








Review

Ancient Faunal History Revealed by Interdisciplinary Biomolecular Approaches

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Abstract: Starting four decades ago, studies have examined the ecology and evolutionary dynamics of populations and species using short mitochondrial DNA fragments and stable isotopes. Through technological and analytical advances, the methods and biomolecules at our disposal have increased significantly to now include lipids, whole genomes, proteomes, and even epigenomes. At an unprecedented resolution, the study of ancient biomolecules has made it possible for us to disentangle the complex processes that shaped the ancient faunal diversity across millennia, with the potential to aid in implicating probable causes of species extinction and how humans impacted the genetics and ecology of wild and domestic species. However, even now, few studies explore interdisciplinary biomolecular approaches to reveal ancient faunal diversity dynamics in relation to environmental and anthropogenic impact. This review will approach how biomolecules have been implemented in a broad variety of topics and species, from the extinct Pleistocene megafauna to ancient wild and domestic stocks, as well as how their future use has the potential to offer an enhanced understanding of drivers of past faunal diversity on Earth.

Keywords: ancient DNA; wild and domestic ancient fauna; ancient genomics; ancient epigenomics; ancient proteomics; ancient lipidomics; stable isotopes; biomolecular archaeology and palaeontology; palaeoecology

1. Introduction

Animals have always been a part of and shaped human history. Additionally, people have played a crucial role in shaping the diversity and dynamics of animal populations, not least in modern times. Through competition for shared resources, early humans are considered to have had limited impact on fauna and its genetic diversity. However, in

more recent history, human pressure has intensified, to the great benefit of some species (e.g., domesticates, commensals) and detriment of others (e.g., through habitat degradation and loss, decrease in diversity), leaving several species at risk of extinction.

Consequently, it is increasingly important for us to gain an understanding of the diversity and dynamics of the palaeofauna, some of which we only know from fossils and the artistic representations made by prehistoric humans millennia ago [1]. Although still methodologically challenging owing to the noise introduced by postmortem damage of the molecules, continuous advances in palaeomics and palaeoecology are making it possible for us to investigate increasingly more ancient faunal diversity (see [2,3]).

To date, a wide range of biomolecules, including proteins, nucleic acids, and lipids, preserved in fossils, artefacts, sediments, and other substrates, have been utilised [2,4–6]. Initial studies focused on reconstructing the palaeoecology and inferring the past diets of ancient fauna from isotopic signatures in bulk collagen ($N(^{15}\text{N})/N(^{14}\text{N})$ that represents the ratio for nitrogen, abbreviated herein as $\delta^{15}\text{N}$, and on $N(^{13}\text{C})/N(^{12}\text{C})$ that represents the ratio for carbon, abbreviated herein as $\delta^{13}\text{C}$), or the $\delta^{13}\text{C}$ composition of bone apatite [7] and, in the last decade, the $\delta^{15}\text{N}$ values of individual amino acids from collagen [8]. Simultaneously, in the 1980s, the first ancient DNA (aDNA) sequence fragment was successfully recovered from the extinct quagga (*Equus quagga quagga*) [9]. Roughly three decades later, the first complete high-quality genome of the woolly mammoth (*Mammuthus primigenius*) was sequenced [10]. In parallel with these developments, the analysis of collagen and non-collagenous proteins and proteomes extracted from ancient bones has developed at a rapid pace [11]. Lipids have been retrieved from frozen carcasses of Late Pleistocene mammoths, horses, and bison [12,13], as well as from ceramic vessels from the transition to agriculture, and have proven useful in determining patterns of animal food consumption by different populations [14,15]. Recently, the epigenetic memory (somatically heritable chemical modifications of the DNA that do not involve modifications of the sequence itself), which is plastic and responsive to the environment, has opened new avenues to the study of the regulatory changes underlying divergence, speciation, and extinction in ancient fauna [16–18]. RNA, a molecule until recently considered an improbable source of information for studying ancient fauna, has provided some first insights into the taxonomy and tissue-specific gene regulation of Late Pleistocene canids [19]. More recently, studies have begun to focus on palaeovirology as a means to elucidate the role of ancient viruses in ancient faunal evolutionary history (e.g., extinctions, island isolations, migrations), in addition to modern consequences on extant species [20,21].

These breakthroughs in ancient biomolecular research over the last decades are instrumental in opening up new perspectives on extinct and extant diversity and their deep-time population histories, ecology, and evolutionary patterns [22–29] not accessible through the analysis of modern molecules alone [30]. With ancient biomolecular research methods becoming increasingly available and powerful, in what ways would multiproxy approaches contribute to a more complete picture of past faunal diversity and evolutionary history?

The aim of this review is to explore the potential of integrated use of multi-biomolecular data identified by the authors for addressing complex questions related to ancient faunal diversity. Within a geochronological and palaeoclimatological context corresponding to the time period before and after the Pleistocene/Holocene transition (~11,700 years before present), estimated to roughly mark the point at which the size of the human population started to increase [31], we intend to consider some major evolutionary events in selected taxa reconstructed through biomolecular research. Ultimately, we will discuss the ways in which multiproxy biomolecular approaches may further our understanding of the evolution and extinction of some emblematic Pleistocene species on the one hand, and of the faunal transformations starting around the Pleistocene/Holocene transition on the other (the most profound being the domestication of a number of species).

2. Evolution and Extinction during the Pleistocene

During the Pleistocene period, from about 2.6 million to 11,700 years ago, the Earth's climate went through cycles with extreme fluctuations between glacial and interglacial conditions. These climatic oscillations forced species to retreat into and expand from refugial areas, still visible in the genetic diversity and current distribution patterns of extant species [32–34]. At the end of the Pleistocene and beginning of the Holocene, the combined impact of these climatic fluctuations [35,36] and human expansion [35,37] disproportionately affected some large mammals, leading to their decline and final extinction (i.e., woolly mammoth, giant deer, woolly rhinoceros, and cave bear) [38]. Below, we will begin by describing two megafaunal species extensively studied from a biomolecular perspective: the cave bear (*Ursus spelaeus sensu lato*) and the woolly mammoth (*Mammuthus primigenius*) (Figure 1), from which abundant remains have been retrieved from circumstances particularly favourable for biological preservation, e.g., cave sediments and permafrost. These pioneering studies, ranging from method development to palaeoecology and population palaeogenomics, effectively laid the foundation for the field of research on biomolecules. Accordingly, these two species may be used as model systems for illustrating how the processes preceding extinction and the contribution to modern species' genomes have been studied.

To further broaden the perspective on the impact of environmental changes on species' diversity and evolution, additional representative Pleistocene taxa will be discussed: the woolly rhinoceros (*Coelodonta antiquitatis*), adapted to the cold of the last ice age, and the bison (*Bison* sp.), which managed not only to survive the other megafaunal species, but to thrive in their wake well into modern times.

2.1. Cave Bears

Cave bears are by far one of the most extensively studied extinct Pleistocene species [39]. They are closely related to the brown bear (*Ursus arctos*) and polar bear (*Ursus maritimus*), from which they diverged some 1.5 million years ago [40]. In contrast to its sister species, the brown bear, with whom cave bears coexisted sympatrically in Eurasia during the Pleistocene, the cave bear was not able to cope with changes in its environment and became extinct around 25,000 years ago [41].

From a biomolecular perspective, traditional isotopic methods based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from bulk protein (collagen), and more recently $\delta^{15}\text{N}$ analyses of individual amino acids, were used to reconstruct the cave bear's dietary preferences. These studies essentially support a herbivorous diet across its range [41–45]. Palaeogenomic studies have revealed a complex evolutionary history within the cave bear species complex with three major groups: the Caucasian group including *praekudarensis* and *kudarensis* taxa; the European group including *spelaeus*, *ingressus*, *eremus*, and *kanivetz* from the Ural Mountains; and the Ural-specific group made up by *rossicus* [40].

Apart from focusing on cave bear palaeoecology and evolutionary history, studies based on isotopes and aDNA have also tried to answer one of the open-ended questions related to cave bear extinction: why did the cave bear go extinct, while the brown bear survived the unstable climate and human expansion in the Late Pleistocene? Consequently, comparative studies on sympatric and/or syntopic cave bear and brown bear populations have been conducted. Palaeodietary inferences showed an omnivorous diet for contemporaneous brown bears that might have played an important role in ensuring species survival, while an apparent lack of dietary flexibility might have made the cave bear vulnerable to decreases in plant biomass quantity and quality related to colder climates [43].

Comparative studies of population dynamics have mainly utilised mitochondrial markers. The first such study compared the demographic history of the extinct cave bear versus that of the extant brown bear, and revealed a constant population size in brown bears during the Late Pleistocene and a drastic decline in cave bears starting about 50,000 years ago [46]. Another study uncovered homing behaviour in cave bears from patterns of

population structure contrasting greater spatial flexibility in brown bears [47], a difference in sociality between the two taxa that might have contributed to the extinction of cave bears.

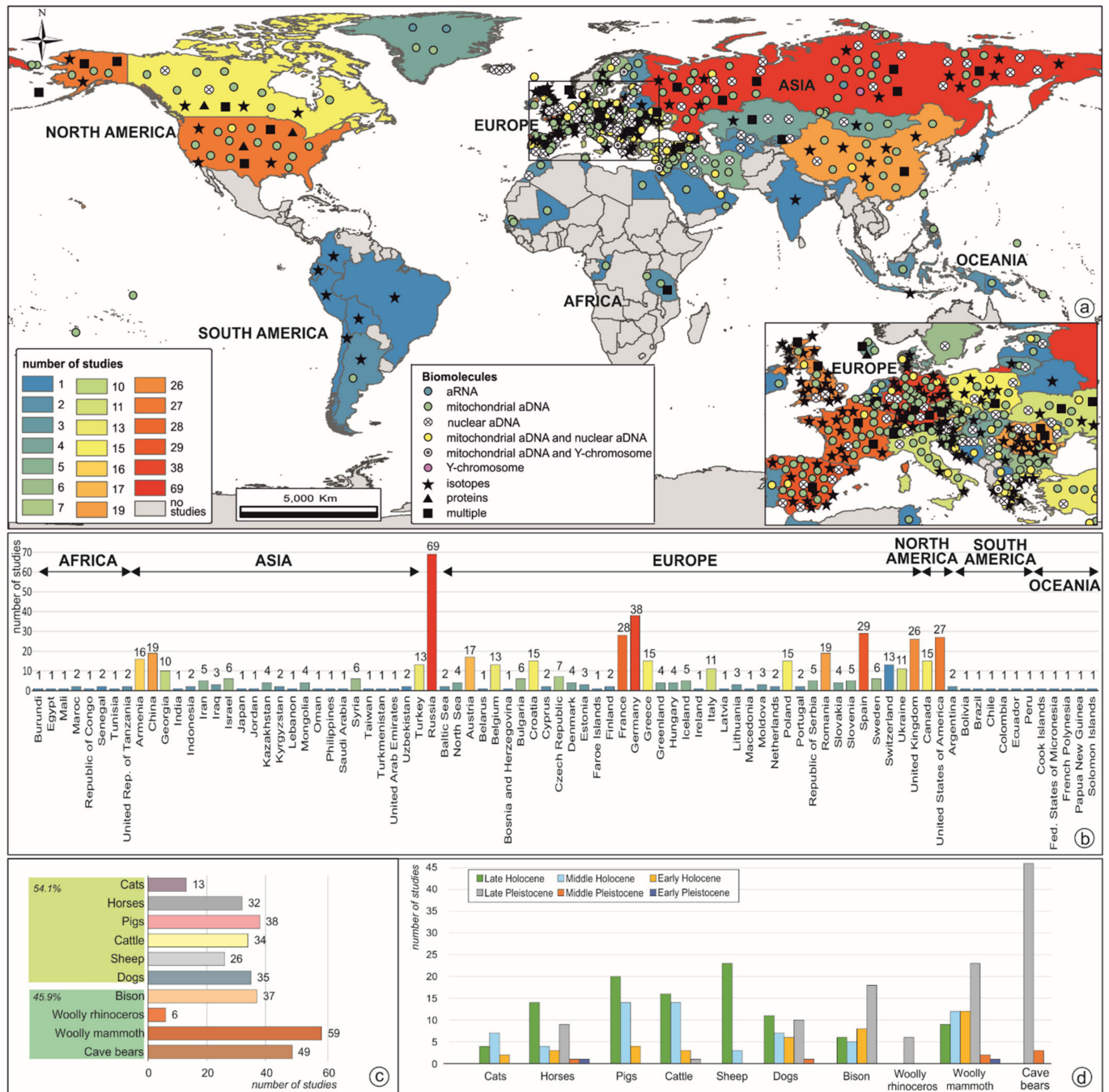


Figure 1. Biomolecular studies within a spatio-temporal context. (a) Global distribution map with the various types of biomolecular and biogeochemical analyses plotted, with inset showing studies in Europe; (b) bar plot showing the number of studies included per country and continent; (c) bar plot showing the number of studies included per taxon; and (d) bar plot showing major temporal stratigraphic divisions (<http://quaternary.stratigraphy.org> (accessed on 7 May 2021)) represented in the studies. Note that the number of studies included does not refer to unique studies as some studies included multiple taxa, geographic locations and time periods.

Even though advances have been made in understanding cave bear’s palaeobiology and evolutionary history, the causes leading to cave bear extinction remain elusive. The debate is ongoing, with most studies suggesting human impact as the major factor based on

an apparent absence of associated substantial climatic changes [39,48–50]. However, palaeoclimate records indicate harsh conditions contemporaneous to inferred evolutionary events that might have contributed to cave bear population decline that started approximately 50,000–40,000 years ago. For instance, the Heinrich 4 event and Campanian Ignimbrite volcanic eruption were two such major events that dramatically changed the landscape of Europe (Figure 2). Studies have shown that the Heinrich 4 event was exceptionally cold and dry [51]. Coupled with one of the most explosive eruptions in the Late Pleistocene, the Campanian Ignimbrite volcanic eruption, which affected large areas of Europe [52], it triggered catastrophic impacts on ecosystems (i.e., diminished food resources, fluoride poisoning), hypothesised to have affected large herbivores and other mammals, including Neanderthals [53,54]. Following the Heinrich 4 event, large areas of Europe experienced a climatic deterioration and progressive continentalization characterized by less precipitation, colder winters, and an open steppe ecosystem, lasting until about 27,000 years ago [55–57], possibly contributing to the loss of genetic diversity inferred in cave bear populations across Europe [39,49,58,59].

Few studies thus far have combined isotopes and aDNA to shed light on cave bear's ecology, evolutionary history, and extinction [45,49,60,61] (Figure 3).

2.2. Woolly Mammoth

One of the most abundant and widespread herbivore species of the last glacial period was the woolly mammoth. They inhabited the productive and cold steppe-tundra that extended from western Europe through Asia into northern North America [62]. At the end of the Pleistocene, however, the woolly mammoth underwent a rapid population decline, and disappeared from most of its former range [63]. Two populations survived into the Holocene, isolated on two small islands: Wrangel Island in northeastern Siberia and St. Paul Island in Alaska [64,65], until the mammoth finally went extinct ca. 4000 years ago (Figure 2).

Both their iconic status and good preservation conditions in the northernmost parts of their distribution range have made woolly mammoths a popular subject for aDNA studies, including the use of their remains to explore evolutionary patterns in endogenous retrovirus-like elements across time [66] (Figures 1 and 3). Early DNA work on the woolly mammoth, however, focused on its evolutionary relationship with extant proboscideans.

Complete mitogenomes and nuclear sequences revealed that it is most closely related to the Asian elephant (*Elephas maximus*) [67–70]. More recent studies have tried to unravel the genetic structure and population size changes within woolly mammoths through time. Whereas the first studies mainly used small nuclear markers, or short stretches of mitochondrial DNA (mtDNA), to tackle these topics [71–75], complete mitogenomes have now become the norm [68,76–81]. Moreover, in their study, the authors of [82] used DNA from samples more than one million years old to explore the genetic relationships between woolly and Columbian mammoths (*Mammuthus columbi*) and their direct ancestors.

These studies have revealed a complex evolutionary history characterized by multiple replacement and local introgression events. Three highly divergent and geographically structured matrilineal clades have been described, but the timing and geographic origins of these clades remain debated [83]. Furthermore, around 25,000 years ago, only one clade persisted after it had replaced the clades endemic to Siberia and Europe in an east-to-west fashion [74,75]. Whether the replacement of mitochondrial clades throughout the woolly mammoth distribution was caused by genetic drift, selective advantage, or coincided with climatic and/or anthropogenic disturbances remains unclear [71,74,75,79].

To study behaviour, palaeodiet, and social structure, stable isotope analysis has been a popular tool. Nevertheless, studies have also used biases in sex ratios derived from genomic data [92], comparisons of the ratio of mitochondrial and nuclear coalescent dates [93], and testosterone from ancient hair shafts to study social structure and life history traits in woolly mammoths [94].

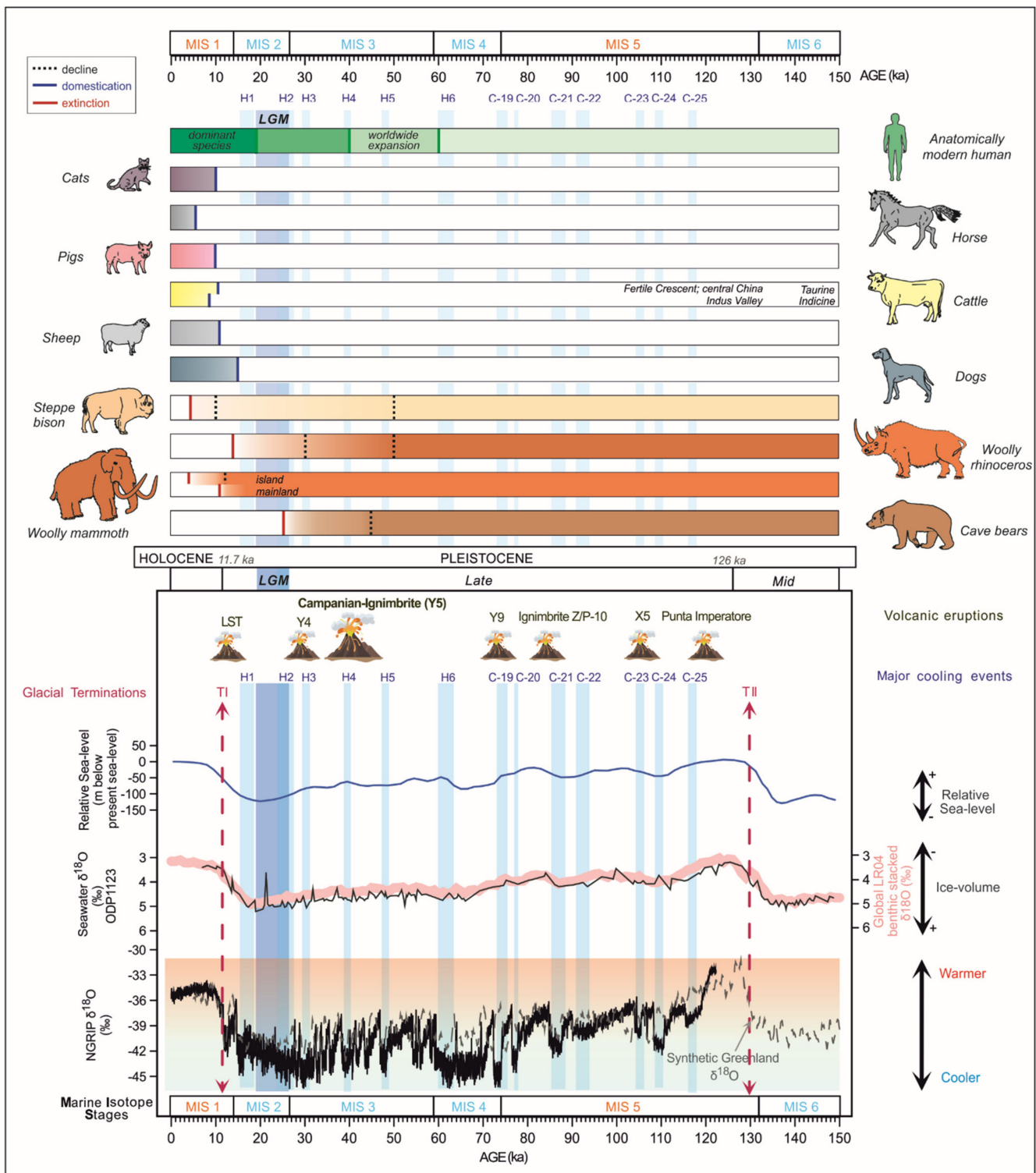


Figure 2. Timelines of taxa in a palaeoenvironmental context. Timelines outlining important evolutionary events in the selected taxa in relation to environmental events and the expansion of anatomically modern humans. Climate variability is represented over the past 150 thousand years (ka) including (synthetic) oxygen isotope record from Greenland ice cores [84,85], seawater oxygen isotope record (Uvigerina $\delta^{18}O$) [86], and global benthic oxygen isotope stack [87] proxies for global ice volume and relative sea-level [88]. LGM refers to the Last Glacial Maximum, TI-TII represent glacial terminations according to [85], cold events represent Heinrich stadials associated with ice-rafting events of the last climatic cycle (H1-H6, C19-C24) [89,90], and selected volcanic eruptions are represented according to [91]. For the sake of clarity, given that the high number of studies included in our review and the vast majority of events studied relate to the Northern Hemisphere, we present reconstructions for the Northern Hemisphere only.

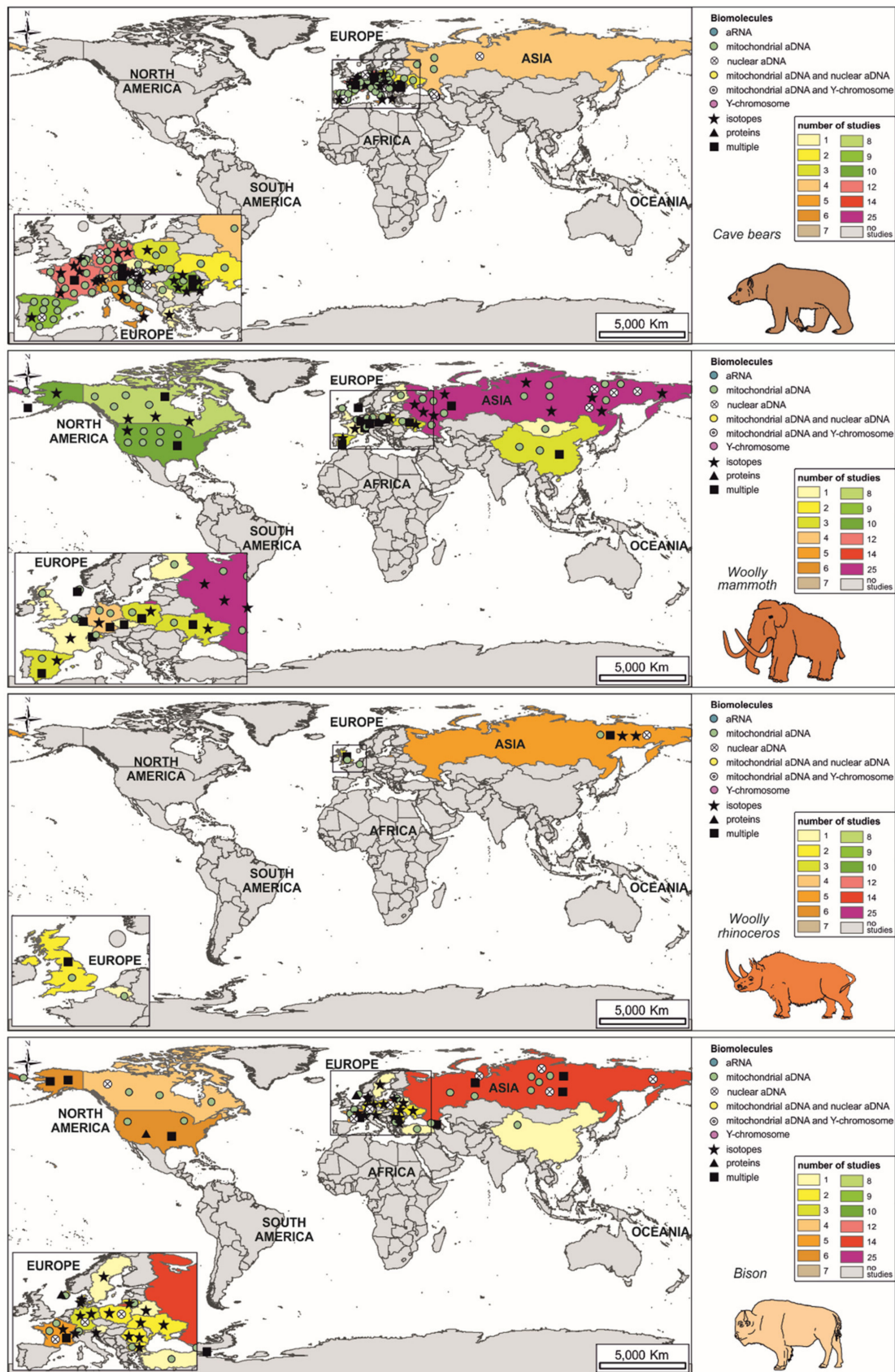


Figure 3. Biomolecular studies on wild taxa. Global distribution map with the various types of biomolecular and biogeochemical analyses plotted separately for cave bear, woolly mammoth, woolly rhinoceros, and bison. Note that the number of studies included does not refer to unique studies as some studies included multiple geographic locations.

Woolly mammoths had a distinct diet rich in C3 plants such as grasses and sedges (e.g., [95,96]), characterised by elevated $\delta^{15}\text{N}$ prints. Multiple hypotheses have been postulated to explain the high $\delta^{15}\text{N}$ values coupled with depleted $\delta^{13}\text{C}$ values, including niche partitioning and coprophagy [95,97–100]. While this pattern is observed in mammoths on both sides of the Bering land bridge, geographic variation in isotopic signatures does exist, reflecting regional differences in precipitation and vegetation [101,102].

A well-studied topic within woolly mammoth research is the timing and cause of its extinction. Two phases within the extinction process have received considerable attention [103]: a first one during the Pleistocene/Holocene transition when mammoths went extinct on the mainland, and a second one during the Holocene when two mammoth populations isolated on islands went extinct, marking the global extinction of the woolly mammoth.

To determine the ultimate cause of the disappearance of the mainland woolly mammoth population at the end of the Pleistocene, studies have used combinations of DNA markers and radiocarbon dates to model the mammoth's distribution in relation to vegetation changes and humans, but the results have remained inconclusive [35,104–106]. Genetic studies on both mitochondrial and nuclear genomes show that the woolly mammoth had a relative stable population size throughout the last glacial period on both sides of the Bering land bridge, but suffered a steep decline around 12,000 years ago, coinciding with the onset of the dramatic climate changes characteristic of the early Holocene [10,74,75]. While studies of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of mammoths from sites on the East European Plains have indicated that extinction was preceded by nutritional stress [29,79,107], no such patterns were found in mammoths from northeastern Siberia, indicating a complex extinction process throughout the woolly mammoth's range [108].

Whereas explanations for the mainland extinction of the woolly mammoth mainly revolve around the relative importance of climate change and anthropogenic effects, other events likely caused the extinction of the woolly mammoth island populations during the Holocene. Using sediment DNA, three coprophilous fungal spore types, and directly dated radiocarbon remains as proxies for megafauna presence, ref. [109] found that the mammoths disappeared on St. Paul Island in Alaska as a result of fresh water scarcity. The circumstances surrounding the extinction of woolly mammoths on Wrangel Island are less clear. Genetic data showed that the early island population went through a bottleneck event and lost much of its genetic diversity, after which it remained constant [72,73], although other studies found extensive genetic drift in the island population [76,110]. Furthermore, stable isotope analysis did not find any evidence for habitat deterioration on the island [108,111]. Altogether, genetic, isotopic, and radiocarbon data all suggest that the extinction must have happened abruptly.

Many studies on woolly mammoths have focused on single biomolecules, whereas more recent studies have shown a trend towards a more integrative approach. For example, ref. [80] combined an extensive series of radiocarbon dates and mitogenome data to establish the origin of the founding population on Wrangel Island and determine the final extinction date of the woolly mammoth approximately 4000 years ago. In another study, ref. [79] showed the strength of combining methods by studying both stable isotopes and mtDNA to get a better understanding of woolly mammoth population dynamics in Central Europe. Despite this work, much uncertainty remains about the extinction of the woolly mammoth.

2.3. Woolly Rhinoceros

Similar to cave bears and woolly mammoths, the woolly rhinoceros (*Coelodonta antiq-uitatis*) was a megaherbivore that was widespread in Eurasia during the Late Pleistocene. Radiocarbon records suggest that the woolly rhinoceros went extinct around 14,000 years ago, after a range contraction towards northeastern Siberia [112] (Figure 2). Although not as well studied as other prominent Pleistocene megafauna, biomolecules such as sta-

ble isotopes and aDNA have contributed to our understanding of the woolly rhinoceros (Figures 1 and 3).

Firstly, stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) extracted from bone, soft tissue, and horn have been used to investigate the diet of woolly rhinoceros [95,113]. The authors of [95] found that the woolly rhinoceros had similar isotopic compositions to woolly mammoths, suggesting that they had a similar staple diet. Furthermore, woolly rhinoceros had seasonal differences in its diet, with more graminoid plants consumed in the summer and wooded and shrub plants during the winter [113]. The results from these stable isotope analyses add to previous analyses based on pollen and macrofossil remains identified from mummified specimens [114,115].

Initial aDNA studies on woolly rhinoceros focused on placing this species in the Rhinocerotidae phylogeny [116,117]. By sequencing short fragments of mtDNA, ref. [116] determined that woolly rhinoceros were most closely related to the extant sumatran rhinoceros (*Dicerorhinus sumatrensis*), and that these taxa diverged ~26–21 million years ago. Following this, ref. [117] constructed the complete mitogenome of woolly rhinoceros, along with other Rhinocerotidae species, and confirmed the previously inferred placement of woolly rhinoceros in the phylogeny.

Later studies have investigated the demographic history of the woolly rhinoceros [104,118,119]. Mitochondrial and nuclear genome data indicate that the population size of woolly rhinoceros increased just prior to the Last Glacial Maximum (LGM) [104,118]. Furthermore, the presence of multiple mitochondrial clades and relatively high genome-wide diversity stipulates that woolly rhinoceros in northeastern Siberia did not experience genetic erosion preceding their extinction [118,119]. Recent stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) evidence found stability in diet in the woolly rhinoceros population in northeastern Siberia over time, suggesting this area was important for maintaining this species during the warming period after the LGM.

Finally, ref. [118] also used aDNA to examine selection in the woolly rhinoceros, finding variants in genes that may be associated with cold-tolerance in this species (e.g., TRPA1). Thus, aDNA and stable isotopes are important biomolecules and biogeochemical traces that have so far shed light on the life and evolutionary history of woolly rhinoceros.

2.4. Bison

Bison is one of the few megafaunal genera that survived the Late Pleistocene/Holocene extinctions in Eurasia and North America. While two present-day representatives exist, the American bison (*Bison bison*) and the European bison (*Bison bonasus*), numerous species have been postulated to have coexisted in the Pleistocene based on morphology (e.g., *Bison priscus*, *Bison schoetensacki*, and *Bison antiquus*, among others) [120]. Both the American and European bison suffered extensive persecution in the 19th century [121], with the European bison being eradicated in the wild in the early 20th century [122]. The current population is the result of an extensive international cooperative breeding program that has made it possible to reintroduce more or less wild herds around Europe.

Notwithstanding the success of the effort to conserve the two species, sharp population declines have nevertheless resulted in reduced morphological and genetic variation in the persisting populations [123,124]. Consequently, research has been dedicated to exploring the extent of the genetic variation lost in the historical bottlenecks (e.g., [125–129]). Similarly, accounts of the ecology and ethology of bison stem from periods when these taxa were already greatly affected by human influence [130]. The ramifications are that only limited knowledge is accessible through the study of these relic bison.

Studies of the evolutionary history of prehistoric bison have been hampered by the morphological similarities between sympatric prehistoric bison species. In addition, bison remains are not easily distinguishable from those of members of the closely related *Bos* genus. Consequently, some of the earliest analyses of ancient bison DNA were conducted to facilitate species identification of bones (and residues on archaeological objects; e.g., [131,132]).

Mitochondrial data have been recovered from numerous bison specimens originating from large parts of its Holarctic distribution (e.g., [125,128,129,133–143]). These studies have, for instance, identified the existence of significant (but only occasionally associated) genetic and morphological variation. They have also been able to detect previously unknown dynamics between bison species and populations: e.g., the movements back and forth of diverse steppe bison (*Bison priscus*) lineages across the Bering land bridge facilitated by climatically induced periodic lowering of the sea level throughout the Pleistocene; the origin and subsequent spread of the American bison from south of the Laurentide and Cordilleran ice sheets; as well as the Late Pleistocene patterns of climatically driven mutual replacements of steppe bison and European bison in Europe.

However, studies using mtDNA, limited by the information obtainable from this uni-parentally inherited locus, have been unable to resolve all the questions about the evolution and taxonomy of the bison species [142]. For example, discordance between the inferred genetic affiliation from mtDNA and Y-chromosome sequences in contemporary European bison has been suggested to be due to a complex ancestry [144]. This is because the Y-chromosome sequence confirms a close relationship to American bison, while the mitochondrial genome, surprisingly, is more similar to the mitogenome of *Bos primigenius/taurus*. Although some ancient genome-wide sequence data, with the potential to resolve this issue, have been published [129,138,139,145,146], the evolutionary history of the European bison, and the reason for the discordance, remain a contested issue [120].

Attempts to reconstruct the past diet and behaviour of prehistoric bison have to date, for the most part, been conducted as separate biogeochemical studies (e.g., [130,147–150]). Without diminishing their significant scientific contribution, we argue that interdisciplinary studies that integrate morphological, isotopic, dietary, and genetic data would contextualise and enhance our knowledge of this enigmatic species complex. We are convinced that this type of integrated analysis can be used not only to relate reconstructions of the palaeoenvironment to the diet and behaviour (e.g., propensity to migrate) of extinct species, but also to investigate relationships between differences in behaviour (and the persisted integrity) of different genetic lineages. So far, with the exception of [138], such studies have mainly been conducted on individual exceptionally preserved specimens (e.g., [134,146]).

3. Faunal Transformations during and after the Late Pleistocene/Holocene Transition

Following the success of biomolecular studies of extinct species, it was not long before palaeo-biomolecular methods were used to investigate the biological history of domesticated species and their co-evolution with the humans who exploited them. Domestication has been described as the sustained human agency in the propagation and care of animals with strong selective advantages for both partners [151], the final consequence of which is the mutual shaping of both visible as direct modifications in the genomes of the animals and indirect patterns of change in the human genome.

The aim of early molecular studies studying the domestication of animals was to identify the wild progenitors and the patterns associated with this process [152,153], and subsequently to map the diversity of stocks in different geographical regions and historical periods, as well as to assess their relation to present-day stocks [154,155].

Domestication of animals by humans was initiated by the taming of the wolf (*Canis lupus*) about 15,000 years ago by hunting and gathering human populations. In the Fertile Crescent at approximately 11,000–10,000 years ago, a shift in human subsistence (from hunting and gathering to herding and cultivation of crops) was most likely triggered by climatic changes related to the global transition from the Late Pleistocene to the Holocene interglacial period [156]. At this time, the first true livestock, domestic sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), and pigs (*Sus scrofa*) [157], appeared. Arguments have also been put forward that the changes in climate after the end of the Late Pleistocene may have led to greater phenotypic and behavioural variation in some species, making them particularly amenable for domestication [158]. This was followed by the domestication of

the horse (*Equus caballus*) in Central Asia, chicken (*Gallus gallus*) in South-East Asia, and cat (*Felix catus*) in Northern Africa, among others, between 5500 and 4000 years ago [156].

3.1. Dogs

The complex issue of dog domestication has been addressed through a combination of single-molecule studies (aDNA sequence and genomic analyses, modern genomic analysis) and interdisciplinary research that integrates genetics, morphological assessment, and stable isotope analysis [159,160] (Figures 1, 2 and 4). Compared with the previous, single-topic studies, the integrated nature of the latter has allowed for a more detailed and complex evaluation of the initial stages of the domestication process.

Ancient DNA [161–163] and modern genomic analyses (e.g., [164]) have established that the dog was the first domesticated species and, even though there is still considerable debate regarding its exact timing, there is a consensus regarding the fact that dogs were domesticated by hunter-gatherers, thus predating the rise of agriculture.

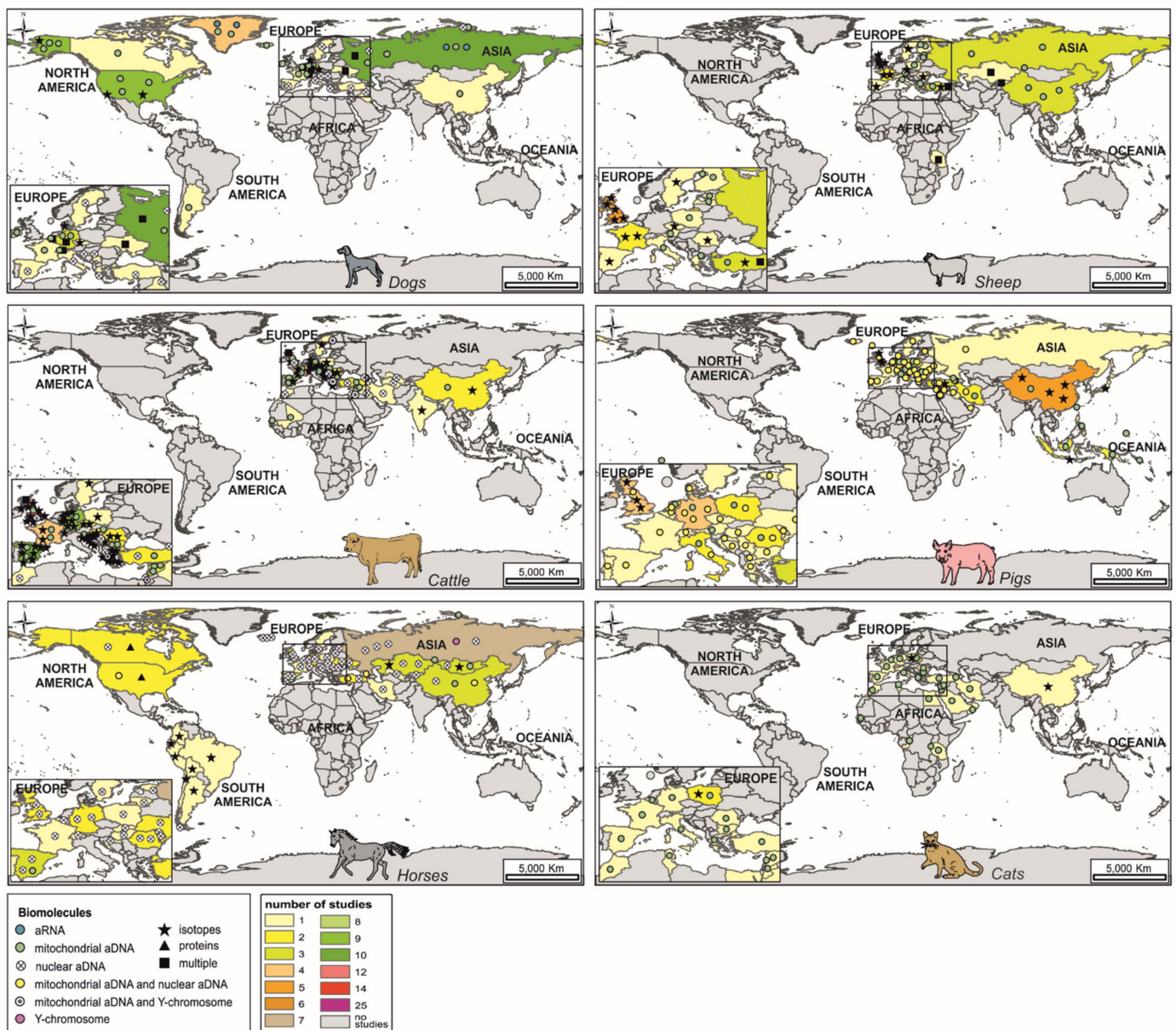


Figure 4. Biomolecular studies on domestic taxa. Global distribution map with the various types of biomolecular and biogeochemical analyses plotted separately for dog, sheep, cattle, pig, horse, and cat. Note that the number of studies included does not refer to unique studies as some studies included multiple geographic locations.

For a long time, it was thought that the ancestor of the domestic dog was the modern grey wolf. While the grey wolf is the closest extant relative of dogs, and there is evidence of post-domestication gene flow between dogs and wolves [155,163–165], modern genomic analysis as well as aDNA analysis of fossil remains have proved that dogs were domesticated from a now-extinct wolf species and do not belong to the same lineage as modern wolves [155,161,163,164]. A Late Pleistocene origin for the most recent common ancestor of dogs and wolves has been suggested by aDNA analysis [161,162] and multidisciplinary studies [159,160].

The geographical origin of dog domestication has yet to be established with certainty, with ancient mitochondrial genomic analysis suggesting a European origin [163], perhaps from multiple and distinct wolf populations [159]. Modern genomic studies, however, propose a Central Asian [166] or Southeast Asian [167,168] origin. The authors of [169] inferred a contribution from Middle Eastern wolves. Moreover, an analysis of ancient mtDNA control region sequences of canid fossil remains from the Siberian Arctic indicates a not exclusively European origin [165]. The possibility of multiple domestication events has been put forward through ancient genomic and mtDNA sequence analysis [170], as well as a potential population replacement in Europe during the Neolithic, by a Near Eastern lineage [171,172]. However, the analysis of mitogenomic data from Neolithic dog remains has failed to corroborate either hypothesis [162].

Nevertheless, following the inception of the domestication process and the growing prevalence of agricultural practices, dogs conformed to the sedentary conditions of living with humans and livestock, as illustrated by two categories of studies. Firstly, modern genomic [173,174] and combined modern and aDNA studies [175] showed signs of selection on genes related to lipid or starch metabolism, behaviour, brain function, and immunity. Secondly, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $N(^{34}\text{S})/N(^{32}\text{S})$ (representing the ratio for sulphur, abbreviated herein as $\delta^{34}\text{S}$) analyses of Stone Age [176,177] and Medieval [178–180] canid remains, have found isotopic signatures suggesting control of dogs' dietary intake and their differential treatment food-wise.

Going forward from aDNA studies, recent advancements in analysing ancient dog specimens have been achieved by examining the yet poorly explored ancient RNA (aRNA) field. For instance, two promising proof-of-concept studies have reported the successful recovery of tissue-specific ancient RNA molecules from the well-preserved remains of a ~14,300-year-old ancient canid [19,181].

The existence of well-preserved short RNA transcripts with known biological functions in ancient specimens [19,181], as well as the ability of RNA molecules to be preserved through extended periods of time in specific conditions, opens the possibility for further analyses on evolution, selection signatures, and regulatory mechanisms at the transcriptomic level. Although the persistence of aRNA is expected to be far shorter than that of aDNA, thus limiting the applicability of this approach for ancient samples, this remains to be tested empirically.

The up and coming field of palaeotranscriptomics has the potential to contribute additional information to the far more mature aDNA field. Further analyses on aRNA sequences possibly surviving in well-preserved ancient and historical specimens might reveal novel insights into the history of extinct species that canonical aDNA studies have so far not been able to provide, for instance, tissue-specific expression profiles or the regulation of molecular pathways by small RNA transcripts such as microRNAs.

3.2. Sheep

Understanding of the complex process of sheep domestication has been greatly aided by the use of various molecular techniques, such as retrovirus integration analysis [182]; SNP analysis [183,184]; stable isotope analysis [185–189]; uni-parentally inherited DNA (mtDNA and Y-chromosomal DNA, both modern and ancient) (e.g., [190–195]); and, of late, large-scale genomic studies performed on modern samples [196–200] (Figures 1, 2 and 4). In addition, the differentiation from the morphologically similar goats (*Capra hircus*) has

been facilitated by collagen-peptide mass fingerprinting [201,202] and recently published ancient mitogenomic sequences [203].

Modern DNA analysis, combined with archaeozoological assessment and aDNA analysis, has shown that initial sheep domestication took place approximately 11,000 years ago in the Fertile Crescent from several Moufloniformic populations [204–207]. From there, domestic sheep were disseminated to Europe, following three separate routes: the Danubian [191], the Northern European [198,208], as well as the Mediterranean [198]. Further analysis of lineage expansions from modern samples indicates two main Asian dispersal waves, with the Mongolian Plateau region acting as the secondary centre of migration towards China and the Indian subcontinent [190,197,199]. The ancient sea route connecting the Middle East to India served as yet another path of sheep dispersal towards the Indian subcontinent [209]. Studies concerned with elucidating local uni-parental genetic diversity of ancient samples before the Iron Age have illustrated the appearance of domestic mitochondrial lineages in the Alpine region [210], Russia [193], Estonia [192], Turkey [194], and China [211,212], while a recent interdisciplinary study, combining mitogenomic analysis and collagen-peptide mass fingerprinting, has illustrated the presence of domestic sheep in the interior of Central Asia ~8000 years ago, 3000 years earlier than previously assessed [203].

Analyses of uni-parentally inherited DNA sequences from modern [205–208,213–216] and ancient samples [194,210,212,217,218] have demonstrated the development of phylogeographic structure following domestication [197], possibly as a consequence of bottlenecks during migration. The clustering of both the deeply divergent rare Y-chromosomal haplotype (HY2) and the mitochondrial lineage C with Iranian mouflon, rather than with the wild mouflon from South East Anatolia, has been suggested to result from wild introgression [196,197], which has been proposed for other rare and geographically restricted mitochondrial lineages [196,197].

Besides wild introgression, the genetic history of sheep is marked by human-mediated trade, strong selective pressure, and admixture between different populations and eventually breeds [192,198,219]. While there are differences in the genetic makeup of different breeds as a result of adaptation to specific production requirements and environments, large-scale nuclear SNP analyses have illustrated that certain key genomic regions, such as those involved in coat colour, morphology (e.g., body size as well as the presence or absence of horns), and reproduction, display similar signs of selection across all breeds [198]. Local practices for breeding and trade during the Iron Age, Middle Ages, and into historical times in northern Europe [191,192] and Italy [217] have also been investigated through analyses of uni-parentally inherited aDNA markers.

Analyses of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $N(^{18}\text{O})/N(^{16}\text{O})$, which represents the ratio for oxygen, abbreviated herein as $\delta^{18}\text{O}$, have similarly been used to examine signs of domestication (e.g., differences in birthing season between wild and domestic sheep) in Neolithic and Bronze Age samples [185–189]. Studies using either aDNA or stable isotopes [220] and multi-proxy studies combining analyses of mtDNA, collagen-peptide mass fingerprinting, and/or stable isotopes [221,222] have mainly focused on examining local management techniques across various historical periods.

3.3. Cattle

The process of cattle domestication has been investigated using various biomolecules ranging from mtDNA [223–226] and Y-chromosomes [227,228] to whole genomes [153,229], and stable isotope analysis [187,230] on both ancient and modern samples (Figures 1, 2 and 4). The progenitor of cattle, the extinct aurochs (*Bos primigenius*), had a wide late Pleistocene and early Holocene distribution, inhabiting the north of Africa, Europe, and Asia [231]. The aurochs' domestication led to the appearance of taurine (*Bos taurus*) and zebu (*Bos indicus*) cattle. The major domestication events took place independently in the Neolithic in a two-step process [232]. First, ~10,500 years ago, taurine cattle were domesticated in the Near East from the western Eurasian *Bos primigenius primigenius*, followed 2000 years later by the

domestication of indicine (zebu) cattle from the southern Asian *Bos primigenius nomadicus* in the Indus Valley [233]. In addition to this, an independent domestication event has been suggested to have occurred at least 10,660 years ago in eastern China. However, the status of this distinct taurine cattle as a ‘true’ domesticate and what contribution it has made to the nuclear gene pool of modern cattle are currently unknown [234].

East Asian cattle are characterised by high genetic diversity, indicative of a complicated history. Firstly, *Bos taurus* was introduced from West Asia ~5000 years ago [235], followed by *Bos indicus* ~3500 years ago [236]. The two species crossbred in central China [237]. Additional admixture between different bovine species has possibly resulted in shared derived alleles, e.g., from the banteng (*Bos javanicus*) into the Chinese Hainan cattle, and from taurine cattle into the yak (*Bos grunniens*) [229].

The domestication of European cattle in the Near East [223,225] is estimated to have involved a low number of individuals (~80 females) and to be the result of the natural mating behaviour of the wild aurochs [225]. Possible gene flow between aurochs and domesticated cattle has also been suggested in both the Near East and Europe [153,238]. Moreover, male-driven adaptive introgression from zebu bulls into taurine stock has been proposed to have been mediated by humans in response to climatic changes (sustained drought), nearly 4000 years ago [239].

The studies on stable isotopes offer new perspectives on the domestication process, with $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{18}\text{O}$ usually used to investigate cattle management strategies. In Central China in the late Neolithic, cattle had a privileged status, as they were fed millet and kept within the settlements all year round [240]. This also contributed to supplementary feeding with leafy fodder becoming a widespread practice [241]. In addition, manipulation of female reproduction, in order to prolong the birthing season and enhance the production of milk, has been proposed to have been common already in the Neolithic based on stable isotope analyses [187,242,243].

An integrated study combining mtDNA, molecular sexing, radiocarbon dating, and stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$), [244] was able to show that the most likely explanation for the presence of the wild north European P haplotype in Late Neolithic cattle from the site Links of Noltland in Orkney originated from the integration of female aurochs into domestic herds prior to the introduction to Orkney.

3.4. Pigs

The pig (*Sus scrofa*), is the only member of the diverse Suidae family that was domesticated [245], and is nowadays one of the most common livestock species worldwide. The long shared history with humans that has gradually shaped the genetic and phenotypic makeup of this widespread and opportunistic species has made it a suitable candidate for molecular genetic studies of domestication processes and evolutionary history.

Unlike other domestic species (e.g., dogs and horses) for which the geographical and temporal (spatio-temporal) origins remain unresolved, for pigs, there is solid evidence from material culture/archaeological material and genetics for the early stages of domestication [246–248]. Pigs were domesticated from the wild boar in East Anatolia and China about 10,000–9000 years ago from two divergent wild boar populations [249,250] (Figure 2). Owing to their omnivorous nature, wild boars are hypothesised to initially have been attracted to anthropogenic habitation sites as an easy way to access food, most probably being domesticated following a commensal pathway [251,252]. The two domestic lineages have subsequently experienced an intertwined genetic history as indicated by the analyses of pig mitochondrial genomes [246,253], microsatellite markers [254], and complete genome sequences [255].

The task of disentangling the multistage domestication process of suids has involved a number of disciplines (e.g., archaeology, biology, anthropology, genetics). Besides the traditional archaeological approach [256,257], additional insights into population dispersal and introgression events have been gained using modern genetic data [258–261]. However, the genetic legacy derived from modern organisms provides only a peek into this protracted

and reticulated process; additional lines of evidence need to be drawn from palaeogenomic research. For instance, while studies of modern domestic pigs and wild boar have shown a lack of a Near Eastern genetic signal in nearly all modern European pigs [246], ancient mtDNA has provided evidence for human-mediated dispersal of domestic pigs from the Near East into Europe associated with the Neolithic expansion [262]. Furthermore, mtDNA analyses from archaeological specimens have shown that the maternal genetic architecture of pig populations has subsequently been influenced by gene flow between local European wild boars and introduced domestic stocks [262–264]. The complex history of translocations between southeastern Europe and Anatolia during the Bronze and Iron Ages [228] and changes in pig management strategies in northern Europe [265] have likewise become apparent by the analysis of maternal ancestry in pig samples from archaeological contexts. Contrary to European pigs, analyses of ancient mtDNA have suggested long-term genetic continuity between ancient and modern Chinese domestic pigs, as well as a lack of maternal genetic contribution from wild boars to modern domestic swineherds throughout East Asia [253].

Despite the unique power of ancient genomes/autosomal DNA to unveil human–pig relations, the vast majority of studies have relied on the analysis of diagnostic regions of the pig mtDNA [262,265–267] (Figure 4). Some studies combine these short stretches of mtDNA with geometric morphometric analyses of the archaeological remains [263,264,268,269]. Only a limited number of studies use mtDNA in conjunction with nuclear markers, such as the coat colour-coding gene MC1R [263,270]. Unknown subtleties pertaining to the spread and dynamics of pigs are only discernible through analyses of datasets sampling multiple geographical regions and time periods. Frantz and his colleagues [270] made a notable contribution in this direction by reconstructing mitochondrial and nuclear sequences of archaeological pig remains from various time periods from across Europe and the Near East.

Besides genomic data, ratios of stable carbon and nitrogen isotopes in bone collagen are useful instruments to explore human–suid relations, particularly reflecting dietary backgrounds, pig origins, and herd management [271,272]. Different foddering regimes have been illustrated for this flexible species by stable isotope signatures of ancient faunal samples from various regions and cultures. For instance, isotopic data of Pre-Pottery Neolithic pigs from Anatolia showed dietary differences between domestic pigs and their wild counterparts, suggesting that they were kept under cultural control [273]. In contrast, domestic pigs in Neolithic China were allowed to roam freely within human settlements much like their wild relatives [274]. Shifts from woodland resources to household waste in the Iron Age [275,276] followed by increased consumption of marine fish in the Middle Ages have been observed in pigs in Britain [277], while millet consumption has been suggested for ancient Chinese pigs [278–280]. Multiple husbandry practices have also been revealed by strontium isotope ratios in ancient Bali [281].

3.5. Horses

The horse is one of the most well studied species genetically, with almost 300 genomes of ancient horses having been sequenced [282] dating back 700,000 years in time [283,284] (Figures 1 and 4). This has contributed significantly to studies on the evolutionary history of the wild horse (*Equus ferus*) (e.g., [283–286]) and to archaeological scenarios of domestication and human movements [282].

An initial domestication of horses happened at least 5500 years ago, possibly in the Western Eurasian Steppe, with the earliest evidence for harnessing, milking, and corralling belonging to the Botai culture of the Eneolithic period in Central Asia [287–290] (Figure 2). However, this lineage does not seem to have contributed significantly to modern domestic horses (*Equus caballus*), but instead gave rise to the feral *Equus przewalski* [288]. Multiple domestication events and possible domestication centers have been proposed [287,291], with the Iberian Peninsula displaying high levels of genetic diversity, as well as now extinct lineages that were still present in the region roughly 4000 years ago [292]. Ancient protein analysis of *Equus* remains dated to ~11,000 years ago [293] also found evidence for the

exploitation of *Equus* in Canada by the Clovis hunters. While the remains of the earliest representative of the lineage that gave rise to modern domestic horses have been found in Hungary [292], neither the site nor time of their domestication are yet known [282].

Studies focused on understanding the genetic signature of domestication [289,294] have shown that modern horses contain high mutational loads, probably as a consequence of domestication or historical breeding practices. Initially, signatures of selection appeared in genes involved in cognitive functions that may have been key for taming horses, while changes in genes involved in locomotory development and the cardiac system may be the result of physiological adaptations to human use [289,294].

Following domestication, horses went through several human-mediated translocations, resulting in multiple population replacements. For instance, the ancestry of the earliest domestic populations of Central Asia was replaced in domestic stocks between 5000 and 4000 years ago. Moreover, after the 7th century, the Arab expansion into Europe and Asia led to changes in the genetic background of horses [287,292,295] and had a significant impact on horse genetic diversity. While modern horses display high levels of mtDNA diversity, representative of ancestral variability [291], they show virtually no Y-chromosome diversity [296]. The fact that ancient (~2800 years ago) horses had considerable Y-chromosome diversity [296] and that the majority of modern male lineages can be traced back to ancestors from the Orient [292,295] suggest that early domestication events involved a larger male stock [282,287] and that the Arab and Mongolian practice of selecting only a limited number of stallions for reproduction led to the observed decrease in Y-chromosome diversity [282,287,292,295]. This is further substantiated by horses dating to the Roman period not having the same decrease in Y-chromosome variability, suggesting that Romans did not practice a similar male-oriented breeding strategy [282,287,292].

Stable isotope analyses of horse remains dating to various periods such as the Pliocene-Pleistocene [297], the Bronze Age [298], and the Early Modern Period [299] have illustrated their dietary preferences in South American regions and the northern Kazakh steppe, as well as the shift in seasonal diet for the Przewalski's horses of the Dzungarian Gobi.

As shown above, biomolecular studies have offered insight into the role and the treatment of horses by distinct historical societies.

3.6. Cats

Little molecular data are available regarding cat (*Felis catus*) domestication (Figures 1 and 3), with much information having been obtained through the study of alternative resources, for example, historical documents, art objects, or osteological material [300]. However, some modern and ancient mtDNA [300–304] and stable isotope [305,306] analyses have been generated.

Felis silvestris, the wild cat, is considered to have diverged into five distinct subspecies: the European wildcat (*F. silvestris silvestris*, clade I), Southern African wildcat (*F. silvestris cafra*, clade II), Central Asian wildcat (*F. silvestris ornata*, clade III), Near Eastern wildcat (*F. silvestris lybica*, clade IV), and Chinese desert cat (*F. silvestris bietii*, clade V) [302,303]. For all modern cats, domestication started ~10,000 years ago, during the Neolithic, involving *F. s. lybica* in the Near East [302,304,307] (Figure 2). The Near East was inhabited by two distinct local populations, one being located in the Fertile Crescent and the other in Egypt [304]. Following domestication, cats, characterised as *F. s. catus* (the sixth subspecies, albeit recognised as the descendant of *F. s. lybica*), underwent human-mediated dispersal from the Near East [300,303].

In Europe, the Greeks, Phoenicians, and Romans are considered to have facilitated the spread of the domesticated cat within the continent. Pre-Roman samples have been identified in Western and Central Europe [308]. Recently, mitochondrial lineages associated with domesticated cats from the Near East was identified in cat remains dated to the Neolithic in Poland. A genetic contribution from individuals associated with both this Neolithic population expansion and the subsequent Roman-mediated spread has been identified in the gene pool of contemporary cats [300].

Studies of stable isotopes, usually $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, have been used to investigate the commensal relationship between the cats and early farmers and to track common migration routes [305,306].

4. Final Remarks and Future Perspectives

In this compilation, our aim has been to outline important evolutionary events for a number of selected species, which have been reconstructed through the use of biomolecular research. For some, we have deliberately chosen to focus on the aspect of domestication, largely omitting research conducted on their wild counterparts. An outline of how different biomolecular and biogeochemical analyses have been used, which questions researchers investigated, and which conclusions have been reached based on their results is provided. Even though mtDNA and stable isotopes from bulk collagen have been used extensively in inferring ancient faunal dynamics (Figures 1 and 5), the number of multiproxy biomolecular studies has increased in the last five years. While still rare, the integrated use of several ancient biomolecules and biogeochemical analyses is expected to provide a more coherent approach, evidently contributing unique insights and a more comprehensive reconstruction than individual proxies. In the future, the progressive reduction in costs for high throughput analyses is expected to remove the necessity for trade-offs limiting multiproxy biomolecular studies to exceptional single finds, and to extend their use to studies of large datasets, when examining ancient diversity in a palaeoenvironmental context.

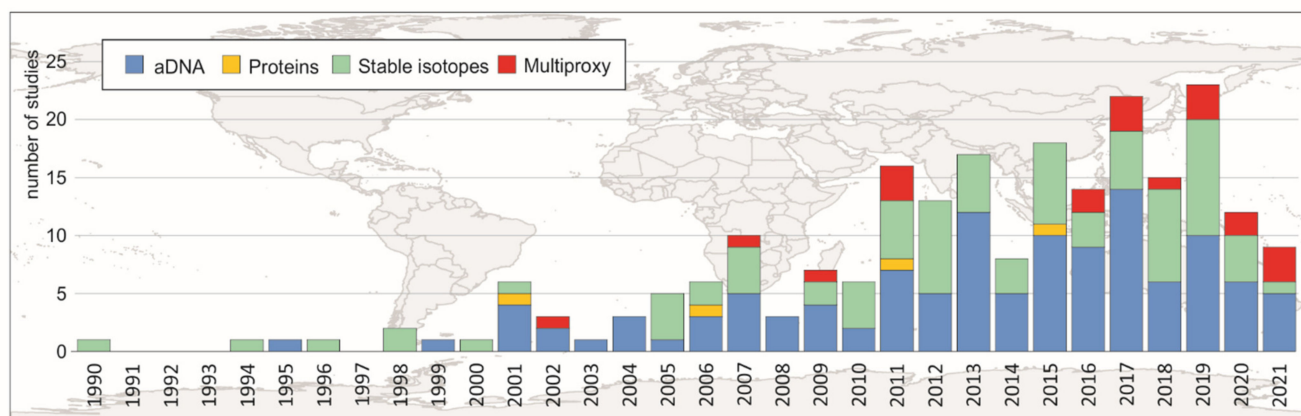


Figure 5. Diachronic trends in biomolecular studies. Bar plot with the number of studies published per year.

In our review, we have focused on a few iconic and well-studied species with a largely Eurasian distribution. Additional studies illustrating the power of multiproxy biomolecular approaches are worth mentioning, like the one from North America by [309]. Using an integrated approach combining osteological age determination, aDNA, and stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), a degree of dietary flexibility not linked to age or haplogroup was demonstrated, supporting the hypothesis of direct human impact (overhunting) as the main factor leading to the decline and subsequent extinction of passenger pigeons (*Ectopistes migratorius*).

While this type of study is relatively more common for issues related to the palaeobiology and palaeoecology of extinct species and for finds from depositional environments with exceptional preservation (i.e., permafrost and caves), integrated analyses (e.g., combinations of stable isotopes, mtDNA, and protein-based methods) have occasionally been employed in studies of domestic species, and of datasets from equatorial and mid-latitude regions. For instance, ref. [310] combined genetic estimates of past effective population size with stable isotope analysis. They were able to infer stable population size and no significant changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures over the last 44,000 years, suggesting that crested moa (*Pachyornis australis*) in New Zealand tracked its habitat through time with little consequence to population size.

The bottom line is that not all data of interest to the study of evolutionary and domestication processes can be found within the boundaries of individual disciplines. The contingent nature of these processes implies that different analytical approaches and biomolecules may be most informative at different points along their development. Despite the limitations imposed by preservation and challenges associated with simultaneous sample extraction for different biomolecular analyses (e.g., aDNA, stable isotopes, and uranium-thorium dating of bone collagen) from limited and/or valuable sources (e.g., rare and small taxa), the adoption of an integrated research design from the onset is expected to enable the co-creation of research questions and the potential for synergistic results. Further development and refinement of biomolecular methods will most likely lead to a reduction in the required sample quantities, adaptations of preparation protocols to facilitate multiple analyses from the same sample, and/or complementary analyses of alternative substrates (e.g., sedimentary aDNA and metabarcoding of bulk bone and middens for tracking presence/absence of species for palaeoenvironmental reconstructions, or the co-evolution of host and microbial/viral pathogens), promoting information-maximization.

With regard to the species addressed in this review, future integrative studies are expected to (1) directly integrate the underlying evolutionary and palaeoenvironmental processes, leading to megafaunal extinctions in the Late Pleistocene at an increasingly fine-scale geographic and temporal resolution; and (2) provide new details on the domestication and dispersal of animals that will contribute to more complex and multifaceted reconstructions of the practices of past societies. Together, the in-depth knowledge that will be gained will provide information available to policy-makers in order to influence measures for the management and conservation of modern counterparts and wildlife in general.

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