Review

Footprints of Wolves and Foxes: Phylogeography and Population History of Canidae

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Posted Date: 27 December 2024

doi: 10.20944/preprints202412.2309.v1

Keywords: Canidae; Phylogeography; Population History

Review

Footprints of Wolves and Foxes: Phylogeography and Population History of Canidae

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Abstract: This review explores the evolutionary history and global expansion of canid species, focusing on the phylogeny and distribution of existing canids, along with the phylogeographic patterns and population history of several key species. It begins by tracing the evolutionary lineage of canids from their origins in the Eocene, emphasizing their significance as one of the oldest extant carnivore groups. The global distribution patterns of canids are significantly influenced by ecological factors, including climate, geographical barriers, dietary preferences, and human activities. The review then summarizes the phylogenetic relationships and worldwide distribution of current canid species. It concludes by examining the phylogeographic characteristics of prominent species within the genus *Canis* (wolves) and *Vulpes* (Arctic fox and red fox). By integrating genomics, archaeology, and ecology, this review offers novel insights into the evolutionary dynamics of canids and highlights key areas for future research, such as enhancing the accuracy of population history inferences, advancing ancient genomics, developing experimental techniques, and fostering interdisciplinary collaboration.

Keywords: Canidae; phylogeography; population history

Evolution and Expansion History of Canids

The Canidae family, a part of the order Carnivora, encompasses wolves, foxes, jackals, dholes, and other species. It is widely believed that canids originated from an ancient group of carnivores known as the Miacidae during the late Eocene, approximately 40 million years ago. At that time, North America and other continents were not yet connected by land. The evolution of canids subsequently followed a pattern of continuous radiation. Tedford et al. identified a significant radiation event at the end of the Oligocene, leading to the formation of three subfamilies: Hesperocyoninae, Borophaginae, and Caninae (Wang et al., 2008). The first two subfamilies, confined to North America, eventually went extinct, primarily due to climate cooling and competition with other carnivores (Van Valkenburgh, 2007), such as felids and saber-toothed cats that invaded from the Eurasian continent. The third subfamily, Caninae, is the one that has successfully dispersed and migrated across the globe.

During the Miocene, significant orogeny occurred, and key geological events, such as the closure of the Isthmus of Panama and the Bering Strait (around 11 million years ago), played crucial roles (Potter & Szatmari, 2009). The expanding island chain of the Isthmus of Panama facilitated the exchange of fauna between North and South America (Montes et al., 2015), while the emergence of the Bering Land Bridge connected North America with Eurasia (Cox, 2000), enabling the bidirectional diffusion of plants, animals, and microorganisms (Jiang et al., 2019; Li et al., 2015; Vershinina et al., 2021). This period, approximately 25 to 8 million years ago, was a peak time for mammalian intercontinental exchanges. The ancestors of modern canids entered Eurasia during the late Miocene through this corridor, and due to their strong exploratory and adaptive abilities, they underwent extensive adaptive radiation. This first major radiation event, around 10 million years ago, gave rise to species such as foxes, wolves, and South American canids, encompassing all extant canid species. Subsequently, a similar diffusion and radiation event occurred in South America, where canids entered from North America via the Isthmus of Panama (2.5 million years ago) and rapidly adapted due to the lack of competing super-predators at that time, resulting in eight genera and 16 species by the Late Pleistocene (Marshall, 1977).

The subfamily Caninae is divided into two major branches: the Canini (dog tribe) and the Vulpini (fox tribe). Canini first appeared in North America during the middle Miocene (7-12 million years ago) as the transitional genus *Eucyon*, while the *Canis* branch emerged during the Miocene-Pliocene transition (5-6 million years ago) and then spread to Europe and Asia. Key events in the history of Eurasian canids include the *Eucyon* event and the *Canis* event, occurring at the end of the Miocene and the beginning of the Pliocene, respectively. In the late Miocene (6 million years ago), species of the genus Eucyon appeared widely, such as *Eucyon monticinensis* in Europe, *Eucyon davisi* in Asia, and *Eucyon intrepidus* in Africa. Following this, Eucyon underwent several radiations in Eurasia and Africa, reaching a relatively high level of diversity in the Pliocene of the Old World (Rook, 2011). During the Pliocene, the diversity of Canini peaked in Asia, marked by the appearance of new *Eucyon* species and an increase in the population of Eucyon davisi (Sotnikova & Rook, 2010). In contrast, the peak of European diversity occurred after the *Canis* event, when species of the *Eucyon* genus were nearly extinct, while the narrowly defined Canis genus underwent extensive diversification.

The fossil record of the Vulpini is relatively sparse, and it is assumed that they underwent moderate divergence in North America during the Early Hemphillian period (9 million years ago), leading to the formation of the original species of the genera *Vulpes* (foxes) and *Urocyon* (gray foxes). The genus *Metalopex*, represented by *Metalopex merriami*, appeared in western North America and the Great Plains. This genus, along with its sister group *Vulpes stenognathus* and the earliest canid *Eucyon*, represents the early stages of the evolutionary branches that include both modern foxes and wolves (Tedford & Wang, 2008). A major dispersal event for the Vulpini occurred around 8.5 million years ago, when one lineage entered North Africa and began differentiating, producing new lineages while also dispersing into Eurasia and North America (Porto et al., 2023). The oldest Vulpes skeletons were found in the Djurab Desert, Chad, Central Africa, in the late Miocene (7 million years ago), predating the appearance of *Eucyon* and other *Vulpes* species in Africa and Europe in more recent periods (L et al., 2007). This suggests that canids may have first spread in Africa before migrating to Europe via a Mediterranean route. Records of *Vulpes* from the Pliocene of North America are poor, whereas *Vulpes* species are widely distributed and diverse in Eurasia (Bartolini Lucenti & Madurell-Malapeira, 2020).

Phylogeny and Distribution of Extant Canids

Extant canids are widely distributed across Eurasia and Africa, comprising 36 species in 12 genera, which are classified into two major tribes: Canini and Vulpini. The Canini tribe, which includes dog/wolf-like canids, is further divided into two subtribes: Canina (true canids) and Cerdocyonina (South American canids). The Vulpini tribe encompasses fox-like canids (Zrzavy et al., 2018). Within the Canina subtribe, the genus *Canis* (wolves and dogs) is accompanied by two monotypic genera—*Cuon* (dhole) and *Lycaon* (African wild dog). The Cerdocyonina subtribe comprises the genus *Pseudalopex* and five monotypic genera, all native to South America. The Vulpini tribe includes three genera: *Otocyon* (bat-eared fox), *Nyctereutes* (raccoon dog), and *Vulpes* (fox). Additionally, the genus *Urocyon* (gray fox), an older and smaller family, remains in southern North and Central America due to their preference for forested areas (Wang et al., 2004). Thus, canids can be broadly categorized into four groups: true canids, South American canids, true foxes, and gray foxes.

Among extant carnivores, the Canidae family is uniquely distributed worldwide, with at least one species present on every continent except Antarctica. Many canids have ranges that extend across entire continents. Geographically, Africa, South America, and Asia boast the highest diversity of canid species, each housing over 10 species. In Africa, where diversity peaks, 8 out of 13 species are endemic. The genera *Canis* (dogs and wolves) and *Vulpes* (foxes) are found in North America, Europe, Africa, and Asia, and have been introduced to Australia by humans. However, six other genera are confined to single continents. For instance, *Chrysocyon* (maned wolf), *Otocyon* (bat-eared fox), *Lycalopex* (South American foxes), and *Speothos* are limited to South America; *Cuon* (dhole) to Asia; *Lycaon* (African wild dog) to Africa; *Urocyon* (gray fox) is exclusive to North and South America; and *Nyctereutes* (raccoon dog) is native to Asia but has been introduced to Europe (Sillero et al., 2004).

From a species-specific perspective, the red fox (*Vulpes vulpes*) and the gray wolf (*Canis lupus*) possess the broadest natural ranges of any terrestrial mammals, spanning the entire Northern Hemisphere and occurring in 81% of the world's countries. Two other species, the golden jackal (*Canis aureus*) and the Arctic fox (*Alopex lagopus*), are found on three continents simultaneously. The red fox (*Vulpes vulpes*) and the Australian dingo (*Canis lupus dingo*) have also reached Oceania with human assistance (Savolainen et al., 2004).

Conversely, some species have highly restricted distributions. For example, Darwin's fox (*Lycalopex fulvipes*), primarily found in the temperate forests of Chiloé Island, was later discovered in Nahuelbuta National Park in Chile, 600 km north of the island (Vilà et al., 2004). Similarly, the island gray fox (*Urocyon littoralis*) is confined to six islands in the California Channel Islands and is also known as the California island fox (Coonan et al., 2013).

The following sections will explore the phylogeographic patterns and population history of key species, focusing on the gray wolf, Arctic fox, and red fox as representatives of the *Canis* and *Vulpes* genera.

Grey Wolf Phylogeography and Population History

Gray wolves (*Canis lupus*) were among the few large predators to survive the Late Pleistocene megafauna mass extinction. This survival may be attributed to their ability to find suitable refuges during the Ice Age and adapt their diet accordingly (Landry et al., 2021). Despite this adaptability, they experienced a severe bottleneck event during this period. Fossil evidence from the eastern Bering Sea reveals a unique haplotype in Late Pleistocene wolves that is absent in modern North American wolves. The skull shape, tooth wear, and isotopic data suggest that the Bering wolf was a distinct, eco-type that became extinct in the Late Pleistocene, along with other megafauna (Leonard et al., 2007).

Based on studies of extinct ancient wolves, Pilot et al. reconstructed the phylogeographic history of European wolves. Two haplogroups were found to overlap geographically, but their frequencies varied significantly between southwestern and eastern European populations. Haplogroup 1 predominates in eastern Europe, while haplogroup 2 is fixed in western Europe. In North America, only haplogroup 1 is present, whereas the eastern Beringian wolf corresponds to haplogroup 2, which was later completely replaced by haplogroup 1. The similarity in population structure changes in wolves across Europe and North America suggests they may be driven by similar ecological processes, warranting further exploration (Pilot et al., 2010).

A comprehensive study of ancient wolves and domestic dogs revealed that the ancient wolf mitochondrial genome was categorized into four haplogroups, but most modern dogs are derived from only one, suggesting a European origin for domestic dogs (Thalmann et al., 2013). However, Loog et al. addressed the limited sample size and geographical constraints of this study by sequencing mitochondrial genomes from more wolves worldwide. Their analysis showed that wolves experienced a bottleneck around the Last Glacial Maximum (LGM) (25ka BP), when Beringian wolf populations expanded east-west, replacing native Pleistocene wolves in both Eurasia and North America. This suggests modern wolves trace their origins to this LGM Beringia wolf expansion driven by climatic shifts across the northern hemisphere (Loog et al., 2020).

This finding aligns with a previous study indicating that modern wolves in Eurasia originated from a single population in the Late Pleistocene, which underwent a sharp reduction in population size before at least 30ka BP (Fan et al., 2016). Further research into Southern European wolf populations found that all present Eurasian wolves share a common ancestor dating back to around 36ka ago, reinforcing the theory that all extant wolves derive from a single founding population (Silva et al., 2020).

Loog's work also explained the star-shaped topologies in modern wolf population genomes, suggesting that wolf population expansion was geographically isolated, limiting gene flow between subgroups. This isolation likely led to differentiation between modern wolf subpopulations and accounts for the large differences between European and East Asian populations observed by Frantz et al. Some of this variability results from mixing events between subpopulations after the LGM (Frantz et al., 2016). After identifying an ancient expansion event in Beringia, Pacheco et al. found that wolves from the Russian Far East and North America shared a common ancestor as early as 34ka BP, indicating divergence before the expansion event (Pacheco et al., 2022).

A 2017 study provided a genetic overview of European wolf populations at three scales: maternal inheritance (mtDNA), paternal inheritance (Y-chromosome), and biparental inheritance (microsatellites and SNPs). These analyses revealed a significant spatial trend in heterozygosity, with the lowest levels in Southwestern Europe and the highest in Northeastern Europe (Hindrikson et al., 2017). This may be due to the fragmentation of wolf populations in Eastern Europe, resulting in relatively small effective local population sizes (Ne), significant genetic differentiation, and low inter-regional migration rates (Sastre et al., 2011). This structure is also linked to human activities, as the persecution of wolves through hunting during the medieval period in many Western European countries led to extinctions in England, Denmark, the Netherlands, and parts of Germany, Switzerland, and France. However, wolf populations in Eastern Europe were less persecuted, enabling higher genetic diversity and larger population sizes (Dufresnes et al., 2018). Recent work comparing the genetic diversity of wolves across Europe using the yardstick method yielded conclusions similar to those described above (Jan et al., 2023).

In summary, ecological factors in the Northern Hemisphere, particularly the bottleneck event and subsequent expansion and replacement of the LGM Beringia wolves, significantly shaped the modern phylogeographic structure of European wolf populations. While wolves do not show specific regional phylogenetic traits globally, there is notable genetic differentiation within European populations. Western Europe has discontinuous populations, while Eastern Europe has larger and more diverse populations, and Italy and the Iberian Peninsula have relatively small isolated populations (Pilot et al., 2014).

The reasons for this population structure require further exploration, especially since Eastern European wolf populations still exhibit a non-random spatial genetic structure despite the absence of obvious geographic barriers. It is suggested that this genetic structure may be influenced by ecological factors such as climate, habitat, and diet composition, with ecological processes strongly affecting gene flow between populations (Pilot et al., 2006). Additionally, human hunting pressures may have further impacted wolf genetic diversity (Ausband & Waits, 2020).

Arctic Fox and Red Fox Phylogeography and Population History

Similar to gray wolves, the Arctic fox (*Vulpes lagopus*) managed to survive the Late Pleistocene mass extinctions, largely due to its exceptional cold adaptations and strong migratory capabilities. Rogers et al. conducted a mitochondrial DNA study on 191 Arctic foxes to investigate their population history. They discovered that several haplotypes were distributed throughout the Arctic, lacking a specific phylogeographic structure, except in highly isolated groups on Iceland. It has been suggested that this pattern may result from a decrease in temperatures during the interglacial period, which led to a northward shift in red fox habitat, creating competition with the Arctic fox. The presence of forest remnants in northern Siberia supports the possibility of red fox habitat in this region (Sher, 1991). Consequently, the Arctic fox may have become extinct in Eurasia and North America during the interglacial period, surviving only on high-latitude islands, and later expanded southward with the onset of the next ice age (11.7 ka BP), forming the modern phylogeographic pattern (DALÉN et al., 2005; Rogers & Harpending, 1992).

A 2007 study aimed at exploring the role of repeated freezing and thawing of sea ice in isolating Arctic fox populations similarly did not detect signs of selection or population expansion at any of the sampled sites in the circumpolar region (Geffen et al., 2007). Genetic diversity was highest in the

Pribilof Islands, with each individual possessing a different mtDNA haplotype. In contrast, populations in Greenland, Iceland, Scandinavia, and the Komandor Islands exhibited lower genetic diversity, with North Greenland showing very low diversity, possibly due to recent colonization or a bottleneck event (Geffen et al., 2007).

Sandra et al. also confirmed the absence of phylogeographic patterns in Arctic foxes but identified differentiation between northern and southern populations on Bylot Island. Their findings suggest that using linear distances to model the dispersal of canid species may lead to biases, particularly in heterogeneous landscapes. They recommended spatially explicit methods, such as spatial principal component analysis (SPCA), for more accurate modeling (Sandra et al., 2017).

The geographic distributions of the Arctic fox and red fox are generally separate on a global scale but overlap at the boundaries of North America and Eurasia. It is widely believed that the northern range of the red fox is determined by resource availability and climate, while the southern range of the Arctic fox is influenced by red fox distribution and interspecific competition (Hersteinsson & MacDonald, 1992). Studies in Northern Norway, where Arctic fox numbers have declined, support this view, showing that interspecies competition in areas of range overlap has significantly impacted Arctic fox populations (Killengreen et al., 2007).

Previous studies have suggested the existence of three distinct branches of red foxes in North America, reflecting colonization events from south to north (Aubry et al., 2009). However, a cytochrome b and isoenzyme study of modern red foxes from southern Europe and other regions concluded that there was little phylogeographic pattern within this limited area (Frati et al., 1998). A subsequent large-scale study, covering 165 samples across Europe and including 35 ancient samples approximately 40,000 years old, examined the European red fox phylogenetic structure by analyzing variation in cytochrome b and mitochondrial control region genes. No evidence of historical bottlenecks or intra-European phylogeographic structure was detected, and the absence of such structure appears consistent over tens of thousands of years, likely due to the high dispersal capacity and adaptability of the red fox. The slight distance segregation in modern populations and time-related divergence could be attributed to random genetic drift. It is likely that European fox populations were not forced into ice age refuges but instead persisted as a single large hybrid population throughout the ice age (Teacher et al., 2011).

Discussion and Perspectives

The evolutionary and dispersal history of canids, supported by a continuous and extensive fossil record worldwide, is relatively well understood. True canids (*Canis*) originated in the Late Eocene and expanded from North America to the Old World around 10 million years ago, undergoing significant radiation and dispersal. Their high mobility and ecological adaptability enabled them to survive the mammalian extinction event following the last glacial maximum (LGM). The exposure of canids to diverse biotic and abiotic pressures in modern times, along with their widespread ancient remains and current distribution, makes them an ideal model for studying genetic diversity, geographic distribution patterns, ecological responses, and population history. This paper reviews the phylogeographic patterns and population histories of representative species from the *Canis* and *Vulpes* genera, specifically the gray wolf (*Canis lupus*), red fox (V*ulpes vulpes*), and Arctic fox (*Vulpes lagopus*).

Summarizing previous studies, it is evident that gray wolves experienced a severe bottleneck between 30,000 and 25,000 years ago, with their common ancestor traceable to at least 30,000 years ago. The earliest divergence occurred between New World and Old World wolf populations, followed by the split between Old World wolves and domestic dogs, confirming that dogs were domesticated in the Old World. Some researchers propose that modern wolves share a common ancestor with a single wolf population from the Late Pleistocene Beringia region. This population underwent a bottleneck during the LGM and subsequently expanded eastward and westward, replacing wolves in North America and northern Eurasia, and gradually spreading into Europe, the Middle East, and other regions.

Present-day wolves exhibit no clear phylogeographic structure globally, although certain patterns of genetic differentiation exist in small regions. For instance, European wolves show low genetic diversity in the southwest and high genetic diversity in the northeast, with relatively small and isolated populations in Italy and the Iberian Peninsula. This is primarily due to the fragmentation of Eastern European wolf populations, leading to smaller effective population sizes (Ne), lower migration rates, and significant genetic differentiation. Additionally, historical human persecution has exerted less pressure on Eastern European wolves, helping preserve genetic diversity and shape the current phylogeographic structure.

Arctic foxes, like wolves, do not display a particular phylogeographic structure on a global scale, with several haplotypes distributed across the Arctic, except for the isolated Icelandic population. This broad distribution may be due to the high frequency of ancestral haplotypes, while emerging haplotypes have not yet spread throughout the species' range. Limited areas, such as Bylot Island, show distinct genetic differentiation between northern and southern populations. Similarly, the high dispersal capacity and adaptability of the red fox result in a lack of significant phylogeographic differentiation globally, a pattern consistent over thousands of years.

Both wolves and foxes exhibit similar patterns of geographic and genetic structure, with no significant global differentiation but some regional differences. These patterns are likely shaped by a combination of ecological factors such as climate, geographic barriers, and diet, as well as human activities and policy changes. Determining which factor serves as the dominant influence requires a comprehensive analysis for specific groups, considering their geographic location, survival age, ecological environment, and the impact of human society.

In the past, population history was primarily inferred from genomic data of extant populations, a method prone to errors due to simplified assumptions about population history, structure, and composition, and dependent on data quality and reference sequence sets. However, with the advent of high-throughput sequencing and techniques like hybrid capture in ancient DNA research, studies of animal phylogenetics and population history have entered the ancient genomics era (Frantz et al., 2020). Researchers now have direct access to ancient genomes to test for events such as migration, mixing, and bottlenecks in populations. To deeply explore the population history of canids, obtaining ancient remains that are as old and widely distributed as possible is crucial. Nonetheless, this approach also has limitations, relying on the availability of abundant and well-preserved skeletal remains, fur, or other ancient materials. Challenges in ancient genomics include developing experimental techniques for different types of animal remains (e.g., bones, skins, sediments), improving sample pretreatment, cleaning, and ancient DNA extraction protocols, enhancing library construction efficiency, and developing algorithms for analyzing short fragments and low-coverage ancient DNA sequences to improve the accuracy of population history inference.

Future research should focus on investigating how ecological factors like climate, geographic barriers, and dietary habits, alongside human activities and policy changes, have jointly influenced the phylogeographic patterns of wolves and foxes. This will require interdisciplinary collaboration, combining knowledge from ecology, genetics, geography, and anthropology to synthesize the interactions of various factors.

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