifying common patterns for phylogenetic trees topologies and network analyses has been shown to be a complex task that is characterised by great variability.

However, the novelty of the research presented in this chapter relies mainly on the comparative approach. Therefore, modern humans have been treated as other mammal species analysed. The first approach to identify similarities between all the species analysed was based on the different phylogenetic tree topologies found. Two main topologies can be identified that help to classify species based on this feature (Figure 3.60). The more representative topology found in 19 species is characterised by at least two main well-supported clades. This topology can be related with an allopatric structure of the populations where each clade has a different geographical origin (Pigot et al. 2010; Gascuel et al. 2015). However, the clades identified for some species analysed are not clearly related with different geographical areas, so the explanation behind this topology is complex and not only geographical arguments may not be the only causal factors. The second main topology was found in nine species and displayed a phylogeny where more than 80% of the haplotype sequences clustered in a main well-supported clade without a strong internal structure (Figure 3.60b). This might indicate the possibility of a demographic history not characterised by not a strong population structure and more likely involving a lack of isolation of populations. Modern humans sequences from the Palaeolithic and Mesolithic showed the second topology (Figure 3.60b) probably indicating that a poor geographical structure of the data and that genetic interchange between populations occurred (Fu et al 2016; Posth et al. 2016). Other species that share this topology with modern humans are not particularly ecologically related to our species, such as *Mustela erminea*, so more analyses were performed.

One of the main difficulties found in this research is related to finding commons pattern for the network analyses. The private allelic richness has shown more interesting results to propose a comparison based on similar patterns observed. Four main patterns were identified based on the distribution of the private allelic richness between species (Figure 4.64).

The first pattern (see Pattern 1 in Figure 4.64) shows and east-to-west cline where the highest values are found in the east and the lowest in the west. Eight species display this general pattern, with some particularities for each of them, where the transition from eastern to

western Europe seems to produce a loss in private alleles. This might indicate that these species have their origin in the east or/and the LGM refugia were more likely located in the east. For *Alces alces*, *Cricetus cricetus*, *Mustela erminea, Erinaceus concolor* and *Lynx lynx* this pattern is in agreement with previous studies, where at least one refugium in the east was suggested for each of these species. For *Castor fiber*, *Mustela nivalis* and *Bison bonasus* the situation is a little bit more complex due to the significant reduction of populations and diversity in recent times for *Bison bonasus* and *Castor fiber* (see Chapter 3). In the case of *Mustela nivalis* this might be reflecting the uncertainty about the subspecies and distinct populations previously found in this species (Lebarbenchon et al. 2010). However, in the case for example, of *Mustela nivalis*, *cyt b* is showing the possibility of pointing to the Carpathians for an important refugium for the species (McDevitt et al. 2012), scenario that is not found in this analysis.

The second pattern (see Pattern 2 in Figure 4.64) identified is related with a western-central belt that comprises the highest values of private allelic richness for *Erinaceus europaeus, Sciurus vulgaris, Sorex minutus,* and *Microtus arvalis*. Interestingly, this is in agreement with similar migration rates for these species and all of them are considered small mammals. The lack of phylogeographic patterns identified for the red squirrel (*S. vulgaris*) is not reflected for the private allelic richness indicating western and central Europe as possible areas of refugium for the species. The haplotype diversity has reinforced these results for *Erinaceus europaeus* and *Microtus arvalis* (Figure 4.63) where the highest diversity is found in central and western Europe indicating the importance of these areas as possible sources of diversity (Stojak et al. 2016). For *Sorex minutus*, the pattern is not as clear as for the other species and the high values for private allelic richness identified in the whole range of the species complicate the resolution. However, the importance of areas in France as a possible refugium has been suggested (McDevitt et al. 2010) and this result would be in agreement with that possibility.

For *Microtus arvalis*, this pattern may reflect a possibility of stable populations in these areas. However, *cyt b* analysis (Stojak et al. 2015) and new ancient DNA study (Baca et al. submitted) are indicated the possibility of a partial turnover during the Late Glacial/Holocene transtion at least in more eastern areas.

The third pattern (see Pattern 3 in Figure 4.64) is the one that is more related to the traditional southern refugia hypothesis (Hewitt 1999, 2004). *Capreolus capreolus*, *Sus scrofa*, *Martes martes* and *Vulpes vulpes* display this pattern were the highest values of private allelic richness are found in the south (east or west) and there is a decrease in private haplotypes in northern

latitudes. For *Capreolus capreolus*, *Sus scrofa* and *Martes martes* southern refugia have been suggested, however, all of them seemed to have complex demographic histories. The domestic (wild boar) and translocation (roe deer) relationships between humans and these species could have also affected the pattern described here (Randi 2005; Larson et al. 2007; Olano-Marín et al. 2014). For *S. scrofa*, modern reintroductions should also be taken into account when considering the significant population reduction that the species went through during the last three or four centuries (Danilkin 2001; Apollonio et al. 2010). *Vulpes vulpes* reflects a pattern that has not been previously reported, as the lack of phylogeographic pattern and homogeneous distribution of the species indicate a possible constant occupation of the territory (Teacher et al. 2011). Surprisingly, in the results here, *V. vulpes* shows a more traditional southern refugial pattern where Iberia, but especially the Balkans, represent important areas for private allelic richness. A new study has provided evidence of this and the possible contribution of Italy and the Balkans to the postglacial colonisation of central European populations (Statham et al. 2018).

The last pattern identified is a traditional "lack of phylogeographic pattern" (see Pattern 4 in Figure 4.64) as presented for example in Hofreiter et al. (2004) for the Late Pleistocene genetic landscape. However, in the present research, the current distribution of private allelic richness and diversity are also identified with a lack of pattern. For eight different species, a homogeneous distribution of private alleles was found and areas with much higher diversity than others were not identified (Figure 4.63 and Figure 4.64).

The absence of phylogeographic patterns in some species, such as wolves (Vila et al. 1999) has been explained by their high migration rate. In this case, the body size of the individuals does not seem the cause for this diversity pattern found, as four of the species are considered small mammals (*Arvicola amphibius*, *Myodes glareolus*, *Lepus europaeus* and *Lepus timidus*). The megafauna is represented by *Cervus elaphus*, *Canis lupus*, *Ursus arctos* and *Homo sapiens*. These species are characterised by a widespread range and this pattern of diversity can be explained by this more homogeneous distribution and their relative lack of ecological restrictions. *Homo sapiens* populations from the Palaeolithic and also the Mesolithic have this pattern, not showing particularly high values in southern areas. However, the private allelic richness is higher in the Mesolithic probably indicating fragmentation of populations in the continent during the LGM (Stewart and Stringer 2012), causing an increasing number of private haplotypes in different regions.

Particularly interesting are the cases of the bank vole, *Myodes glareolus*, and the red deer, *Cervus elaphus*, where phylogeographic patterns have been widely described and studies (Skog et al. 2009). For *cyt b*, this lack of phylogeographic patter has never been reported, and for example the bank vole, is well known for revealing a complex phylogeographical pattern with up to seven proposed clades, including some with subclades, allowing the resolution of both "northern" and "southern" refugia (Filipi et al. 2015). The results found here are not showing this strong phylogeographic structure, however, are consistent with multiple refugia and colonisation events (Filipi et al. 2015).

In the case of red deer, the results here does not seem to complement the role of northern Spain as a possible refugium and in the recolonisation phase after the LGM (Meiri et al. 2013; Rey-Iglesia et al. 2017). However, this new pattern could be potentially influenced by recent movement of the species (Perez-Espona et al. 2009, Olano-Marín et al. 2014). For the brown bear, on the other hand, this analysis is confirming the complex genetic landscape of the species. This has been reinforced by a recent study (Ersmark et al. in prep) where this complexity in the genetic history of the brown bear in Europe has been demonstrated.

Knowledge of the genetic diversity per species and per geographical region has helped with an understanding of the complexity of identifying a general pattern of diversity in the European continent. Relevant patterns were not found (Figure 4.63) and only certain differences between species were found (Table A3.1 in Appendix 3). The species that displayed a southern higher private allelic richness are interestingly the ones that are the significantly different species (Table A3.1 in Appendix 3). This might indicate that haplotype diversity is a good diversity index to identify clear latitudinal differences in diversity but not such a good proxy for the identification of refugial populations that show relatively less differentiation.

This analysis reinforces the results of chapter 3, showing that haplotype diversity, taken alone, provides misleading inferences for identifying refugia, even when diversity is shown on maps on a species-by-species and region-by-region basis (Maggs et al. 2008). The high haplotype diversity found, for example, across modern humans in the Palaeolithic and Mesolithic complicates any identification of possible refugia from the haplotype diversity values (Figure 4.63). However, the complementary analysis of the individual phylogeographic patterns based on phylogenetic tree topologies, networks and private allelic richness values are given insight to some patterns in all the species compared.

The geographical distribution of the species seems to be primarily shaped by species' biological traits such as tolerance ranges and adaptive capacity. Northern areas in the European

continent do not seem to be as hostile or barren as previously considered reinforcing the idea that simple regional restrictions cannot dictate the phylogeographic patterns observed (Pedreschi et al. 2018). The interpretation of the traditional expansion/contraction model for diversity does not seem to explain the different patterns shown in this chapter. The presence of dissimilar patterns that are shared by a different number of species can contribute to a better understanding of the influence of climate on their demographic history and also helping to find common ecological traits that contribute to shape those patterns. Further investigations, through other genetic markers and methodological approaches, may provide further insight into these patterns, helping to identify the recolonisation of these species after the LGM.

4.5 Conclusion

The interspecific analysis for all the species, with sufficient numerical and geographical coverage in Europe, enables a comparison between different individual species and includes inferences on the location of refugia for differently adapted mammal taxa. Furthermore, the resultant patterns from different phylogeographical studies are combined here to obtain a better understanding of each species' demographic histories.

Being aware of the caveats involved in using only one mtDNA marker, revealing a small part of the evolutionary history of a species, the twenty-nine species seemed to display different patterns. Hence, it is difficult to infer only one or two models to describe this variability. The individualistic response of the species is shown by the species-specific patterns presented here for 29 species and is defining the main results of this chapter. However, from the perspective of the diversity and private allelic richness, the results show four different patterns of distribution that can help to understand better certain phylogeographic affinities between species. Modern humans, from the Palaeolithic and the Mesolithic, are defined by one of these patterns characterised by a lack of phylogeographic structure where the genetic diversity indices analysed seem to be homogeneous across the different geographical regions analysed.

Chapter 5. Cyprus as an ancient hub for house mice and humans

5.1 Introduction

Knowledge of human history has traditionally been inferred from documentary evidence, material artefacts and remains from humans. Remains from animals, particularly domesticated and commensal species, have also provided information about the human cultures with which they were associated. Recently, these approaches have been enriched by the use of genetic data from modern and ancient human DNA (Haak et al. 2010; Hervella et al. 2012; Malmström et al. 2015; Lazaridis et al. 2017). Many species have been linked with human migration and other anthropogenic activities and therefore may reflect a similar phylogeographic pattern (e.g. Jones et al. 2013; Thomson et al. 2014; Heintzman et al. 2016; Herman et al. 2017). These organisms are considered bioproxies or 'living artefacts' of human migration history and can complement our knowledge of the archaeology and phylogeography of humans (Jones et al. 2013).

Several domestic species have already been used as bioproxies for human movement because of their close association with our species. For example, the spread of Neolithic culture to Europe has been corroborated by the domestication process of pigs (Larson et al. 2007) and goats (Naderi et al. 2007). Rats (Matisoo-Smith and Robins 2004; Naderi et al. 2007; Wilmshurst et al. 2008) and cats (Koch et al. 2015) have also been used as commensal bioproxies to track more recent movements. Furthermore, pathogens and parasites can also be used as proxies that show histories of colonisation and demography (Jones et al. 2013).

The western house mouse (*Mus musculus domesticus*) has been a commensal species since the beginning of stored grain (Weissbrod et al. 2017). Humans and mice have migrated together for about 12,000 years (Bonhomme and Searle 2012) travelling by land but also by boat (Cucchi and Vigne 2006). The colonisation history of the house mouse has been demonstrated to be informative in the study of the human population who transported them (Förster et al. 2009; Searle et al. 2009; Hardouin et al. 2010; Jones et al. 2012, 2013); Gabriel et al. 2015). One of the main examples of this close association between human and house mouse has been demonstrated for the Vikings. Viking mouse haplotypes were found on Madeira, suggesting a possible Viking visit to the island, unrecorded in historical records (Gündüz et al. 2001; Förster et al. 2009; Searle et al. 2009). Among subfossil house mouse remains on

Madeira found in 2010, radiocarbon dates of a house mouse mandible pre-date Portuguese colonisation and match the Viking hypothesis (Rando et al. 2014). In this context, house mouse phylogeography has been a powerful complementary tool to aid archaeologists and historians to understand recent human movement.

Due to its location and richness in natural resources, Cyprus provides the key context for understanding the dynamics of human migration and trade, from mobile foragers to early farmers and later regional polities, sedentism and seafaring, together with the associated socio-cultural changes in the Eastern Mediterranean (Knapp 2013). Recent excavations (e.g. Simmons and Mandel 2007) confirm early human activity in the Late Epipalaeolithic, identifying sites that suggest seafaring foragers and fishers made seasonal return journeys from the Levantine shores to Cyprus between 11000 and 9000 cal BC to exploit local terrestrial and marine resources. The earliest Neolithic occupation and permanent settlement on Cyprus goes back to ca. 9000 cal BC, showing evidence for cultivated or even domesticated cereals and pulses virtually contemporaneous with earliest appearances in the Levant and Anatolia. Triggered by increasingly unstable environmental conditions on the mainland, this represents the 'first successful overseas migration of farmers in the Mediterranean' (Knapp 2013), which would have also entailed transport of plants and animals (Vigne et al. 2014). In the course of the prehistoric Bronze Age, regional interaction through seaborne trade contacts between Cyprus, Anatolia and the Aegean increase, to become even more established, and extended to Egypt, during the protohistoric Bronze Age (Knapp 2013).

The Mediterranean basin is an area of considerable importance in understanding the close relationship between humans and the western house mouse. The initial commensalism of the house mouse began in the Near East (Cucchi et al. 2005). The range of house mice may have expanded slowly in the Near East by natural dispersal, but they had the potential to make rapid progress across the Mediterranean on boats (Cucchi 2008). The earliest evidence of such human-mediated transport is the presence of house mouse remains at an archaeological site from the Early Preceramic Neolithic on the island of Cyprus (late 9000 and 8000 BC) (Cucchi et al. 2002).

Although the house mouse arrived in Knossos, Crete, during the Bronze Age (2500 – 1000 BC), it is only during the Iron Age (1000 BC - 300 AD) that the house mouse spread throughout the western Mediterranean basin and to Western Europe (Cucchi et al. 2005). Around 1000 BC, the Phoenicians were the most prominent traders and they are therefore the most likely mediators of these mouse expansions (Bonhomme et al. 2011). House mice feed on stored

grain but even though agriculture spread over much of Western Europe during the Neolithic, the species did not spread out of the extreme east of the Mediterranean at that time (Cucchi et al. 2005) probably because: (1) there was limited human maritime exchange between the eastern and western Mediterranean at this early stage, and (2) there was competition with the native wood mouse (*Apodemus sylvaticus*), which may also have been commensal in small Neolithic settlements (Cucchi et al. 2005), such as Skara Brae, Orkney (Romaniuk et al. 2016).

Being the first island in the Mediterranean colonised by mice makes Cyprus an interesting case study. Indeed, records from the archaeological site of Mylouthkia (situated close to Paphos on the west of the island) showed that the first introduction of the house mouse occurred during the Neolithic period, approximately 8000 BC (Cucchi et al. 2002). The house mouse colonisation history should, therefore, reflect the ancient migration of Neolithic people, Mycenaean Greeks, Phoenicians, Romans, Francs and Ottomans. The substantial genetic diversity found in the mouse mitochondrial D-loop, with seven differentiated haplogroups described in Cyprus, is a consequence of the island being at a maritime crossroads, with a consequently complex colonisation process shaped by many introductions of house mice from several origins (Macholán et al. 2007; Bonhomme et al. 2011). Human trade and migration related to secondary colonisations can also be inferred through nuclear markers, such as microsatellites, through data on genetic relationship of populations and levels of genetic diversity (Hardouin et al. 2010; Jones et al. 2011b).

The purpose of this study is threefold: (1) to establish the different sources of house mice that colonised Cyprus, using the mitochondrial D-loop, (2) to establish the timing of these migrations and (3) to investigate the population structure of the house mouse on the island using microsatellites. We then compare these results with the previously known pattern of human migration to and from the island and consider the value of the house mouse as a bioproxy for studying modern human movement.

5.2 Material and Methods

5.2.1 Sample collection

A total of 191 house mice (*Mus musculus domesticus*) were collected in Cyprus in 2013 and 2015 (Table A4.2 in Appendix 4). The mice were sampled by trapping at 27 sites distributed across the island (Figure 5.1), and an additional 33 samples were collected from Patras, Greece, due to the historical link between Cyprus and Greece. Farms and agricultural settings

were targeted. The sampling follows the scheme from Ihle et al. (2006) and was made in order to minimise the sampling of highly related mice from the same family. All these samples were collected following local regulations for field collection of small mammals.

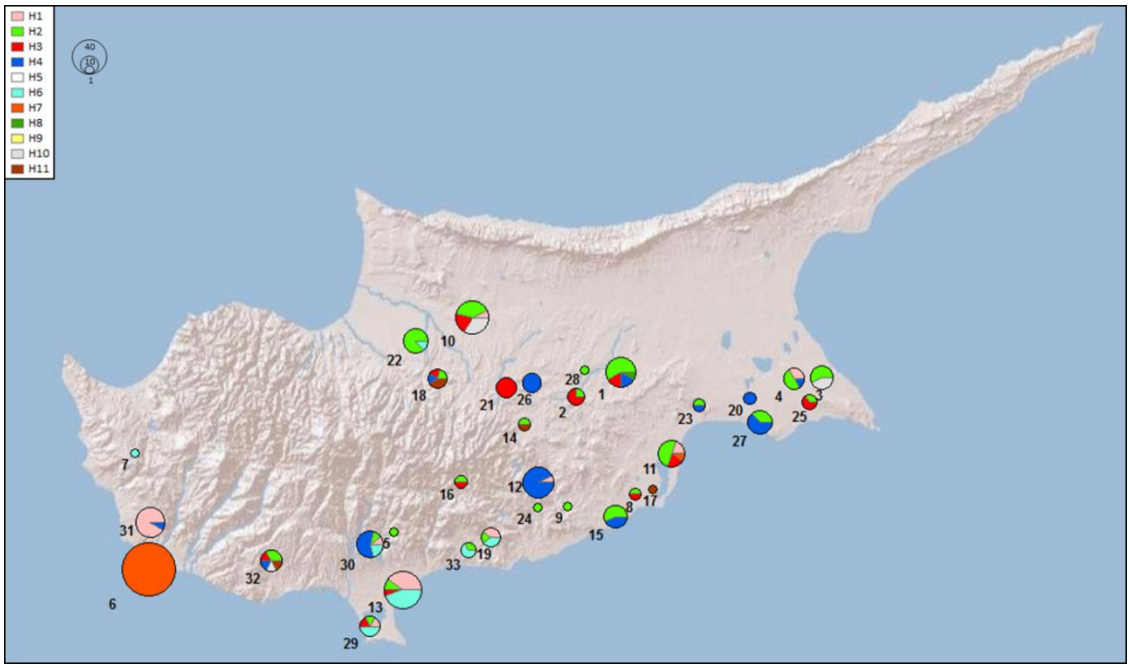

Figure 5.1 Map of *Mus musculus domesticus* sampling localities (numbered) on Cyprus and frequencies of each of the eleven different haplogroups (H1–H11) described by Bonhomme et al. (2011). These data incorporate new samples described here and those from Cucchi et al. (2006) and Bonhomme et al. (2011). 1. Athienou, 2. Dali, 3. Deryneia, 4. Frenaros, 5. Gerasa, 6. Geroskipou, 7. Kathikas, 8. Kiti, 9. Kofinou, 10. Kokkinotrimithia, 11. Larnaka, 12. Lefkara, 13. Limassol, 14. Lythrodontas, 15. Mazotos, 16. Melini, 17. Meneou, 18. Mitsero, 19. Monagroulli, 20. Ormideia, 21. Pera, 22. Peristerona, 23. Pyla, 24. Skarinou, 25. Sotira, 26. Tseri, 27. Xylophagou, 28. Agios Sozomenos, 29. Akrotiri, 30. Lemesos, 31. Paphos, 32. Post Geri, 33. Pyrgos. The size of the pie chart is related to sample size.

5.2.2 Mitochondrial DNA sequencing and analysis

Genomic DNA was extracted using the DNeasy Tissue Kit (Qiagen), following manufacturers' instructions. Mitochondrial D-loop (= control region) sequences of 894 bp were generated using the primers and protocol previously described in Hardouin et al. (2010).

To infer the phylogenetic relationships of *M. m. domesticus* in the Mediterranean basin, northern Europe and the Near East, our data set was combined with 1319 previously published sequences downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank/). The sequences were aligned using CodonCodeAligner Ver. 6.0.2 (CodonCode Corporation, Dedham, MA, USA),

BioEdit ver.7.2.5 (Hall 1999) and Seaview 4.5.4 (Gouy et al. 2010). A list with references of all the sequences used in the present study is available in Table A4.1 in Appendix 4.

There has been some divergence in the earlier literature regarding the assignment for the main haplogroups described for *M. m. domesticus* with two main nomenclatures independently developed (Bonhomme et al. 2011; Jones et al. 2011). There is an almost exact correspondence between the main clades described (1=C1; 2=C; 3, 5, 9=B; 4=F; 7=D; 8=D1; 10=A; 11=E) (Bonhomme and Searle 2012); the nomenclature of Bonhomme et al. (2011) was primarily used in this study, with occasional reference to the nomenclature by Jones et al. (2011).

Haplotype diversity and nucleotide diversity were calculated using DnaSP 5.10.1 (Librado and Rozas, 2009). The substitution model, TN+G, was selected using JMODELTEST, version 2.1.7 (Darriba et al. 2012), based on the Aikike Information Criterion (AIC, cAIC) and the Bayesian Information Criterion (BIC). This model was used in subsequent phylogenetic and population genetic analyses. The phylogenetic tree was calculated using MrBayes v. 3.2 (Ronquist et al. 2012) with a MCMC for 2 million generations, with the first 25% discarded as burn-in. *Mus musculus castaneus* (AF088879) and *Mus musculus musculus* (U47532) were used as outgroups. The aligned haplotypes were used to construct a NeighbourNet network with the hypothesis-poor algorithm of Huson and Bryant (2006) implemented in the Splitstree package (v. 4.10) with P distance as a default setting.

The mismatch distribution (MMD) was obtained using DnaSP v. 5.10.1 (Librado and Rozas, 2009), and compared with the expected distribution under a model of population growth. The (mutational) time since expansion was calculated as $\tau = 2\mu t$, where τ [tau] is a parameter deduced from MMD, t is the time since expansion in generations and μ is the mutation rate following Rogers and Harpending (1992). The D-loop mutation rate of 2 x10-7 substitutions site-1 generation-1 , inferred by Förster et al. (2009), was used assuming 1, 2 and 3 generations per year (Förster et al., 2009). Two neutrality test statistics, Tajima's D (Tajima 1989) and Fu's FS (Fu 1997), were used to detect recent population expansion. By comparing the value of the tests with distributions obtained by randomly placing the observed number of mutations onto 10,000 coalescent simulations of the genealogy, the significance of any departure from neutrality was determined.

Further demographic analyses were performed using BEAST, version 2.3.2 (Bouckaert et al., 2014). For each of the mitochondrial lineages identified on Cyprus, individual coalescent genealogies and skyline models (Drummond et al. 2005) of the effective female population size

were co-estimated using a shared model of sequence evolution. Separate genealogies and demographic models were used as the distinct maternal lineages are presumed to be independent and the result of separate introductions to the island.

With this model, the generation time is confounded with population size, so relative rather than absolute values of population size are estimated and used to show the pattern of demographic change with actual time. Base frequencies, kappa values for transition/transversion rates, and the α parameter of the gamma distribution of rates were all estimated along with the other parameters of the model.

The molecular clock rate was fixed at 4 x 10-7 substitutions site-1 year-1. This clock rate was previously estimated from mitochondrial D-loop variation and was based on the timing of the Neolithic expansion (Rajabi-Maham et al. 2008). It is broadly similar to rates that were estimated from mitochondrial genetic variation that had accumulated in other Eurasian rodents during the Holocene (Herman et al. 2014; Martinková et al. 2013). Given that intraspecific molecular clock rates are time dependent (Ho et al. 2005; Ho et al. 2014), it is important to use a clock rate estimated from genetic variation that accumulated over a similar timescale to the house mouse colonization of Cyprus.

As all the sequences belong to a single species, little variation in branch rate was expected; therefore a strict molecular clock was used. Prior parameter distributions are shown in Appendix 4 (Table A4.5). All simulations were repeated without sequence data to test the joint distributions of parameters obtained with the priors alone and to ensure that the results were not unduly influenced by these.

Posterior parameter distributions were obtained from 4 separate MCMC chains which were each run for 100 million generations, using different random seeds. The first 10 million generations were discarded as burn-in. The Log files were examined using TRACER, version 1.6 (Rambaut et al. 2014), to check for convergence. The log files were combined using LOGCOMBINER in BEAST, version 2.3.2 package. Bayesian Skyline Plots (BSP), showing the pattern of demographic change in each lineage, were obtained using TRACER version 1.6 (Rambaut et al. 2014). Maximum clade credibility (MCC) trees were identified from the posterior samples of genealogies, for each haplogroup, and posterior probability support for branches within each haplogroup were visualised using FigTree2 (http://tree.bio.ed.ac.uk/software/figtree/).

All the Cypriot and Greek house mouse mitochondrial D-loop sequences generated in the course of the study were deposited in GenBank (accession numbers MG937349-MG937536 and MG950367-MG950397)

5.2.3 Microsatellite typing and analysis

All the Cypriot and Greek house mice were genotyped for 18 unlinked autosomal microsatellites as in Hardouin et al. (2010). The microsatellite data were analysed and scored with GeneMapper (Applied Bioscience). This dataset was combined with Hardouin et al. (2010) and Linnenbrink et al. (2013) in order to compare the Cypriot data with Western European and Iranian populations. In order to calibrate the microsatellite allele size of the two datasets subsamples of individuals from the previous studies were genotyped with the new samples, without any discrepancies observed. The heterozygosity and the mean allele number per locus were calculated using Genetix 4.03 (Belkhir et al. 2004). Allelic richness was calculated using the rarefaction method available in HP-RARE (Kalinowski 2005).

A Discriminant Analysis of Principal Components (DAPC) (Jombart et al. 2010) was performed using the R-package adegenet (Jombart 2008); http://www.r-project.org/). This multivariate analysis derived the probability of individual membership in each different group. The software covered a range of possible clusters representing the total number of populations in the dataset. Principal components were retained as predictors for discriminant analysis in the individuals studied.

To address the differences within the island, STRUCTURE (Pritchard et al. 2000) was used. The software implemented a Bayesian clustering analysis. To find the possible number of clusters (K) into which our data can be divided, ten runs for each cluster were performed and the likelihoods were recorded. K was chosen using the criterion of Evanno et al. (2005). To draw the STRUCTURE diagram, CLUMPP (version 1.1.2 (Jakobsson and Rosenberg 2004)) and Distruct (Rosenberg 2004) softwares were used.

5.3 Results

5.3.1 Phylogenetic analysis

A NeighbourNet network was drawn using 529 haplotypes derived from the 1540 sequences, comprising our 221 new sequences (189 from Cyprus and 32 from Greece) and previously

published data (Figure 5.2a). Figure 5.2a presents the 529 haplotype network showing 11 identifiable haplogroups. This analysis helped the haplogroup identification in the Bayesian phylogenetic tree (Figure 5.2b) which are defined based on the network analysis. The 11 haplogroups showed in this study correspond exactly with the ones described in Bonhomme et al. (2011).

The 189 Cypriot sequences collected for this study can be seen in Figure 5.1. A total of 32 haplotypes, belonging to 9 of the 11 described haplogroups, were found in Cyprus (Figure 5.1). The haplotype diversity (*h*) and nucleotide diversity (π) were calculated for all the Cypriot samples together, giving values of 0.93 (*h*) and 0.00981 (π), respectively. The high values probably reflect the presence of unrelated mitochondrial DNA (mtDNA) sequences due to multiple house mouse introductions. This result is consistent with the high variability previously described on Cyprus (Macholán et al. 2007; Bonhomme et al. 2011).

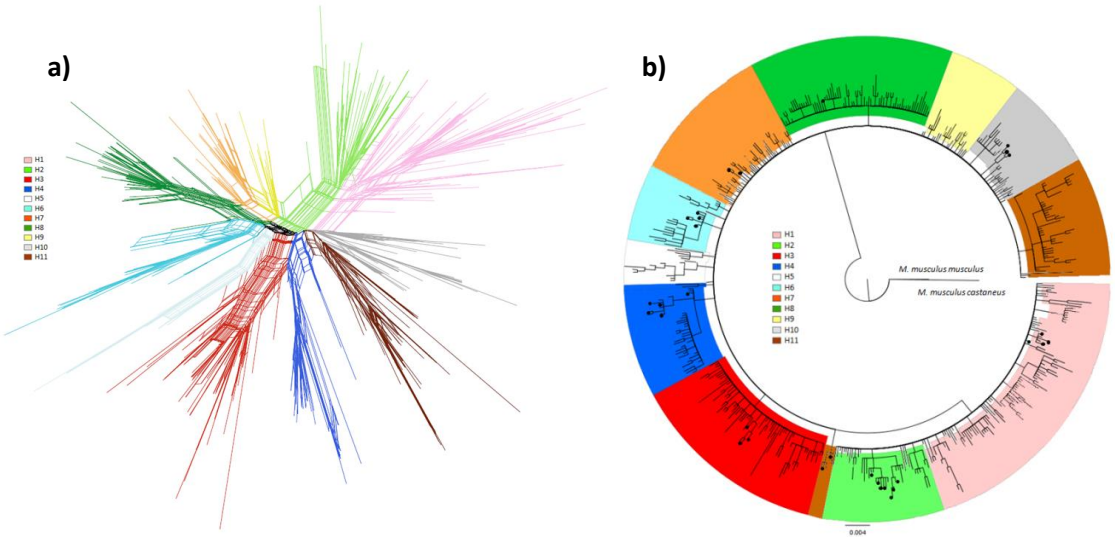

Figure 5.2 *Mus musculus domesticus* D-loop genealogy. (a) NeighbourNet network for the 529 haplotypes described from 1540 individual mitochondrial D-loop sequences. (b) Bayesian tree generated with MrBayes for 529 house mouse D-loop haplotypes described here and previously published. The numbered haplogroups defined by Bonhomme et al. (2011) are displayed by different colours; some of these haplogroups are paraphyletic in our analysis. Haplotypes present on Cyprus are represented with black dots.

A total of 65% of the Cypriot samples belong to three major haplogroups (H2, H4 and H7; i.e. clades C, F and D of Jones et al. (2011)). H2 is high in frequency around the Mediterranean basin and in the Near East, whereas H4 is present in 17% of the Cypriot samples and was previously associated with the British Isles and Norway (Searle et al. 2009). H7 was only found on two locations in Cyprus, Geroskipou and Larnaka (only one individual), (Figure 5.1; Table

A4.2 in Appendix 4) however it is distributed around the Mediterranean, with high frequency in North Africa, and also on the European continent (Figure 5.4).

5.3.2 Demographic analysis and dating

In Cyprus, demographic expansions of haplogroups H1, H3, H4 and H6 began ca. 500 years ago, according to the Bayesian skyline plots (BSPs; Figure A4.1 in Appendix 4) and unimodal mismatch distributions (MMDs; Figure A4.2 in Appendix 4). The expansion times from the MMDs with two generations give the closest correspondence with the timings obtained with the coalescent model, which is measured in real time, rather than generations (Figure 5.3; Table A4.3 in Appendix 4). The respective tMRCAs for these haplogroups are somewhat earlier, up to ca. 900 years ago (Figure A4.1 and Table A4.3 in Appendix 4), but these latter dates refer to the coalescence of the haplogroup members from Cyprus within the overall population, that is the time at which their ancestors diverged from the remainder of the haplogroup, rather than the colonisation or onset of demographic expansion on the island.

Demographic expansion of haplogroup H2 began about 1,400 years ago, according to both the skyline plot (Figure A4.1 in Appendix 4) and unimodal mismatch distribution (Figure A4.2 in Appendix 4) with two generations per year (Table A4.3 in Appendix 4), while the coalescence time was again earlier, ca. 3,700 years. The coalescence of haplogroup H7 was ca. 3,200 years ago (Figure A4.1 and Table A4.3 in Appendix 4), but this is due to the presence of a single divergent sequence from Larnaka, whereas the remaining 39 sequences are all identical and from Geroskipou (Figure 5.1; Table A4.2 in Appendix 4). This pattern of variation precludes the use of the mismatch distribution to estimate the timing of the demographic expansion and also confounds the skyline model (Figure A4.1 in Appendix 4), however the MMD (Figure A4.2 in Appendix 4) and the Bayesian genealogy (not shown) are consistent with recent introductions of this haplogroup to Cyprus rather than the tMRCA of ca. 3,000 years ago. The coalescence (tMRCA) of haplogroup H10 was about 2,400 years ago but the demographic expansion did not begin until ca. 2,000 years ago, according to the MMD with two generations per year (Figure 5.3; Table A4.3 in Appendix 4). The fit to this model was poor (Figure A4.2 in Appendix 4) and the coalescent model did not recover any signal of expansion (Figure A4.1 in Appendix 4), perhaps due to the rare appearance of this haplogroup in our sample (nine specimens). The coalescence and onset of demographic expansion for haplogroup H11 are recent, within the last 1,000 years, according to the Bayesian genealogy and mismatch models (Figure 5.3; Table A4.3 in Appendix 4) and although the latter appears to fit well (Figure A4.2 in

Appendix 4), the skyline model did not recover any demographic change (Figure A4.1 in Appendix 4), presumably due to the small sample size of only five sequences. Only one sequence was attributed to haplogroup H8, precluding further analysis.

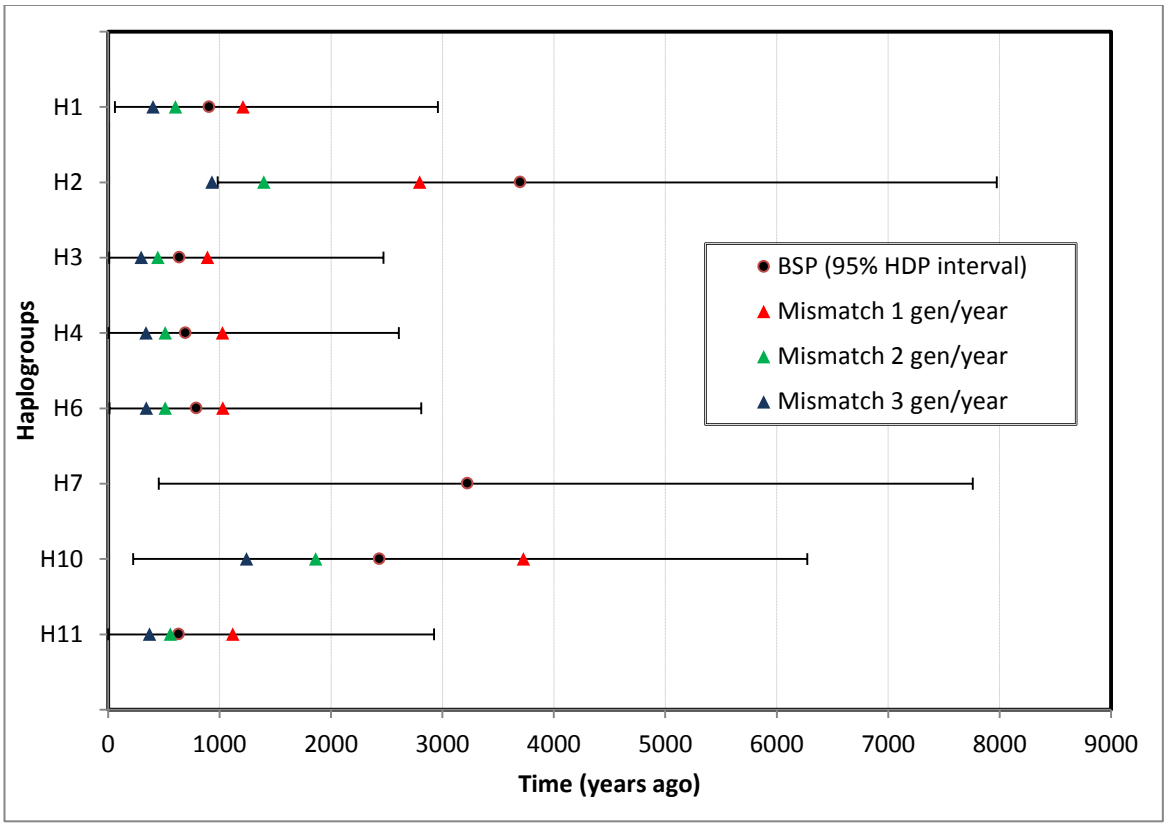

Figure 5.3 A summary of dates inferred from molecular data, for each *Mus musculus domesticus* haplogroup on Cyprus. The onset of demographic expansion estimated from mismatch distributions (MMD), using the mutation rate from Förster et al. (2009) and assuming one, two or three generations per year. Median tMRCA, from Bayesian genealogy sampling in Beast 2.3.2, is shown together with its 95% HPD limits.

Tajima's *D* values were negative for all haplogroups except H10 (Table A4.3 in Appendix 4), although only one was statistically significant (H7), indicating an excess of rare nucleotide site variants compared to what would be expected under a neutral model of evolution. An excess of low-frequency polymorphisms relative to expectation indicates a population size expansion (Tajima 1989). All the haplogroups, except H10, showed evidence of recent expansion. The more sensitive Fu's F_S also indicated expansion, except for H7, H10 and H11. This result is in agreement with BSP analysis however it might be due to subsequent replacement, given the rarity of H10 and H11 in the analysed sample, as mentioned before (H10=9 specimens; H11=5 specimens).

5.3.3 Population structure on Cyprus

A total of 18 microsatellites were analysed for all newly collected samples (Table A4.4 in Appendix 4). Heterozygosities, as well as mean numbers of alleles, were calculated for Cyprus. These values were compared with previous data from Hardouin et al. (2010) and Linnenbrink et al. (2013) to compare the Cypriot genetic diversity to that recorded for European and Iranian populations (Table 5.1). Those three datasets were calibrated using samples from Hardouin et al. (2010) that were re-genotyped. Mice from Cyprus displayed a very high observed heterozygosity (0.73) when compared to continental European populations (France, Germany and Greece; Table 5.1). The genetic diversity found in Cyprus is comparable to that in Iran (expected heterozygosity 0.89, average number of alleles per locus 15.1 – see Table 5.1). The two relatively recently founded populations of Cameroon (0.48) and Kerguelen (0.44) displayed low genetic diversity as expected (Table 5.1) (Hardouin et al. 2010; Ihle et al. 2006). The mean number of alleles per locus varied among localities across Cyprus from 1.38 to 8 with an overall mean of 4.06 (Table A4.4 in Appendix 4). The values for the expected heterozygosity within locations are similar to those from Western Europe, for example Cologne-Bonn, Germany (0.85), Massif Central, France (0.86) and Patras, Greece (0.83) (Table 5.1). The observed heterozygosity found on other islands are lower than on Cyprus (La Palma (0.75), Madagascar (0.67), Kerguelen (0.44) or Gough Island (0.70) (Duplantier et al. 2002; Hardouin et al. 2010; Bonhomme et al. 2011; Gray et al. 2014).

Table 5.1 Population genetic parameters for the 18 microsatellite loci typed in *Mus musculus domesticus* on Cyprus and other localities (previous studies; see text). N = number of individuals, H_{exp} = expected heterozygosity, H_{obs} = observed heterozygosity.

Countries/ Island group	Location	N	H_{exp}	H_{obs}	Mean number of alleles	Allelic richness
Antipodes Island	Antipodes Island	18	0.44	0.51	3.06	2.79
Auckland Island	Auckland Island	13	0.42	0.39	3.17	2.93
Cameroon	Kumba	46	0.61	0.48	6.67	4.3
Cyprus	Cyprus	191	0.84	0.73	15.89	7.66
Falkland Islands	New Islands	12	0.44	0.41	3.20	3.09
France	Anjou	20	0.81	0.62	9.39	7.28
France	Divonne les Bains	12	0.80	0.60	8.44	7.57
France	Espelette	38	0.77	0.60	9.94	6.85
France	Louan-Villegruis	12	0.76	0.67	6.83	6.39
France	Severac le Château	65	0.86	0.73	13.11	8.16

France	Nancy	15	0.80	0.66	8.28	7.2
Germany	Cologne-Bonn	58	0.85	0.61	12.83	8.13
Germany	Schömberg/Langenbrand	18	0.79	0.55	8.06	6.82
Greece	Patras	33	0.83	0.67	10.61	7.52
Iran	Ahvaz	46	0.89	0.81	15.17	9.14
Kerguelen	Cochons/ Cimetière	97	0.37	0.35	2.78	2.24
Kerguelen	Port-aux-Français	41	0.48	0.44	4.10	3.06
Macquarie	Macquarie island	40	0.42	0.38	3.33	2.61

Seven different clusters (K=7) were identified in the DAPC (Figure A4.3a in Appendix 4). All the continental populations from France, Germany, Greece and Iran clustered together, for Axis 1 and two representations. The population from Cameroon formed a separate cluster, probably due to the relatively recent colonisation event of this country by the house mouse. The Cyprus population also formed its own cluster, as expected for an island, but is more closely related to the European and the Iranian populations than the one from Cameroon (Figure A4.3a in Appendix 4).

The population structure on Cyprus was also investigated using DAPC (Figure A4.3b in Appendix 4). The number of detected clusters was coincident with the lowest BIC value identified for the DAPC analysis. Four clusters (K=4) were identified. The main cluster is composed by the populations collected in 22 locations. The specimens from Geroskipou formed a separate cluster possibly because the mice were collected in a restricted geographic area. Two other clusters were found, the first one is formed by specimens in Skarinou and Lefkara which are geographically close (8 km – Figure 5.1), which might explain the pattern. The second cluster is formed by Pyla and Gerasa although these populations are geographically distant (68 km – Figure 5.1). This pattern could be explained by a putative direct connection between the locations or as an artefact due to the small sample size at both locations (Pyla=2 specimens and Gerasa= 1 specimen).

A STRUCTURE analysis was performed on Cyprus to investigate population structure on the island. A value of K=4 was also found, in accordance with the DAPC (Figure A4.3b in Appendix 4). The most differentiated subpopulation is Geroskipou. Limassol and Monagroulli formed a second cluster, Lefkara and Pera a third one, all the rest of the island clustered together (Figure 5.5). In order to investigate the population structure further, we decided to remove individuals sampled in the outlier population of Geroskipou. In this scenario, K=9 was found. Locations like Limassol, Pera, Pyla and Tseri form separate clusters. The rest of the populations were more admixed, probably reflecting high gene flow across the island.

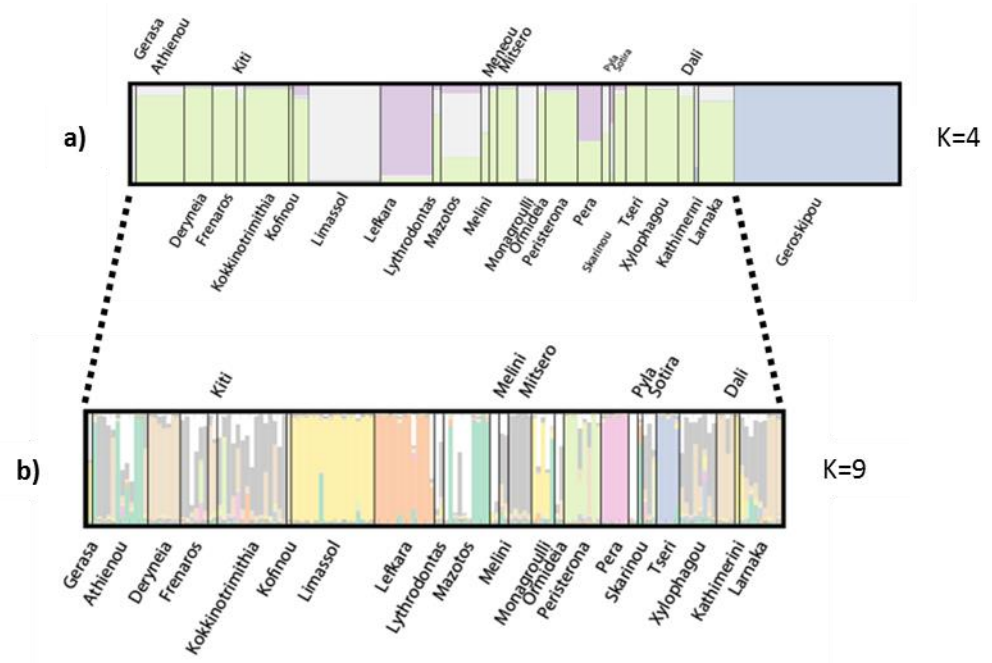

Figure 5.5 STRUCTURE analysis for the different locations across Cyprus. a) The results for the Structure analysis with K=4 are shown, represented by different colours. b) Structure analysis without Geroskipou (K= 9), represented by different colours. Each vertical bar represents a single individual, as well as the likelihood to belong to a given population group.

5.4 Discussion

5.4.1 Multiple colonisation events

The phylogenetic analyses revealed the presence of nine D-loop haplogroups on Cyprus out of the eleven haplogroups described for the western house mouse by Bonhomme et al. (2011). All five clades recognised in the alternative nomenclature scheme of Jones et al. (2011) were found on Cyprus. This mitochondrial diversity suggests a complex scenario with multiple colonisation events. This result was expected as Cyprus was the first island to be colonised by house mice in the Mediterranean basin (Cucchi et al. 2002). Due to its location in the eastern Mediterranean, Cyprus was a centre of commercial trade and this could have led to the high number of house mouse haplogroups found. House mouse populations on islands are considered to be resilient to new introductions (Hardouin et al., 2010), however with these results, it is suggested that there were potentially many more introductions of house mice than are apparent from these nine possible successful colonisation events. It is also likely that some of the haplogroup populations are derived from more than one introduction as well, as multiple colonisation events are already implied by the presence of individuals from the different haplogroups. The signature of the founding females will generally be kept in the

matrilineal line, being rare for invading females to successfully integrate into an existing population (Bonhomme and Searle 2012) making mtDNA a good signature of founding females and providing an indicator of human exchanges (Jones et al. 2013).

The molecular dating suggests that there may have been two main waves of colonisation (Fig. 4; Table A4.3 in Appendix 4), given that the tMRCAs and expansion dates from the MMDs for the haplogroups fall into two groups of broadly similar dates. However, the 95% HPD ranges in the coalescent analyses are wide and there is considerable overlap between them, so this suggestion must be treated with caution. Furthermore, it is important to bear in mind that the tMRCAs represent the estimated coalescence times for the haplogroup members from Cyprus, but their divergence from the remainder of the respective haplogroup might have occurred before the colonisation of Cyprus. This could be the case if members of the haplogroup successfully colonised Cyprus on more than one occasion, or this variability was present among the original colonists.

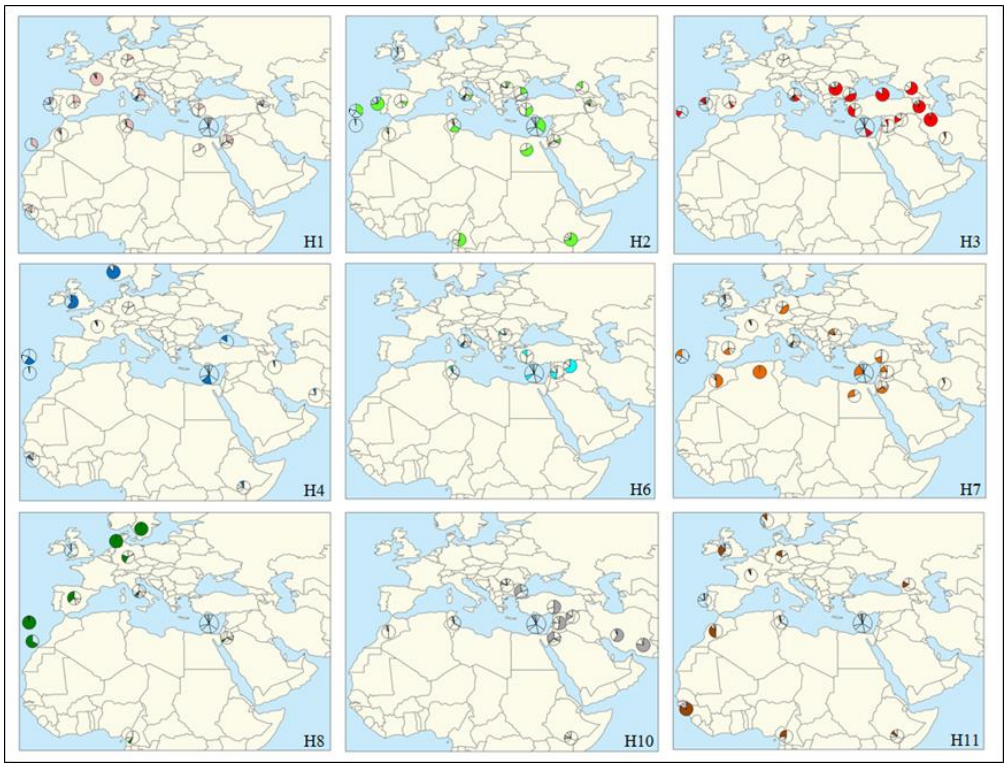

Figure 5.4 Geographical distributions in the Mediterranean and nearby areas for all the *Mus musculus domesticus* of all the D-loop haplogroups identified in Cyprus and constituent haplotypes. The pie charts display the proportion of individuals with the main haplogroups found on Cyprus.

Nevertheless, the presence and timing of these two putative waves of colonisation does seem plausible in the context of human history. The earlier wave, represented by members of haplogroups H2 and H10, dates to ca. 2,400-3,700 years ago, according to the coalescent

genealogy sampling (Figure 5.3; Table A4.3 in Appendix 4). These two haplogroups are present in the Near East (Figure 5.4), where *M. m. domesticus* originated, so this earlier colonisation is plausible. The time of introduction coincides with the Bronze Age or Phoenician cultures, when the volume of trade may have increased in the eastern Mediterranean. According to the molecular dating, their introduction was much more recent than the Neolithic, whereas there is evidence from the zooarchaeological record that the house mouse was present in Cyprus already by ca. 8,500 cal (Cucchi et al. 2002), suggesting that either the genetic signature of these earlier colonists has been replaced by that of more recent introductions or that current sampling does not cover the full range of mitochondrial genetic variation on Cyprus.

The demographic expansion of haplogroups H2 and H10 was delayed until much more recently, ca. 1-2,000 years ago (Figure A4.1 and Table A4.3 in Appendix 4). Once again the 95% HPD margins are broad, due to the nature of the coalescent modelling and the limited resolution of the data, therefore the signal and timing of this expansion must be treated with caution. Assuming that the dates are correct, the difference may be due to standing genetic variation within a single introduced population, more than one introduction from the source population, or delayed demographic expansion following introduction at the date of coalescence. The last of these could relate to changing ecological factors such as increasing agriculture or urbanisation, but is the least likely explanation, given the presence of clear splits within the trees inferred for each haplogroup.

The second wave of colonisation involved members of five haplogroups (H1, H3, H4, H6 and H11) and coalescent genealogy sampling dates this to the last millennium, from ca. 1,000 years ago (Figure 5.3; Table A4.3 in Appendix 4), although once again the uncertainty in this date should be acknowledged. If the date is accepted, this wave of introductions might be explained by the level of trade across the Mediterranean by that time. By then, the house mouse appears to have been arriving from two different directions, both the Near East and Western Europe, in the case of haplogroups H4 and H6 (Figure 5.4). Once again, the demographic expansion of these populations was more recent than their coalescence, in this case ca. 500 years ago, and the most likely explanation is that there were multiple introductions from the source population.

Our results support the findings of Cucchi et al. (2006) and Bonhomme et al. (2011) concerning a complex introduction scenario with a notable presence of H2 and H4. The widespread H2 is geographically associated with the Near East and the Mediterranean basin. H4 (clade F) is found at highest frequency in Nordic countries and the British Isles (Figure 5.4) and is a lineage

found in the Near East that apparently was spread around the northeast Atlantic by the Vikings (Searle et al. 2009). H8 (clade D) has also been associated with Scandinavia (Searle et al. 2009). Interestingly, H8 was detected in Madeira and the Canary Islands and could represent a possible Viking introduction (Förster et al. 2009). We are not suggesting a Viking introduction on Cyprus although there are data suggesting trade between Cyprus and Scandinavia during the Bronze Age (Ling et al. 2014); the introduction of H8 is most likely due to more recent trade. Only 8.5% of our samples belonged to H1, although this haplogroup was the most common (37%) in Cyprus in Bonhomme et al. (2011). This difference may reflect our much increased sampling effort all across Cyprus (Figure 5.1). The high mitochondrial diversity suggests that the ecological conditions found on the island were favourable to establish large local populations of new migrants (Bonhomme et al. 2011). Propagule pressure must also have been high due to the central location of Cyprus in the Mediterranean Sea.

5.4.2 House mice as a proxy to study human movement and genetic diversity

Associations between house mice and human phylogeography have been well described and accepted, especially in the peripheral distribution of the species, for example in northern and western Europe in association with Viking movements (Gündüz et al. 2001; Förster et al. 2009; Searle et al. 2009) or between Australia and the British Isles, demonstrating that the house mouse was brought to Australia during the British colonisation (Gabriel et al. 2011). Cyprus has a more complex history and it is more difficult to identify specific associations between human travellers and the house mouse haplogroups introduced. There are two possible reasons for this, firstly the high level of trade in the Mediterranean and secondly the geographical location of Cyprus, close to the origins of commensalism of *M. m. domesticus* with humans (Cucchi et al. 2005). However, even if the signal is not very clear, it does give a good insight into the relationships and trading activities of the island.

As house mice are moving using human-mediated transportation, their genetic diversity might correlate with human genetic diversity (Jones et al. 2013). The association between genetic diversity in mice and humans has been described in the Faroe Islands (Jones et al. 2011b). In this particular case low genetic diversity was found for both humans and mice. This relationship is also found on Cyprus where human genetic variability is relatively high, for example studies of Cypriot populations have revealed high mtDNA variability with six mtDNA haplogroups out of ten present across the island and high haplotype diversity (0.994) (Irwin et al. 2008; Badro et al. 2013). As expected from the geographical location of the island, Cypriot

people are related to Near Eastern populations (Jordanians, Lebanese, Palestinians and Syrians) (Badro et al. 2013). Future ancient DNA studies in this geographic region might help resolve the different waves of mouse introduction indicated by the present research.

5.4.3 Population structure in Cyprus

The 18 microsatellites genotyped for this study indicate a large mean number of alleles, high allelic richness and high heterozygosity on Cyprus when compared to other islands or even to continental populations (Hardouin et al. 2010; Linnenbrink et al. 2013). Indeed, similar high variability was, for example, present in Iran, which is also a phylogeographic melting pot for house mice (Hardouin et al. 2015). Furthermore, this similarity between Iran and Cyprus was confirmed in the DAPC analysis, which shows the population from Ahvaz in Iran closest to Cyprus (Figure A4.3a in Appendix 4). Interestingly, little population structure was found on the island (Figure 5.5; Figure A4.3b in Appendix 4), potentially because of a high level of goods transportation, and so mice, all around the island.

5.5 Conclusion

As expected for a commensal species, the western house mouse is characterised by a complex history shaped by founder events, genetic drift and admixture. Cyprus seems to be a good model that represents this complexity due to different introductions that are related to human movements or transport. The substantial house mouse genetic variability found on the island reflects the level of human genetic diversity there. Two main waves of introductions could be tentatively identified and dated, the first one corresponding to the Bronze Age and the second one to more recent movements. Genetic variation in house mice from Cyprus does, therefore, appear to be concordant with the complex human history of the island. As a result, Cyprus is unusual, because genetic variation in populations on islands is often low, due to the genetic dominance of the first colonisations. Instead, Cyprus has high genetic diversity reflecting the hub-like nature of the island with respect to traffic of both humans and mice.

Chapter 6. Travellers to the north: ancient DNA from the first house mice in the British Isles

6.1 Introduction

The western house mouse (*Mus musculus domesticus*) is nowadays a widely distributed commensal species that is closely associated with human settlements. Although present during the Bronze Age in the Netherlands and elsewhere in Europe (Brothwell 1981; Ijzereef 1981), it is thought that they probably did not spread widely into Europe from the Near East until the Iron Age (Cucchi et al. 2005). As a non-native British species, the earliest records in Britain date from the Late Bronze Age (Brady and Ellison 1975; Bell 1990; Lawson 2000). However, as these may not be secure (O'Connor 2010), house mice probably did not arrive into Britain until the Iron Age period, and then firstly into southern England (Harcourt 1979; Coy 1984), where the presence of structures to store grain, which represent an ideal niche for house mice, would have helped their introduction (O'Connor 2001).

Within the last 3,000 years alone, the British Isles have had multiple waves of human immigration. Demographic changes in human populations can lead to similar changes in the house mouse due to the close relationship between the two species, such that the house mice niche has been shaped by humans (Gabriel et al. 2011). Phylogeographic studies have shown that historical human movements impacted on current house mouse population patterns (Searle et al. 2009; Hardouin et al. 2010; Gabriel et al. 2011; Lippens et al. 2017). However, until now, conclusions have been drawn regarding the founding populations and colonisation routes based on modern phylogeography. Ancient DNA analysis of early house mice from Britain can test these assumptions and help us to understand the origins of the earliest house mouse populations in the British Isles.

Islands are interesting for the varied ways in which they can be colonised, as species can arrive by natural 'sweepstake' dispersal (Simpson 1940) or introduced by humans (Martinkova et al. 2013). In this study, we aim to identify the first colonisation of western house mouse in Britain, and the possible route that these first arrivals followed, based on ancient DNA (aDNA). To this end, ancient house mouse mitochondrial DNA (mtDNA) control-region sequences were obtained from four different Iron Age archaeological sites in southern England in an effort to sample some of the first populations that arrived to the British Isles. To understand the

phylogeographic history of the species, all modern mtDNA control-region data available for Britain were incorporated into the analyses.

6.2 Material and Methods

The archaeological record of small rodents are adversely affected by their small size, and sieving of soil into a minimum mesh of 2mm is necessary to recover them (O'Connor 2001; O'Connor and Barret 2006). The small size of the bones also makes them problematic for radiocarbon dating, as a single bone will rarely yield enough collagen for direct analysis. Therefore, the dating of mouse material often requires dating by context and association with artefacts.

A total of 16 ancient mouse mandibles from four British archaeological sites were collected, ranging from the Late Bronze Age to the Roman period (Figure 1) – Potterne, Wiltshire (n=7); Battlesbury Bowl, Wiltshire (n=5); North West Farm, Dorset (n=2); and Druce Farm Roman Villa, Dorset (n=2).

The site of Potterne, near Devizes, Wiltshire, was excavated by Wessex Archaeology between 1982-84, and comprises an extensive accumulation of dark anthropogenic soil deposits, up to 2m deep in places, covering an area of 3.5 ha. The 'midden-like' deposits are rich in artefacts and ecofacts, which result from the accumulation of manure and refuse from stock keeping and the repeated dumping and trampling of waste from human occupation and activities on and around the site over a 500 year period. Pottery typology and radiocarbon dating of charcoal from different levels within the deposit, and other cut features, suggest a date of 1,200-600 BC, encompassing the Late Bronze Age into the very Early Iron Age period (Lawson 2000). In addition to a large hand-recovered animal bone assemblage dominated by domestic mammals, small mammal remains were also recovered, mainly from sieved environmental samples, and house mouse remains have been identified from every level (Locker 2000). Although it was not possible to obtain radiocarbon dates from the mice directly to confirm this Late Bronze Age date, a radiocarbon date of 1,460-990 cal. BC (2σ) was obtained from charcoal that came from the same posthole as mouse mandible OG06 (Lawson 2000). The assumption is that all the mice remains are contemporary with the associated archaeological materials of Late Bronze Age (c. 1,200-600 cal. BC) and date from the same layers and contexts, although Locker (2000) does caution that some small mammal remains may have filtered down the deposit from higher levels.

The later prehistoric site of Battlesbury Bowl lies along a narrow chalk ridge immediately to the north of Battlesbury Camp, an Iron Age hillfort near Warminster, Wiltshire. Excavations by Wessex Archaeology in 1999 revealed features of Late Bronze Age to Middle Iron Age dates (base on ceramic style), including ditches, post holes, and almost 200 pits (Ellis and Powell 2008). The faunal assemblage is one of the largest collections of Early to Middle Iron Age faunal material from Britain. The presence of both house mouse and wood mouse in both the hand-recovered assemblage and the environmental sieved samples has been reported (Hambleton and Maltby 2008). The mouse mandibles included in this study came from the fills of pits (OG08, OG09, OG11, OG12) and a posthole (OG10), all of which were assigned Early to Middle Iron Age dates. Radiocarbon dating of a pig humerus, from the same context as mouse mandible OG11, provided a date of 420-100 cal. BC (2σ) (Ellis and Powell 2008).

The site at North West Farm, just outside the village of Winterborne Kingston to the north of Bere Regis, forms part of a programme of archaeological fieldwork, the Durotriges Project, designed to investigate native and Romano-British settlement across Dorset, focusing specifically on the archaeologically distinct Iron Age Durotriges tribe. The mouse remains were recovered from a chalk deposit (340) within one of three large storage pits in Trench H of the 2017 fieldwork season.

Druce Farm villa, Puddletown, Dorset, comprises a series of stone and flint constructed and timber post built buildings arranged on a courtyard plan surrounded by a series of ditched enclosures with features associated with industrial use (e.g. kilns/ovens and pits) (Ladle *in prep*). The site displays a number of phases of use between the 1st and 4th century AD. The samples were obtained from an extensive deposit of remains of microfauna which lay on the intact mosaic floor of a room in the main range of buildings, sealed by a deposit of degraded plaster and roof tiles. Analysis of the site and the deposit are ongoing (Ladle *in prep*), but this appears to represent a deposit of owl pellets, most likely derived from barn owls, which accumulated when the building was going out of use, and which was sealed by the collapsed roof. The mosaic floor has been typologically dated to the 4th century AD. Two water vole mandibles from the deposit were subjected to radiocarbon dating to elucidate the date of the building collapse, and returned dates of 1719 +30 BP (249-391 cal AD 95% probability) and 1768+30 BP (208-346 cal AD 95% probability). More details regarding the archaeological sites can be found in Table A5.1 and Text A5.1 in Appendix 5.

The morphological identification of the mouse mandibles was not easily resolved as the characters published to distinguish house mouse *Mus* spp. from *Apodemus* spp. (Chaline et al.

1974; Hilson 1986) are not thought to be reliable. Most identification characteristics depend on the state of wear of the teeth, or have not been tested against a number of individuals of each species, in the manner achieved for the identification of red deer (*Cervus elaphus*) versus fallow deer (*Dama dama*) (Lister, 1996). Specifically, some of the specimens (OG04, OG05, OG07, OG08 and OG09) were either missing the M1**,** where the distinguishing characters are present or are in an advanced wear stage. Therefore, mandibulae were sampled if they were recognisable as murids and could conceivably belong to either *Mus* or *Apodemus*.

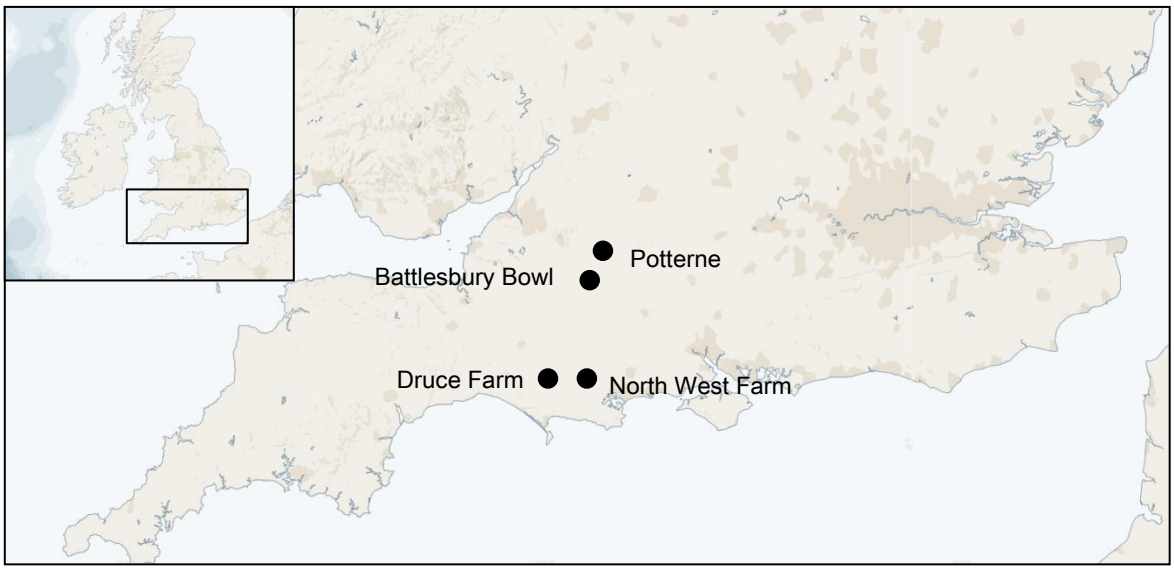

Figure 6.1 Map of the archaeological sites sampled in this study.

6.2.1 DNA Extraction and Amplifications.

Sample processing was done at the Ancient DNA Facility of the University of Huddersfield (England) under dedicated clean-room conditions supplied by a positive air pressure system. Full body suits, hairnets, gloves and face masks were worn throughout the sampling, extraction and PCR set-up processes. All tools and surfaces were constantly cleaned with LookOut® DNA Erase (SIGMA Life Sciences), as well as with bleach, ethanol and long exposures to UV light.

The surface of the mandibles was decontaminated by UV radiation for 10 minutes on each side. Whole or partial jaws were shaken with a steel ball inside a metal shaker in a Mixer Mill (Retsch MM400) for 15 seconds at 30x frequency. DNA was extracted from the resulting 10-50mg of powder produced, following the protocol by Yang et al. (1998) with modifications by MacHugh et al. (2000). Blank controls were included throughout the sampling procedure, extraction, PCR set-up to monitor for possible contamination.

The mtDNA sequences were amplified and sequenced in 12 overlapping 121 to 150 bp fragments (Table 6.1) covering a 915 bp fragment of the control region. Seven primer pairs were designed specifically for this study and five were taken from Jones et al. (2012) with minor modifications (Table 6.1). Each pair amplified overlapping fragments including the most variable region (between positions 15381 and 15663).

Three of the pairs of primers (2b, 2c and 3) were designed to be able also to amplify the other similarly sized murids of the *Apodemus* spp. (Table 6.1). This aided the identification at the genus level of jaws that presented identification issues and were not clearly attributed at the species level.

Table 6.1 Primers used to amplify the ancient mitochondrial DNA control-region sequence. Seven primers were designed for this study, while five were taken from Jones et al. (2012).

Fragment name	Primer Name	Primer sequences (5'-3')	Size (bp)	Reference
Fragment 1	Mm-1F	GCACCCAAAGCTGGTATTCT	146	Jones et al. 2012
	Mm-1R	TTTTATGACCTGAACCATTGATT		Modified from Jones et al. 2012
Fragment 2	Mm-2F	CCAAGCATATAAGCAAGTACAT	141	Jones et al. 2012
	Mm-2R	GTATGTCAGATAACACAGATAT		inverted
Fragment 2a	Mm-2aF	CAATATATATACCATGAATATTATCTTAA	121	This study
	Mm-2aR	AAGGGGATAGTCATATGG		This study
Fragment 2b	Mm-2bF	ATCTGTGTTATCTGACATACACC	150	This study
	Mm-2bR	TTTAATGGGCCCGGAGCGAGAA		This study
Fragment 2c	Mm-2cF	ACTATCCCCTTCCCCATTTGG	143	This study
	Mm-2cR	GTAAGAACCAGATGTCTGATAA		This study
Fragment 3	Mm-3F	TCTACCATCCTCCGTGAAA	145	Modified from Jones et al. 2012
	Mm-3R	TATGGGCGATAACGCATTTGAT		Jones et al. 2012
Fragment 4	Mm-4F	CTTTATCAGACATCTGGTTCTT	124	Jones et al. 2012
	Mm-4R	CACAGTTATGTTGGTCATGG		This study
Fragment 4b	Mm-4bF	CTTAAATAAGACATCTCGATGG	142	This study
	Mm-4bR	TAGACTGTGTGCTGTCCTT		This study
Fragment 5	Mm-5F	CTTTCATCAACATAGCCGTCAA	129	Jones et al. 2012
	Mm-5R	CATTTATGTCTAACAAGCATGAA		This study
Fragment 6	Mm-6F	CACCTACGGTGAAGAATCATT	146	Jones et al. 2012
	Mm-6R	TGTTTTTGGGGTTTGGCATTAA		Jones et al. 2012
Fragment 7	Mm-7F	CTCAATACCAAATTTTAACTCTC	144	Jones et al. 2012
	Mm-7R	GTCATATTTTGGGAACTACTAG		Jones et al. 2012
Fragment 8	Mm-8F	CTATCAAACCCTATGTCCTGA	140	Jones et al. 2012
	Mm-8R	CTTGTTAATGTTTATTGCGTAA		Modified from Jones et al. 2012

The alignment of the sequences from this study and previously published house mouse sequences from Britain (Prager et al. 1993; Nachman et al. 1994; Searle et al. 2009; Jones et al. 2010) were used to create a Bayesian inference phylogenetic tree with MrBayes (Ronquist et al. 2012), using the parameters previously calculated in JModelTest (Posada 2008). The analysis was run for 5 million generations with four chains and with a 25% burn-in. We used FigTree v.1.3.1. in order to visualise the tree and clades/haplogroups were assigned and named following previous nomenclature (Bonhomme et al. 2011; Jones et al. 2010) (1=C1; 2=C; 3, 5, 9=B; 4=F; 7=D; 8=D1; 10=A; 11=E).

A median-joining network (Bandelt et al. 1999) was constructed in POPART (Leigh and Bryant 2015) for all the modern control-region sequences from Britain and the ancient sequences obtained for *Mus musculus domesticus* in this study.

6.3 Results

In total, genetic material from 13 samples was obtained, of which eight individuals were identified as *Mus musculus domesticus* , four as *Apodemus sylvaticus*, and one as *Apodemus flavicolis* (Table 6.2). The Bronze Age site (North West Farm) only yielded DNA for one individual, attributed to *A. sylvaticus.* Therefore, the presence of the western house mouse in Britain during the Bronze Age remains unconfirmed by molecular analysis. The Roman period site (Druce Farm) also yielded only *A. sylvaticus* (n = 2). Other *Apodemus* spp. were found at the Iron Age sites of Potterne (one *A. sylvaticus*; n = 1) and Battlesbury (*A. flavicolis*; n = 1). However, in both of these sites, we found eight *M.m. domesticus* samples (three at Potterne and five at Battlesbury). These results highlight the uncertainty in the identification of Murid species in the archaeological record based on jaw morphology.

Table 6.2 Details of the ancient murid samples analysed in this study.

Specimen	Location	Period	MtDNA Species ID	Total Length (bp)
OG01	Potterne, Wiltshire	Iron Age	*Mus musculus domesticus*	74
OG02	Potterne, Wiltshire	Iron Age	*Mus musculus domesticus*	772
OG03	Potterne, Wiltshire	Iron Age	*Mus musculus domesticus*	576
OG04	Potterne, Wiltshire	Iron Age	*Mus musculus domesticus*	772
OG05	Potterne, Wiltshire	Iron Age	no amplification products	n/a
OG06	Potterne, Wiltshire	Iron Age	*Apodemus sylvaticus*	304

OG07	Potterne, Wiltshire	Iron Age	*Mus musculus domesticus*	744
OG08	Battlesbury Bowl, Wiltshire	Iron Age	*Mus musculus domesticus*	772
OG09	Battlesbury Bowl, Wiltshire	Iron Age	*Mus musculus domesticus*	744
OG10	Battlesbury Bowl, Wiltshire	Iron Age	*Mus musculus domesticus*	354
OG11	Battlesbury Bowl, Wiltshire	Iron Age	no amplification products	n/a
OG12	Battlesbury Bowl, Wiltshire	Iron Age	*Apodemus flavicolis*	259
OG13	North West Farm, Dorset	Bronze Age	*Apodemus sylvaticus*	255
OG14	North West Farm, Dorset	Bronze Age	no amplification products	n/a
OG15	Druce Farm, Dorset	Roman Period	*Apodemus sylvaticus*	131
OG16	Druce Farm, Dorset	Roman Period	*Apodemus sylvaticus*	104

The longest fragment obtained for *M.m. domesticus* was 772 bp (OG04), from position 122 to 893 of the reference house mouse mitogenome. The shortest fragment (OG01) had a length of 74 bp, so we were unable to assign it to a clade.

All house mouse individuals analysed here date to the Iron Age, and clustered in two main clades/haplogroups (D1/8 and E/11), described previously in modern samples from Britain (Table 6.3). Two individuals clustered in clade D1 and six individuals belonged to cluster E (Figure 2). Interestingly, clade F/4, the most widespread clade in Britain today, was not present in our sample set. Three samples (OG04, 07 and 08) belonged to the same haplotype, and the rest of the sequences were unique.

Unfortunately, the fragments obtained for the *Apodemus* spp. are too short for meaningful integration into wood mouse (*A. sylvaticus*) or yellow-necked (*A. falvicolis*) mouse phylogeographies. Phylogeographic studies based on the control region for wood mice species are scarce, so that further exploration of the data was not possible.

Table 6.3 Variable positions in control region sequences of archaeological *Mus musculus domesticus* samples from the British Isles between positions 122 and 893, compared with the reference house mouse mitogenome. Differences are indicated, whilst a period denotes identity. Missing sequence data are denoted by question marks. Sequence codes are given in the first column. In the final column, each sample has been assigned to a mitochondrial clade by means of its relative position in a Bayesian phylogenetic tree and the mutations sites compared with modern samples.

	122	123	123i	124	125	134	136	147	150	151	162	164	172	173	174	193	194	199	201	203	218	272	304	339	532	545	630	632	676	703i	703v	703vi	703vii	703viii	703ix	703x	703xi	703xii	703xiii	703xiv	737	867	869	883	887	Clade
U47430	**T**	**A**	*****	**A**	**A**	**T**	**A**	**T**	**T**	**C**	**A**	**C**	**A**	**T**	**A**	**A**	**C**	**T**	**A**	**C**	**C**	**T**	**C**	**A**	**C**	**C**	**A**	**A**	**T**	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	*****	**C**	**G**	**G**	**A**	**T**	**E**
OG01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	.	.	.	.	.	.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	E
OG02	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	T	.	.	.	.	.	.	*	*	*	*	*	*	*	*	*	*	*	.	.	.	.	.	E
OG03	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	?	?	.	.	?	?	?	?	?	?	?	?	?	?	?	?	?	T	.	.	.	.	E
OG04	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*	*	*	*	*	*	*	*	*	*	*	.	.	.	.	.	E
OG07	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	?	.	.	.	.	.	.	.	*	*	*	*	*	*	*	*	*	*	*	.	.	.	.	.	E
OG08	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*	*	*	*	*	*	*	*	*	*	*	.	.	.	.	.	E
OG09	.	.	*	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	T	.	T	?	.	.	T	T	.	.	C	*	*	*	*	*	*	*	*	*	*	*	.	A	.	.	C	D1
OG10	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	.	.	.	T	.	T	.	.	T	T	T	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	.	.	C	D1

6.4 Discussion

Britain is at the periphery of the western European expansion of *M. m. domesticus* if, as believed, the subspecies started its spread from the Near East associated with modern humans at around 8000 BC (Cucchi et al. 2005; Hardouin et al. 2015).The phylogeography of the western part of the Atlantic geographical range of the western house mouse has been particularly well studied (Förster et al. 2009; Searle et al. 2009; Jones et al. 2011). Britain has a relatively high genetic variation based on haplotype diversity and the presence of different clades (Searle et al. 2009).

This study complements the understanding of the colonisation of the British Isles by the western house mouse by showing that two clades, D1 and E, were present in southern Britain during the Iron Age. These two clades may represent different human movements into Britain.

Clade D1 has been previously suggested to play a fundamental role in the distribution of the species across the Atlantic coast. Sequences of this clade are common in northern Germany today as well as Scandinavia, but also in more peripheral regions such as Madeira and the Canary Islands (Gündüz et al. 2001; Förster et al. 2009; Bonhomme et al. 2011). The colonisation of these islands by clade D1 has been attributed to Danish Viking movements first to Madeira and then to the Canary Islands followed by the Portuguese settlement (Förster et al. 2009; Bonhomme et al. 2011). The presence of this clade also in the Faroe Islands (Jones et al. 2011b) has also shown a more complex scenario than a simple Norwegian Viking colonisation (related with clade F) as has been previously suggested and pointed to a more southern Norwegian origin or even a possible continental origin (Jones et al. 2012). However, the presence of this haplogroup in Britain since the Iron Age is more in agreement with an introduction from continental Europe rather than a later Danish Viking introduction. If clade D1 is, as supported by this and other phylogenetic analyses (Jones et al. 2011), a subclade that derives from clade D, it can be hypothesised that the continental route took more time and probably allowed the appearance of this clade in western Europe (including Scandinavia). We can also infer this from the distribution and high frequency of D1 in western Europe and lower representation in the east (Figure 6.3).

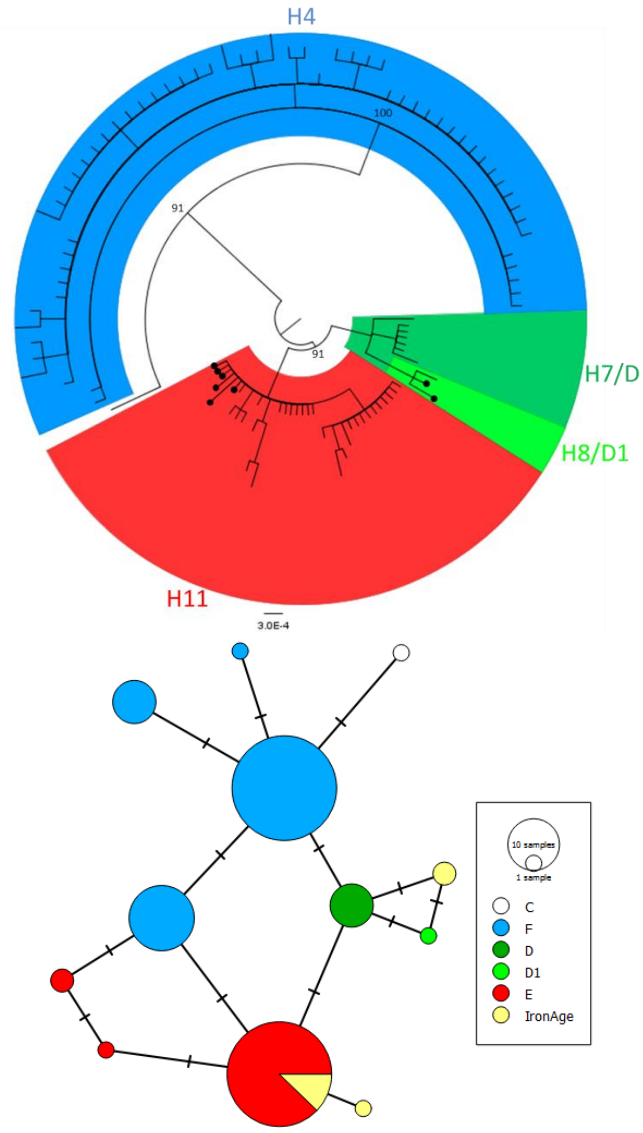

Figure 6.2 a) Bayesian phylogenetic tree for all the British mtDNA control-region sequences. Ancient samples indicated with a black dot. b) Median-joining network calculated with POPART for all British sequences available.

Clade E is well represented in modern southern British samples, but also in areas in the north of the country, as well as in Ireland (Searle et al. 2009; Jones et al. 2011). Searle et al. (2009) noted that the distribution of E appears to reflect the colonisation of Britain from the European mainland during the Iron Age. As this clade is not well represented in central Europe, it has been suggested that it did not arrive with people overland but via a maritime route, possibly transported from the Mediterranean by the seafaring Phoenicians in the late Bronze Age/Iron Age (Bonhomme and Searle 2012). However, the presence of E in northern France may provide evidence that this area was the continental source of British house mouse populations (Jones et al. 2011), which has been further supported by zooarchaeological evidence of house mice in this area during the Iron Age (Cucchi et al. 2005). The presence of E

in the Iron Age in Britain demonstrates that the introduction occurred at least as early as in the Iron Age, and was the result of an ancient expansion caused, most likely, by trade routes between Mediterranean cultures (Phoenicians and Greeks) and the Atlantic seaboard, including Britain, during this time (Cunliffe 2001).

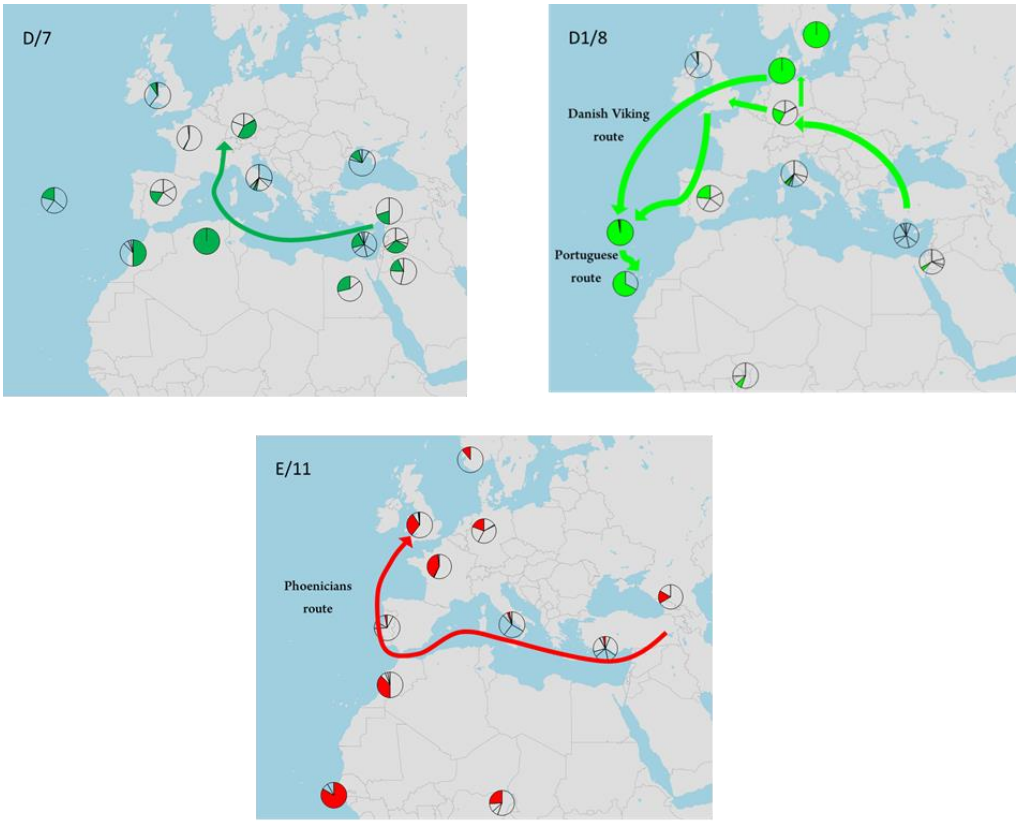

Figure 6.3 Maps of the distribution of clade D/7 (a), D1/8 (b) and E/11 (c). The hypothesised routes are represented with colour arrows.

The distribution data for the western house mouse mtDNA clades from both ancient and modern British DNA samples allow us to make a synthesis for the island's first colonisation. Five main clades are represented in modern British samples (C, F, D, D1 and E), while only two of these have been found in the Iron Age sites analysed (D1 and E). The presence of these two clades in Britain since the Iron Age had previously been hypothesised from the analysis of modern samples (Bonhomme and Searle 2012; Jones et al. 2012). This study provides the first direct evidence of the presence of D1 and E in Britain from at least the Iron Age period.

6.5 Conclusion

The presence of clades D1 and E during the Iron Age in Britain has provided evidence of an early house mouse colonisation that may be related with Iron Age expansions of humans. This

is in agreement with what has been previously suggested for clade E, but gives a new perspective on the origins of clade D1 in Britain, which has traditionally been linked to the movements of Danish Vikings.

Chapter 7. Discussion

7.1 Overview of the thesis

In recent times many advances have been made in order to collect and analyse genetic data from many different mammal species and identify the main phylogeographic patterns inferred by these data. Despite most of scientific studies addressing phylogeographic questions, there is a traditional species-specific scheme that analyses the data from the perspective of each taxon. Few studies use a holistic approach, covering multiple taxa, and try to understand common patterns. This thesis has investigated different approaches in comparative phylogeography to understand the demographic patterns for mammal species and to compare them, searching for similarities and differences between them.

Europe has been the principal area of study given the extensive amount of genetic data that is available. This research has laid its foundations in recompiled these data, reanalysed it, in a new framework, common across different taxa and interpreting the results based on an integrative approach. Nevertheless, the "genetic record" has some deficiencies such as varying levels of resolution based on genetic markers and/or fragment lengths. The standard method developed during this research has constructed a common framework that allowed the comparison between species (Chapter 2).

Genetic diversity has been the core of this research by describing the diversity distribution across Europe, helping to identify areas of richness and purity in modern distributions (Chapter 3). Genetic diversity and phylogeographic patterns have been examined for each species, describing the main results found in a more traditional and descriptive phylogeographic approach (Chapter 4). For each species, new phylogeographic inferences have been discussed, contradicting or reinforcing previous knowledge by using a meta-analysis of the genetic data available for the control region. Common trends in Europe for genetic diversity were also analysed and compared between species including an assessment of the importance of the LGM to the current patterns (Chapter 4). In the last two chapters of this thesis (5 and 6), the commensal species, the western house mouse, has been studied in two different insular contexts and from the perspective of modern and ancient DNA analyses. This helps to understand the pattern of human colonisation and the human transport of this species.

This chapter discusses the key findings of this research in the context of existing knowledge and their relevance to the understanding of comparative phylogeography in Europe. Research limitations are also considered and suggestions made as to future research.

7.2 Findings and original contribution to knowledge

The developed method in Chapter 2 to assess the comparative approach between different mammal species and the reliability of genetic diversity indices, with the reconstruction of phylogeographic patterns, assigned the context for the comparative analysis developed in the thesis. Meta-analyses like this are a useful tool in collecting data from numerous studies to identify common effects with increased power (Borenstein et al. 2009). It has proved to be a simple and clear approach to introduce an extensive meta-analysis perspective into genetic data providing useful insights for phylogeographic purposes. The methods previously developed by Pedreschi et al. (2018) and Lumibao et al. (2017) have been expanded and updated to be applied to mammal species with a European range and using the same genetic marker. This method has been applied to 29 different mammal species in Europe.

The genetic diversity paradigm to understand refugia has also been tested in a new common framework (Chapter 3 and 4). First, in Chapter 3 general trends in Europe were identified indicating the more complex relationship between latitude and diversity previously reported. This study shows that the southern richness and northern purity for genetic diversity are not confirmed when a large number of taxa is added to the equation and that southern areas showed no higher diversity than northern regions. Furthermore, three different temporal periods were compared (Pleistocene, Holocene and Modern) for twelve species where ancient DNA was available. This analysis showed a higher diversity during the Pleistocene for seven species and not significant variation in four species. Only *Homo sapiens* were found to be more diverse in the Holocene than in the Pleistocene.

Each of the mammals has been analysed individually after having systematically reviewed the literature and compiling the genetic data available, reanalysing it and interpreting it (Chapter 4). This section of the chapter probably represents the first attempt to describe the phylogeography of such an extensive number of species using the same genetic marker and has contributed to a better understanding. The disparity in patterns found suggest that species responded differently to climatic changes, as previously suggested (Stewart et al. 2010) and that species-specific analyses also need to be considered in the context of the previous work developed.

In Chapter 4, a new approach to identify potential refugial areas in the continent has been established based on identifying areas were private allelic richness displayed high values and complemented by haplotype diversity indices and phylogenetic tree topologies. This research continues the comparative approach legacy (Taberlet et al. 1998; Petit et al. 2003; Hewitt 2004; Maggs et al. 2008) but adding new formulas to try to identify similarities between species. Four different patterns have been identified contributing a new framework where the species can be compared. Modern humans, from the Palaeolithic and the Mesolithic, are defined by one of these patterns characterised by a lack of phylogeographic pattern found where the genetic diversity indices analysed seem to be the same across the different geographical regions analysed.

In Chapter 5, two main waves of colonisation were found in the Mediterranean island of Cyprus for the western house mouse, *Mus musculus domesticus*, inferred by modern mtDNA data. These two different colonisation events are likely related to human transport first during the Bronze Age/Iron Age, and second with more recent transportation. This study was complemented by the microsatellite analysis to understand the variability within the island complementing the mtDNA approach, confirming the high gene flow found in the island between populations.

In Chapter 6, the first ancient DNA study in the British Isles for the western house mouse has been developed. The presence of two main clades during the Iron Age in Britain has provided evidence of an early house mouse colonisation that may be related with Iron Age human expansions.

7.3 Implications

The use of the method developed in Chapter 2 allows for quantitative analysis of the genetic data based on the database produced and the analysis in a common framework for all the species included in this research. This method is used in Chapters 3 and 4. The main implication of Chapter 3 is that the general trend of genetic diversity based on mammals is less straightforward than previously presented in the literature. The framework provided by this study should aid with more and different genetic indices to address the general pattern of diversity in Europe.

In Chapter 4, each species is presented individually but the compilation and reanalysis of all the available sequences have given insight and a new perspective on the treatment of the genetic data and the need for more extensive analyses as a literature review on their own can be misleading and studies that might be difficult to compare between them seem to be the rule rather than the exception. In this same chapter, the comparative approach has proved the importance of using the same genetic marker to infer phylogeographic patterns.

The geographical ranges of mammals alter as climate changes, but predicting how each species will respond is still difficult (Helmuth et al. 2002; Broitman et al. 2009). Understanding the distributions during previous climatic events, such as the LGM, provide valuable insights into migration and a population's resistance to changes. Genetic data have been essential to understanding the evolutionary legacy of the ice ages (Hewitt 1996, 2004) and this will continue in the upcoming years.

The main implications of Chapters 5 and 6 are related to highlighting that the analysis of modern and ancient sequences can be complementary. Both approaches can give important perspectives to address phylogeographic questions related to the species of interest, but also being used as a bioproxy for human dispersal, as the western house mouse has proved in these two studies.

7.4 Research limitations

The examination and testing of general relationships that enable asking phylogeographical questions on a larger scale than usually possible at a single taxon study level are allowed by meta-analyses (Kaiser et al. 2006). However, there are specific limitations associated with such a study. Below is a summary of the limitations encountered during this research, however, the specific research limitations are covered in each chapter and discussed accordingly.

7.4.1 Mitochondrial DNA as a marker

One of the main caveats of this research is related with the genetic marker used. The well-studied mitochondrial DNA has been the centre of this thesis and also the most common genetic marker used to infer phylogeographic patterns (Petit et al. 2005; Galtier et al. 2009). MtDNA benefits from a higher rate of mutation than nuclear DNA, so that the events that allow for the reconstruction of the genealogy are more frequent, being able to resolve branching structure in the maternal genealogy (Macaulay and Richards 2013). These are the main reasons for selecting it to address this project; however, it can only reveal a small part of

the evolutionary history of a species. One of the caveats for using mtDNA is that the benefit of the high mutation rate is engendered by mutation at the same positions, leading to alternative branching orders being equally plausible for sets of sequences. Some critiques to mtDNA phylogeography often ignore that this marker has led the way in the reconstruction of many different species demographic histories from genetic data.

Nuclear DNA studies have revealed different phylogeographic and demographic histories for some species (e.g. Posth et al. 2017) but have also confirmed similar results for both markers (e.g. Hardouin et al. 2010). Chapter 5 is the only study in this thesis that analyses both, mtDNA and nuclear DNA, and showed how both markers could be used to complement each other. In order to achieve a reliable study comparing different species, this marker has to be constant through the different species' analyses.

7.4.2 Short fragment used

The short fragment of mtDNA used in this research is also a matter of possible concern. Due to the difficulties found in the compilation of the data (see Chapter 2) and in order to include the largest number of sequences per species as possible, for some species, the fragment length used has been reduced (see Chapter 3 and 4). This has a clear impact on the phylogeographic inference, however, for most of the species, this short length has not represented a loss of resolution of the main populations, clades or haplogroups previously described in the literature. Although it is important to point out that the individual phylogeographic patterns seen in some species may be altered by this constraint and the interpretation of the results has to be taken carefully.

7.4.3 Common framework

The constructed database (Chapter 2) with all the sequences, number of individuals, geographical areas, countries and reference information may have missed some studies and sequences that were not found during the literature process and the collection of the data from Genbank. Some sequences were not added to the analysis due to a lack of information, for example, the exact number of individuals represented by the data. Moreover, the lack of geographical coordinates in GenBank, or in the publication itself has not allowed a full reconstruction (see Gratton et al. 2016). Finally, sequences published or submitted to GenBank after January 2018 have not been added to the database as a cut-off date, after which the analysis was done had to be agreed. This may have an impact on the studied phylogeography

of the different taxa (Chapters 3 and 4), however, new data is unlikely to change the interpretation of the data and it will not change the main conclusions of the thesis.

7.5 Recommendations for future research

This thesis has highlighted issues regarding the use of genetic data as "big data" to identify common patterns and to generate a common framework to analyse it. However, these big data have proved to be "dirty" and contain errors and incomplete information. This has been a common pattern found in the research. The lack of complete information has affected the choice of some species and has introduced caveats on others (see limitations below). Therefore, the first recommendation is to publish and submit a complete record of the sequences uploaded to GenBank database. The geographical coordinates, the number of individuals that share the same haplotype, the information regarding studies that have not yet been published, are issues that need to be addressed and improved. Gratton et al. (2016) found that only 6.2% of tetrapods surveyed in GenBank submissions reported geographical coordinates, without any increase in recent years. Enhancing georeferencing of genetic data must be continued to help researchers to address phylogeographic questions with more confidence. New databases, such as BOLD (Ratnasingham and Herbert 2007) and GeOMe (Deck et al. 2017), are also trying to ensure scientific reproducibility allowing syntheses of big data.

The second set of recommendations are those relating to the implications of this research for general trends and patterns. The difficulty behind this has been addressed previously (Taberlet et al. 1998; Maggs et al. 2008; Pedreschi et al. 2018) and has been confirmed in this thesis. Accepting paradigms of phylogeography based on model species (that are most likely based on small sample sizes and limited geographical areas covered) can prevent new questions being asked. Therefore, a deeper understanding of the complexity seen in phylogeography will be achieved if more new hypotheses that contradict or reinforce certain ideas are acknowledged. Many ideas have also been developed to explain the disparities in phylogeographic histories including the existence of southern refugia (Hewitt 2000), cryptic northern refugia (Stewart and Lister 2001), microrefugia (Rull et al. 1988, Rull 2009) or refugia within refugia (Gómez and Lunt 2007). These different paradigms demonstrated the complexity behind the phylogeographic patterns and in many occasions seems to be ignored or not well considered.

The third group of recommendations are related to the last two chapter of this thesis (5 and 6). The phylogeographic studies in the commensal species *Mus musculus domesticus*, have

proven to be very useful to gain new knowledge of human movement. As seen here, the modern and ancient analyses of DNA sequences can (and should) be complementary. However, despite the complexity behind the phylogeny of *Mus musculus domesticus,* the uncertainty in the nomenclatures traditionally used for the species (Bonhomme et al. 2011; Jones et al. 2011) needs to be resolved. The use of ancient DNA analyses may help to gain resolution on this matter.

7.3 Conclusion

The work presented in this thesis shows a new common framework for meta-analyses in phylogeography. The collection of such genetic data as part of ongoing new efforts can contribute to understanding general patterns of diversity and phylogeography. The species analysed in this research have shown that genetic diversity trends in the European continent are characterised by a more complex pattern than previously described. Despite this complexity, the most important outcome, and hopefully the area where this study will be most influential, is with the approach that can help to identify possible refugial areas and the postglacial colonisations by species. It is hoped that outcomes from this research will influence the study of phylogeography using a common framework for different species. Both the findings and limitations of this study will be able to give a better context for future research in the field of specific taxon phylogeography (Chapter 4, 5 and 6) and also into comparative phylogeography (Chapter 2, 3 and 4). Modern human phylogeography pattern from the short control region has been contextualised in the patterns observed for other mammal species, showing a homogeneous distribution across the continent. The western house mouse has also been confirmed as an excellent bioproxy to understand human movement in more recent times, especially on insular scenarios such as Cyprus and Britain.

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9. Appendices

9.1 Appendix 1

Table A1.1 225 species (including marine mammals and bats) considered for the database at the beginning of this project indicating the number of entries found in Genebank for the control region, D-loop and *cyt* b.

Species	Terrestrial/Non Endemic	Control Region	D-loop	CytB
Acomys minous (Crete Spiny Mouse)	✗	✗	✗	✗
Alces alces (Eurasian Elk)	✓	308	112	32
Apodemus agrarius (Striped Field Mouse)	✓	18	151	60
Apodemus alpicola (Alpine Field Mouse)	✓	1	1	0
Apodemus epimelas (Western Broad-toothed Field Mouse)	✓	0	1	18
Apodemus flavicollis (Yellow-necked Field Mouse)	✓	20	35	4
Apodemus mystacinus (Eastern Broad-toothed Field Mouse)	✓	41	57	16
Apodemus sylvaticus (Long-tailed Field Mouse)	✓	5	16	4
Apodemus uralensis (Herb Field Mouse)	✓	3	2	144
Apodemus witherbyi (Steppe Field Mouse)	✓	0	0	21
Arvicola amphibius (European Water Vole)	✓		59	91
Arvicola sapidus (Southern Water Vole)	✓	7	89	98
Arvicola scherman (Montane Water Vole)	✓	0	3	2
Atelerix algirus (North African Hedgehog)	✓	0	15	59
Balaena mysticetus (Bowhead Whale)	✗	✗	✗	✗
Balaenoptera acutorostrata (Common Minke Whale)	✗	✗	✗	✗
Balaenoptera borealis (Sei Whale)	✗	✗	✗	✗
Balaenoptera edeni (Bryde's Whale)	✗	✗	✗	✗
Balaenoptera musculus (Blue Whale)	✗	✗	✗	✗
Balaenoptera physalus (Fin Whale)	✗	✗	✗	✗
Barbastella barbastellus (Western Barbastelle)	✓	0	29	54
Bison bonasus (European Bison)	✓	79	169	70
Bos primigenius (Aurochs)	✓	21	93	
Canis aureus (Golden Jackal)	✓	14	37	77
Canis lupus (Gray Wolf)	✓	4968	4301	2815
Capra ibex (Alpine Ibex)	✓	5	2	9
Capra pyrenaica (Iberian Wild Goat)	✓	32	7	37
Capreolus capreolus (European Roe Deer)	✓	122	734	168
Castor fiber (Eurasian Beaver)	✓	34	61	19
Cervus elaphus (Red Deer)	✓	846	870	575

Chionomys nivalis (European Snow Vole)	✓	10	18	63
Cricetulus migratorius (Gray Dwarf Hamster)	✓	0	2	64
Cricetus cricetus (Black-bellied Hamster)	✓	0	180	126
Crocidura canariensis (Canarian Shrew)	✗	✗	✗	✗
Crocidura leucodon (Bicolored Shrew)	✓	3	3	84
Crocidura pachyura (North African White-toothed Shrew)	✗	✗	✗	✗
Crocidura russula (White-toothed Shrew)	✓	41	45	117
Crocidura sicula (Sicilian Shrew)	✗	✗	✗	✗
Crocidura suaveolens (Lesser Shrew)	✓	0	0	197
Crocidura whitakeri (Whitaker's Shrew)	✗	✗	✗	✗
Crocidura zimmermanni (Cretan White-toothed Shrew)	✗	✗	✗	✗
Cystophora cristata (Hooded Seal)	✗	✗	✗	✗
Delphinapterus leucas (Beluga)	✗	✗	✗	✗
Delphinus delphis (Short-beaked Common Dolphin)	✗	✗	✗	✗
Dicrostonyx groenlandicus (Northern Collared Lemming)	✓		19	350
Dinaromys bogdanovi (Martino's Snow Vole)	✓	0	0	53
Dryomys nitedula (Forest Dormouse)	✓	0	0	50
Eliomys melanurus (Asian Garden Dormouse)	✗	✗	✗	✗
Eliomys quercinus (Garden Dormouse)	✓	0	0	53
Eptesicus bottae (Botta's Serotine)	✓	0	0	39
Eptesicus nilssonii (Northern Bat)	✓	0	1	31
Eptesicus serotinus (Serotine)	✓	69	24	131
Erignathus barbatus (Bearded Seal)	✗	✗	✗	✗
Erinaceus europaeus (Western European Hedgehog)	✓	315	82	378
Erinaceus roumanicus (Northern White-breasted Hedgehog)	✓	60	13	3
Eschrichtius robustus (Gray Whale)	✗	✗	✗	✗
Eubalaena glacialis (North Atlantic Right Whale)	✗	✗	✗	✗
Felis silvestris (Wild Cat)	✓	117	21	197
Feresa attenuata (Pygmy Killer Whale)	✗	✗	✗	✗
Galemys pyrenaicus (Pyrenean Desman)	✓	1	267	311
Glis glis (Edible Dormouse)	✓	0	2	52
Globicephala macrorhynchus (Short-finned Pilot Whale)	✗	✗	✗	✗
Globicephala melas (Long-finned Pilot Whale)	✗	✗	✗	✗
Grampus griseus (Risso's Dolphin)	✗	✗	✗	✗
Gulo gulo (Wolverine)	✓	271	5	53
Halichoerus grypus (Grey Seal)	✗	✗	✗	✗

Homo sapiens (Human)	✓			
Hyperoodon ampullatus (North Atlantic Bottlenose Whale)	✗	✗	✗	✗
Hystrix cristata (Crested Porcupine)	✓	29	47	23
Kogia breviceps (Pygmy Sperm Whale)	✗	✗	✗	✗
Kogia sima (Dwarf Sperm Whale)	✗	✗	✗	✗
Lagenodelphis hosei (Fraser's Dolphin)	✗	✗	✗	✗
Lagenorhynchus acutus (Atlantic White-sided Dolphin)	✗	✗	✗	✗
Lagenorhynchus albirostris (White-beaked Dolphin)	✗	✗	✗	✗
Lemmus lemmus (Norway Lemming)	✓	42	1	29
Lepus arcticus (Arctic Hare)	✓	3	63	8
Lepus capensis (Cape Hare)	✓	64	245	165
Lepus castroviejoi (Broom Hare)	✓	15	1	11
Lepus corsicanus (Corsican Hare)	✗	✗	✗	✗
Lepus europaeus (European Hare)	✓	305	563	267
Lepus granatensis (Granada Hare)	✓	15	226	239
Lepus timidus (Mountain Hare)	✓	151	188	258
Lutra lutra (Eurasian Otter)	✓	86	14	53
Lynx lynx (Eurasian Lynx)	✓	74	17	47
Lynx pardinus (Iberian Lynx)	✗	✗	✗	✗
Marmota marmota (Alpine Marmot)	✓	1	0	18
Martes foina (Beech Marten)	✓	15	53	55
Martes martes (Pine Marten)	✓	55	153	160
Martes zibellina (Sable)	✓	166	188	158
Megaptera novaeangliae (Humpback Whale)	✗	✗	✗	✗
Meles meles (Eurasian Badger)	✓	23	75	65
Mesocricetus newtoni (Romanian Hamster)	✗	✗	✗	✗
Mesoplodon bidens (Sowerby's Beaked Whale)	✗	✗	✗	✗
Mesoplodon densirostris (Blainville's Beaked Whale)	✗	✗	✗	✗
Mesoplodon europaeus (Gervais' Beaked Whale)	✗	✗	✗	✗
Mesoplodon mirus (True's Beaked Whale)	✗	✗	✗	✗
Micromys minutus (Eurasian Harvest Mouse)	✓	81	13	94
Microtus agrestis (Field Vole)	✓	2	2	431
Microtus arvalis (Common Vole)	✓	287	138	1086
Microtus bavaricus (Bavarian Pine Vole)	✗	✗	✗	✗
Microtus brachycercus (Calabria Pine Vole)	✗	✗	✗	✗
Microtus cabrerae (Cabrera's Vole)	✗	✗	✗	✗
Microtus duodecimcostatus (Mediterranean Pine Vole)	✗	✗	✗	✗
Microtus felteni (Balkan Pine Vole)	✗	✗	✗	✗

Microtus gerbei (Pyrenean Pine Vole)	✗	✗	✗	✗
Microtus guentheri (Günther's Vole)	✓	33	1	45
Microtus levis (East European Vole)	✗	✗	✗	✗
Microtus liechtensteini (Liechtenstein's Pine Vole)	✗	✗	✗	✗
Microtus lusitanicus (Lusitanian Pine Vole)	✗	✗	✗	✗
Microtus multiplex (Alpine Pine Vole)	✗	✗	✗	✗
Microtus oeconomus (Tundra Vole)	✗	✗	✗	✗
Microtus savii (Savi's Pine Vole)	✗	✗	✗	✗
Microtus subterraneus (European Pine Vole)	✗	✗	✗	✗
Microtus tatricus (Tatra Vole)	✗	✗	✗	✗
Microtus thomasi (Thomas's Pine Vole)	✓	164	2	161
Miniopterus schreibersii (Schreiber's Bent-winged Bat)	✓	0	223	434
Monachus monachus (Mediterranean Monk Seal)	✗	✗	✗	✗
Monodon monoceros (Narwhal)	✗	✗	✗	✗
Mus macedonicus (Macedonian Mouse)	✓	7	120	2
Mus musculus (House Mouse)	✓	7523	2795	3321
Mus spicilegus (Mound-building Mouse)	✓	32	4	5
Mus spretus (Western Mediterranean Mouse)	✓	8	7	28
Muscardinus avellanarius (Hazel Dormouse)	✓	0	12	42
Mustela erminea (Stoat)	✓	119	220	330
Mustela eversmanii (Steppe Polecat)	✓	5	7	5
Mustela lutreola (European Mink)	✓	7	44	27
Mustela nivalis (Least Weasel)	✓	122	140	159
Mustela putorius (Western Polecat)	✓	0	32	50
Myodes glareolus (Bank Vole)	✓	92	129	1525
Myodes rufocanus (Grey Red-backed Vole)	✗	✗	✗	✗
Myodes rutilus (Northern Red-backed Vole)	✗	✗	✗	✗
Myomimus roachi (Roach's Mouse-tailed Dormouse)	✗	✗	✗	✗
Myopus schisticolor (Wood Lemming)	✓	0	1	62
Myotis alcathoe (ALCATHOE MYOTIS)	✓	0	0	35
Myotis aurascens (STEPPE WHISKERED BAT)	✓	0	0	36
Myotis bechsteinii (Bechstein's Myotis)	✓	48	4	7
Myotis blythii (Lesser Mouse-eared Myotis)	✓	6	39	50
Myotis brandtii (BRANDT'S MYOTIS)	✓	515	144	43
Myotis capaccinii (Long-fingered Bat)	✓	0	0	1
Myotis dasycneme (Pond Myotis)	✓	0	0	1
Myotis daubentonii (Daubenton's Myotis)	✓	1	135	76
Myotis emarginatus (Geoffroy's Bat)	✓	0	0	51
Myotis myotis (Greater Mouse-eared Bat)	✓	61	143	99
Myotis mystacinus (Whiskered Myotis)	✓	0	0	22

Myotis nattereri (Natterer's Bat)	✓	38	0	89
Myotis punicus (Maghreb Mouse-eared Bat)	✓	27	0	1
Myotis schaubi (Schaub's Myotis)	✓	0	0	4
Neomys anomalus (Southern Water Shrew)	✓	0	0	32
Neomys fodiens (Eurasian Water Shrew)	✓	2	2	39
Nyctalus azoreum (Azores Noctule)	✗	✗	✗	✗
Nyctalus lasiopterus (Giant Noctule)	✓	0	427	219
Nyctalus leisleri (Lesser Noctule)	✓	15	30	31
Nyctalus noctula (Noctule)	✓	2	3	14
Odobenus rosmarus (Walrus)	✗	✗	✗	✗
Orcinus orca (Killer Whale)	✗	✗	✗	✗
Oryctolagus cuniculus (European Rabbit)	✓	474	343	103
Ovibos moschatus (Muskox)	✓	240	19	32
Pagophilus groenlandicus (Harp Seal)	✗	✗	✗	✗
Phoca vitulina (Harbour Seal)	✗	✗	✗	✗
Phocoena phocoena (Harbour Porpoise)	✗	✗	✗	✗
Physeter macrocephalus (Sperm Whale)	✗	✗	✗	✗
Pipistrellus kuhlii (Kuhl's Pipistrelle)	✗	✗	✗	✗
Pipistrellus maderensis (Madeira Pipistrelle)	✗	✗	✗	✗
Pipistrellus nathusii (Nathusius' Pipistrelle)	✗	✗	✗	✗
Pipistrellus pipistrellus (Common Pipistrelle)	✓	160	103	122
Pipistrellus pygmaeus (Pygmy Pipistrelle)	✓	112	42	39
Pipistrellus savii (Savi's Pipistrelle)	✗	✗	✗	✗
Plecotus auritus (Brown Big-eared Bat)	✓	29	26	21
Plecotus austriacus (Gray Big-eared Bat)	✓	15	14	49
Plecotus kolombatovici (Kolombatovic's Long-eared Bat)	✓	18	3	2
Plecotus macrobullaris (Mountain Long-eared Bat)	✓	8	85	72
Plecotus sardus (Sardinian Long-eared Bat)	✗	✗	✗	✗
Plecotus teneriffae (Tenerife Long-eared Bat)	✗	✗	✗	✗
Prolagus sardus (Sardinian Pika)	✗	✗	✗	✗
Pseudorca crassidens (False Killer Whale)	✗	✗	✗	✗
Pteromys volans (Siberian Flying Squirrel)	✓	4	2	72
Pusa hispida (Ringed Seal)	✗	✗	✗	✗
Rangifer tarandus (Reindeer)	✓	918	1403	703
Rhinolophus blasii (Blasius's Horseshoe Bat)	✓	9	7	14
Rhinolophus euryale (Mediterranean Horseshoe Bat)	✓	3	23	16
Rhinolophus ferrumequinum (Greater Horseshoe Bat)	✓	121	174	89
Rhinolophus hipposideros (Lesser Horseshoe Bat)	✓	375	375	397
Rhinolophus mehelyi (Mehely's Horseshoe	✓	4	14	10

Bat)				
Rupicapra pyrenaica (Pyrenean Chamois)	✗	✗	✗	✗
Rupicapra rupicapra (Northern Chamois)	✗	✗	✗	✗
Saiga tatarica (Mongolian Saiga)	✗	✗	✗	✗
Sciurus anomalus (Caucasian Squirrel)	✗	✗	✗	✗
Sciurus vulgaris (Eurasian Red Squirrel)	✓	92	507	157
Sicista betulina (Northern Birch Mouse)	✗	✗	✗	✗
Sicista subtilis (Southern Birch Mouse)	✓	0	5	20
Sorex alpinus (Alpine Shrew)	✗	✗	✗	✗
Sorex antinorii (Valais Shrew)	✓	40	0	113
Sorex araneus (Eurasian Shrew)	✓	266	97	56
Sorex arunchi (Udine Shrew)	✓			
Sorex caecutiens (Laxmann's Shrew)	✓	2	1	115
Sorex coronatus (Crowned Shrew)	✓	0	0	17
Sorex granarius (Lagranja Shrew)	✓	0	0	7
Sorex isodon (Even-toothed Shrew)	✓	1	0	9
Sorex minutissimus (Eurasian Least Shrew)	✓	225	152	298
Sorex minutus (Eurasian Pygmy Shrew)	✓	158	0	344
Sorex samniticus (Appenine Shrew)	✗	✗	✗	✗
Spalax graecus (Balkan Blind Mole Rat)	✗	✗	✗	✗
Spalax leucodon (Lesser Mole Rat)	✗	✗	✗	✗
Spermophilus citellus (European Ground Squirrel)	✓	8	0	134
Spermophilus suslicus (Speckled Ground Squirrel)	✓	108	12	3
Stenella coeruleoalba (Striped Dolphin)	✗	✗	✗	✗
Stenella frontalis (Atlantic Spotted Dolphin)	✗	✗	✗	✗
Steno bredanensis (Rough-toothed Dolphin)	✗	✗	✗	✗
Suncus etruscus (White-toothed Pygmy Shrew)	✗	✗	✗	✗
Sus scrofa (Wild Boar)	✓	5138	5601	1993
Tadarida teniotis (European Free-tailed Bat)	✗	✗	✗	✗
Talpa caeca (Mediterranean Mole)	✗	✗	✗	✗
Talpa europaea (European Mole)	✓	0	2	367
Talpa levantis (Levantine Mole)	✓	0	0	18
Talpa occidentalis (Iberian Mole)	✓	2	0	31
Talpa romana (Roman Mole)	✓	0	0	120
Talpa stankovici (Stankovic's Mole)	✓	0	0	19
Tursiops truncatus (Common Bottlenose Dolphin)	✗	✗	✗	✗
Ursus arctos (Brown Bear)	✓	792	415	396
Ursus maritimus (Polar Bear)	✓	509	143	398
Vespertilio murinus (Particoloured Bat)	✓	0	53	29
Vormela peregusna (Marbled Polecat)	✓	0	21	20

Vulpes lagopus (Arctic Fox)	✓	80	100	57
Vulpes vulpes (Red Fox)	✓	137	708	328
Ziphius cavirostris (Cuvier's Beaked Whale)	✗	✗	✗	✗

9.2 Appendix 2

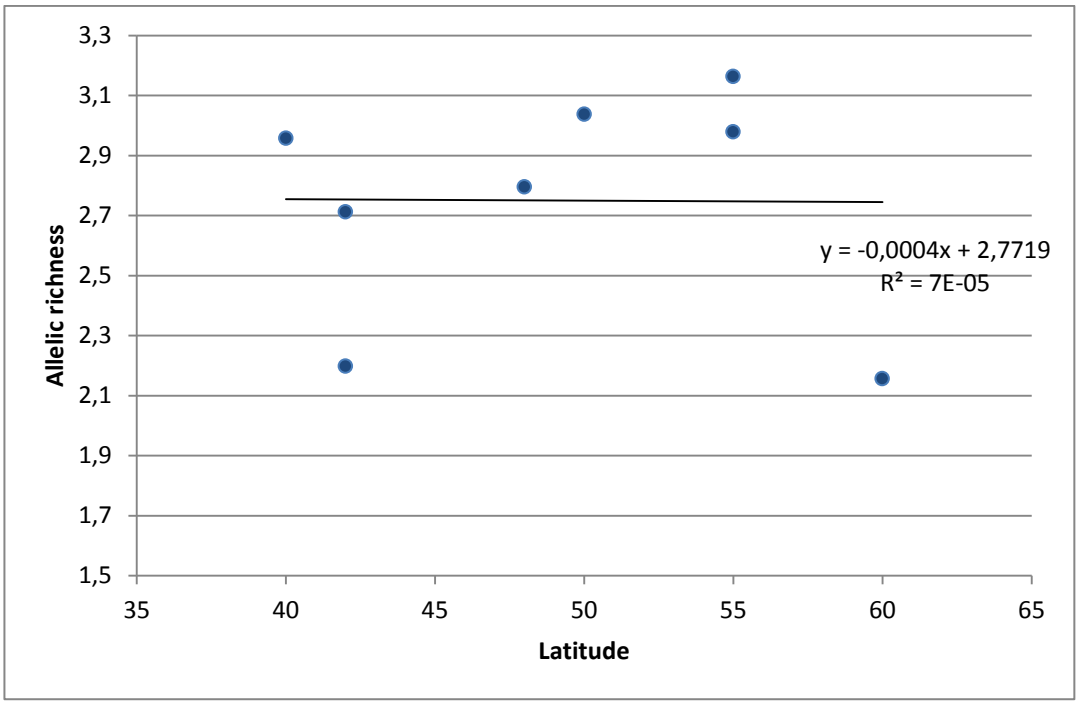


Figure A2.1 Private allelic richness examined in relation to latitude. The private allelic richness was not found to be correlated with the latitudinal distribution (slope of the linear regression P>0.05).

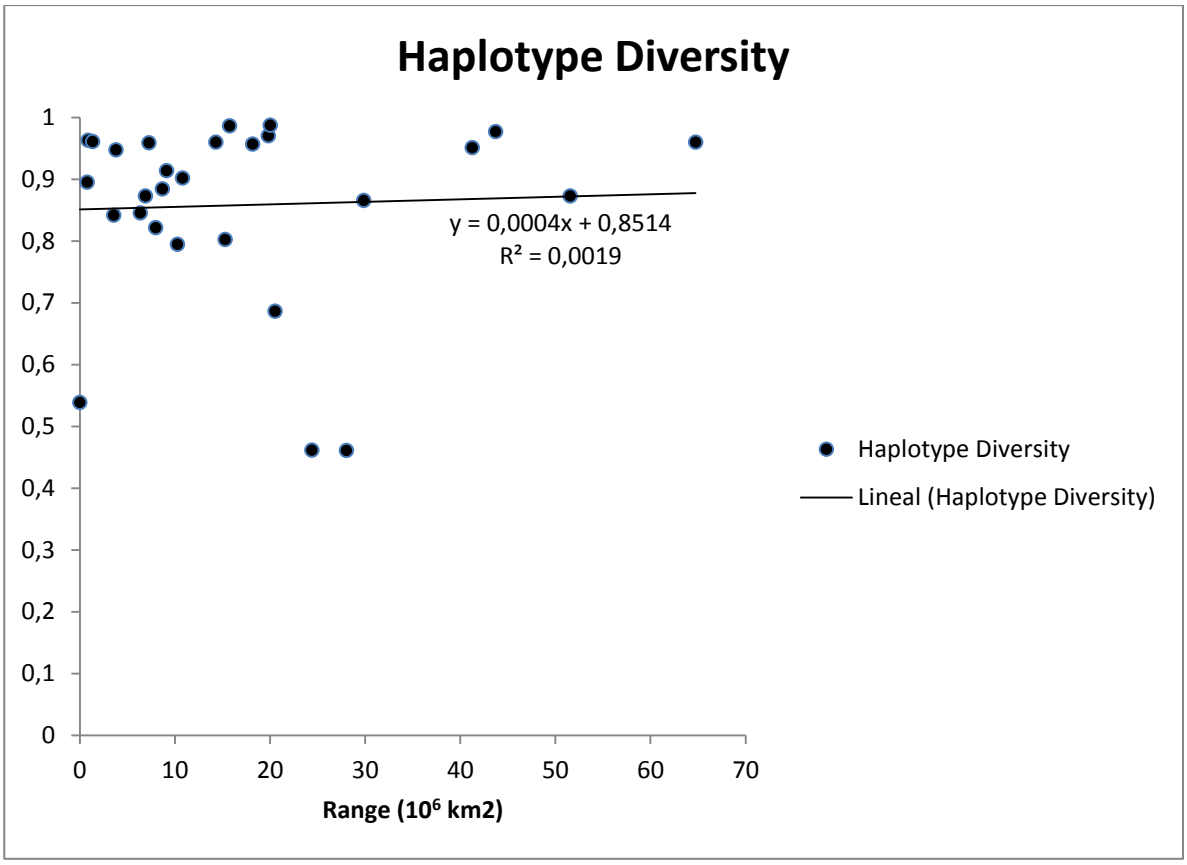


Figure A2.2 MtDNA haplotype diversity indices of all 29 mammal species examined in relation to area. Species mtDNA diversity indices were not found to consistently correlate with area.

9.3 Appendix 3

Table A3.1 Results of the Wilcoxon Signed Rank Test (see, for example, Hollander and Wolfe (1973) to compare haplotype diversity values between species and regions performed between pairs of species. The results show that certain species can only be considered significantly different ($p<0.05$, indicating in yellow).

	Alces alces	Arvicola amphibiu	Bison bonasu	Bos primigeniu	Canis lupus	Capreolus capreol	Castor fiber	Cervus elaph	Cricetus cricetu	Erinaceus europae	Erinaceus concol	Gulo gulo	Lepus europae	Lepus timidu	Lemmus lemm	Lynx lynx	Martes marte	Microtus arval	Mustela ermin	Mustela nival	Myodes glareol	Rangifer tarandi	Sciurus vulgari	Sorex minutu	Sus scrofa	Ursus arctos	Vulpes lagopu	Vulpes vulpe	Homo sapiens
Alces alces																												
Arvicola amphibius																												
Bison bonasus																												
Bos primigenius						0,014266187								0,036031686									0,036031686					0,014266187
Canis lupus						0,034610558				0,036031686							0,034610558											0,022494271
Capreolus capreol				0,014266187	0,034610558			0,020862582																0,036031686				
Castor fiber																												
Cervus elaphus						0,020862582								0,036031686														0,014266187
Cricetus cricetus																												
Erinaceus europae					0,036031686																		0,036031686					
Erinaceus concolor																												
Gulo gulo																												
Lepus europaeus																								0,036031686				
Lepus timidus				0,036031686				0,036031686									0,036031686											
Lemmus lemmus																												
Lynx lynx																												
Martes martes					0,034610558									0,036031686										0,036031686				
Microtus arvalis																												
Mustela erminea																												
Mustela nivalis																												
Myodes glareolus																												
Rangifer tarandus																												
Sciurus vulgaris				0,036031686						0,036031686																		
Sorex minutus																												
Sus scrofa						0,036031686							0,036031686				0,036031686											0,036031686
Ursus arctos																												0,022494271
Vulpes lagopus																												
Vulpes vulpes				0,014266187	0,022494271			0,014266187																	0,036031686	0,022494271		
Homo sapiens																												

9.4 Appendix 4

Figure A4.1 Bayesian skyline plots showing effective female population size (*Nef x* T), in thousands, with time for each D-loop haplogroup detected in *Mus musculus domesticus* on Cyprus. The solid line is the median and the dashed lines are 95% highest posterior density (HDP) limits.

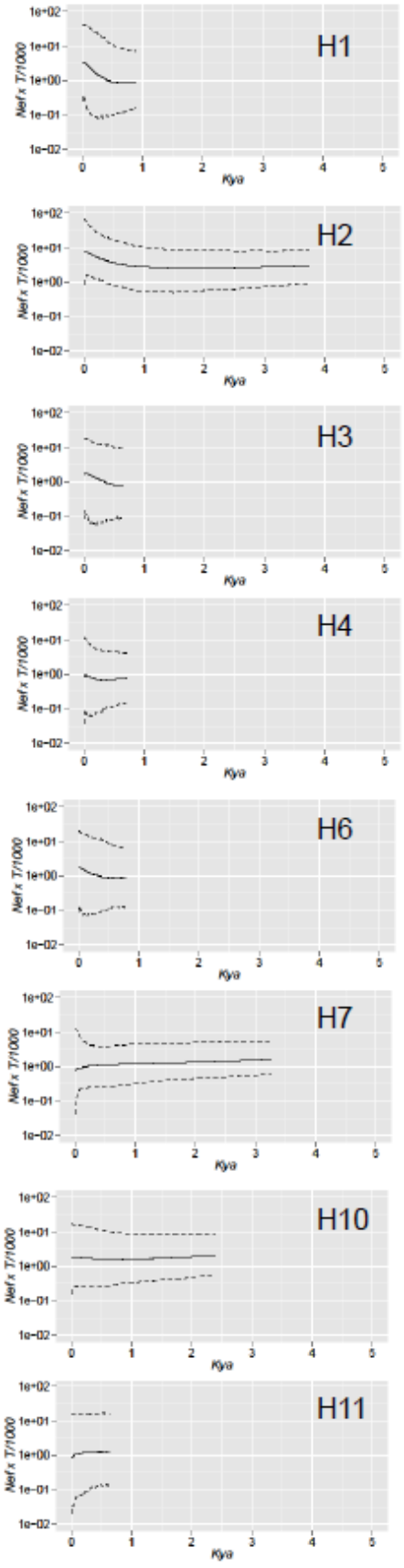


Figure A4.2 Mismatch distributions for each D-loop haplogroup represented by the Cypriot *Mus musculus domesticus* samples. Observed values and the expected distribution according to the constant population size model. Harpending's raggedness index (r), as calculated in DnaSP v. 5.10.1 (Librado & Rozas, 2009), is also indicated.

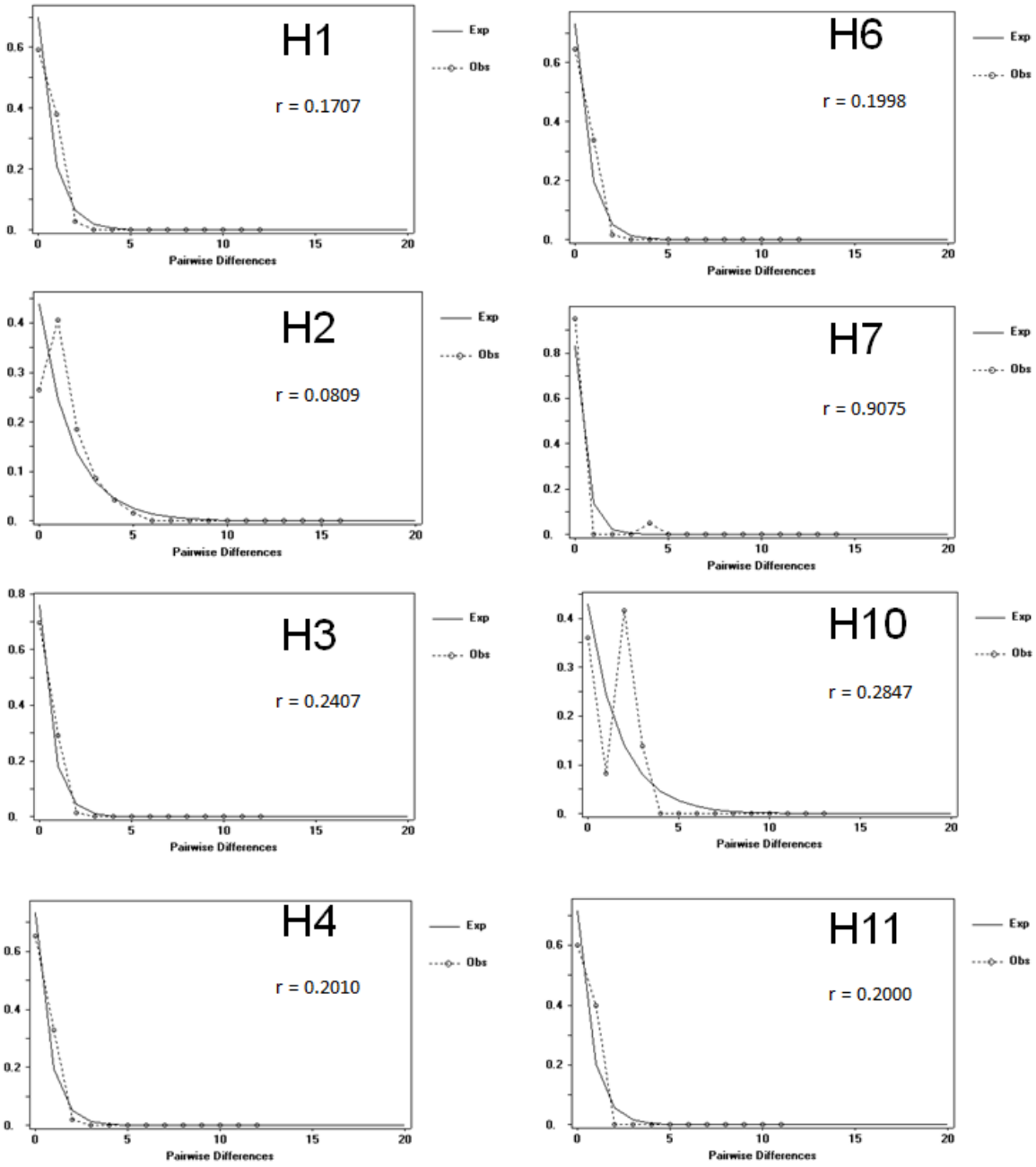
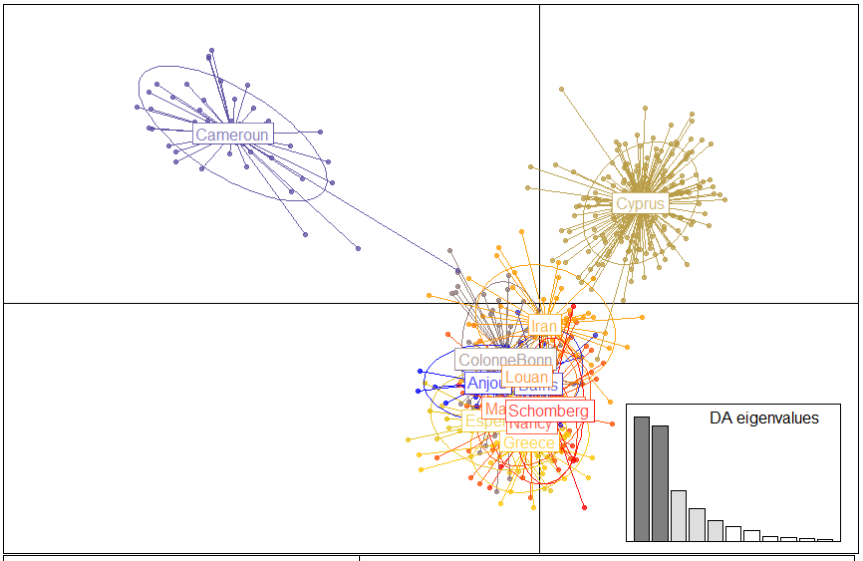


Figure A4.3 Discriminant Analysis of Principal Components (DAPC) based on microsatellite data comparing populations of *Mus musculus domesticus* typed by us and in published studies (see text). The first two principal components of DAPC are represented using population locations as prior clusters. Populations are labelled inside their 95% inertia ellipses and dots represent individuals from **(a)** France (multiple locations), Germany (multiple locations), Greece, Iran, Cameroun and Cyprus; **(b)** All the locations from Cyprus. The DAPC eigenvalues correspond to a ratio of between to within group variance calculated for each function.

a)



b)

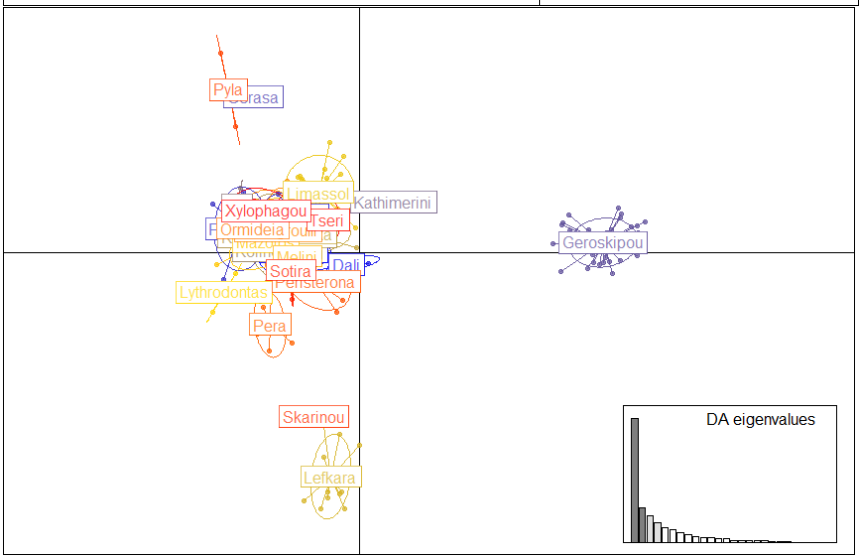


Table A4.1 Detailed publication references, number of individuals and geographical locations included in the alignment.

References	Number of individuals	Locations
(Prager et al., 1993)	232	British Isles (5), Croatia (2), Denmark (114), Egypt (5), Germany (60), Greece (1), Israel (2), Italy (2), Morocco (3), Peru (1), Portugal (1), Scandinavia (30), Spain (2), Switzerland (2) and USA (2)
(Nachman, Boyer, Searle, & Aquadro, 1994)	51	British Isles (12), Greece (7), Italy (25), Spain (6) and Switzerland (1)
(Prager, Tichy, & Sage, 1996)	9	Austria (1), Croatia (1), Georgia (2) and Norway (5)
(Gündüz, Rambau, Tez, & Searle, 2005)	100	Turkey (100)
(Ihle, Ravaoarimanana, Thomas, & Tautz, 2006)	124	Cameroon (27), France (56) and Germany (41)
(Geraldes et al., 2008)	11	Israel (11)
(Rajabi-Maham, Orth, & Bonhomme, 2008)	133	Bulgaria (24), Iran (78) and Italy (31)
(Förster et al., 2009; Gündüz et al., 2001)	200	Madeira (124), Portugal (76)
(Searle et al., 2009)	77	British isles (77)
(Bonhomme et al., 2011)	383	Algeria (12), Canary Islands (140), Cyprus (38), Egypt (2?), France (9), Georgia (4), Germany (7), Israel (11), Kenya (11), Lebanon (58), Morocco (29?), Qatar (2), Senegal (12), Spain (3), Syria (12) and Tunisia (33)
Total	1319	

Table A4.2 Collection sites for *Mus musculus domesticus* on Cyprus and allocation of individuals to the eleven mitochondrial haplogroups as defined in Bonhomme et al. (2011).

			Total	Number of individuals in each haplogroup										
Population	Latitude	Longitude	N	1	2	3	4	5	6	7	8	9	10	11
Athienou	N 35°03.897'	E 33°31.208'	12		7	2	2				1			
Dali	N 35°03.344'	E 33°25.527'	4		1	3								
Deryneia	N 35°03.344'	E 33°57.505'	7		4								3	
Frenaros	N 35°03.117'	E 33°54.367'	6	2	3		1							
Gerasa	N 34°46.418'	E 32°59.355'	1		1									
Geroskipou	N 34°45.444'	E 32°28.401'	39							39				
Kathikas	N 34°55.028'	E 32°26.125'	1						1					
Kiti	N 34°50.221'	E 33°33.112'	2		1	1								
Kofinou	N 34°49.185'	E 33°24.094'	1		1									
Kokkinotrimithia	N 35°09.919'	E 33°11.304'	15	1	6	3							5	
Larnaka	N 34°58.055'	E 33°36.211'	10	2	5	2				1				
Lefkara	N 34°50.302'	E 33°20.185'	13	1			12							
Limassol	N 34°39.765'	E 32°56.141'	20	8	2	1			9					
Lythrodontas	N 34°58.188'	E 33°18.237'	2		1									1

Mazotos	N 34°48.040'	E 33°30.454'	8		5		3				
Melini	N 34°51.893'	E 33°09.786'	2		1	1					
Meneou	N 34°51.031'	E 33°35.484'	1								1
Mitsero	N 35°03.200'	E 33°06.611'	5		1	1	1				2
Monagroulli	N 34°45.780'	E 33°13.190'	5	2	1			2			
Ormideia	N 35°00.208	E 33°48.452'	2				2				
Pera	N 35°02.248'	E 33°16.407'	6			6					
Peristerona	N 35°07.353'	E 33°03.688'	8		7			1			
Pyla	N 35°00.292'	E 33°41.679'	2		1		1				
Skarinou	N 34°49.061'	E 33°20.025'	1		1						
Sotira	N 35°00.636'	E 33°56.388'	3		1	2					
Tseri	N 35°02.790'	E 33°19.271'	5				5				
Xylophagou	N 34°58.413'	E 33°49.796'	8		3		5				

Table A4.3 Neutrality test statistics, Tajima's *D* and Fu's F_S, with significance determined from 10,000 coalescent simulations. Dates estimated in years, for time to most recent common ancestor (tMRCA), with median and 95% highest posterior density (HPD) range; and onset of demographic expansion (tau) from mismatch distributions according to different estimations of number of generations per year. All statistics relate to house mouse mitochondrial haplogroups, treated as populations.

							Molecular date estimates (in years)					
							BEAST analysis			Mismatch distribution analysis		
Haplogroup	N	Tajima's *D*	*p*-value	Fu's F_S	*p*-value	Tau value	95% HPD lower	tMRCA median	95% HPD upper	1 Generation per year	2 Generations per year	3 Generations per year
H1	29	-1.028	0.168	-1.563	0.080	0.433	60	907	2959	1210	605	403
H2	58	-0.682	0.280	-3.708	0.035	1.001	983	3699	7974	2796	1398	932
H3	24	-0.890	0.179	-0.919	0.259	0.319	9	640	2472	892	446	297
H4	40	-0.416	0.320	-0.366	0.381	0.367	3	694	2609	1026	513	342
H6	20	-0.812	0.190	-0.775	0.257	0.368	11	791	2811	1029	514	343
H7	40	-1.880	<0.0001	0.241	0.530	0	454	3226	7760	NA	NA	NA
H10	9	0.794	0.790	0.909	0.745	1.333	223	2434	6273	3727	1863	1242
H11	5	-0.816	0.280	0.090	0.198	0.400	0	634	2925	1118	559	372

Table A4.4 Locations, coordinates and number of *Mus musculus domesticus* individuals analysed for microsatellite data and the mitochondrial D-loop, with measures of variation. N = number of individuals, H_{exp} = expected heterozygosity, H_{obs} = observed heterozygosity

			Microsatellites				Mitochondrial DNA	
Location	**Latitude**	**Longitude**	**N (individuals)**	**H_{exp}**	**H_{obs}**	**Mean number of alleles per locus**	**N (individuals)**	**N (haplotypes)**
Athienou	N 35°03.897'	E 33°31.208'	12	0.74	0.77	6.78	12	5
Dali	N 35°03.344'	E 33°25.527'	4	0.60	0.65	3.83	4	3
Deryneia	N 35°03.344'	E 33°57.505'	7	0.67	0.78	4.67	7	3
Frenaros	N 35°03.117'	E 33°54.367'	6	0.71	0.79	5.28	6	4
Gerasa	N 34°46.418'	E 32°59.355'	1	0.19	0.39	1.39	1	1
Geroskipou	N 34°45.444'	E 32°28.401'	41	0.66	0.71	4.61	39	2
Kathimerini	N 34°55.028'	E 32°26.125'	1	0.36	0.72	1.72	1	1
Kiti	N 34°50.221'	E 33°33.112'	2	0.54	0.75	2.78	2	2
Kofinou	N 34°49.185'	E 33°24.094'	1	0.28	0.56	1.56	1	1
Kokkinotrimithia	N 35°09.919'	E 33°11.304'	15	0.78	0.74	7.83	15	9
Larnaka	N 34°58.055'	E 33°36.211'	9	0.75	0.76	6.44	10	6
Lefkara	N 34°50.302'	E 33°20.185'	13	0.57	0.71	4.00	13	3

Limassol	N 34°39.765'	E 32°56.141'	18	0.78	0.77	8.00	20	5
Lythrodontas	N 34°58.188'	E 33°18.237'	2	0.52	0.67	2.78	2	2
Mazotos	N 34°48.040'	E 33°30.454'	10	0.73	0.72	5.72	8	2
Melini	N 34°51.893'	E 33°09.786'	2	0.57	0.67	2.89	2	2
Meneou	N 34°51.031'	E 33°35.484'	2	0.63	0.81	3.17	1	1
Mitsero	N 35°03.200'	E 33°06.611'	5	0.70	0.81	5.00	5	4
Monagroulli	N 34°45.780'	E 33°13.190'	5	0.68	0.73	4.22	5	3
Ormideia	N 35°00.208	E 33°48.452'	2	0.65	0.83	3.28	2	1
Pera	N 35°02.248'	E 33°16.407'	6	0.5	0.68	2.89	6	1
Peristerona	N 35°07.353'	E 33°03.688'	8	0.69	0.74	5.61	8	3
Pyla	N 35°00.292'	E 33°41.679'	2	0.44	0.75	2.11	2	2
Skarinou	N 34°49.061'	E 33°20.025'	1	0.25	0.50	1.50	1	1
Sotira	N 35°00.636'	E 33°56.388'	3	0.62	0.62	3.39	3	3
Tseri	N 35°02.790'	E 33°19.271'	5	0.43	0.62	2.44	5	1
Xylophagou	N 34°58.413'	E 33°49.796'	8	0.71	0.73	5.61	8	3

Table A4.5 Prior parameter distributions from coalescent genealogy sampling with Beast 2.3.2 applied to all available *Mus musculus domesticus* D-loop sequences from Cyprus (published and new data here). Substitution and clock model parameters were linked, tree parameters unlinked.

Parameter	Prior distribution	Range	Initial value
Kappa1	Lognormal (1.0/1.25)	0 – inf	1
Kappa2	Lognormal (1.0/1.25)	0 – inf	1
Gamma shape	Lognormal (1.0/1.25)	0 – inf	1
Frequencies	Uniform	1.0e-9 - 1.0	0.25
Strict clock rate	----	----	4e-4
Tree (each haplogroup)	Coalescent BSP		Random tree
Population size (each haplogroup)	Jeffrey's (1/x)	1.0e-9 - 1.0e12	100,000
Pop. groups (Cyprus only Haplogroup 1)	----	----	5
Pop. groups (Cyprus only Haplogroup 2)	----	----	5
Pop. groups (Cyprus only Haplogroup 3)	----	----	5
Pop. groups (Cyprus only Haplogroup 4)	----	----	5
Pop. groups (Cyprus only Haplogroup 6)	----	----	4
Pop. groups (Cyprus only Haplogroup 7)	----	----	5
Pop. groups (Cyprus only Haplogroup 10)	----	----	3
Pop. groups (Cyprus only Haplogroup 11)	----	----	3

9.5 Appendix 5

Table A5.1. Table of archaeological *Mus/Apodemus* specimens studied, with associated period and context information.

Specimen	Location	Period	Context information
OG01	Potterne, Wiltshire	Iron Age	N35 134 122 Cutting 12
OG02	Potterne, Wiltshire	Iron Age	W35 221 5 159 Cutting 12
OG03	Potterne, Wiltshire	Iron Age	W35 202 565 Cutting 12
OG04	Potterne, Wiltshire	Iron Age	W35 202 564 Cutting 12
OG05	Potterne, Wiltshire	Iron Age	W35 221 5160 Cutting 12
OG06	Potterne, Wiltshire	Iron Age	W35 3716 5.676R Cutting 12
OG07	Potterne, Wiltshire	Iron Age	W35 221 5160 Cutting 12
OG08	Battlesbury Bowl, Wiltshire	Iron Age	W4896 4817 <2143>
OG09	Battlesbury Bowl, Wiltshire	Iron Age	W4896 4817 <2143>
OG10	Battlesbury Bowl, Wiltshire	Iron Age	W4896 4174 <2010>
OG11	Battlesbury Bowl, Wiltshire	Iron Age	W4896 5137
OG12	Battlesbury Bowl, Wiltshire	Iron Age	W4896 5056
OG13	North West Farm, Dorset	Bronze Age	NWF17 340 "2" bag 79
OG14	North West Farm, Dorset	Bronze Age	NWF17 340 "1" bag 78
OG15	Druce Farm, Dorset	Roman Period	DF13 (2) (197) HXAM
OG16	Druce Farm, Dorset	Roman Period	DF13 (2) (197) HXAM

Text A5.1:

Battlesbury Bowl

The site of Battlesbury Bowl, lies along a narrow chalk ridge immediately to the north of Battlesbury Camp, an Iron Age hillfort near Warminster, Wiltshire. Excavations by Wessex Archaeology in 1999 revealed features of Late Bronze Age-Middle Iron Age dates (base on ceramic style), including ditches, post holes, and almost 200 pits (Ellis & Powell 2008). The faunal assemblage is one of the largest collections of Early-Middle Iron Age faunal material from Britain. Hambleton & Maltby (2008) report the presence of both house mouse and wood mouse in the hand-recovered assemblage and from environmental sieved samples. The mouse mandibles included in this study come from the fills of pits (OG08, OG09, OG11, OG12) and a posthole (OG10) all of which were assigned Early-Middle Iron Age dates. Radiocarbon dating of a pig humerus, from the same context as mouse mandible OG11, provided a date of calBC (2σ) 420-100 (Ellis & Powell 2008).

Potterne

The later prehistoric site of Potterne, near Devizes, Wiltshire, was excavated by Wessex Archaeology between 1982-4 and comprises an extensive accumulation of dark anthropogenic soil deposits up to 2m deep in places, covering an area of 3.5 ha. The 'midden-like' deposits are rich in artefacts and ecofacts and result from the accumulation of manure and refuse from stock keeping and the repeated dumping and trampling of waste from human occupation and activities on and around the site over a 500 year period. Pottery typology and radiocarbon dating of charcoal from different levels within the deposit and other cut features suggest a date of 1200-600BC, encompassing the Late Bronze Age into the very Early Iron Age period (Lawson 2000). In addition to a large hand-recovered animal bone assemblage dominated by domestic mammals, small mammal remains were also recovered mainly from sieved environmental samples. Locker (2000) reports that house mouse remains were identified from every level although it was not possible to obtain radiocarbon dates for the mice to confirm their Late Bronze Age date. However, a radiocarbon date of 1460-990 (2σ) cal BC (Lawson 2000:) was obtained from charcoal that came from the same post hole one of the mouse specimens included in this study (OG06). The assumption is that all the mice remains are contemporary with the associated archaeological materials of Late Bronze Age (c.1200-600BC) date from the same layers and contexts, although

Locker does caution that some small mammal remains may have filtered down the deposit from higher levels.

North West Farm

The site at North West Farm, just outside the village of Winterborne Kingston to the north of Bere Regis forms part of a programme of archaeological fieldwork, The Durotriges Project, designed to investigate native and Romano-British settlement across Dorset, focussing specifically in the archaeologically distinct Iron Age Durotriges tribe.

The land, which is sub-divided in to large land parcels bounded primarily by mature hedge and fence and post field divisions, is primarily under arable cultivation with parcels set-aside for pasture and habitat creation. The underlying geology comprises Upper Chalk.

The site lies in an area of known archaeological monuments, sites and findspots recorded on the Dorset Historic Environment Record, although none of these occur within the site or within its immediate vicinity. The invasion of southern Britain by Rome is usually treated as if it was a single, dramatic event, with the Roman legions fighting a lengthy and bitter war of conquest. The Durotriges Project is reconsidering the Iron Age to Roman transition through a detailed programme of field survey, geophysical investigation and targeted excavation. Previous seasons of investigation focused upon an enclosed later Iron Age 'banjo' settlement containing round houses, storage pits (containing enigmatic human and animal hybrid ritual offerings) , a later Iron Age Durotrigan cemetery and the remains of a 4th century Roman villa. In 2014 a small yet significant late Roman cemetery, with five inhumations recorded in close vicinity to the Roman villa, was recorded while in 2015 an extensive undefended Late Iron Age settlement of the scale of a small town, consisting of an estimated 100-150 roundhouses was identified.

In 2017 a series of later Bronze cylindrical cuts or pits were excavated across three trenches some of which incorporated domestic 'midden' waste material, whilst a few also contained copper and iron working debris. The term 'storage pit' has generally applied to these features although no definitive evidence as to the nature of material being stored has yet been recovered. If intended as functional elements within a settlement these features may have been designed to function as a cold store for dairy produce or as a silo for grain with each pit acting as a silo designed to contain the surplus perhaps on an annual basis.

The mouse remains were recovered from a chalk deposit (340) within one of three large storage pits in Trench H of the 2017 fieldwork programme. The almost circular pit measured 3.46m at its widest and was 2.13m deep. The sides of the pit were generally steep becoming vertical and then undercut below a depth of 0.75m. The base was flat, sloping gradually from NE to SW. A total of 37 fills were recorded filling the pit, and within the excavated half of the pit the base was entirely lined by a thin, 10-15mm deep black deposit with a very high concentration of charred organic remains (341). This material was sealed by a series of chalk rubble deposits (340, 385, 383 and 381) interpreted as being derived from erosion and collapse of the pit sides after it went out of use. These were interspersed with deposits of soil (384, 382 and 375) which have been interpreted as deliberate deposits within the same timeframe and may have been organic based.

A subsequent sequence of fills were piled against the north east side of the pit characterised as thin banded deposits of chalk and soil, potentially representing alternating episodes of organic waste, possibly cess disposal and the capping/covering of this material with clean chalk, followed by substantial deposits of chalk rich soil representing a deliberate deposition of material and gradual accumulations of back fill material.

Druce Farm Roman Villa

Druce Farm villa, Puddletown, Dorset, comprises a series of stone and flint constructed and timber post built buildings arranged on a courtyard plan surrounded by a series of ditched enclosures with features associated with industrial use (e.g. kilns/ovens and pits) (Ladle in prep). The site displays a number of phases of use between the 1st and 4th century AD. The samples were obtained from an extensive deposit of remains of microfauna which lay on the intact mosaic floor of a room in the main range of buildings, sealed by a deposit of degraded plaster and roof tiles. Analysis of the site and the deposit are ongoing (Ladle in prep; Randall in prep), but this appears to represent a deposit of owl pellets, most likely derived from barn owls, which accumulated when the building was going out of use, and which was sealed by the collapsed roof. The mosaic floor has been typologically dated to the 4th century AD. Two water vole mandibles from the deposit were subjected to radiocarbon dating to elucidate the date of the building collapse, and returned dates of 1719 +30 BP (249-391 cal AD 95% probablilty) and 1768+30 BP (208-346 cal AD 95% probablilty).

Initial analysis indicates that the deposit is dominated by field vole (*Microtus agrestis*), which makes up almost half of the material identified to species. Shrews contributed a further third of the material, with a similar amount identified as *Apodemus*. A small selection of elements could be attributed to bank and water voles, song birds and amphibians, mainly frogs. The identification of the single example of potential *Mus musculus domesticus* as *Apodemus* is therefore not surprising given the nature of the deposit. It does however confirm the general picture of abandonment of the site at the point that the deposit was forming, with the owls predating the microfauna of the surrounding landscape, rather than taking advantage of house mice present within adjacent buildings.