Patterns of diversification and geographic distribution of Canidae over time

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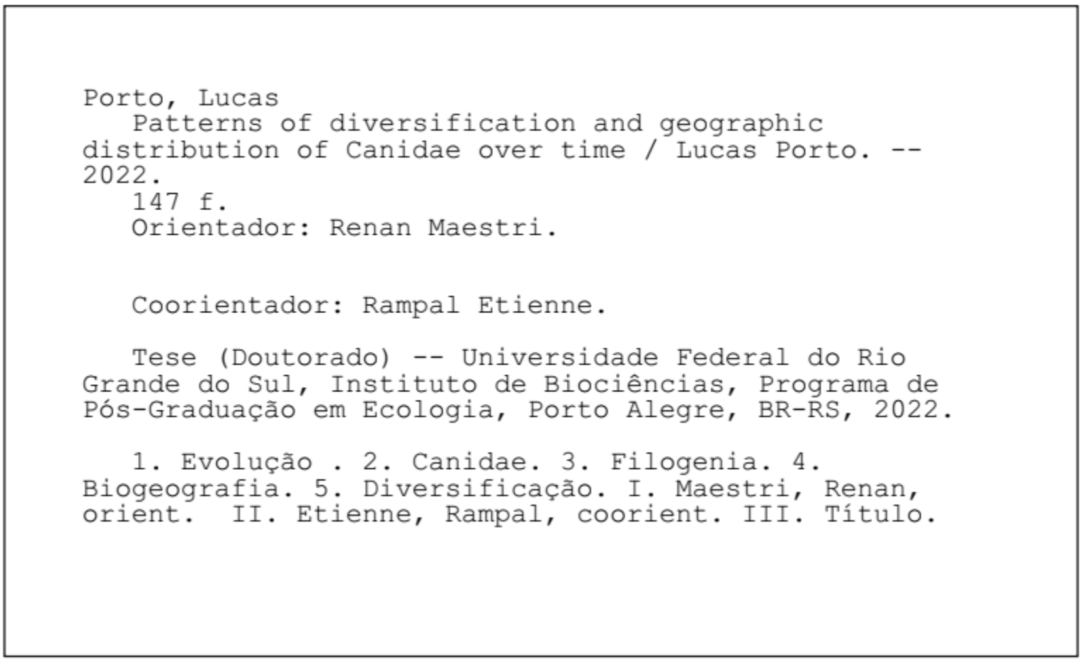

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CONTENTS

ENGLISH ABSTRACT

In this thesis I aimed to shed light on several aspects of Canidae distribution in the past, present, and future. My goals were 1) to obtain a more detailed understanding of the evolutionary processes that led to the rise and fall of several species of canids. 2) to identify the factors influencing the distribution of species in the present. and 3) to understand how canids respond to climate change, and what are the future prospects for the taxon. Chapter 1 focused on the past, and aims to answer whether the colonization of new environments by canids triggered an explosive radiation process. I was able to show that major events of canid dispersal — to South America and North Africa — are associated with peaks in diversification rates, suggesting an evolutionary radiation process right after the geographic colonization of new continents after leaving North America around 11 million years ago (Mya). The timing of radiations suggests that this pattern for the whole tree was generated by ecological opportunity after the entrance in new continents by South American canids and foxes, but also by the diversification of wolves within North America. In Chapter 2, I look at the present in order to identify the mechanisms that structure Canidae assemblages across the planet. I discovered how distinct parts of the globe are phylogenetically structured, and how these patterns are most likely to have originated. I show that there are regions over the planet that present phylogenetically closed related species, such as South America, Middle East, and a large part of Asia, while Northern Asia, Europe, and a major part of North America present co-occurring lineages that are more evolutionary distant to each other than would be expected by chance. However, I demonstrated that both phylogenetic distribution patterns are better explained by environmental filters than species interactions and human impact. This supports what I suggested in Chapter 1, where the differences in the ecological settings between continents, such as vegetation cover and temperature, may be responsible for the disparity among clades' evolutionary rates, being a plausible source of ecological opportunity for canids. Furthermore, in Chapter 2 I assumed that the measure of body size dissimilarity would be a proxy for past competition among canids, which in turn would have an influence on the distribution patterns of the lineages. I found that two environmental variables (temperature and vegetation cover) have a strong influence on body size dissimilarity, suggesting that such variables influence certain aspects in different continents (e.g., resource availability), which in turn may have culminated in past competition events between canids. Chapter 3 focused on the future distribution of canids. I modeled the potential distributions of all 36 extant Canidae species in pessimistic climate scenarios for the future to evaluate their response to climate change. I showed that climate change will make most species of canids reduce their distributions, while a few have the potential to benefit from future conditions and expand their ranges. But two species, *Atelocynus microtis* and *Chrysocyon brachyurus*, which live in South America, are very concerning cases as both are predicted to undergo considerable habitat loss in their future and do not show the capacity to adapt given the current pace of climate change. *A. microtis* lives in the Amazon rainforest, while *C. brachyurus* inhabits the Cerrado in Brazil, and both environments are constantly suffering from wildfires and habitat fragmentation, reducing the available area for organisms that need extensive distribution areas (Sillero-Zubiri et al., 2004). I also indicate that species with higher potential to evolutionary rescue are the ones that gain area or lose only a small part of their future distributions, while the ones which are going to lose a large part of their future distribution will need a higher evolutionary change to maintain their populations. In Chapter 4, I look again at the past of Canidae. This time, I used a new extension of the secsse (Several Examined and Concealed States-Dependent Speciation and Extinction) model (Herrera-Alsina et al. 2019) to explore even more the rich and well-documented records of extinct Canidae species, which give us a great opportunity to fill the puzzle in the evolutionary history of Canidae. With this new approach, this chapter helps to understand which traits (geographic areas) promote (or not) diversification over the last 13 Mya, and how important it is to include fossil information on diversification analyses, due to the distinct interpretations we can get from incomplete trees.

Key-words: Biogeography; Canidae; Diversification; Evolution; Phylogeny.

RESUMO EM PORTUGUÊS

Nesta tese, tive como objetivo esclarecer vários aspectos da distribuição de Canidae no passado, presente e futuro. Meus objetivos foram: 1) obter uma compreensão mais detalhada dos processos evolutivos que levaram à ascensão e queda de várias espécies de canídeos; 2) identificar os fatores que influenciam a distribuição das espécies no presente; e 3) compreender como os canídeos respondem às mudanças climáticas e quais são as perspectivas futuras para o clado. O Capítulo 1 teve como foco o passado e visa responder se a colonização de novos ambientes por canídeos desencadeou um processo explosivo de radiação. Pude mostrar que grandes eventos de dispersão de canídeos – para a América do Sul e Norte da África – estão associados a picos nas taxas de diversificação, sugerindo um processo evolutivo de radiação logo após a colonização geográfica de novos continentes após deixar a América do Norte há cerca de 11 milhões de anos (Mya). O tempo das radiações sugere que esse padrão para toda a árvore foi gerado pela oportunidade ecológica após a entrada em novos continentes por raposas e canídeos sul-americanos, mas também pela diversificação de lobos na América do Norte. No Capítulo 2, examino o presente para identificar os mecanismos que estruturam as assembleias de canídeos em todo o planeta. Descobri como partes distintas do globo são filogeneticamente estruturadas e como é mais provável que esses padrões tenham se originado. Mostro que existem regiões do planeta que apresentam espécies filogeneticamente relacionadas, como América do Sul, Oriente Médio e grande parte da Ásia, enquanto o Norte da Ásia, Europa e grande parte da América do Norte apresentam linhagens co-ocorrentes que são evolutivamente mais distantes entre si do que seria esperado por acaso. No entanto, demonstrei que ambos os padrões de distribuição filogenética são melhor explicados por filtros ambientais do que interações de espécies e impacto humano. Isso corrobora o que sugeri no Capítulo 1, onde as diferenças nas configurações ecológicas entre os continentes, como cobertura vegetal e temperatura, podem ser responsáveis pela disparidade entre as taxas evolutivas dos clados, sendo uma fonte plausível de oportunidade ecológica para os canídeos. Além disso, no Capítulo 2, presumi que a medida da dissimilaridade do tamanho do corpo seria um proxy para a competição passada entre os canídeos, o que, por sua vez, influenciaria os padrões de distribuição das linhagens. Descobri que duas variáveis ambientais (temperatura e cobertura vegetal) têm forte influência na dissimilaridade do tamanho corporal, sugerindo que tais variáveis influenciam certos aspectos em diferentes continentes (por exemplo, disponibilidade de recursos), o que por sua vez pode ter culminado em eventos passados de competição entre canídeos. O Capítulo 3 focou na distribuição futura de canídeos. Modelei as distribuições potenciais de todas as 36 espécies de Canidae existentes em cenários climáticos pessimistas para o futuro para avaliar sua resposta às mudanças climáticas. Mostrei que a mudança climática fará com que a maioria das espécies de canídeos reduza suas distribuições, enquanto algumas têm o potencial de se beneficiar das condições futuras e expandir seus alcances. Mas duas espécies, *Atelocynus microtis* e *Chrysocyon brachyurus*, que vivem na América do Sul, são casos muito preocupantes, pois prevê-se que ambas sofrerão uma perda considerável de habitat no futuro e não mostram capacidade de adaptação devido ao ritmo atual das mudanças climáticas. *A. microtis* vive na floresta amazônica, enquanto *C. brachyurus* habita o Cerrado no Brasil, e ambos os ambientes sofrem constantemente com incêndios florestais e fragmentação de habitat, reduzindo a área disponível para organismos que precisam de extensas áreas de distribuição (Sillero-Zubiri et al., 2004). Indico também que as espécies com maior potencial de resgate evolutivo são aquelas que ganham área ou perdem apenas uma pequena parte de suas distribuições futuras, enquanto as que vão perder grande parte de sua distribuição futura precisarão de uma mudança evolutiva maior para manter suas populações. No Capítulo 4, volto a olhar para o passado dos Canidae. Desta vez, usei uma nova extensão do modelo secsse (Several Examined and Concealed States-Dependent Speciation and Extinction) (Herrera-Alsina et al. 2019) para explorar ainda mais os registros ricos e bem documentados de espécies extintas de Canidae, que nos dão uma grande oportunidade de preencher o quebra-cabeça na história evolutiva dos Canidae. Com esta nova abordagem, este capítulo ajuda a compreender quais os traços (áreas geográficas) que promovem (ou não) a diversificação nos últimos 13 milhões de anos, e quão importante é incluir informação fóssil nas análises de diversificação, devido às distintas interpretações que podemos obter das árvores incompletas.

Palavras-chave: Biogeografia; Canidae; Diversificação, Evolução; Filogenia.

INTRODUCTION AND OUTLINE OF THE THESIS

Historical background

Among the several purposes that scientists have dedicated their lives to for hundreds of years, understanding species distribution patterns across the planet is perhaps one of the most fascinating. Advances in navigation enabling travelling to distant lands made us realize that *Homo sapiens* was not the only one that colonized different parts of the planet. Two hundred years ago, naturalists found organisms of the same species in different places, and tried to figure out how and why they were there. Darwin joined on the Beagle trip very motivated by these questions, so much that his book ‘On the Origin of Species’ is mainly based on observing the geographical distribution of biological groups. The discoveries that took place between the 18th and 19th centuries led to the establishment of the field of biogeography, and this is the focus of this thesis: the study of the patterns of geographic distribution of organisms and the factors that determine these patterns. More than two centuries after the origin of biogeography, we still lack knowledge on many aspects of how life is distributed on Earth, and in this thesis, I will focus on the Canidae family to provide some insights about how the distribution of life can be regulated by several forces and stochastic events over time.

Beyond local habitats

Generally, species distribution patterns can be explained by their ecology and history, but for now I will only focus on the historical part. A species occurs in a given place because its ancestors evolved there or dispersed to it in the past. Biogeographers use the current distribution of species to look into their past and discover the mechanisms responsible for generating such geographical patterns. The continental drift theory by Wegener (1912) and later the plate tectonics theory (Harrison 2009; Leprieur et al. 2016; Descombes et al. 2017; Pellissier et al. 2018) were a big step in this sense, as mechanisms that not only helped to understand why similar fossil species were found on different continents, but also to explain a large part of the diversity of life on Earth today. It is crucial to unravel these mechanisms because they act on the three factors that control species richness in a certain location — the rate of speciation, the rate of extinction, and the dispersal of species from other locations (Etienne et al., 2019; Mittelbach et al., 2007; Wiens et al., 2006; Wiens & Donoghue, 2004). However, numerous parameters can drive these historical factors in complex ways (Mittelbach & Schemske, 2015; Rolland et al., 2014).

Traits

Traits can have a prominent effect on the evolution of species. A trait can hinder or foster diversification depending on the evolutionary pressure they experience (Jablonski, 2008). Some traits can open up new ecological opportunities, being considered as key innovations. In this way, higher dispersal ability can increase speciation rates of species (Claramunt et al., 2012). By contrast, other traits can be dead ends, leading initially to more species, but ultimately leading to extinction of lineages. For example, one of the

Darwin’s finches, the mangrove finch, seems to be on an evolutionary dead end because its mating signals isolate a part of its population with a few individuals, making them more likely to become extinct (Brumm et al., 2010).

The distribution of species can be considered an emergent trait, and this is what I explore during Chapters 1 and 4, where I investigate the timing and location of biogeographical events, and associate these events with estimates of shifts in speciation and extinction rates through time and across clades. The information about where species are can be associated with the ecological opportunities that past lineages have undergone upon arriving in a new environment. Dispersal events to new regions can trigger exceptional shifts in species diversification (Algar & Mahler, 2016; Mahler et al., 2010; Mahler & Losos, 2010). In addition, the range of species distribution is also linked to the likelihood of speciation and extinction, as small-ranged species are more likely to become extinct, whereas large-range species will experience more habitat heterogeneity, increasing the chances of speciation (Kennedy et al., 2017; Uribe-Convers & Tank, 2015).

The community context

If we seek to understand the current distribution of species, we cannot just use the historical data to get answers. While past events shaped the current distribution of species, the past and current interaction with the environment and biotic components influence the capacity for a species to survive, and must be taken into account (Pearson & Dawson, 2003). Sometimes evolutionary approaches end up focusing only on separate lineages, trying to understand what happened to them over time, but we can also evaluate them in a community context, where our focus becomes the pool of species in one place and not the lineages separately. Thus, we can evaluate how species interact with each other and with the environment, which shapes their distributions at the present.

Chapter 2 was conceived from an initial idea that I had to just understand how the lineages of Canidae are different from each other due to their past evolutionary history. For this, one of the first tests that I did with the phylogeny of Canidae was the analysis of principal coordinates of phylogenetic structure (PCPS; Duarte, 2011), which describes phylogenetic gradients across the array of grid cells (Duarte et al., 2012). in Figure 1, I show how the phylogenetic information of the three major clades of extant canids is distributed in just two axes of the PCPS. However, this image raised a lot more questions, because by that time I was no longer only interested in knowing the phylogenetic distribution pattern of Canidae, but I also wanted to understand why it was like that. In other words, what factors were responsible to generate the pattern I saw in Figure 1? Thus, Chapter 2 was developed to answer this main question.

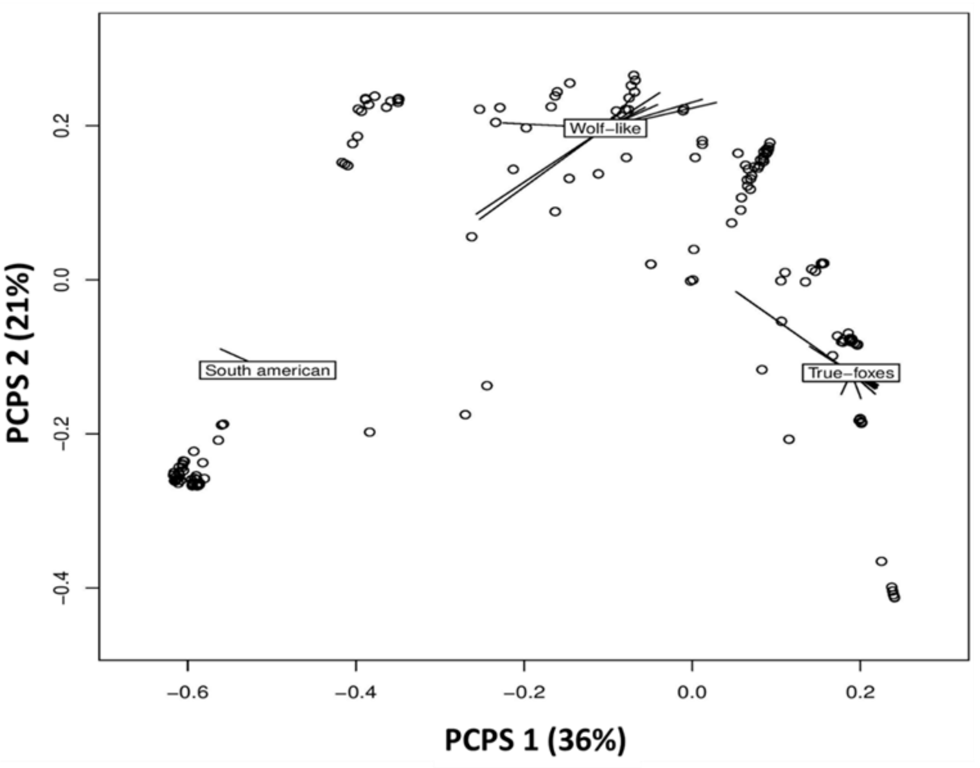

Figure 1. Phylogenetic information of Canidae distributed over the two main axes of the PCPS analysis. Axis 1 is more related to the information near to the root of the tree and is responsible for explaining 36% of the shown pattern, while axis 2 is more related to the information near the present, explaining 21% of the clade's distribution. Each black circle means one grid cell with the same dimensions as used in Chapter 2. The three major clades of Canidae are shown here.

The external environment and biotic competition are the main explanations for phylogenetic and functional diversity patterns in community structure (Cadotte & Tucker, 2017). We can incorporate species' traits and their phylogenetic information to assess patterns of community assembly and obtain randomized communities by permuting the presence-absence pattern on the phylogenetic tree (Webb et al., 2002). Even with the pitfalls that these approaches can bring (Mayfield and Levine 2010; HilleRisLambers et al. 2012; Pigot and Etienne 2015; Cadotte and Tucker 2017), they can still be very informative on how patterns of traits or phylogenetic dispersion change in response to the environment. After organisms disperse to a new environment, they will depend on some factors to be able to successfully colonize it and spread (Cadotte & Davies, 2016). The so-called 'environmental filters' are thought to play a strong role upon the arrival in the new area, while competition is more important as succession progresses (Cadotte & Tucker, 2017). Thus, we can compare our observed data with null models of trait and phylogenetic information to test if species within communities are phylogenetically or functionally more different or similar to each other than would be expected by chance (Cadotte & Davies, 2016; Cadotte & Tucker, 2017). If species in a community are more phylogenetically distant to each other than expected, this pattern is assumed to be caused by competition. However, if species are phylogenetically closer than expected, this can be explained by the action of environmental filters (Webb et al., 2002), although this may also be due to filtering of competition traits (Mayfield & Levine 2010; HilleRisLambers et al., 2012). Even without a definite answer to the cause of the phylogenetic community pattern, it is interesting to study how it varies across the globe. This is what I do in Chapter 2.

Niche structure

Environmental factors and interactions among species are very important to understand the current distribution patterns of biodiversity. However, many studies in recent years have investigated the effects of climate change on the future of biodiversity due to anthropogenic factors (Flores-Tolentino et al., 2020; IPCC, 2021; Kosanic et al., 2018; Pimm et al., 2014). This concern is increasing because recent climate change has become one of the main drivers of shifts in the geographical distributions of species (Pacifici et al., 2015; Parmesan et al., 2011). Pimm et al. (2014) already showed that the pace of climate change induced by humans is much faster than past predictions indicated, and the present extinction rates are likely a thousand times higher than the background extinction rates. Thus, the impacts that human society can impose on the future of Canidae is a case of concern and must be evaluated.

Chapter 3 was conceived because of this concern that I had after the reports from Pimm et al. (2014), and throughout this part of the thesis I show how climate change will affect canids in the future. Understanding how canids are affected by changes in the landscape, and being able to predict their future distributions is essential to outline conservation strategies for different species.

Understanding the response of biodiversity to climate change is of great importance because future geographic distributions help scientists to evaluate potential areas that run a greater risk, and to develop strategies to reduce the impacts of climate change on biodiversity (Parmesan et al., 2011; Pereira et al., 2010). Therefore, studies have investigated how future climate scenarios can affect whole ecological communities (Albouy et al., 2012; Ihlow et al., 2012; Nolan et al., 2018; Sommer et al., 2010), and showed that climate change can impose a biotic homogenizing effect on the fauna, reducing the diversity of communities (Magurran et al., 2015). Basically, this process can be generated by the extinction of specialist species with small distributions and expansion of ranges of generalist species, with large distributions (Longman et al., 2018; Magurran et al., 2015; McKinney, 1997).

Most of the attempts to predict the future distribution of biodiversity are made using Ecological Niche Models (ENMs), which combine the relationship between species distributions and environmental data. ENMs still are our most reliable tools to shed light on future distributions of species, as they allow us to integrate several climatic scenarios and distinct prediction algorithms that take into account distinct aspects of species ranges (Guisan et al., 2017). However, the effectiveness of ENMs to predict potential distributions rely on the data we use and their quality (Ishihama et al., 2019), and so far, few studies have aimed to clarify this dependence. Although ENMs are not foolproof, they are still a useful alternative to the IUCN spatial database, as ENMs are expected to improve our understanding of conservation areas by estimating species potential distributions in unsurveyed ranges and by reducing survey bias (Elith et al., 2010; Elith & Leathwick, 2009).

The Canidae family

Few biological groups have a well-documented fossil history, detailed trait datasets, reliable distribution maps, and are distributed on a global scale. The Canidae family is one of them, which allows us to tackle several topics not only about canids, but also related to general evolutionary processes and species' relationship with their environment. The origin of Canidae dates around 40 million years ago in North America, an epoch where this continent did not have land connections to any other continent (Wang & Tedford, 2008; Prothero, 2013). Through time, diversification events gave rise to the subfamilies Hesperocyoninae, Borophaginae and Caninae (Wang et al., 2004). The first two are now extinct and were restricted to North America, while Caninae radiated over almost the entire planet allowed by two geological events when North America connected with Eurasia and South America because of the Bering Strait and the Isthmus of Panama (Geffen et al., 1996; Montes et al., 2015; Sillero-Zubiri et al., 2004; Wang & Tedford, 2008). After crossing to new continents, and dispersing all over the planet, Caninae diversified into 111 species, of which only 36 are still alive today (Wang & Tedford, 2008). The phylogeny of Caninae is separated into three major clades: true wolves, South American canids, and Vulpini (Figure 2A) (Porto et al., 2019; Wang & Tedford, 2008).

The canid history is marked by their repeated tendency to evolve both hypocarnivorous and hypercarnivorous forms. Hypercarnivorous species evolved within each subfamily, and hypocarnivorous species evolved within two of the three (all but the Hesperocyoninae). Hypocarnivory was most fully expressed in the Borophaginae (Wang et al. 1999). Among the Caninae, the tendency has not been quite as strong, with only a single lineage, *Nyctereutes*, developing such trait. However, the three major clades of Caninae include multiple hypercarnivore lineages (Sillero-Zubiri et al., 2004). The evolution of hypercarnivorous forms in Caninae appears to have occurred at least partly in response to a reduced diversity of other hypercarnivorous taxa at a time when the two previously dominant carnivorous in North America, Hesperocyoninae and Borophaginae, were on their way to extinction, probably due to climate change and competition from Caninae (Wang & Tedford, 2008).

Among the extant families of carnivores, modern canids are the only family to have a truly worldwide distribution (except Antarctica, and not taking into account the Dingo in Australia) (Figures 2B, 2C, and 2D), and interact with several other species (Fleming et al., 2017). Many canids have distributions that span at least a whole continent. Red foxes (*Vulpes vulpes*) and grey wolves (*Canis lupus*) have the most extensive natural range of any land mammal (with the exception of humans), inhabiting the whole Northern Hemisphere, and being present in 81% of countries around the world (Sillero-Zubiri et al., 2004).

Whereas some canids are declining globally under the pressure of habitat degradation and fragmentation, others have managed to survive in human-dominated landscapes. This overlap with humans results in competition for resources, which is at the heart of the conflict between many wild canids and man (Sillero-Zubiri et al., 2004; Di Marco & Santini, 2015). Records of *Canis latrans* within urban areas are increasing every year in North America (Poessel et al., 2013). In addition, other species such as the African wild dog (*Lycaon pictus*) lost a large part of its historical distribution as a direct consequence of human activities (Di Marco & Santini, 2015). This is a cause for concern, because canids are mostly predators, fulfilling a variety of roles within the ecosystems where they occur, and their loss could be devastating for the communities.

Historically, humans had negative views towards wild canids in several parts of the world, but mainly in the USA and Europe (Mech, 1981). These views have often been generated by a fear of the larger species, and by the recurrent issue of wild canids predating on livestock (Sillero-Zubiri et al., 2004). Europeans, for instance, exterminated whole populations of wild canids around Europe. Furthermore, the British were responsible in 1876 for the last known canid extinction, the Falkland wolf (*Dusicyon australis*) (Macdonald & Sillero-Zubiri, 2004). In North America, grey wolves (*Canis lupus*) and coyotes (*Canis latrans*) were actively hunted, which almost led to the local extinction of these two species in this continent in the 1930s (Mech, 1981). After realizing the damage to the ecosystem caused by the removal of wolves, measures were taken in the United States to prevent their hunting (Sillero-Zubiri et al., 2004). In 1995 wolves were re-introduced to Yellowstone National Park as part of a plan to regenerate the park that had lost much of its diversity due to large numbers of elks, which no longer had predators to regulate their population. Studies indicated that wolves led to greater biodiversity, preying primarily on elk, which generated opportunities for several other species to establish at the park again. Now, throughout the whole United States, natural populations of wolves are re-establishing themselves (Dobson, 2014; Boyce, 2018). A similar example is happening in Europe as a result of protection plans for wolves. After centuries of persecution, there are wolf packs roaming not only in wild areas but also in well-populated landscapes across Europe. Wolf populations are re-establishing themselves in France, Germany, the Netherlands, and Denmark (Chapron et al., 2014; Gula et al., 2020).

As canids have a well-documented fossil history, marked by several episodes of global change over the last 40 Mya, and suffer distinct biotic and abiotic pressures in the present, Canidae represent an ideal group to investigate patterns of diversification, distribution and response to environmental changes.

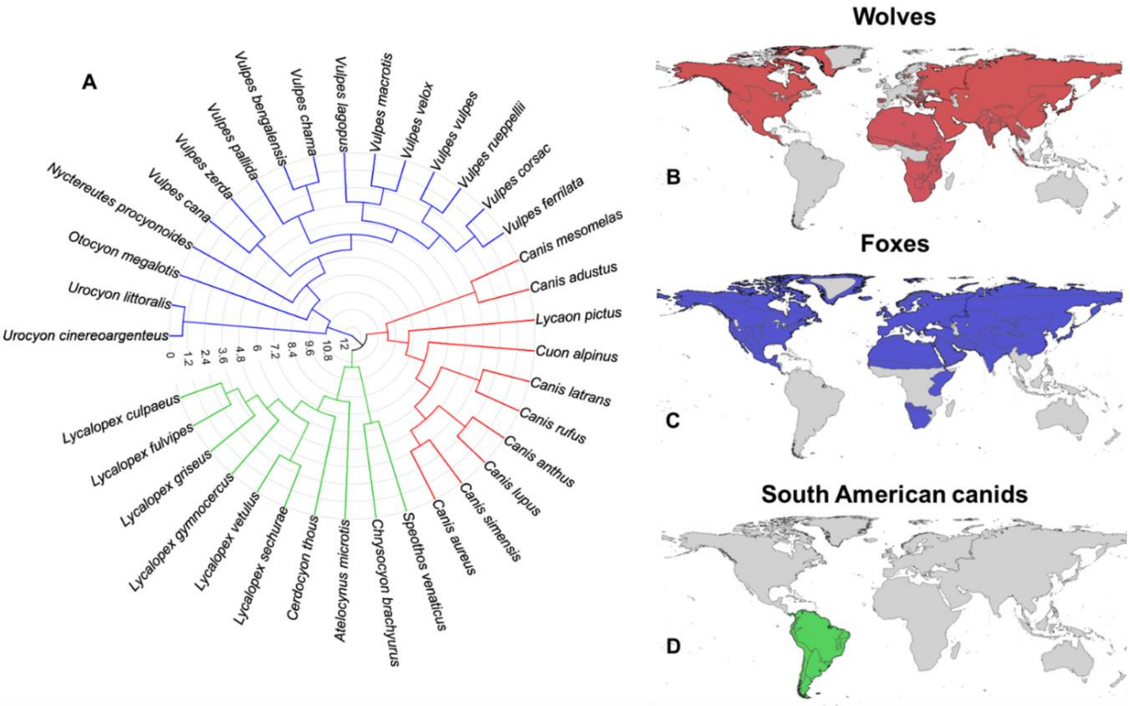

Figure 2. Phylogenetic information of the three major clades of Caninae presenting all the 36 extant species of canids (A). The geographical distribution of each clade is also showed (B, C and D). The dated (Mya) phylogenetic tree is from Porto et al. (2019). The distribution maps were created overlaying the IUCN polygons of the species within each clade. The distribution maps match in color with the clades in the phylogeny (Wolves - red, Foxes – blue, South American canids – green)

Thesis outline

Several questions concerning the distribution patterns of Canidae in past, present, and future are addressed in this thesis. Below I give an overview of the different chapters and the main objectives and goals behind them.

The main topic of the **first chapter** is understanding whether and how often colonization events trigger explosive radiations. Evolutionary radiations are often associated with the colonization of initially empty ecological space as a result of ecological opportunity. I traced the paths that Canidae lineages used to disperse around the world, and compared these routes with speciation rates at the moment when lineages entered into new regions. I was able to demonstrate a major peak in the speciation rate of Canidae right after the clade started to go into new environments, and throughout this chapter I discuss what are the most likely causes for such effects on the diversification of canids.

An ecological community can be shaped by several biotic and abiotic factors, including competition and habitat filtering. Usually, both forces act together to assemble the pool of species in a given area, and although we know the roles that both play, we often do not understand the contribution that each force has in certain communities. The **second chapter** deals with this issue, testing how the phylogenetic structure of the Canidae family varies across the world, and what are the actual contributions of the environment and competition to shape the observed distribution patterns.

How will canids be affected by future climatic scenarios? And will the populations be able to keep pace with climate change? Together with a quarter of all known mammals, canids are currently threatened with extinction, suffering the consequences of the human contact, as they lose their home ranges due deforestation, and are constantly being hunted. In the **third chapter** I point to how severe the next decades will be for canids in different parts of the planet, showing that not only many species (27) will lose large parts of their distributions, but also that some will not be able to even maintain their viable populations in the face of climatic pressures. On the other hand, nine species have the potential to benefit from future climatic conditions and expand their ranges, occupying areas previously inhabited by other canids.

The Canidae consist of lineages with very distinct characteristics. Some lineages are endemic to specific regions, while others have distributions that span three different continents. In addition, canids are found all over the planet, but not in every single place, which makes regions species-rich and others species-poor. Therefore, what is the cause of these unbalanced patterns in clade distributions across the planet? Are there regions that contributed more for the diversification of lineages than others? In the **fourth chapter**, I explore Canidae past one more time in order to obtain more answers about species diversification and dispersal around the world. Here, I extend the secsse model and feed this new version with the geographic information of canids and their complete phylogenetic tree to assess the contributions that biogeographic states had on canid rates of speciation and extinction. In addition, I shed light about how incorporating fossil information into trees can change the interpretation we can get from the diversification processes.

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CHAPTER 1

Explosive diversification following continental colonizations by canids

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Abstract

Colonization of a new environment may trigger an explosive radiation process, defined as an accelerated accumulation of species in a short period of time. However, how often colonization events trigger explosive radiations is still an open question. We studied the worldwide dispersal of the subfamily Caninae, to investigate whether the invasion of new continents resulted in explosive radiations. We used a combination of phylogenetic analyses and ancestral area reconstructions to estimate ancestral ranges of 56 extant and extinct species of Caninae, as well as variation in speciation and extinction rates through time and across clades. Our findings indicate that canids experienced an explosive radiation event when lineages were able to cross the Bering Strait and the Isthmus of Panama to reach Eurasia and South America, respectively, around 11 million years ago. This large number of species arising in a short period of time suggests that canids experienced ecological opportunity events within the new areas, implying that the differences in the ecological settings between continents may be responsible for the variation in clade dynamics. We argue that interaction with other carnivores probably also affected the diversification dynamics of canids.

Keywords: Ancestral range estimation, Canidae, Dispersion routes, Ecological opportunity, Evolutionary radiation, Geographical distribution.

Introduction

Evolutionary radiations are phenomena in which a large number of species arise in a short period of time (Lovette and Bermingham 1999, Schluter 2000, Rabosky and Lovette 2008, Losos 2011). Such radiations have contributed substantially to the earth's biodiversity (Lovette and Bermingham 1999; Rabosky and Lovette 2008; Losos 2011; Morlon et al. 2012). Evolutionary radiations are often associated with the colonization of initially empty ecological space as a result of ecological opportunity, i.e. when species have access to new resources that are little used by other taxa (Schluter 2000). Geographic colonization of areas previously unoccupied by potential competitors or occupied by competitively inferior organisms is therefore an ideal setting for an evolutionary radiation to unfold (Stroud and Losos 2016), i.e. to generate cladogenesis accompanied by ecological and morphological disparity among lineages (Harmon et al. 2003).

Detecting evolutionary radiations requires knowledge of how speciation and extinction rates varied over time (Rabosky and Lovette 2008). The common assumption is that diversification is highest at the beginning of the radiation (Schluter, 2000; Etienne & Haegeman, 2012). In the last decades, the number of robust and reliable molecular phylogenies has increased together with methods to extract information about the tempo and mode of evolution from them (Nee 2006; Rabosky et al. 2007; Etienne and Haegeman 2012; Etienne and Rosindell 2012; Etienne et al. 2012; Revell 2012; Yu et al. 2015; Morlon et al. 2016; Herrera-Alsina et al. 2019). Patterns of evolutionary radiations have been identified for a variety of organisms (Burbrink and Pyron 2010; Wagner et al. 2012; Tran 2014; Arbour and López-Fernández 2016; Maestri et al. 2017; van Els et al. 2019). Once the timing of shifts in diversification rates has been established, one can compare them to major shifts in biogeographical distribution that characterize entrance in new geographic areas to find support for the hypothesis that this entrance triggered the radiation.

An ideal group to investigate patterns of diversification in continental evolutionary radiations is that of the Canidae, because their evolutionary history is marked by episodes of dispersal and colonization of new environments. Furthermore, canids are distributed all over the planet, have a rich fossil history, and well-resolved phylogenetic relationships between both extinct and extant species (Finarelli 2007; Porto et al. 2019). The family Canidae originated in North America approximately 40 million years ago (Mya), an epoch where this continent did not have land connections to any other continent (Wang and Tedford 2008; Prothero 2013). Within Canidae, successive radiations gave rise to three subfamilies by the end of the Oligocene: Hesperocyoninae, Borophaginae, and Caninae. The first two are now extinct and were restricted to North America, while Caninae radiated over almost the entire planet allowed by two geological events (Geffen et al. 1996; Cox 2000; Sillero-Zubiri et al. 2004; Wang and Tedford 2008; Potter and Szatmari 2009): the emergence of the Bering Strait and the Isthmus of Panama, both around 11 Mya (MacNeil 1965; Hopkins 1967; Montes et al. 2015). Today, the Caninae is separated into three major clades: true-wolves, Cerdocyonina, and Vulpini (which we hereafter will refer to as wolves, South American canids, and foxes, respectively) (Wang and Tedford 2008).

In this study, we used phylogenetic information of the subfamily Caninae to investigate the timing and location of major dispersal events, to explore the biogeographical processes that led to the present canid distribution, and to associate biogeographical events with estimates of shifts in speciation and extinction rates through time and across clades.

Materials and Methods

Taxon sampling and phylogenetic information

We used the phylogenetic tree from Porto et al. (2019) as the base for our study. This tree was constructed with molecular and osteological data, through Bayesian inference, and presents all the 37 extant canids in the world. To increase accuracy in the ancestral range estimation, we added 19 extinct species (Table S1) to this tree following taxonomic information from the digital paleobiology dataset, *Fossilworks* (Alroy 1998). We performed a literature review in *Fossilworks* in search of articles that presented information on the most likely taxonomic position that the extinct species would fit into. With this information we added the species to the phylogeny at the most likely nodes, resulting in a phylogeny of 56 species (representing 46.7% of all known species of the Caninae subfamily, based on Wang & Tedford (2008)). We only added extinct species that had a detailed description of their past geographical distribution in the literature, and thus we could generate maps (polygons) with the occurrence points to classify these species into the eight biogeographic regions used here (Fig. 1). We dated the phylogeny again, using the fossil information of the 19 species and the fossil ages that were used by Porto et al. (2019). We used *Leptocyon vafer* (Leidy 1858) and *Leptocyon vulpinus* (Matthew 1907) as the outgroup for the biogeographical analyses because it is known that both species originated in North America during the Miocene, so the root of the phylogeny will be fixed where the subfamily Caninae originated. The phylogeny is shown in Fig. S1.

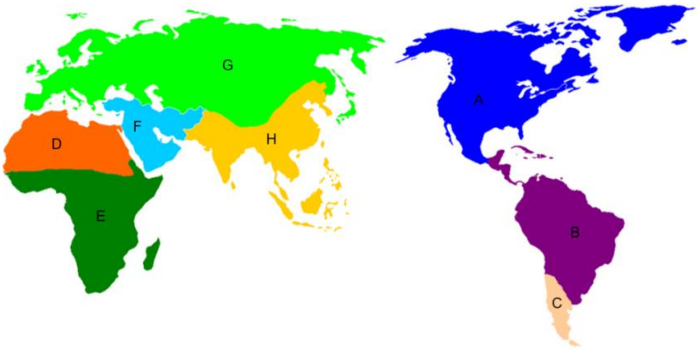

Figure 1. Eight biogeographic regions delimitated for our ancestral range estimation analysis based on the patterns of the beta-sim index of mammal species from Kreft & Jetz (2010), and the distribution shapes from IUCN (2017). The regions delimitated are North America (A), Northern South America (B), Southern

South America (C), Northern Africa (D), Sub-Saharan Africa (E), Middle East (F), Northern Eurasia (G), and Southern Eurasia (H).

Ancestral range estimation

To estimate ancestral ranges, we divided the world into eight biogeographic regions (Fig. 1) based on the patterns of the beta-sim index of mammal species from Kreft & Jetz (2010), and on the distribution shapes of the extant species taken from IUCN (2008). We categorized all the 56 canids into one or more biogeographical regions based on their distributions as given in (IUCN 2008) (Table S1).

We performed an ancestral range estimation using *RASP* 4.0 (Yu et al. 2015). Six models of ancestral range estimation were fitted and compared: The Dispersal-Extinction Cladogenesis Model (DEC), a likelihood version of the Dispersal-Vicariance Analysis (DIVALIKE), the likelihood version of the Bayesian Analysis of Biogeography (BAYAREALIKE), as well as "+J" versions of these three models, that include founder events of speciation. DEC assumes that one daughter lineage will always have a range of one area and, at least, one daughter lineage inherits the range of the ancestor lineage. DIVALIKE allows that all daughter lineages have two or more areas, but this model does not allow sympatric speciation. BAYAREALIKE assumes the daughter lineages will have the same range as their ancestor. For more details on the assumptions of these different models see Matzke (2013). We compared the predictions of these different models rather than selecting the best-fit model based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Akaike 1973) because it has been argued that this model selection may be biased (Ree and Sanmartín 2018). The number of sampled trees was set to 1×10^6.

To understand how canids dispersed worldwide, we used the informative matrices (Appendices S1 and S2) of the ancestral range estimation analysis, which summarize the most likely paths by which ancestral lineages followed. These matrices contain all the events that occurred in each ancestral node of the tree (Yu et al. 2015). Based on this data, we derived, in a form of a palaeoscenario, the dispersal routes that the lineages of Caninae followed during their evolutionary history.

Speciation and extinction rates

We estimated speciation and extinction rates through time and across clades using the Bayesian Analysis of Macroevolutionary Mixtures version 2.6 (*FossilBAMM*) (Mitchell et al. 2019). *FossilBAMM* implements an automatic reversible-jump Markov Chain Monte Carlo algorithm (rjMCMC), which enables the detection of changes in the rates of speciation and extinction of canids, allowing us to visualize rate peaks over time with non-ultrametric trees, even with an incomplete fossilized history. Speciation and extinction rates were calculated for the whole tree and separately for the three major clades of Caninae (wolves, foxes, and South American canids). Each analysis was performed using four chains, with 20×10^6 iterations, and samples were obtained every 1000 cycles. We removed the first 20% of the collected samples as burn-in. We used the *BAMMtools* package (Rabosky et al. 2014) in the *R* environment (R Development Core Team 2020) to plot and visualize the results from *BAMM*. that allows estimates to be made. To detect rate shifts over the tree, we extracted the potential rate shifts and associated parameters, together with their relative probabilities, from all the collected samples (80%).

While *BAMM* has been criticized in the literature (Moore et al., 2016), Rabosky et al., (2017) have argued that previous criticisms about *BAMM* are incorrect or unjustified, although it is true that the method, like many others in the same family of models, is not exactly correct (Laudanno et al. 2020). More importantly, over the last few years, several studies have demonstrated that most inferences seem to be robust when estimating diversification in distinct groups of animals (Rabosky et al. 2013; Shi and Rabosky 2015; Chang et al. 2019; Rabosky 2020).

Results

Ancestral range estimation

We provide a detailed analysis of the predictions of the DEC + J model and then compare the predictions of the other models to this model (Fig. 2B) because DEC + J was the model that presented less uncertainty during node reconstruction compared to the others. According to DEC + J, the ancestor of the three major clades of Caninae originated in North America, but the first lineage to disperse out of this continent was the lineage that led to the South American canids, around 10.4 Mya. After a long period, diversifying in the north part of South America, the South American canids dispersed to Patagonia through three lineages (Fig. 3A - M2, M4, and M6), around 4 and 3 Mya, originating four species. Two South American lineages dispersed back to North America around 4.8 Mya (Fig. 3A - M3 and M5), giving rise to *Chrysocyon nearcticus* and *Cerdocyon avius*.

Wolves went for the first time to the Old world through two lineages between 9.5 and 7 Mya, which dispersed to Africa and Asia, respectively (Fig. 3B - M1 and M3), and gave rise to four species that were distributed in a great part of these continents. Wolves experienced a long period diversifying within North America until around 4.5 Mya, when a lineage (Fig. 3B - M5) dispersed to Sub-Saharan Africa. *Canis lupus* and *Vulpes vulpes*, which are the species with the largest current biogeographic distributions, originated from endemic lineages of North America, dispersing to other areas in a relatively short time, 3.4 Mya. Within the wolf clade, the extinct species of *Canis dirus* and *Canis nehringi* originated from a lineage that dispersed to South America around 1 Mya (Fig. 3B - M7 and M8).

Foxes also originated in North America, but dispersed to the Sub-Saharan Africa around 9 Mya (Fig. 3C - M1). The most important dispersal event for foxes was the event M2, around 8.5 Mya when a lineage went to North Africa. From this ancestor, the foxes started a diversification process inside North Africa generating new lineages in this area, but also dispersing to other areas, such as Eurasia (Fig. 3C - M3 and M5) and North America (Fig. 3C - M7). Unlike the wolves, foxes had their center of diversification in North Africa.

The other five biogeographic models used here estimated ancestral ranges in slightly distinct ways. DIVALIKE + J resembles the DEC + J generating a similar ancestral estimation for foxes and South American canids. However, under DIVALIKE

+ J, the ancestral lineages of wolves had an area expansion, around 11 Mya, inhabiting a great part of the north-hemisphere. Then, around 9 Mya, it seems that a retraction in their distributions occurred, originating more geographically restricted lineages (Fig. S2). BAYAREALIKE + J is similar to DEC + J for the diversification of both wolves and foxes (Fig. S3). They differ in predictions for the South American canids. The estimation of BAYAREALIKE + J suggests that, for this clade, the first lineages inhabited a wide distribution (North America and a great part of South America), different from the DEC + J model that shows the diversification of this clade occurring within South America only. The DEC, BAYAREALIKE, and DIVALIKE models (Figs. S4, S5, and S6), in which the J parameter is not present, are all similar to DEC + J for the clade of foxes and South American canids. However, they all differ from the DEC + J model because the predictions for wolves were more similar to those of DIVALIKE + J, where the ancestral lineages of wolves had an expansion and then a retraction in their distributions before originating the extant lineages.

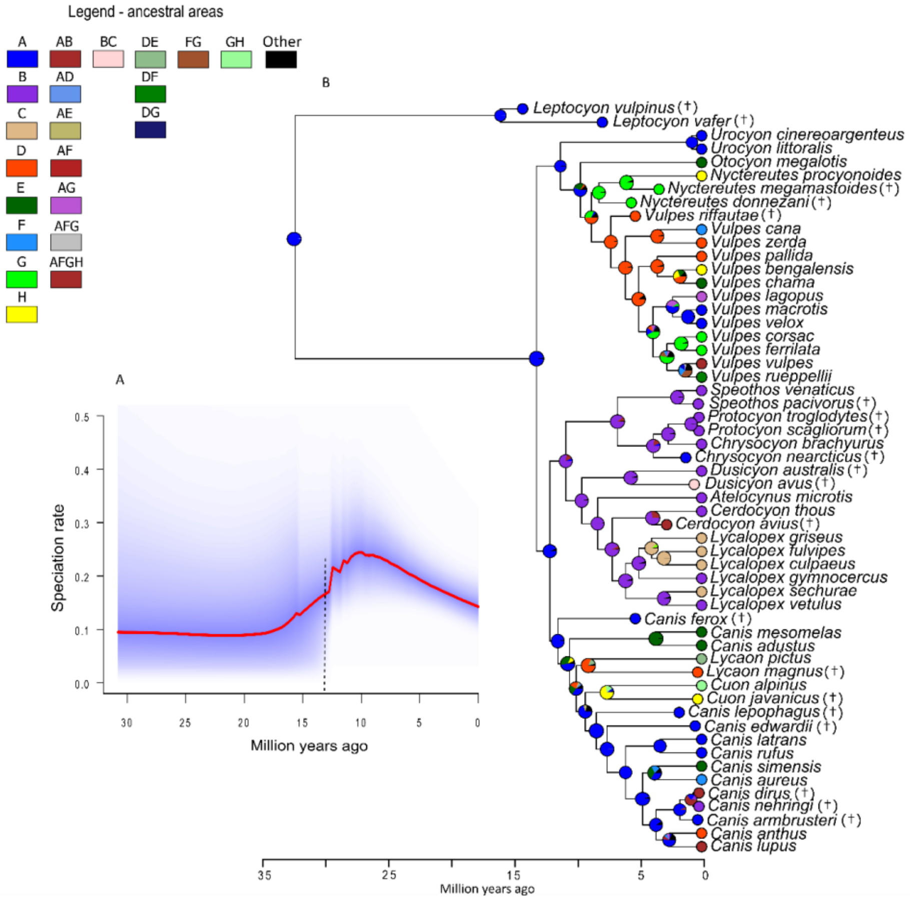

Figure 2. Speciation rate for the whole tree (A), phylogenetic tree, and ancestral range reconstruction under DEC + J (B). The probability of the ancestral areas of the lineages is indicated at the nodes of the tree, and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left). The black dashed line indicates the time of significant rate shift (A). The species with the symbol (†) are the extinct species added to the tree.

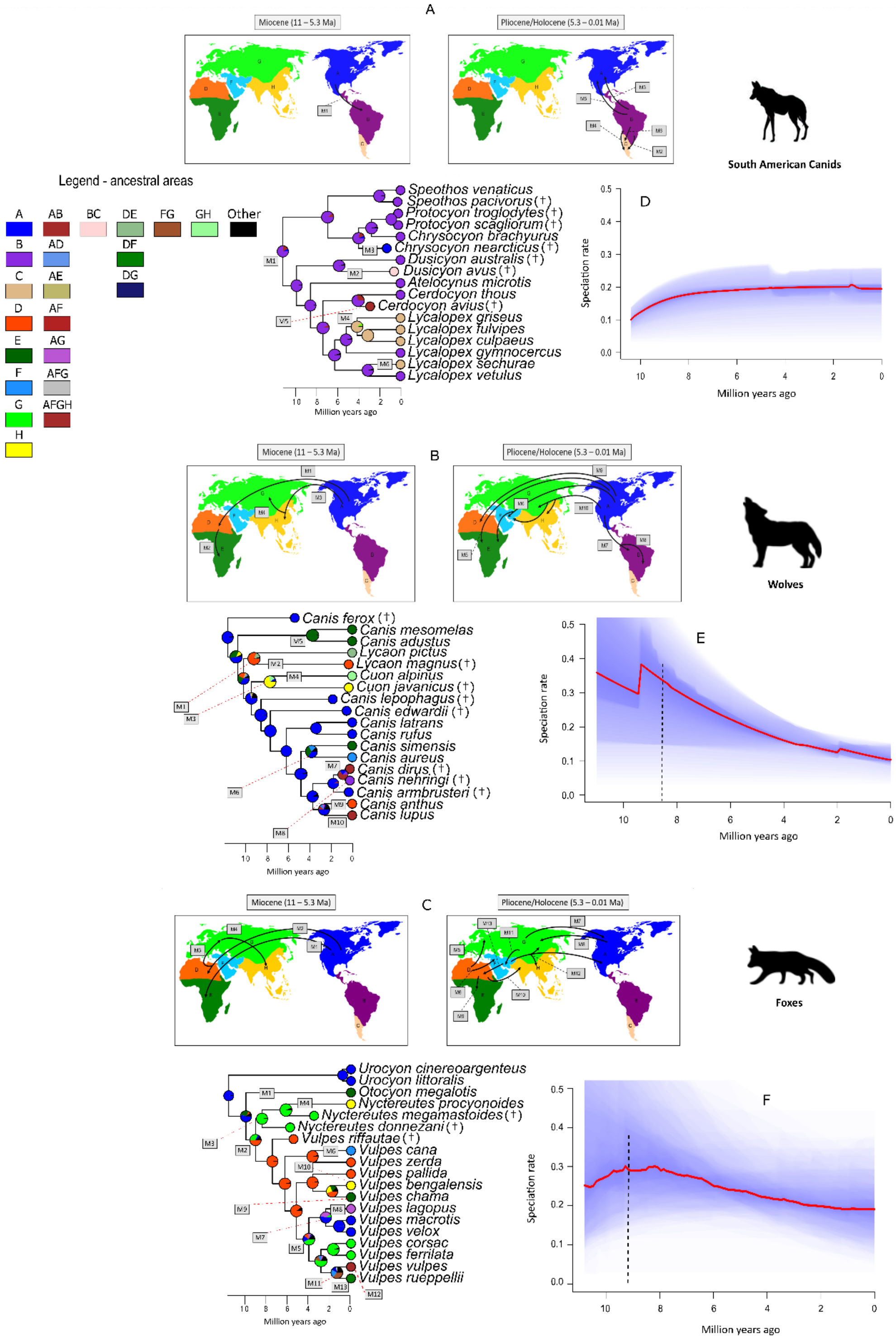

Figure 3. Ancestral range estimation for the South American canids (Cerdocyonina) (A), wolves (B), and foxes (C) under DEC + J model. The hypothetical dispersal routes that lineages used are indicated by black arrows. The probability of the ancestral areas of the lineages is indicated at the nodes of the tree, and the color-coded circles at the tips represent the current areas occupied by each lineage. The respective areas that the colors represent are indicated in the maps. All the dispersal events that occurred over the tree are coded as moments (M1, M2…M*x*) and are also indicated in the maps at the respective times that occurred (Miocene or Pliocene/Holocene). We also show the speciation rates for the three major clades: South American canids (D), wolves (E), and foxes (F). The peaks in the speciation rates occurred ~ 9 Mya for the three major clades separately. Black dashed lines indicate the time of significant rate shifts (D, E, and F). The species with the symbol (†) are the extinct species added to the tree.

Speciation and extinction rates

Peaks in speciation rates through time were coincident for Canids (whole tree) and each of its major subclades (Figs. 2A, 3D, 3E, and 3F), around 12 - 8 Mya. Therefore, changes in speciation rates were triggered in parallel across different lineages. The peak for the Caninae tree starts at 12 Mya ($\lambda = 0.25$). The results for the three clades separately showed that in wolves, foxes, and South American canids the peaks occurred at ~ 9 Mya ($\lambda = 0.37$; $\lambda = 0.28$ and $\lambda = 0.16$). After the rate peaks, South American canids stabilized their speciation rate, whereas the speciation rate of wolves and foxes declined. For the whole tree, the extinction rate remained at its highest value until 17 Mya ($\mu = 0{,}13$), and after that, the rate began to decline over time (Fig. S7A). The extinction in wolves presented a peak 6 Mya ($\mu = 0{,}12$), while in foxes and South American canids the extinction rates of both clades were constant over time ($\mu = 0.1$ and $\mu = 0.02$) (Fig. S7B, S7C and S7D).

We detected three significant rate shifts during the speciation of Canidae: one for the whole tree (Fig. 2A) and the other two for the clades of wolves and foxes, respectively (Figs. 3E and 3F). The uncertainty during the speciation rate estimations was higher when clades were analyzed separately due to the removal of many species for the comparison between clades.

Discussion

Our findings show that major events of canid dispersal — to South America and North Africa — are associated with peaks in diversification rates, suggesting an evolutionary radiation process right after the geographic colonization of new continents. Moreover, the pattern presented by the speciation rates in the clades of wolves and foxes, as well as for the whole tree, with a decline in the speciation rate after a peak in the emergence of new lineages is characteristic of an explosive radiation (Schluter 2000; Rabosky and Lovette 2008). Our results contrast with those of Liow & Finarelli (2014), which showed stable diversification rates of carnivores over the last 22 Ma.

The speciation rate of Caninae increased substantially shortly after canids arrived in the Old World and South America around 10 Mya (Fig. 2A). The timing of radiations suggests that this pattern for the whole tree was generated by ecological opportunity after the entrance in new continents by South American canids and foxes, but also by the diversification of wolves within North America. For the first two clades, the peaks in speciation rates occurred at the same time as these lineages entered in North Africa and South America (Fig. 3D and 3F). The absence of competitors and the new types of vegetation in Africa (deserts) (Zhang et al. 2014) and South America (tropical forests), may have generated the ecological opportunity and subsequent Caninae diversification in these continents. This ecological opportunity hypothesis must still be tested with ecological data.

Wolves had their peak around 9 Mya, but it seems that their explosive diversification was not triggered by the entrance in new areas, but probably due to the great turnover in the North American herbivorous fauna associated with the expansion of grasslands, resulting in ecological innovations in canids (Cox 2000; Janis et al. 2000;

Figueirido et al. 2015). As our results showed, during the Miocene, there were not many dispersion events among biogeography areas that could explain the peak in wolves` speciation (Fig. 3B). Therefore, the explosive diversification that wolves underwent in North America was probably due to the changing environment in this continent rather than the colonization of new areas.

We note that not all dispersal events to new areas led to radiations. Dispersal events M3 and M4 in wolves and M4 in foxes, all in Eurasia, did not increase the speciation rates of both clades (Figs. 3B, 3C, 3E, and 3F). It is likely that the large number of other carnivores in this area (e.g., Felidae, Barbourofelidae, and Hyaenidae) (Werdelin and Solounias 1991; Zhanxiang 2003; Wang and Tedford 2008) imposed strong competition on canids, which may have resulted in a slowdown in the rate of speciation of these clades. Intense competition with other carnivores may explain why Eurasia was not the center of diversification for any of the three major clades of Canidae.

In addition, wolves and foxes showed a decrease in the speciation rate, as well as the whole tree, after their peak (Fig. 2A, 3E, and 3F). This brings us to another characteristic of explosive radiations, declining speciation through time due to a presumed saturation of available ecological opportunity (Schluter, 2000; Harmon et al., 2003; Rabosky & Lovette, 2008, Etienne et al. 2012). In foxes, a plausible explanation would be that niches became filled over time, mainly in North Africa (diversity-dependence). Wolves, mainly in North America, may have experienced competition with other carnivores that came from Eurasia, such as felids (Johnson et al. 2006). These interactions may have contributed to the decay in the speciation rate and the increase in the extinction rate of wolves (Silvestro et al. 2015; Pires et al. 2017), as biotic interactions such as competition can constrain evolutionary dynamics (Pires et al. 2015). Wolves in North America may also have had their dispersal out of the continent limited by the carnivores in Eurasia (Werdelin and Solounias 1991; Zhanxiang 2003; Wang and Tedford 2008) through an incumbency effect (Rosenzweig and Mccord 1991), which could explain the great diversification of wolves only in North America.

The three major clades of canids showed distinct dispersal patterns over the world. Wolves and foxes, even though they have very similar geographic distributions nowadays, did not coexist in the same biogeographical regions for much time in the past. Because of the large number of speciation events in wolves on the North American continent, it is evident that the center of diversification of the wolves was North America, while foxes had their center of diversification in North Africa. Furthermore, our results suggest different arrival times of some species in certain biogeographic regions than previously known in the literature. For example, the ancestral range estimation indicated that the first canid to arrive in the Old World was the ancestor of both species, *Lycaon magnus* and *Lycaon pictus* (Fig. 3B - M1) about 9 to 8.5 Mya, differently from Crusafont-Pairó (1950) who proposed, with fossil data, that the *Canis cipio* as the first canid to disperse out of North America around 8 to 7 Ma.

Foxes and South American canids seem to have undergone a diversification process distinct from wolves. The diversification center of foxes, North Africa, is a desert environment that originated around 7 Mya (Zhang et al. 2014). Because it is a desert, food is probably very scarce for large predators such as lions and leopards, which now live in sub-Saharan Africa, but during the last five million years also inhabited parts of the Sahara (Johnson et al. 2006; Wilson and Mittermeier 2009; de Manuel et al. 2020). In this scenario, foxes may have had an ecological opportunity to occupy this area due to the generalist behavior that this clade evolved, as demonstrated by Porto et al. (2019), not overlapping their niches with other carnivores. A similar process probably occurred with the South American canids. Once in South America, the lineage that dispersed from North America faced an environment dominated by forest (Zachos et al. 2001; Potter and Szatmari 2009; Strömberg 2011) and a fauna composed mostly of large herbivores and lacking potential competitors (Wang and Tedford 2008).

Our results are based on separate analyses for the biogeographic ancestral reconstruction and for the shifts in diversification rates. Ideally, a single analysis should be used for this, such as GeoSSE (Goldberg et al. 2011) or other state-of-the-art SSE-type approaches (Beaulieu and O'Meara 2016; Herrera-Alsina et al. 2019), which can link the diversification rate directly to the biogeographic distribution of the lineage. However, these are currently computationally very demanding when there are many states which is the case here, and they have not been developed for phylogenies with fossil data. Similarly, the detection of ecological opportunity affecting diversification rates suggests the use of diversity-dependent diversification models (Etienne and Haegeman 2012; Etienne et al. 2012). This requires a combination of diversity-dependence diversification with ancestral state reconstruction, which has not yet been implemented.

Conclusion

We studied changes in speciation rates of Caninae in the light of distribution data to provide a detailed description of the dispersal and diversification of the subfamily Caninae through the world over the last 31 Ma. The spatial patterns indicated that Caninae underwent an evolutionary radiation process when entering in Africa and South America, suggesting that the differences in the ecological settings between continents may be responsible for the disparity among clades dynamics. We also suggest that the new environment arising in North America over the last 10 Mya was the major responsible for wolves` radiation rather than dispersion events outside this continent. Interaction with other carnivores, which came from Eurasia to North America, may have affected the speciation dynamics of wolves over the last 9 Mya.

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Supplementary material

Appendices and R scripts will be available at the online public repository of this thesis.

Figures

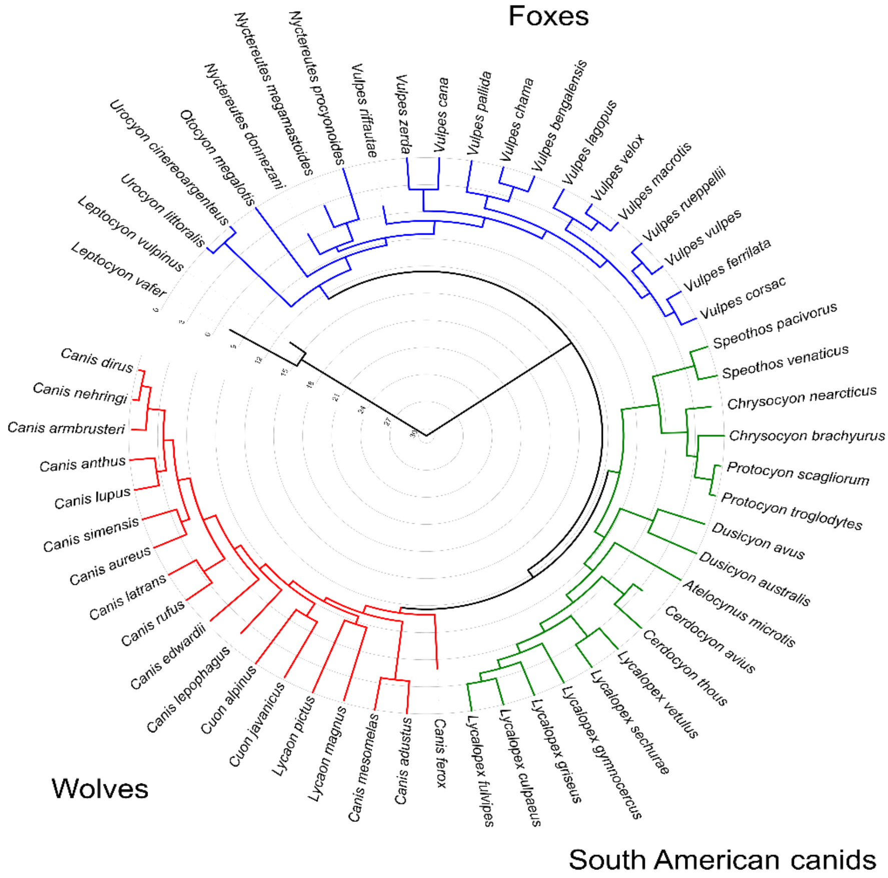

Figure S1. Phylogenetic tree with 56 species of canids used during our analyses. This tree was constructed by adding 19 extinct species to the phylogeny of extant canids of Porto et al. (2019). The three major clades of Caninae are identified by the colors red (Wolves), blue (Foxes), and green (South American canids).

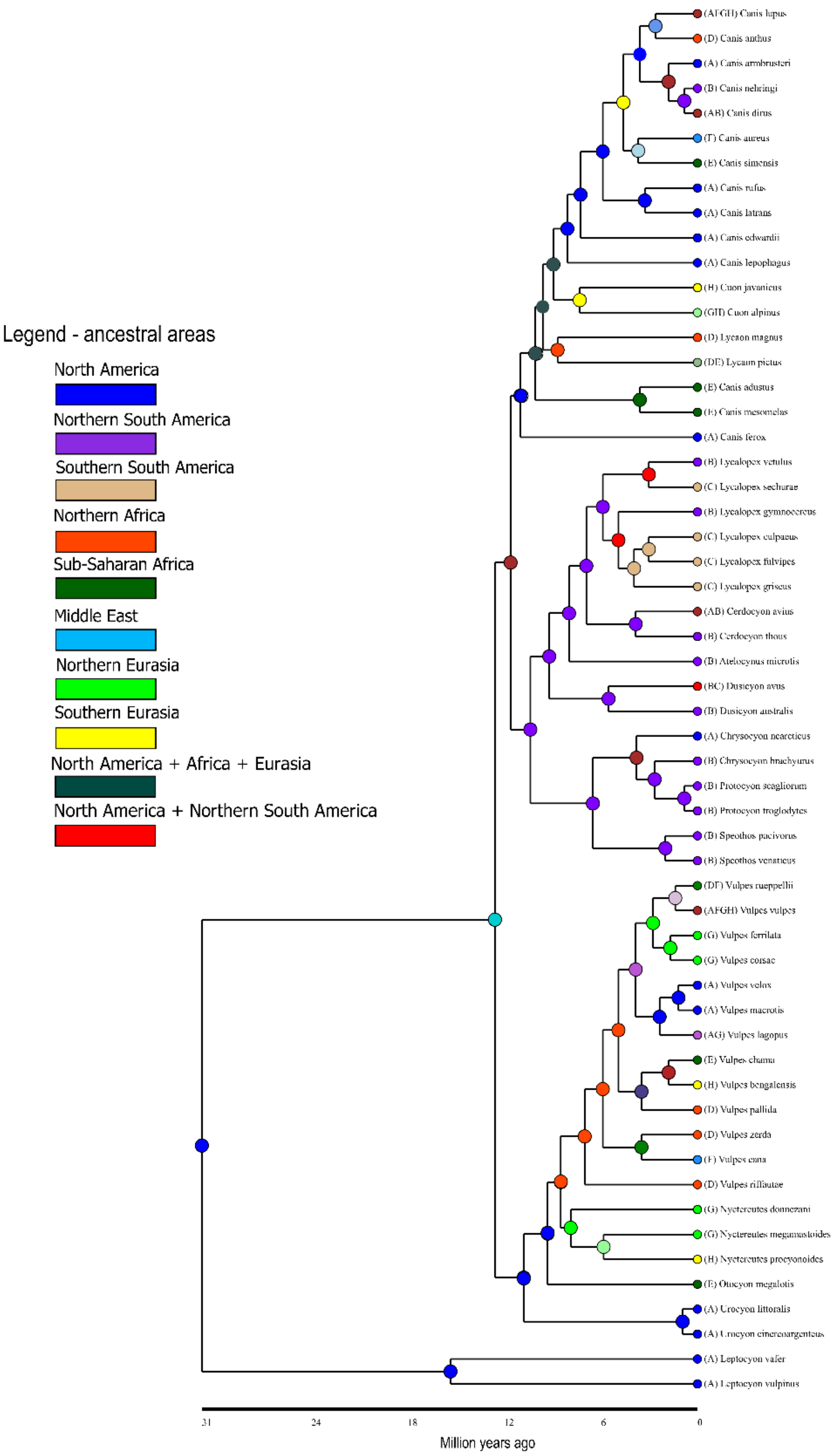

Figure S2. Phylogenetic tree and ancestral range reconstruction for the whole tree under DIVALIKE + J. The ancestral areas of the lineages are indicated at the nodes of the tree and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left).

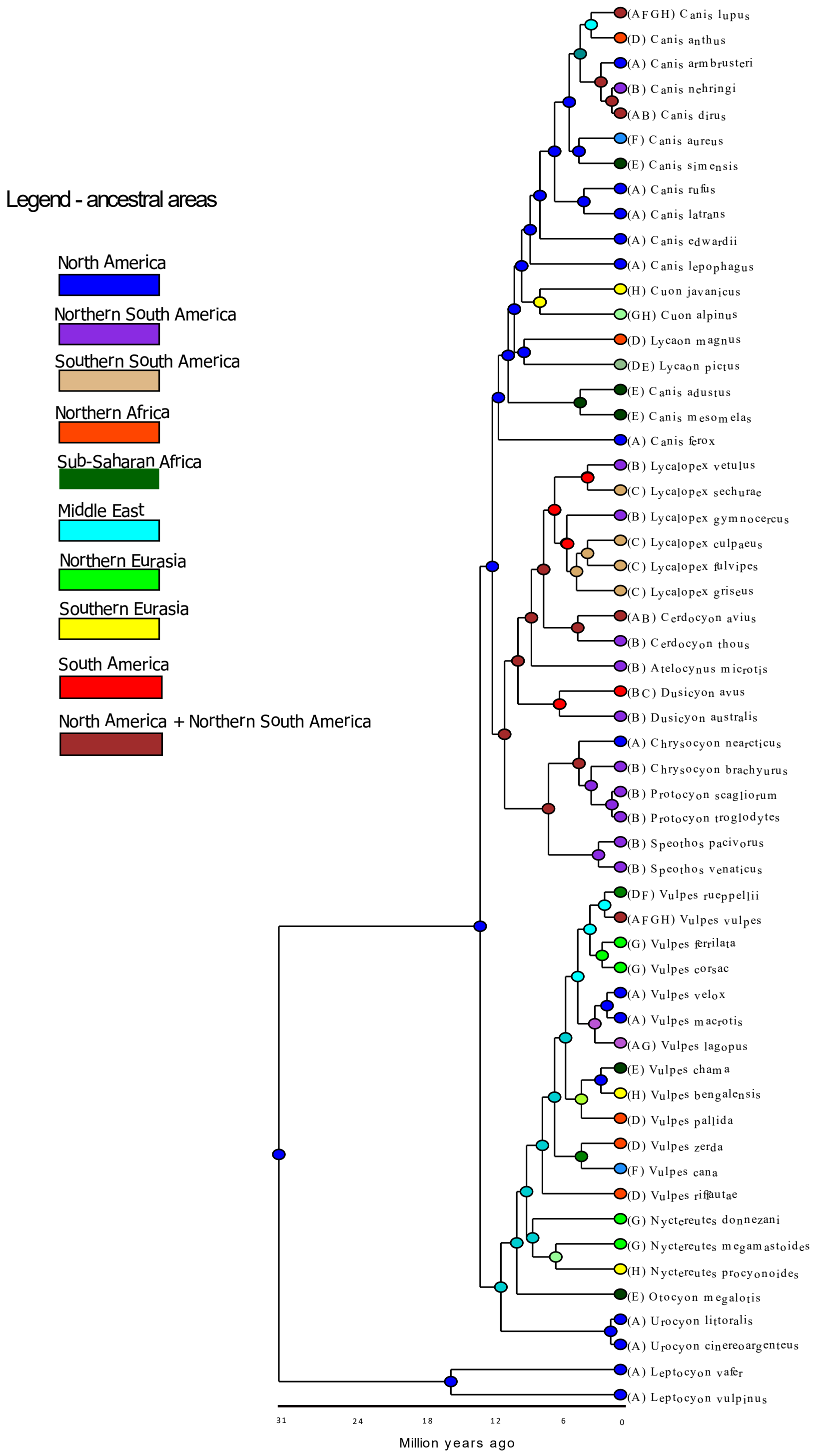

Figure S3. Phylogenetic tree and ancestral range reconstruction for the whole tree under BAYAREALIKE + J. The ancestral areas of the lineages are indicated at the nodes of the tree and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left).

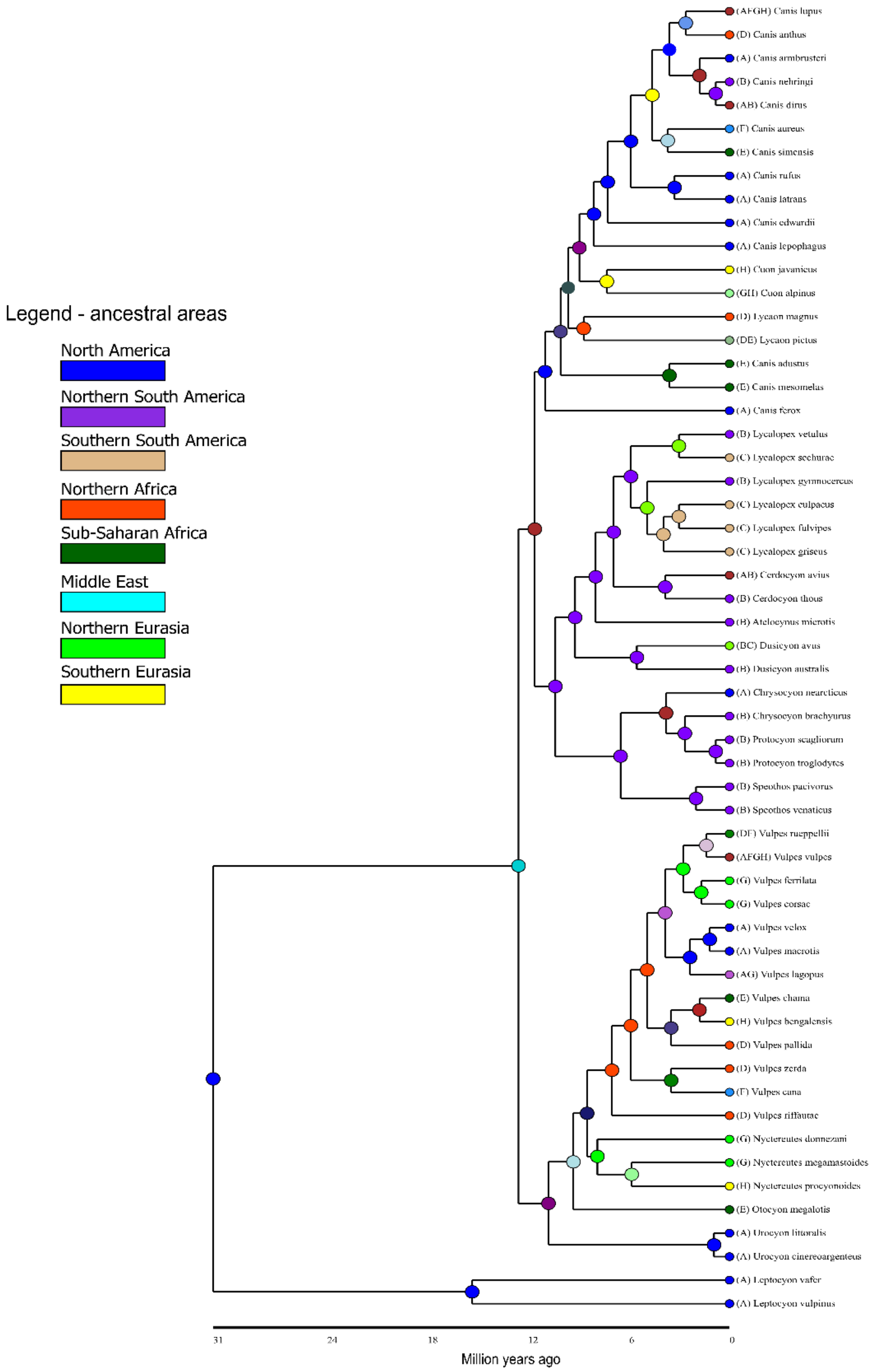

Figure S4. Phylogenetic tree and ancestral range reconstruction for the whole tree under DIVALIKE. The ancestral areas of the lineages are indicated at the nodes of the tree and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left).

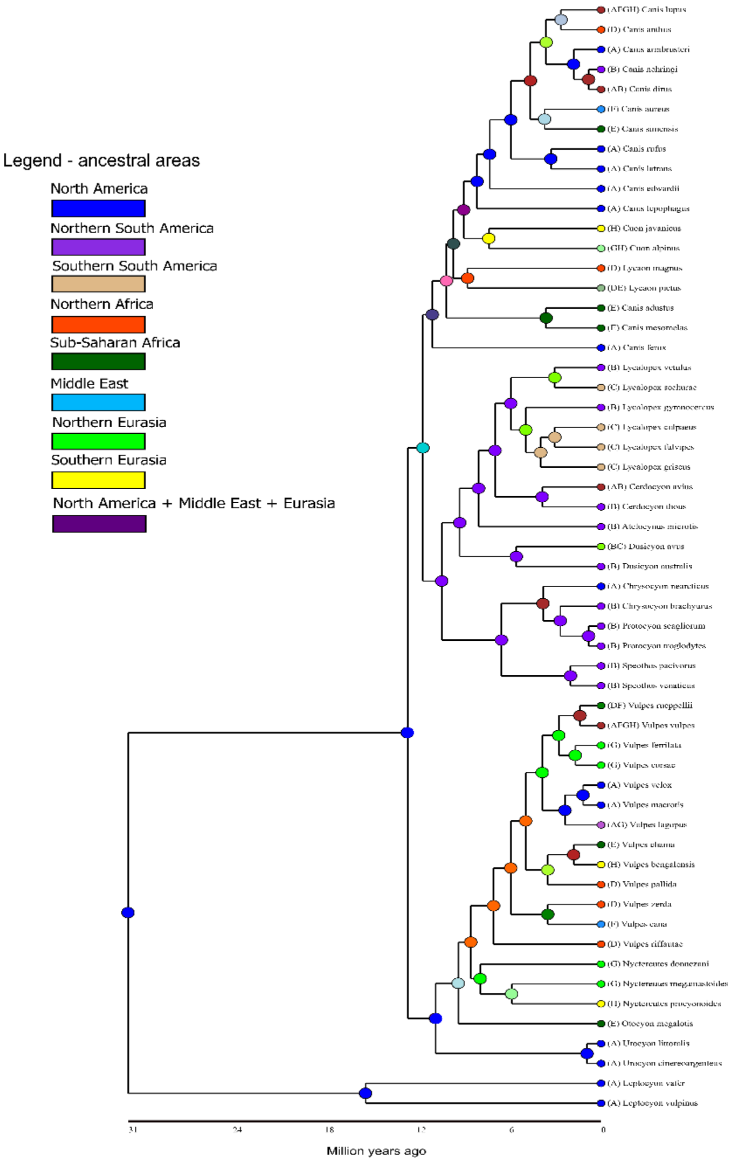

Figure S5. Phylogenetic tree and ancestral range reconstruction for the whole tree under DEC. The ancestral areas of the lineages are indicated at the nodes of the tree and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left).

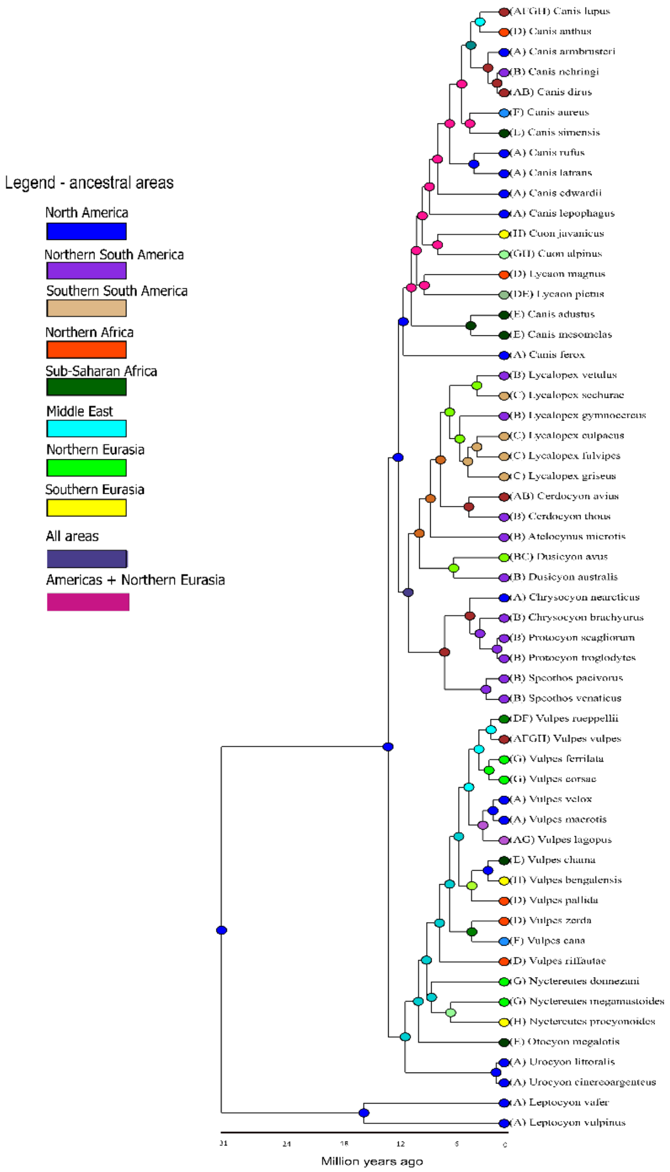

Figure S6. Phylogenetic tree and ancestral range reconstruction for the whole tree under BAYAREALIKE. The ancestral areas of the lineages are indicated at the nodes of the tree and the color-coded circles at the tips represent the current areas occupied by each lineage. The colors represent the different biogeographic regions as indicated in the legend (left).

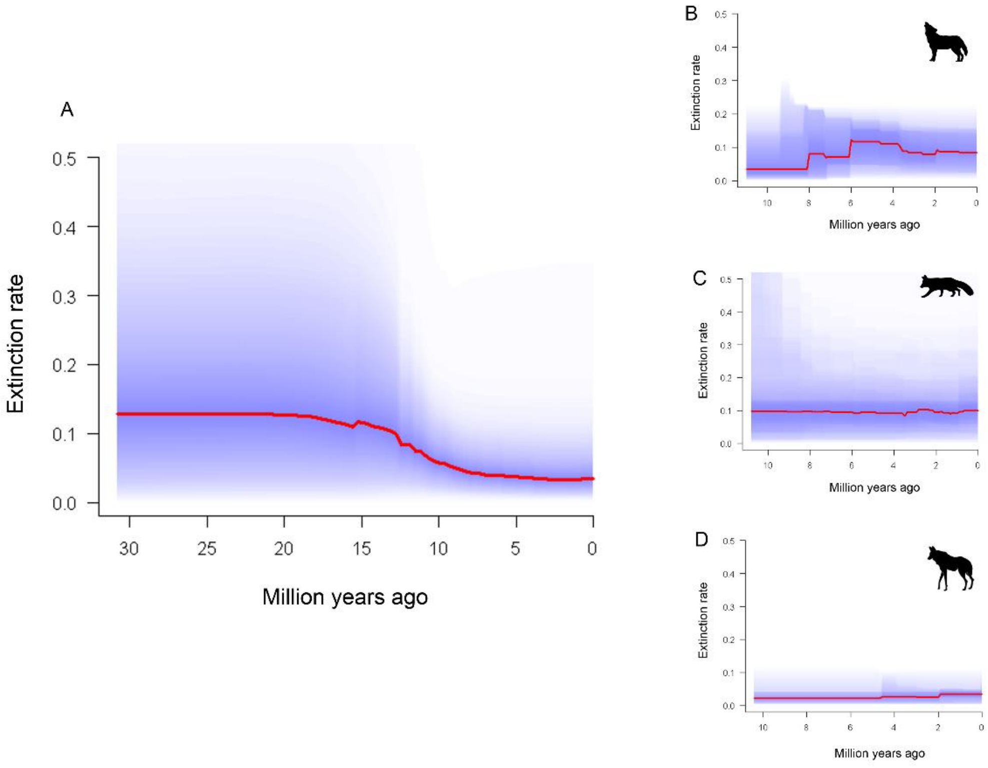

Figure S7. Extinction rates for the whole tree (A) and for the three major clades of Caninae: wolves (B), foxes (C), and South American canids (D).

Table list

Table S1. List of the 56 species of Canidae included in our study with the distribution areas that they belong based on our eight biogeographical regions (Fig. 1 in the main text). The original descriptor is also specified. Species marked with (*) are the 19 extinct canids include in the tree of Porto et al. (2019).

Species	**Biogeographic area**	**Descriptor**
Canis lupus	ACE	Linnaeus, 1758
Canis anthus	D	Cuvier, 1820
Canis aureus	C	Linnaeus, 1758
Canis simensis	D	Rüppell, 1840
Canis rufus	A	Audubon and Bachman, 1851
Canis latrans	A	Say, 1823
Cuon alpinus	E	Pallas, 1811
Lycaon pictus	D	Temminck, 1820
Canis adustus	D	Sundevall, 1847
Canis mesomelas	D	Schreber, 1775
Lycalopex vetulus	B	Lund, 1842
Lycalopex sechurae	B	Thomas, 1900
Lycalopex gymnocercus	B	Fischer, 1814
Lycalopex culpaeus	B	Molina, 1782

Lycalopex fulvipes	B	Martin, 1837
Lycalopex griseus	B	Gray, 1837
Cerdocyon thous	B	Linnaeus, 1766
Atelocynus microtis	B	Sclater, 1883
Dusicyon australis †	B	Kerr, 1792
Chrysocyon brachyurus	B	Illiger, 1815
Speothos venaticus	B	Lund, 1842
Vulpes rueppellii	DC	Schinz, 1825
Vulpes vulpes	ACE	Linnaeus, 1758
Vulpes ferrilata	E	Hodgson, 1842
Vulpes corsac	E	Linnaeus, 1768
Vulpes velox	A	Say, 1823
Vulpes macrotis	A	Merriam, 1888
Vulpes lagopus	AE	Linnaeus, 1758
Vulpes chama	D	Smith, 1833
Vulpes bengalensis	E	Shaw, 1800
Vulpes pallida	D	Cretzschmar, 1826
Vulpes zerda	D	Zimmermann, 1780
Vulpes cana	C	Blanford, 1877
Nyctereutes procyonoides	E	Gray, 1834
Otocyon megalotis	D	Desmarest, 1822
Urocyon littoralis	A	Baird, 1857
Urocyon cinereoargenteus	A	Schreber, 1775
**Canis dirus* †	AB	Leidy, 1858
**Canis armbrusteri* †	A	Gidley, 1913
**Leptocyon vafer* †	A	Leidy, 1858
**Leptocyon vulpinus* †	A	Matthew, 1907
**Cuon javanicus* †	E	Desmarest, 1820
**Canis ferox* †	A	Miller and Carranza-Castaneda, 1998
**Canis edwardii* †	A	Gazin, 1942
**Lycaon magnus* †	D	Ewer and Singer, 1956
**Canis lepophagus* †	A	Johnston, 1938
**Vulpes riffautae* †	D	de Bonis et al., 2007
**Cerdocyon avius* †	AB	Torres and Ferrusquia, 1981
**Chrysocyon nearcticus* †	A	Tedford et al., 2009
**Dusicyon avus* †	B	Burmeister, 1866
**Canis nehringi* †	B	Ameghino, 1902
**Protocyon troglodytes* †	B	Lund, 1838
**Protocyon scagliorum* †	B	Giebel, 1855
**Nyctereutes donnezani* †	E	Depéret, 1890
**Nyctereutes megamastoides* †	E	Pomel, 1842
**Speothos pacivorus* †	B	Lund, 1839

CHAPTER 2

Competition and environmental gradients structure Canidae assemblages across the planet

Lucas M. V. Porto, Rampal S. Etienne and Renan Maestri

Abstract

The phylogenetic information of assemblages carries the signature of ecological and evolutionary processes that assembled these communities. Closely related species, under similar environmental conditions, are likely to present similar traits due to environmental filtering. However, if species are too similar, it is unlikely that they will co-occur because of competitive exclusion. Here, we investigated how the phylogenetic structure of Canidae is affected across the globe by the environment and competition. We first identified phylogenetically clustered and overdispersed Canidae assemblages over the planet. Then, we apply Structural Equation Models in these communities in order to identify the effect that temperature, vegetation cover, human impact, and body size dissimilarity have on the global distribution of canids. South America and Asia present a high concentration of clustered communities, whereas Central America, Europe, and North America show phylogenetically overdispersed assemblages. Vegetation cover and human impact are the most important variables to explain the patterns of phylogenetic structure in overdispersed and clustered communities, respectively, followed by temperature and body size dissimilarity. Interestingly we found that more body size dissimilarity is associated with more clustering in clustered communities, but with more overdispersion in overdispersed communities. Canidae patterns of cluster and overdispersion suggest habitat filtering as the main force acting on Canidae assemblages. We conjecture that competition may still have played an important role, because character displacement seems to have driven species to diverge in their body sizes.

Keywords: Clustering, community assembly, habitat filtering, NRI, overdispersion, phylogenetics.

Introduction

The assembly of an ecological community is influenced by several biotic and abiotic factors (Webb, 2000; Webb et al., 2002; Westoby, 2006), including competition and habitat filtering. On the one hand, the competitive exclusion principle predicts that ecologically similar species cannot coexist if resources are limiting, and under phylogenetic trait conservatism, this implies that communities will be phylogenetically overdispersed (Darwin, 1859; Elton, 1946; Leibold, 1998; Webb et al., 2002). On the other hand, phylogenetically closely related species likely share traits that allow them to tolerate a specific environment (Jarvinen, 1982; Weiher et al., 1998; Webb et al., 2002; Di Marco & Santini, 2015), which implies phylogenetic clustering of species in an ecological community. Because this also applies to traits that are linked to competitive ability, competition may also lead to phylogenetic clustering (Mayfield & Levine, 2010; HilleRisLambers et al., 2012). If one can rule out this possibility, patterns of phylogenetic overdispersion or clustering are indicative of competition and habitat filtering respectively if the relevant traits are phylogenetically conserved. If traits are not conserved, overdispersion may be due to trait convergence of distant species, and clustering could be a result of historical processes that limited species' dispersion from their ancestral ranges (Webb, 2000; Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007).

Webb (2000) and Webb *et al.* (2002) described how communities can be tested for phylogenetic overdispersion or clustering by comparing the value of a community metric to that of a null distribution of randomized communities. One such metric is the net relatedness index (NRI), where negative values of NRI are indicative of overdispersion, while positive values indicate clustering (Webb, 2000; Webb *et al.*, 2002). They suggested that randomized communities can be obtained by permuting the presence-absence pattern on the phylogenetic tree. Pigot & Etienne (2015) argued that such a permutation approach does not yield a proper null distribution because it ignores speciation, colonization, and extinction dynamics. They developed a method that does take these processes into account and found that a null community (i.e. without habitat filtering or competition, but with speciation, colonization and extinction dynamics) would be overdispersed relative to the randomized community resulting from permutation. While absolute values for phylogenetic dispersions are therefore difficult to interpret, relative values are still informative: one can still compare dispersion patterns between communities and ask why some communities are more overdispersed or clustered than others. Many studies have used the phylogenetic approach described by Webb (2000) and Webb *et al.* (2002) to understand how the phylogenetic information of clades is structured through space (Cavender-Bares et al., 2004; Helmus et al., 2007; Kress et al., 2009; Kraft & Ackerly, 2010; Goberna et al., 2014; Yang et al., 2014; Miazaki et al., 2015; Cadotte & Tucker, 2017; Pérez-Valera et al., 2017; Zhang et al., 2018; Kusumoto et al., 2019). The majority of these studies have shown that overdispersion dominates at small scales, while clustering explains the structure of communities better at large scales. These findings demonstrate that the interpretation of the mechanisms acting in a community is scale-dependent (Webb et al., 2008). In this light, it is interesting to note that a large number of studies on phylogenetic structuring of communities are at small scales (see Cardillo, Gittleman, & Purvis, 2008).

Another difficulty in studies on the phylogenetic structure of communities relates to how abiotic and biotic factors are treated as independent forces acting on a community. Although habitat filtering and competition are contrasted in their effect on community structure, they occur together in natural communities (Ackerly, 2003; Cadotte & Tucker, 2017). Over the last decade, several studies have attempted to understand how much each mechanism influences communities (Kraft & Ackerly, 2010; Goberna et al., 2014; Cadotte & Tucker, 2017; Pérez-Valera et al., 2017; Zhang et al., 2018; Kusumoto et al., 2019). The results have been inconclusive. Cadotte & Tucker (2017) noted that “it is likely that most observational data reported as evidence for environmental filtering, in fact, reflect the combined effects of the environment and local competition.” To overcome these issues, one needs a detailed analysis of whether traits are conserved or not on a phylogenetic tree and of how patterns of phylogenetic dispersion vary with environmental variables.

Here, we assess patterns of phylogenetic dispersion in the family Canidae across the world. As canids are present in all continents, except in Antarctica (Wang & Tedford, 2008; Wilson & Mittermeier, 2009), and have a well-resolved phylogenetic tree (Porto *et al.*, 2019), they are an ideal group to test how the phylogenetic structure of a whole clade is structured over the world by the influence of environmental and competition forces. The phylogeny of extant canids presents 36 species distributed in three distinct clades (Porto et al., 2019) with a variety of patterns: multiple species of a single genus, multiple genera of only one species, species with continental distributions, and also geographically restricted species. We explore, using Structural Equation Models (SEM), how dispersion pattern relates to environmental variables and a measure of competition among canids (dissimilarity in body size).

Material and methods

Data compilation

Canids’ range maps were compiled from the IUCN Red List for all the 36 species (IUCN, 2019). We processed these maps using ArcGIS (ESRI, 2019) to generate a presence-absence matrix of species within defined grids cells of 300 x 300 km (hereafter, assemblages). From these grids, we extracted average values for three environmental variables (mean temperature, vegetation cover, and human footprint) (Center for International Earth Science Information Network, 2005; Fick & Hijmans, 2017; USGS, 2019). Temperature and vegetation cover are two of the most commonly used suites of variables in studies that evaluate species distribution (Porfirio et al., 2014), while human footprint was included in the models following Di Marco & Santini (2015), who found that human impacts explain the distribution of terrestrial mammals better than biological traits. Canid body size were obtained from the Handbook of the Mammals of the World (Wilson & Mittermeier, 2009) and also from the Animal Diversity Web (ADW) (Myers et al., 2018) (Table S1).

We then calculated for each grid cell the body size dissimilarity among the canids within each assemblage using the decoupled trait approach proposed by De Bello *et al.* (2017) (*dcFdist*). This approach calculates functional differences between species accounting for the shared evolutionary history. Thus, we can measure how different canids within communities are, based on their body size, while accounting for their ancestry. Body size dissimilarity was used as a measure of competition. We are assuming here that dissimilarity has resulted from past competition and has led to character displacement, as already suggested by Smith *et al.* (2004) and Lomolino (2005) for mammals. Therefore, the greater the body size dissimilarity within an assemblage, the greater was the competition in that assemblage. Analyses were performed in R 4.0-2. (R Development Core Team, 2020) using the raster package 3.3-13 (Hijmans & Etten, 2012).

Phylogenetic data analyses

We used the phylogeny presented by Porto *et al.* (2019) that includes all 36 extant canid species and one recently extinct. The phylogeny was constructed through Bayesian inference based on 23 genes and 68 osteological characters. We removed the extinct species *Dusicyon australis* from this tree because there is no environmental data available for the region where the species lived before the year of its extinction (1876). To investigate how body size is distributed over the phylogeny, we calculated its phylogenetic signal using the K-statistic (Blomberg & Garland, 2003) with the R package Phytools 0.7-47 (Revell, 2012). Values of $K < 1$ describe less phylogenetic signal than expected under a Brownian motion model of character evolution, while values of $K > 1$ describe data with greater phylogenetic signal than expected under Brownian motion.

To analyze phylogenetic dispersion patterns over the planet, we first calculated the standardized effect size of mean pairwise distances in communities (MPD) for each assemblage using the package Picante 1.8-2 (Kembel et al., 2010). Expected MPD was obtained by 1000 randomizations (999 iterations for each). We then calculated the net relatedness index (NRI) from MPD as follows:

$$NRI = -1 \times \frac{Observed\ MPD - Expected\ MPD}{SD(Expected\ MPD)}$$

Larger (positive) NRI values imply a more phylogenetically clustered assemblage while smaller (negative) NRI values indicate more phylogenetic overdispersion.

Structural equation models

To test the influence of biotic and abiotic variables on NRI patterns we used Structural Equation Models (SEM) (Mitchel, 1992; Wang et al., 2013). SEM allow testing the contribution of different variables while accounting for potential correlations between them. We did not specify *a priori* whether any of these correlations had positive or negative effects. We tested four models (Figure 1). Our predictor variables were mean temperature, vegetation cover, human footprint, and body size dissimilarity. We assumed they all affect NRI values. The models differ as follows. Model 1 assumes that the human footprint has an impact on global temperature, which in turn affects vegetation cover. Model 2 is similar to model 1, but the human footprint affects vegetation cover, and the temperature is influenced by both variables. None of these two models have the influence of environmental variables on body size, but Models 3 and 4 do. In Model 3, body size is assumed to be influenced by vegetation and temperature, because higher values of these variables indicate more resources. Vegetation influences temperature in areas with high human density. Temperature influences vegetation cover, because in general, higher temperatures are associated with tropical forests. In Model 4, human footprint has an effect on temperature and vegetation due to urbanization, and different from Model 3, there is no influence of vegetation on temperature.

Because SEM analyses on all assemblages (phylogenetically overdispersed and clustered) simultaneously could mask some effect related to the predictor variables, besides analyzing all data together, we also conducted the SEM analyses separately for assemblages with negative NRI values and assemblages with positive NRI values. We conducted these analyses through maximum-likelihood estimation using the R package lavaan 0.6-7 (Rosseel, 2012), and the models were compared using the Akaike information criterion (AIC) (Akaike, 1973). Spatial autocorrelation was taken into account during the analyses using the package semTools 0.5-3 (Jorgensen et al., 2020).

Another way to identify the mechanisms acting in communities would be applying the null model of assembly proposed by Pigot & Etienne (2015), DAMOCLES. The model considers the historical effects of speciation, colonization, and local extinction acting over time to determine the present composition of the community. However, DAMOCLES needs more species than we usually have in our communities to reliably estimate parameters.

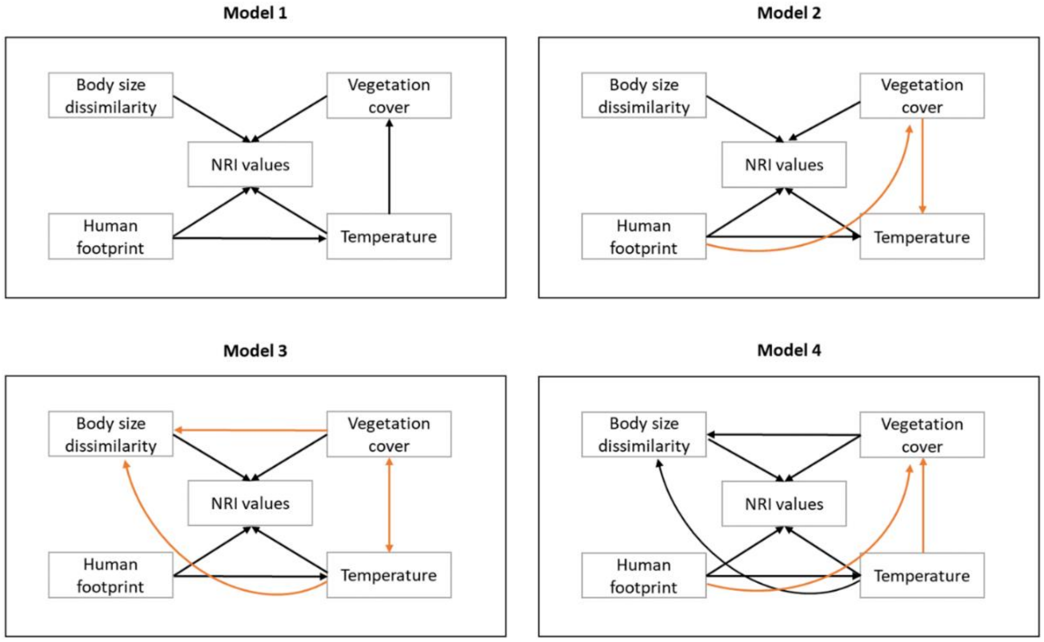

Figure 1. Schematic representations of the four Structural Equation Models tested in this study. The same models were used for negative, positive, and for all NRI values through separate analyses. Arrows indicate

the direction of the variables' effects. Orange arrows indicate different effects added to the model compared to the previous model.

Results

Phylogenetic signal in body size was high across the phylogeny of canids ($K = 1.31$, $P < 0.01$). The NRI values distributed over the world showed that there are phylogenetically overdispersed and underdispersed communities in different continents (Figure 2A). South America and Asia generally have high positive NRI values, whereas Central America, Europe, a large part of North America, and some regions in Asia show negative NRI values. Mean temperature, vegetation cover, human footprint, and body size dissimilarity also varied considerably across the world (Figures 2B, 2C, 2D, 2E).

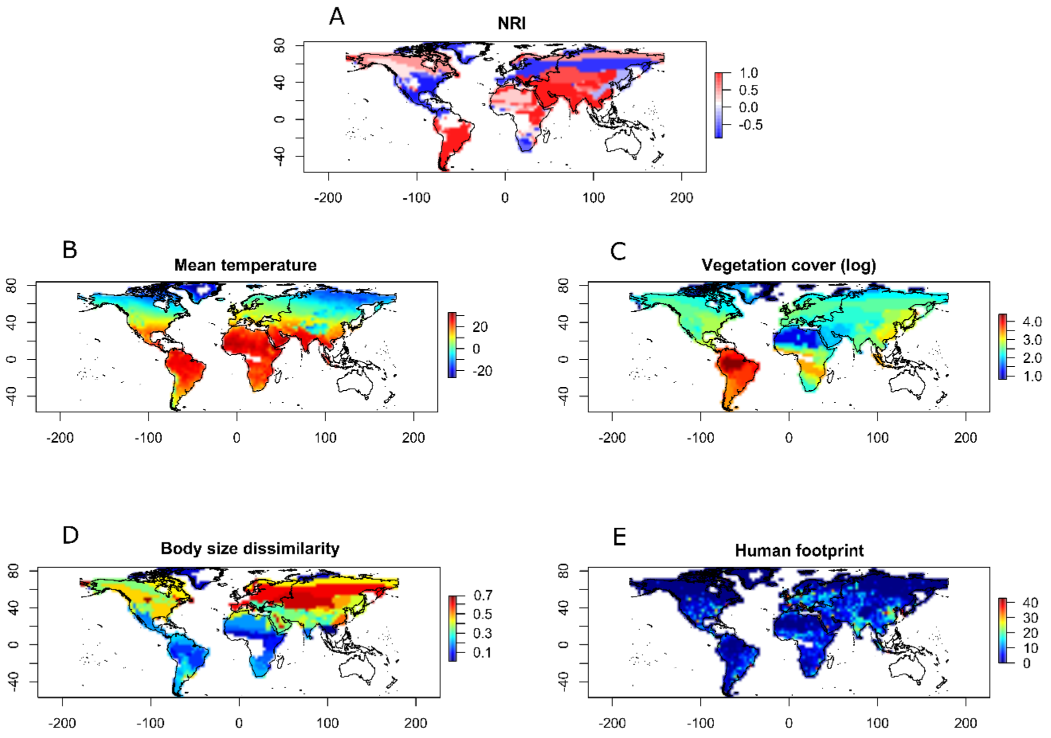

Figure 2. NRI and variables used in this study plotted over the world. (A) NRI values for each assemblage showing that phylogenetic dispersion of canids varies spatially. Assemblages colored in blue present negative NRI values indicating that species within these areas are phylogenetically more dissimilar. Assemblages colored in red represent positive NRI values, where species are phylogenetically more similar. (B) Values of the global average temperature used in this study measured in Celsius (°C). (C) Global pattern of log-transformed vegetation cover percentage. (D) Body size dissimilarity (cm) among canids for each pixel. (E) Values of the human footprint (people per square kilometer).

Structural Equation Model 4 was selected as the best model for the three NRI analyses (negative, positive, and all data together), more than three AIC units better than the second-best model in all cases, model 3 (Table 1). The weights of model 4 were 0.832, 0.866, and 0.886 for negative, positive and all data together analyses, respectively. Model 3, on the other hand, presented weights of 0.167, 0.133, 0.113. Models 1 and 2, with no influence of environmental variables on body size dissimilarity, had a very poor performance in the model comparison. In Model 4, all predictor variables influence NRI values, but also the human footprint influences vegetation and temperature, which in turn influences vegetation cover and body size dissimilarity.

For all NRI data (Figure 3A), model 4 shows that the environmental variables temperature ($P < 0.01$, effect = 0.37) and vegetation ($P < 0.01$, effect = -0.19) were the most important to explain the phylogenetic distribution of canids (Table 2). Model 4 also shows that body size dissimilarity and human footprint had very weak and non-significant effects on NRI (-0.01 and 0.002, respectively).

Table 1. Akaike information criterion ranking of the four models of Structural Equation Models tested for negative, positive, and total NRI values.

Models	df	Negative NRI			Positive NRI			Total NRI		
		AIC	Δ	W	AIC	Δ	W	AIC	Δ	W
4	13	3295.996	0	0.832	16755.383	0	0.866	27995.420	0	0.886
3	14	3299.202	3.206	0.167	16759.117	3.734	0.133	27999.539	4.119	0.113
2	10	3513.220	217.224	5.6E-53	17980.139	1224.756	9.66E-100	29029.366	1033.946	2.6E-132
1	10	3525.275	229.279	1.3E-55	17997.486	1242.103	1.6E-127	29050.563	1055.143	6.7E-140

Table 2. Results of the best-fitting Structural Equation Model (model 4) for total NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		**Estimate**	**Std Err**	**z-value**	***P***	**Effect**
NRI ~	Body size dissimilarity	-0.041	0.094	-0.436	0.663	-0.012
	Human footprint	0.000	0.002	0.061	0.951	0.002
	Temperature	0.017	0.001	12.829	< 0.01	0.374
	Vegetation cover	-0.003	0.000	-7.172	< 0.01	-0.186
Temperature ~	Human footprint	0.666	0.051	13.094	< 0.01	0.323
Vegetation cover ~	Human footprint	0.494	0.131	3.774	< 0.01	0.097
	Temperature	0.756	0.063	11.906	< 0.01	0.307
Body size dissimilarity ~	Temperature	-0.006	0.000	-16.927	< 0.01	-0.426
	Vegetation cover	0.000	0.000	1.480	0.139	0.037

** P of the model (<0.01)*

For analyses on only the communities with positive NRI values, model 4 indicated that the environmental variables are still the most important to explain the phylogenetic composition within assemblages. Human footprint ($P < 0.01$, effect = 0.34) and temperature ($P < 0.01$, effect = 0.26) had the largest effects on canid assemblages (Figure 3B, Table 3). Body size dissimilarity also presented a significant effect on NRI (the more dissimilar the community in terms of body size, the more similar they are phylogenetically), smaller than the effect of human footprint, but close to that of temperature. Furthermore, temperature had a strong influence on body size ($P < 0.01$, effect = -0.57) (Figure 4B).

Table 3. Results of the best-fitting Structural Equation Model (model 4) for positive NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		**Estimate**	**Std Err**	**z-value**	***P***	**Effect**
Positive NRI ~	Body size dissimilarity	0.446	0.069	6.479	< 0.01	0.238
	Human footprint	0.001	0.000	11.076	< 0.01	0.335
	Temperature	0.006	0.001	6.981	< 0.01	0.259
	Vegetation cover	-0.000	0.000	-1.281	0.20	-0.039
Temperature ~	Human footprint	0.047	0.004	10.610	< 0.01	0.318
Vegetation cover ~	Human footprint	0.027	0.010	2.686	< 0.01	0.086
	Temperature	0.473	0.069	6.902	< 0.01	0.222
Body size dissimilarity ~	Temperature	-0.007	0.000	-22.262	< 0.01	-0.565
	Vegetation cover	-0.001	0.000	-6.564	< 0.01	-0.167

** P of the model (<0.01)*

Table 4. Results of the best-fitting Structural Equation Model (model 4) for negative NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		**Estimate**	**Std Err**	**z-value**	***P***	**Effect**
Negative NRI ~	Body size dissimilarity	-0.203	0.038	-5.309	< 0.01	-0.226
	Human footprint	0.037	0.017	2.214	0.03	0.096
	Temperature	-0.004	0.001	-4.026	< 0.01	-0.242
	Vegetation cover	0.519	0.064	8.091	< 0.01	0.485
Temperature ~	Human footprint	11.582	0.937	12.357	< 0.01	0.453
Vegetation cover ~	Human footprint	-0.012	0.012	-1.014	0.31	-0.033
	Temperature	0.010	0.000	22.149	< 0.01	0.722
Body size dissimilarity ~	Temperature	-0.006	0.001	-6.333	< 0.01	-0.334
	Vegetation cover	0.700	0.063	11.136	< 0.01	0.588

** P of the model (<0.01)*

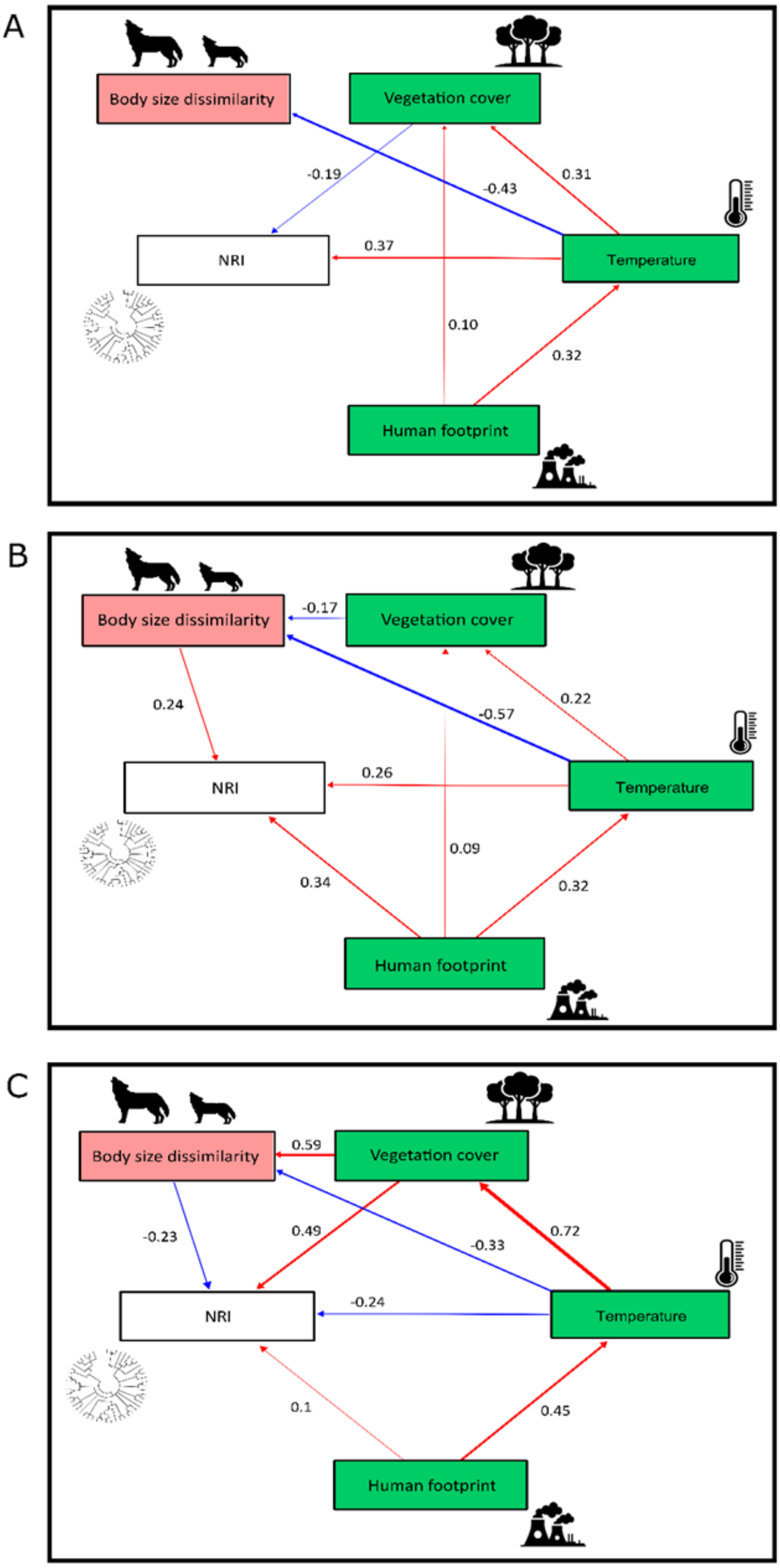

Figure 3. Best-fitting Structural Equation Model for the total NRI (A), clustered communities - positive NRI (B), and overdispersed communities - negative NRI (C) values. Positive and negative effects are indicated by red and blue arrows, respectively. Arrow thickness is scaled to illustrate the relative effect of each variable. Only significant effects (arrows) are shown (*P* < 0.05).

For analyses on only the negative NRI communities (Figure 3C), the environmental variables are still the ones with the largest influence on phylogenetic dispersion. Based on model 4, vegetation cover is the most important variable ($P < 0.01$, effect = 0.49), suggesting that as vegetation cover increases, species within these communities become phylogenetically closer. Temperature ($P < 0.01$, effect = -0.24) and body size dissimilarity ($P < 0.01$, effect = -0.23) also had a considerable negative effect on NRI (i.e., the less dissimilar the community in terms of body size, the more dissimilar they are phylogenetically). For the negative NRI analysis, correlations among the environmental variables, and the effect of the environment on body size dissimilarity were larger than in the analysis of all NRI values together (Table 4). In addition, vegetation cover presented a positive effect on body size ($P < 0.01$, effect = 0.59) (Figure 4A).

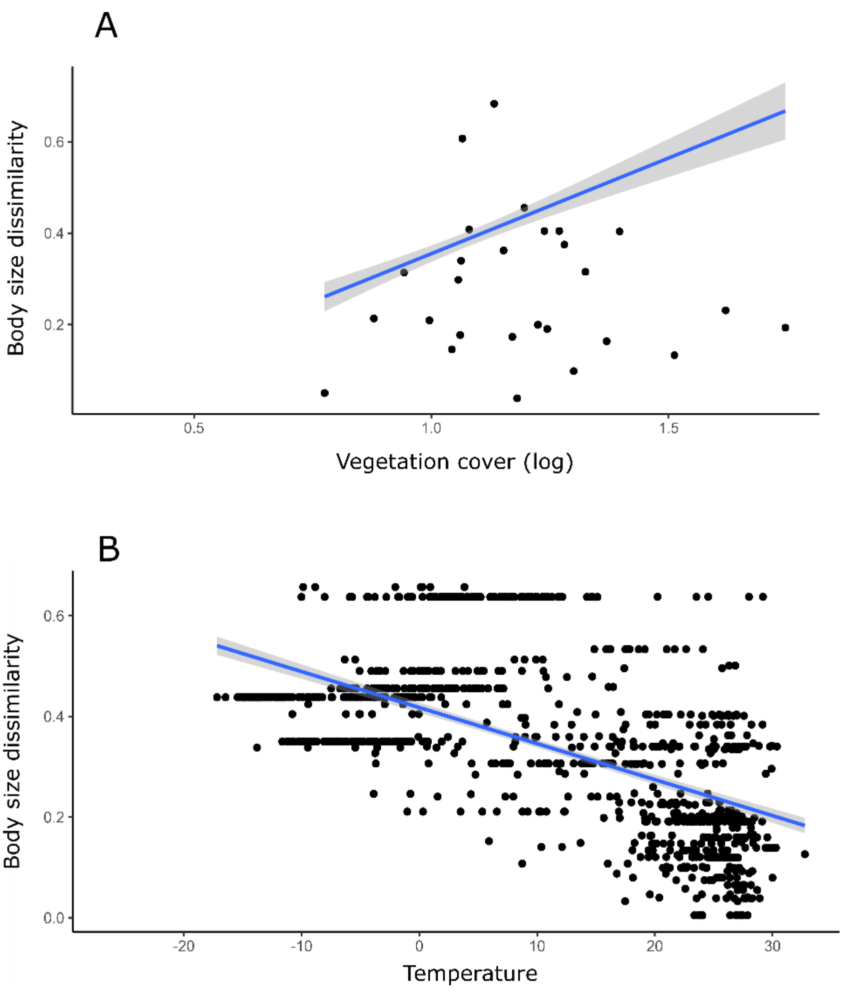

Figure 4. (A) Correlation between vegetation cover and body size dissimilarity within overdispersed communities ($R^2 = 0.12$, $P < 0.01$). (B) Correlation between temperature and body size dissimilarity within clustered Canidae assemblages ($R^2 = 0.37$, $P < 0.01$).

Discussion

The composition of canid communities across the world shows both negative and positive values of NRI and is influenced by distinct factors in different continents. However, it seems that the environment plays a greater role than traits related to biotic factors to explain the phylogenetic composition of Canidae assemblages. This pattern was maintained when NRI was analyzed as a whole and separately, but the effects of variables were much stronger in the separate analyses (Figures 3A, 3B and 3C) which supports our idea that it is necessary to separate the phylogenetic information to have a better understanding on how these variables structure Canidae assemblages through space.

Body size dissimilarity among canids was not the main factor structuring assemblages with negative NRI values. In these communities, the vegetation cover has the greatest effect, where canids become less closely related as vegetation cover increases. However, the best model suggests that overdispersed communities are maintained due to the combined effect of temperature and body size dissimilarity (Figure 3C). Nevertheless, our model shows that the environmental variables have a larger effect on overdispersed communities than body size dissimilarity. We can observe on the map how overdispersed assemblages vary across the environmental gradient (Figures 2A and 2C), showing that these communities in the Northern hemisphere are associated with low vegetation cover.

Interestingly, the relationship between body size dissimilarity and NRI has a different direction in positive and negative NRI communities. In positive NRI communities more phylogenetic clustering is associated with more body size dissimilarity, while in negative NRI communities more phylogenetic overdispersion is associated with more body size dissimilarity. Note that body size dissimilarity has been corrected for phylogenetic signal, so this larger similarity in body size is more than can be expected from shared evolutionary history. Hence, this implies that species are much more dissimilar in their body sizes at very negative NRI values (highly overdispersed communities) and very positive NRI values (highly clustered communities) than at small positive and negative NRI values (communities with random phylogenetic structure). In clustered communities this may be explained by character displacement after speciation: competition may have driven phylogenetically related species to diverge in their body sizes. In overdispersed communities this may be explained by character displacement after secondary contact. These explanations assume that clustered communities undergo mostly sympatric speciation whereas overdispersed communities assemble through immigration after allopatric speciation. This seems to be in line with the results from Porto *et al.* (2021), on the origin and dispersal of the Canidae lineages. They show that highly clustered communities, such as South America, the Middle East and South Asia, present several lineages that originated within these regions. South America, for example, is inhabited only by species of a single clade — endemic to this continent. Furthermore, highly overdispersed regions, such as North America, Europe and South Africa, are inhabited by lineages of distinct clades, where many have their origins outside these regions.

The overdispersed pattern presented by assemblages of canids living in North America, Europe, and the northern part of Asia is probably due to a large number of distinct species of the genera *Vulpes*, *Canis*, and *Urocyon* that coexist within these areas and are very phylogenetically distant, being separated around 12 million years ago (Ma) (Porto et al., 2019). Species from these three genera have very distinct diet, habitat type, and social behavior (Wang & Tedford, 2008; Wilson & Mittermeier, 2009).

For phylogenetically clustered assemblages, the combined effect that human footprint and temperature have on NRI values suggests that habitat filtering plays an important role within these communities. The effect of human impact suggests that as human population density increases, canids become phylogenetically closer (Figure 3B). This is in line with Di Marco & Santini (2015) who demonstrated that human impacts predict the geographical distribution of terrestrial mammals better than the biological traits of species. While past events shaped the current distribution of species (Davies et al., 2007), current environmental forces influence the capacity for species to survive in different regions (Pearson & Dawson, 2003). Endemic canids of South America, like those from the genus *Lycalopex*, and also species from the Northern hemisphere, such as *Vulpes lagopus* are constantly losing habitat and being killed by humans (Hoffmann et al., 2011). By contrast, even though human activity in North America is large, this region still has a highly overdispersed pattern. This might be explained by the large number of species of the *Canis* genus that live within this region. Several species in this clade, such as the coyote (*Canis latrans*) (Poessel et al., 2013), have shown high plasticity to co-exist with humans, being able to live and obtain resources near to urban areas.

Temperature also presented a positive effect in phylogenetically underdispersed assemblages, suggesting that warm regions on the planet, such as deserts and tropical forests, can impose a much greater environmental filter on canids than cold regions. Our finding is contrary to what was proposed by Dobzhansky (1950), who argued that biotic factors are more limiting in the tropics, while abiotic conditions are more important at higher latitudes. However, our finding may not be so surprising given that the first ancestors of the living canids were probably packing hunters with medium body sizes, around 70 cm (Wang & Tedford, 2008; Porto et al., 2019). Deserts and tropical forests may act as a strong filter to canids with such a lifestyle because food is scarce in deserts and pack hunting is difficult inside dense forests. An alternative explanation may be differential diversification rates. Pigot & Etienne (2015) showed that allopatric speciation creates overdispersed patterns, suggesting that for canids speciation might be higher at higher latitudes. Extinction must then also be higher at high latitudes to explain the lower diversity at these communities (Weir & Schluter, 2007).

We emphasize the better performance that models with environmental variables influencing body size dissimilarity had compared to the ones that did not. This suggests environmental control of body size dissimilarity. For overdispersed assemblages, places with more vegetation cover probably influenced competition in a way that biotic interactions may have led to character displacement. In underdispersed communities, temperature strongly affects body size dissimilarity, showing that as temperature increases, species become similar in their sizes (less dissimilarity). As body size is well known to be a good proxy for species' ecological niches (De Roos et al., 2003; Nakazawa et al., 2010), this is strong evidence for habitat filtering in warmer places, which can generate ecologically similar Canidae assemblages.

Even though canids are not dispersal limited, because they can travel long distances (Wang & Tedford, 2008; Wilson & Mittermeier, 2009), they may still tend to be found in higher numbers near to their center of diversification than far from it. This can also help understand the phylogenetic structure of the Middle East + Northern Africa, and South America, which, based on the fossil records and biogeographical models, had major diversification events of foxes and South American canids, respectively (Wang & Tedford, 2008; Porto et al., 2021). Ecological speciation within these regions might have generated species' phylogenetic clustering. In these areas the number of endemic species is high, and speciation tends to generate similar trait values (Gillespie, 2004).

The majority of studies of the phylogenetic structure within communities concerns plants or focus on small geographic scales. Nevertheless, some studies with vertebrates at large spatial scales have demonstrated contrasting patterns of phylogenetic composition. Cooper, Rodríguez, & Purvis, (2008) found a tendency of overdispersion in assemblages of New world monkeys, Australasian possums, and North American ground squirrels. Yan *et al.* (2016), however, found phylogenetic clustering for Mammalia, Aves, Reptilia, and Amphibia from China. And Cardillo (2011) demonstrated an unstructured phylogenetic pattern on African carnivore's assemblages. Here we presented a case where both patterns are important to understand community composition across the planet, depending on the region studied.

Larger geographical scales are expected to generate more phylogenetic clustering than overdispersion because the rate of speciation increases with more space available (Losos & Schluter, 2000) due to higher habitat heterogeneity (Kneitel & Chase, 2004), and thus sister species are more likely to co-occur at larger scales. Even though we found many areas with phylogenetic clustering (Figure 2A), there were also many areas with overdispersed patterns, indicating that the scale we used (300 km × 300 km) may still be too small for clustering to kick in. Therefore, we anticipate that using an even larger scale, e.g. the biome scale, will reveal clustering. Studying community structure at that scale, however, is no longer very informative, exactly because of the large expected biogeographic contribution to phylogenetic dispersion.

The results presented here agree with the ideas proposed by Mayfield & Levine (2010) about how competition can drive clustered patterns in specific situations, making it complicated to trust relatedness indices within communities to separate the real role of biotic and abiotic factors. Here we managed to show the distinct effects of each variable acting on assemblages, partitioning the phylogenetic structure of communities and applying structural equation models to them. Without this methodology, it could have led us to wrong conclusions as we would have only considered the effect that different variables have on dispersion patterns in communities, but not considering the effects they have on each other.

The mechanisms that influence the assembly of a community can act in complex ways (Ricklefs, 1987, 2015). In this study we used both a phylogenetic approach and an approach based on current environmental variables and traits. We demonstrated that canid community composition over the world presents significant patterns of clustering and overdispersion. These patterns follow mainly the environmental gradient, suggesting habitat filtering as the main force acting on Canidae assemblages, but competition may also have played a key role in shaping the communities through character displacement.

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Supplementary material

Appendices and R scripts will be available at the online public repository of this thesis.

Table S1. Body size of the 36 species of canids used in this study.

Species	Body size (cm)
Atelocynus microtis	86
Canis adustus	85.5
Canis aureus	78
Canis anthus	78
Canis latrans	84
Canis lupus	108.5
Canis mesomelas	88
Canis rufus	112
Canis simensis	94.4
Cerdocyon thous	67.25
Chrysocyon brachyurus	105
Cuon alpinus	111.75
Lycaon pictus	115.75
Nyctereutes procyonoides	59.75
Otocyon megalotis	53.35
Lycalopex culpaeus	69
Lycalopex fulvipes	52.15
Lycalopex griseus	58.05
Lycalopex gymnocercus	65.85
Lycalopex sechurae	64
Lycalopex vetulus	58.5
Speothos venaticus	66.25
Urocyon cinereoargenteus	56.9
Urocyon littoralis	53
Vulpes bengalensis	47
Vulpes cana	57.35
Vulpes chama	57.35
Vulpes corsac	47.5
Vulpes ferrilata	56.25
Vulpes macrotis	50.25
Vulpes pallida	46.5

Vulpes rueppellii	47.5
Vulpes velox	52
Vulpes vulpes	63.5
Vulpes zerda	36.4
Vulpes lagopus	60

CHAPTER 3

The effect of climate change on the distribution of Canidae

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Abstract

Land use by humans and climate change have been seriously affecting the distribution of species resulting in a quarter of all known mammals currently threatened with extinction. Here, we modeled the present and future potential distributions of all 36 extant Canidae species to evaluate their response to future climate scenarios. In addition, we tested if canids were likely to experience evolutionary rescue, which could allow some species to adapt to climate change. Our results suggest that global warming will cause most species to lose or maintain their ranges, while a few will have the potential to benefit from future conditions and considerably expand their geographic distributions. Some canids have the potential to experience evolutionary rescue, but *Atelocynus microtis* and *Chrysocyon brachyurus* are two concerning cases that do not show this capacity to adapt given the current pace of climate change. We also reveal that most Canidae hotspot regions are outside protected areas, which may be useful for the identification of key areas for conservation.

Keywords: adaptation, ecological niche models, environmental change, geographical ranges, Haldanes.

Introduction

The pace of climate change induced by humans is much faster than predicted previously (Pimm et al., 2014). Ceballos et al. (2015) showed that the rate of vertebrate species loss over the last century is up to 100 times higher than the background extinction rate. This anthropogenic pressure causes habitat loss and increased competition from invasive organisms (Butchart et al., 2010), which leads to species extinction (Ceballos et al., 2015; May & Lawton, 1995), and thus has serious impacts on global biodiversity. Over the last decades, several studies have shown how human impacts affect the structure of ecosystems and how these changes can backfire and affect humans negatively with floods, fires, air pollution, heat waves, and vector-borne diseases (Bellard et al., 2012; Cardinale et al., 2012; Goberna et al., 2014; Kortsch et al., 2015; Nadeau et al., 2017; Parmesan & Yohe, 2003; Pecl et al., 2017; Woodward et al., 2010). Some species are more susceptible to extinction than others due to their traits, including: reproductive rate, habitat specialization, body size, and geographic range (Davidson et al., 2009; Fritz & Purvis, 2010). Therefore, understanding how species are going to respond in future scenarios of climate change is necessary to predict the impact of the loss of certain species on ecosystems, and it will be useful for conservation of biodiversity.

Until recently, evolution was thought to play no substantial role in a population's resilience when facing a rapid environmental change (Ferrière et al., 2004). The common idea was that a population in decline, exposed to a deteriorating environment, would become extinct. However, Gonzalez et al. (2012) and Bell (2013) coined and matured the idea of evolutionary rescue (ER). In an ER scenario, adaptive processes could be triggered in some resistant individuals of the population under environmental stress, allowing them to rapidly proliferate and counter the rate of decline of the population, thereby changing our perspective on communities with populations that are threatened with extinction (van Eldijk et al., 2020).

The most used tools to evaluate how species are dealing with climate change are ecological niche models (ENMs) (Araújo & New, 2007; Ehrlén & Morris, 2015; Elith et al., 2010; Guisan & Thuiller, 2005). ENMs use mathematical modelling of a species' relationship with environmental variables, and predict habitat suitability for that species based on known occurrence data (Araújo et al., 2011; Guisan & Thuiller, 2005). ENMs based on climate data have proven extremely useful in assessing the effectiveness of the distribution of protected areas (Catullo et al., 2008), assessing species vulnerability to local land-use changes (Santos et al., 2013), predicting distributions of rare species (Marino et al., 2011; Rheingantz et al., 2014), and predicting possible responses to climate change by species and ecosystems (Moor et al., 2015; Sobral-Souza et al., 2018).

However, the use of ENMs with climatic variables alone has been debated in several studies (Diniz-Filho et al., 2019; Elith et al., 2010; Synes & Osborne, 2011), mainly because ENMs do not incorporate intrinsic characteristics of the populations, relying on the idea that all the mechanisms that affect species` distributions are captured by the environmental data (Diniz-Filho et al., 2019). However, niche models that use traits (morphological and physiological) or genetic data are complex and do not work well when the niches of several species are modeled simultaneously (Norberg et al., 2012).

The attempt to predict responses of species to climate change is further limited by uncertainties surrounding climatic predictions - with slight differences existing between different general circulation models (GCM) - and by uncertainties about the possibilities of measuring evolutionary rescue.

Recently, Diniz-Filho et al. (2019) applied a macroecological framework to estimate responses to evolutionary change and the likelihood of evolutionary rescue; they proposed the *H* value (Haldanes) to estimate the evolutionary change required by species to maintain their populations in future environmental scenarios, giving a biological and evolutionary meaning to temperature variations that species will experience. According to the framework proposed by Diniz-Filho et al. (2019), the greater the variation in temperature between present and future, the greater the *H* value, and consequently, the more difficult it is for the species to experience an ER scenario. Likewise, the fewer generations the species can have until the future, the higher the *H*. In short, the smaller the temperature difference and the larger the number of generations, the more likely it is for evolutionary rescue to happen, and for a species to persist in the face of climate change.

WWF (2018) showed an average 60% decrease in vertebrate populations, and a quarter of all known mammals are currently threatened with extinction (IUCN, 2020). Within this group, the canids (family Canidae) is an excellent group to test the impacts of climate changes on future distributions, as they are distributed in all continents, except Antarctica (Sillero-Zubiri et al., 2004; Wang & Tedford, 2008), and because as medium-large mammals they are more prone to extinction than smaller species (Rija et al., 2020). Like other species, canids are affected by the consequences of urbanization and climate change: coyotes (*Canis latrans*) and red foxes (*Vulpes Vulpes*) have been observed in urban areas in North-America (Lombardi et al., 2017; Mueller et al., 2018; Poessel et al., 2013, 2017), while the red fox has invaded a habitat in northern Europe that was previously occupied only by the arctic fox (*Vulpes lagopus*) (WWF, 2018). Understanding how canids are affected by changes in the landscape, and being able to predict their future distributions is essential to outline conservation strategies for different species.

Here we use climate-based ENMs to: 1) model the distribution of all canids under present climate conditions, 2) predict possible changes in Canidae distribution under climate change in the next 54 years (2075), and identify species at risk of losing some or all of their current range, but also assess if some species could enlarge it; and 3) identify which species are most likely to adapt to changing climatic conditions and therefore avoid the negative effects of temperature change.

Materials and methods

Occurrence and environmental data

Species occurrence data for all canids were taken from VertNet (Constable et al., 2010) and the Global Biodiversity Information Facility (GBIF, 2020) online databases. The number of occurrence points is shown in Tables S1, and cover all the known distribution of the 36 species used here (which correspond to 100% of the living Canidae species). We spatially filtered the data using SDMToolbox 2.0 (Brown et al., 2017), in ArcGis 10.3.1 (Environmental Systems Resource Institute, 2019), to remove duplicate occurrence points. As there are different classifications for the Canidae family in relation to the number of species (Bardeleben et al., 2005; Perini et al., 2010; Zrzavy & Ricánková, 2004), here we use the most recent canid phylogeny proposed by Porto et al. (2019) to define which species of Canidae (*n* = 36 - Table S1) would be considered here to model their potential distributions.

For environmental variables, we downloaded a digital elevation model (DEM) (IUCN, 2019) and the standard 19 Worldclim bioclimatic variables for the present and future (2075) (Hijmans et al., 2005). In addition, we used the distance to freshwater as a variable, which we measured using the Natural Earth River and lake maps, and the Euclidean distance tool in ArcGis. To clarify the environmental data we masked the variables and imported them into R 4.0-2 (R Development Core Team, 2020) and tested for multicollinearity using variance inflation factor (VIF) tests with the package regclass 1.6 (Petrie, 2020) and pairwise plots. Highly correlated variables (VIF score > 10 or Pearson correlation > 0.7 respectively) were eliminated one at a time, starting with the variable(s) deemed to possess the least ecological relevance based on the VIF tests.

Ecological niche modelling

ENMs for the present were performed using the R package SDM 1.0-89 (Naimi & Araújo, 2016). To model species' niches for the present, we generated 10.000 random background points within a mask equivalent to the species' known IUCN ranges, buffered to 220 km (or approximately two decimal degrees), producing a presence-absence matrix of species within defined grids cells (pixels). We built ensembles (objects with a weighted averaging over all predictions from several fitted models) of four different models: Maxent, Support Vector Machine (SVM), Random Forest (RF), and Boosted Regression Tree (BRT). For all models, we used 90% as training data and 10% were retained as test points. Models were only accepted if they had acceptable True Skill Statistic (TSS - calculated as the sum of specificity + sensitivity – 1) and Area Under the Curve (AUC) values (0.7 being the minimum accepted AUC, 0.6 the minimum TSS (Allouche et al., 2006)). We used both TSS and AUC to evaluate the models because they assign different weights depending on the sample size of the data used (Guisan et al., 2017), and hence we believe our results to be more robust if both criteria are met.

In order to verify whether the ENMs and IUCN polygons agree, we compared the current distribution maps of all species of canids available at IUCN against the maps created here through ENMs. IUCN maps were generated by minimum convex polygons, which represent the realized niche of the species, while the ENMs here bring a more detailed notion of their fundamental niche.

We modelled the future distribution of species based on the most pessimistic climate scenario for the year 2075 (RCP 8.5 - Representative Concentration Pathway) from IPCC (2007). We chose this scenario because it seems to have become the most realistic one over the last years, and can even be under-estimating future concentrations of atmospheric carbon (Christensen et al. (2018). RCP 8.5 assumes high global CO_2 concentration, a high rate of human population growth, and an increased use of energy and land. We used an ensemble of three General Circulation Models (GCMs): Access1.0 (exhibits a high skill score with regard to historical climate), HadGEM2 (has a good representation of extreme El Niño events), and MIROC5 (also has a good representation of extreme El Niño events, and represents all RCPs scenarios well). Maps of suitability (present/future) are shown on a continuous scale to better visualize the potential distribution of species.

Evolutionary rescue calculations

H values were calculated for each of the 36 canids to predict whether they can adapt to climate change and prevent the loss of their habitat. We assumed that temperature is a representation of the species' niche (tolerance) most closely reflecting climate change. For each species, changes in maximum temperature of the warmest month (Bio05) across the entire range were estimated, and the temperature change in each cell was calculated as the average of the future temperature (in the warmest month) minus the average of the present temperature (in the warmest month). Following Diniz-Filho et al. (2019), H values were calculated using:

$$H = \frac{\frac{Y_0 - Y_t}{Y_{sd}}}{g}$$

where Y_0 is the mean temperature at the present, Y_t is the mean temperature at time t in the future, Y_{sd} is the standard deviation of the present temperature tolerance (assuming a constant variance between generations), and g is the number of generations between present and future. The generation lengths for all canid species was compiled from the Animal Diversity Web (ADW - Myers et al., 2018) and PanTHERIA (Jones et al., 2009) (Table S1). The higher the value of H, the greater the rate of evolutionary change needed for a species to experience ER, and consequently, the more difficult it is to maintain its population facing a climatic change scenario.

For the evolutionary rescue analyses, we used the threshold maps (binary) for each species, produced with the suitability maps because they show presence/absence values based on the specificity and sensitivity of the model (Liu et al., 2015).

Results

Ecological niche modelling

All ENMs produced acceptable accuracy values for TSS and AUC. After testing highly correlated variables, only five were not excluded and were used to model canid niches, they are: distance to freshwater (DIST), the maximum temperature in the warmest month (Bio05), precipitation in the driest month (Bio14), elevation (DEM).

To check the reliability of the ENMs we compared their predictions on the present distributions with the actual current distributions according to IUCN polygons (realized niche) (Appendix - Figure S1 – S36). With the exception of a single species, *Canis lupus*, the distribution polygons fall within the areas that the ENMs demonstrate to be suitable for the species to occupy (fundamental niche). Species richness maps for the present generated by ENMs (Figure 1) and by polygons (Figure S37) show very similar patterns of species overlap, generally maintaining the same hotspot locations in the Middle East + Northeast Africa region and western part of the USA. However, there is an exception: the richness map based on polygons shows the presence of Canis lupus in the Middle East region towards India, but this is not predicted by the ENMs (see Discussion). Because of the high similarity our ENM predictions seem highly reliable, and we therefore compare our future ENM predictions with ENM predictions for the present, as they are better comparable (both describe the fundamental niche).

Our models indicated that 27 species were predicted to experience range contractions under climate change, while 9 were predicted to expand in range overall (Table S2). In all three Canidae clades (wolves, foxes, and South-American canids), we find that most species will contract their ranges, and a few will expand their ranges (Figure S38A-S38C). We discuss them now in more detail.

The South-American canids (Figure S38C), *Atelocynus microtis*, *Lycalopex fulvipes*, and *Lycalopex sechurae* are predicted to see future climate suitability fall below their modelled threshold across their entire ranges (Table S2), losing a large part of their geographical distributions (Appendix - Figures S39, S40, and S41). In contrast, *Cerdocyon thous* is the only South-American canid that was predicted to have a considerable expansion in its geographical area under future conditions; moreover, the ENM predicts that *C. thous* will occupy areas within the Amazon Forest not inhabited before (Table S2, and also see Appendix - Figure S38C and Figure S42).

In the clade of wolves, *Canis latrans* and *Canis rufus* are probably going to lose a large part of their ranges in North America, while *Canis anthus* and *Canis lupus* are expected to increase their distributions, mainly in desert areas such as the Middle East, for both species, and the deserts in the USA for *C. lupus* (Table S2, and also see Appendix - Figure S38A, Figure S43, and Figure S44).

Some of the fox species are predicted to suffer severe losses in their ranges (Table S2 and Figure S38B). Among them, *Urocyon littoralis* stands out: even though it is considered an endangered species at the moment, the ENMs predicted that *U. littoralis* will lose 28.6% of its (small) current distribution (Table S2). *Vulpes chama*, *Vulpes bengalensis,* and *Vulpes velox* also were predicted to have a considerable decrease in their geographical ranges. By contrast, *Vulpes corsac*, *Vulpes vulpes*, *Otocyon megalotis*, and *Urocyon cinereoargenteus* will probably experience range expansions under future climatic conditions. In fact, the ENM predicted that *V. vulpes* will increase 5.7% of its distribution, inhabiting new areas such as the Middle East, Northern Canada, and Greenland (Appendix - Figure S45).

The richness map of the present (Figure 1) shows that the overlap of different species is very low around the planet. The map also points to two hotspot areas for canid diversity, one in the western part of the USA (Figure 1A), and another in the Middle East + Northeast Africa region (Figure 1B). The richness map for the future (Figure 2) shows that patterns of richness are predicted to change under future climatic conditions, where the main changes will be in the hotspot areas. The USA hotspot is predicted to reduce its area considerably due to the low species overlap in the future. By contrast, The Middle East + Northeast Africa hotspot is predicted to increase in size.

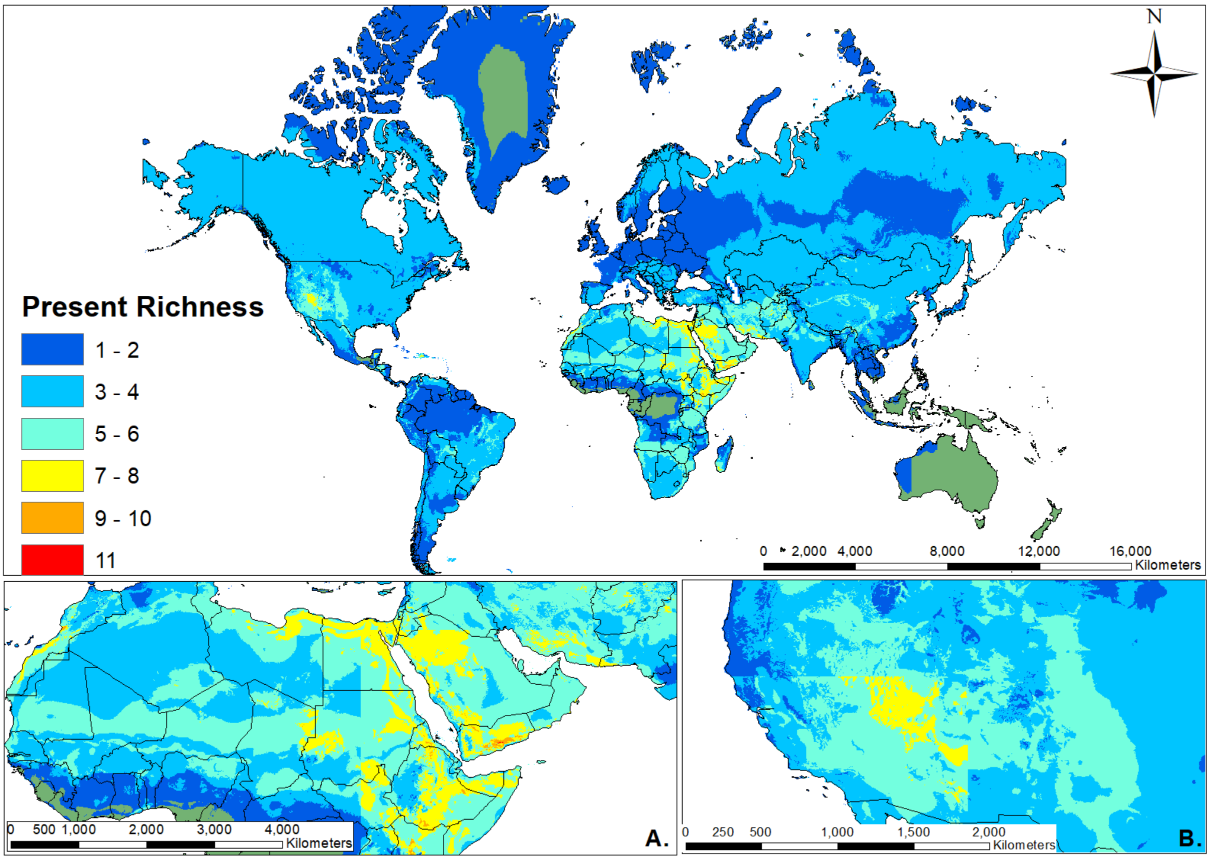

Figure 1. Species richness map of Canidae for the present produced by ENM. The richest areas (hotspots) were identified in the Middle East + Northeast Africa region (A) and western part of the USA (B). The legend on the left shows the number of overlapping species.

The ENMs indicated species that do not overlap currently will start to overlap in their distributions, and even those that overlap in only small parts of their distributions will suffer considerable increases in their overlap areas. In South America, *C. thous* is predicted to invade areas where only *A. microtis* and *Speothos venaticus* live, inside the Amazon rainforest (Appendix - Figures S39, S42, and S46). With the great expansion of *V. vulpes'* geographical distribution, this species is expected to overlap its area with *V. bengalensis*, *Vulpes rueppellii*, and *Vulpes zerda* (Appendix - Figures S45, S47, S48, and S49). In addition, *C. lupus* will probably overlap in areas occupied before only by *V. bengalensis*, *V. rueppellii*, *V. zerda*, and *Canis aureus* (Appendix - Figures S44, S47, S48, S49, and S50).

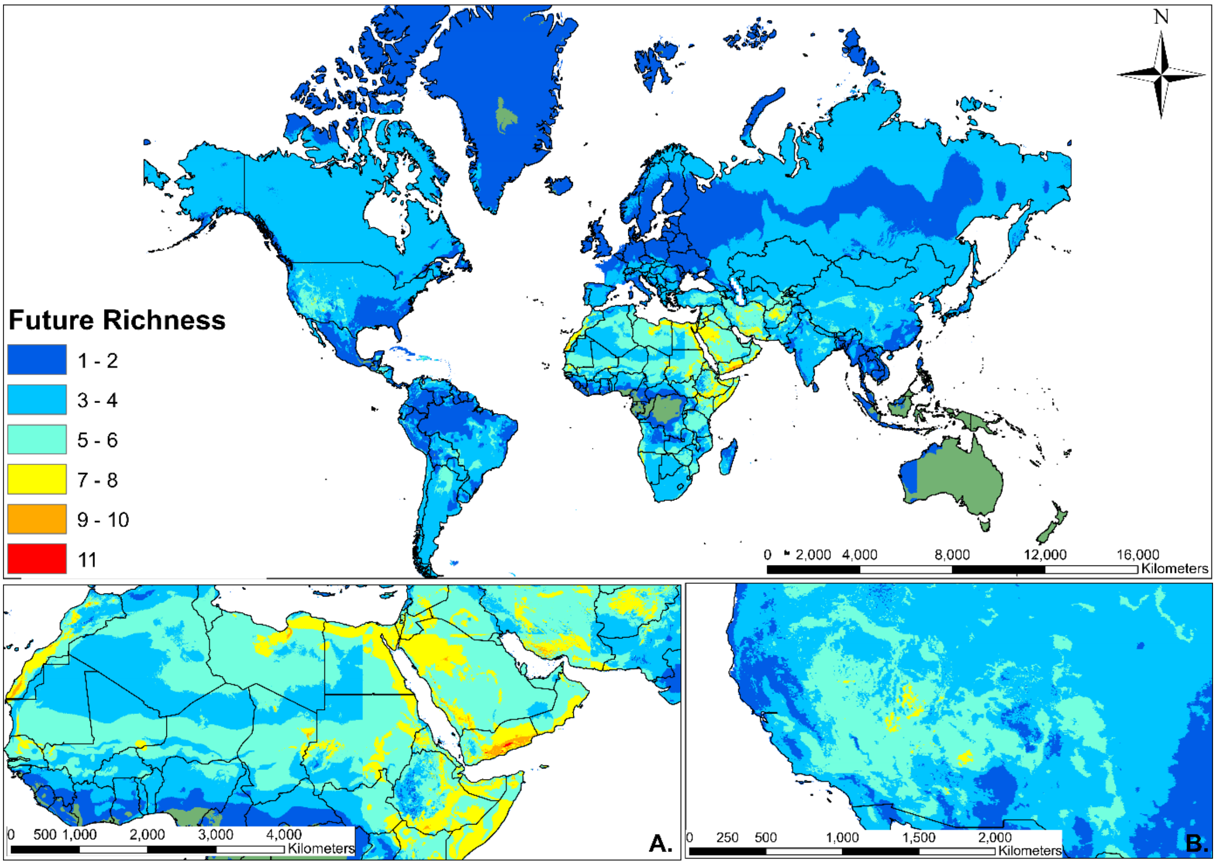

Figure 2. Species richness map of Canidae under future climate conditions produced by ENM. The richest areas (hotspots) were identified in the Middle East + Northeast Africa region (A) and western part of the USA (B). The legend on the left shows the number of overlapping species.

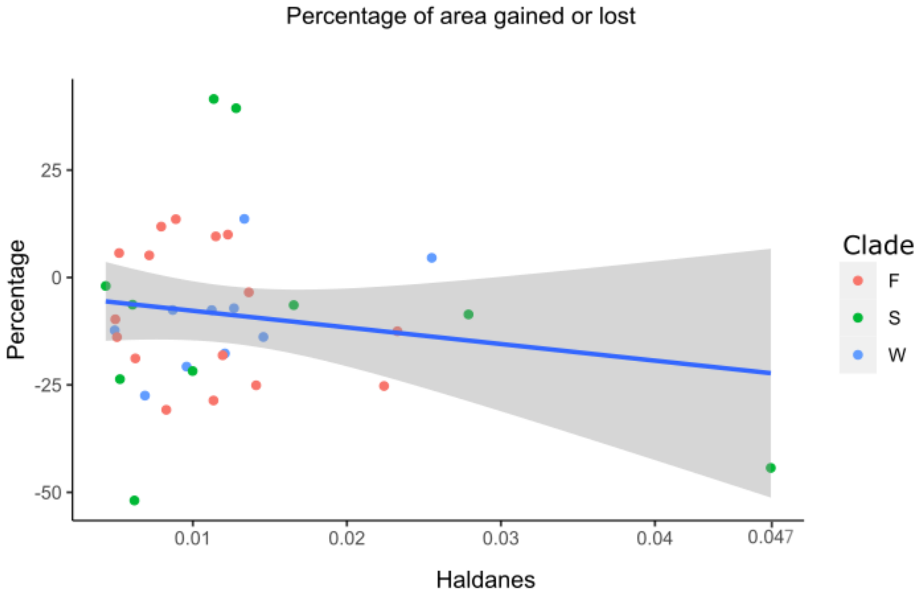

Figure 3. Plot representing the relationship between the percentage of area gained or lost by canids in relation to *H* values. The higher the *H* value, the lower the likelihood of evolutionary rescue. Red, green,

and blue dots are species from the clades of foxes, South-American canids, and wolves, respectively. $R^2 = -0.187$ ($P < 0.05$).

Evolutionary rescue

Most of canids presented evolutionary rates around 0.01 Haldanes (Table S2). The highest *H* value was found for *A. microtis* (*H* = 0.047 Haldanes), and the lowest value was from *Lycalopex griseus* (*H* = 0.004 Haldanes) (Table S2).

We found a significant weak negative correlation between change in range size and evolutionary potential: species that are predicted to undergo more habitat loss according to the ENMs have a lower potential for ER, according to the *H* values (Figure 3).

Discussion

We applied models of evolutionary rescue, using temperature and generation cycle as intrinsic characteristics of canids, together with ENMs to understand the magnitude of the effects of climate change on Canidae distribution. Predictions for the future by ENMs, derived from the IPCC worst climate change scenario, suggested that climate change will affect canids in distinct ways, where some species will expand or maintain their distributions, while most will suffer a large reduction in their suitable areas. Furthermore, the calculated Haldanes suggest that for some species it will be more difficult to keep up with the pace of temperature changes than others. We detected a weak negative correlation between habitat loss and potential for evolutionary rescue, indicating that the species with higher potential to evolutionary rescue are the ones that gain area or lose only a small part of their future distributions, while the ones which are going to lose a large part of their future distribution will need a higher evolutionary change to maintain their populations. *Atelocynus microtis,* for example, is predicted to lose about half of its potential distribution and has the highest *H* value among canids (*H* = 0.047 Haldanes). This negative correlation is to be expected because larger differences between present and future temperatures will increase *H* and will also make it more likely that range sizes will change.

Our results suggest that global warming will be devastating to the Canidae family as a whole. However, even in this pessimistic scenario, some species have the potential to benefit from future conditions and considerably expand their geographic distributions. In general, several taxa, including mammals, birds, amphibians, and reptiles, are expected to experience drastic range reductions (Araújo & New, 2007; Diniz-filho et al., 2009; Hidasi-neto et al., 2019; Lawler et al., 2009; Maiorano et al., 2011; Peterson et al., 2002). In a scenario such as this, several communities will probably lose phylogenetic and functional diversity (Davis et al., 1998; Hidasi-neto et al., 2019), and considering the number of interactions that will be lost within these areas, the ecological impacts due to indirect effects may be stronger than the direct effects of climate change on species' distributions (Davis et al., 1998; Peterson et al., 2002). Carnivores, through population regulation, can promote the coexistence of several species by reducing interspecific competition (Paine, 1966). Because canids, being carnivores, hunt distinct animals, they end up regulating the population dynamics of their prey, which is an important factor for maintaining biodiversity (Sanders et al., 2013; Sanders & van Veen, 2012).

In South-America, there is a very concerning situation, where *A. microtis* will probably contract its range substantially and undergo fragmentation of its distribution within the Amazon Forest, while *C. thous* will expand. *A. microtis* is ecologically restricted to very specific resources and conditions (Sillero-Zubiri et al., 2004; Wilson & Mittermeier, 2009). By contrast, *C. thous* is a generalist species with a large distribution across South-America (Sillero-Zubiri et al., 2004). Currently, the status of *A. microtis* is "Near Threatened" (IUCN, 2019), but considering the climate change effects shown here, and the fact that the Amazon Forest has been suffering with wildfires and an intense deforestation process over the last decades (Exbrayat et al., 2017; INPE, 2019), *A. microtis* is probably experiencing a substantial habitat loss followed by a very likely increase in the number of direct encounters with another competitor. Thus, we suggest that its "Near Threatened" status must change, at least, to "Vulnerable".

A similar situation applies to *V. vulpes* and *V. lagopus*. The first one has a wide distribution over the northern hemisphere, while the second is restricted to areas covered by snow around The North Pole, but both species overlap in the Tundra of North America and Eurasia (Hersteinsson & Macdonald, 1992; Sillero-Zubiri et al., 2004). Over the past few years there has been an increase in the number of encounters between the two species due to the warming temperatures that are gradually melting the Arctic ice cap, reducing the available area for *V. lagopus*, but making it possible for *V. vulpes* to expand its distribution to the north into arctic tundra in Eurasia and North America (Gallant et al., 2012). This reality is even more aggravating in the future scenario shown here, considering the large area loss by *V. lagopus* to *V. vulpes* (Figure S51). However, Gallant et al. (2012) suggested that food scarcity in these areas seems to explain the dynamics of the geographical overlap of both two species better than climate warming. Nevertheless, the effects of area loss must still be taken into account to outline conservation strategies for *V. lagopus*.

The loss of species has severe impacts on the functioning of ecosystems (Cardinale et al., 2012; Kennedy et al., 2002; Lyons & Schwartz, 2001; Pimm et al., 2014). In general, reductions in the number of species (functional groups) decrease the efficiency of communities to capture resources, and convert these into biomass (Balvanera et al., 2006; Cardinale et al., 2012; Quijas et al., 2010). Our niche models detected two major richness hotspots for Canidae: one in the Middle East + North East Africa and one in North America. The former is predicted to undergo a small expansion, mainly due to the range expansion of *C. lupus*, *C. anthus*, and *V. vulpes* over these areas, and the capacity of *C. lupus* and *V. vulpes* to live around urban areas (Sillero-Zubiri et al., 2004; Wang & Tedford, 2008; Wilson & Mittermeier, 2009). This capacity can also explain the wide distribution of both species around the world. The other hotspot area, in North America, is expected to experience a considerable area reduction. This can be explained by the small portion of this hotspot that is within protected areas in the USA, according to Brum et al. (2017).

Here, the ENMs for all canids (appendix) agreed well with the current distribution of canids, suggesting that the methodology we applied is reliable to assess the impacts of climate change on Canidae, taking into account their main niche dimensions. *Canis lupus* is the only species for which the ENMs for the present did not encompass the entire distribution presented by its polygon, because it is not predicted to occur in the Middle East. This might be explained by the presence of a single population found in that region, which results in the distribution of the species to be extended to areas that are not suitable. The IUCN distribution maps are widely used in several studies for different purposes (Kyne et al., 2020; Porto et al., 2021; Shier, 2015; Zhang et al., 2019), and are defined as the area within the outermost limits of known occurrence for a species, but this area is not an estimate of the extent of occupied habitat, it only measures the general extension of the localities in which the species is found (Gaston & Fuller, 2009). Thus, polygons are highly susceptible to sampling biases. Nevertheless, it is important to point out that ENMs for the future suggest that *Canis lupus* will expand its distribution to the Middle East, which could be an indication that this region is already becoming suitable for the species.

Our methods assumed that the prey of the Canidae will respond to environmental changes at the same rate as their (apex or medium-level) predators. Indeed, climate change has already been observed to have wide-ranging trophic effects (Gilman et al., 2010), and physiological and behavioral effects in other species (Parmesan, 2006). Modelling the effect of climate change on species' communities and trophic interactions has proven extremely difficult, but these interactions can have serious impacts on species distributions (Sanders et al., 2013; Sanders & van Veen, 2012). These trophic interactions may be further disrupted by invasive species, the spread of which could be accelerated by climate change (Hellmann et al., 2008).

Looking at the *H* values, two cases are very concerning. *Atelocynus microtis* and *Chrysocyon brachyurus* present higher *H* values compared to other canids (0.047 and 0.027, respectively), and based on Diniz-Filho et al. (2019), these species have a lower potential for evolutionary rescue. Although *H* values and ENMs try to elucidate the future of species, they have distinct points of view about the effects of climate change on canids, and therefore should not be compared. However, these two approaches can shed light on Canidae responses to the future of the planet. *H* values suggest that some species have less potential than others to adapt fast enough to temperature changes, but ENMs indicate that some of them may increase their range, because more suitable habitats will become available for them due to climate change. Thus, in these cases ecological processes seem to prevail over evolutionary ones.

Unfortunately, very little is known about ER in nature to compare with our findings, mostly because the idea that evolution may influence the persistence of a population facing a rapid environmental change is very recent. Nevertheless, Diniz-Filho et al. (2019) already suggested that the use of the ER approach for wider geographical areas might not be that simple. They suggested that in order to obtain a standard temperature deviation, the real temperature tolerances must be known. However, no lab values were available for any wild canid, meaning that only values obtained from range estimations and ENMs could be used. Nonetheless, both may underestimate a species' true temperature tolerance. For example, while we have extracted values of mean Bio05 (maximum temperature in the warmest month), sometimes these values are well below the highest value seen within a species range.

The biogeographic patterns observed in this study may provide useful information for assessing how canids are distributed in the present over the planet, being an alternative to the distribution polygons provided by IUCN (2020). Climate change is projected to play an essential role in the geographical distribution of canids, so our predictions can be used to identify key areas for conservation strategies. This should receive special attention because as we showed, most of the Canidae hotspot regions are not located within protected areas.

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Supplementary material

Appendices and R scripts will be available at the online public repository of this thesis.

Figures

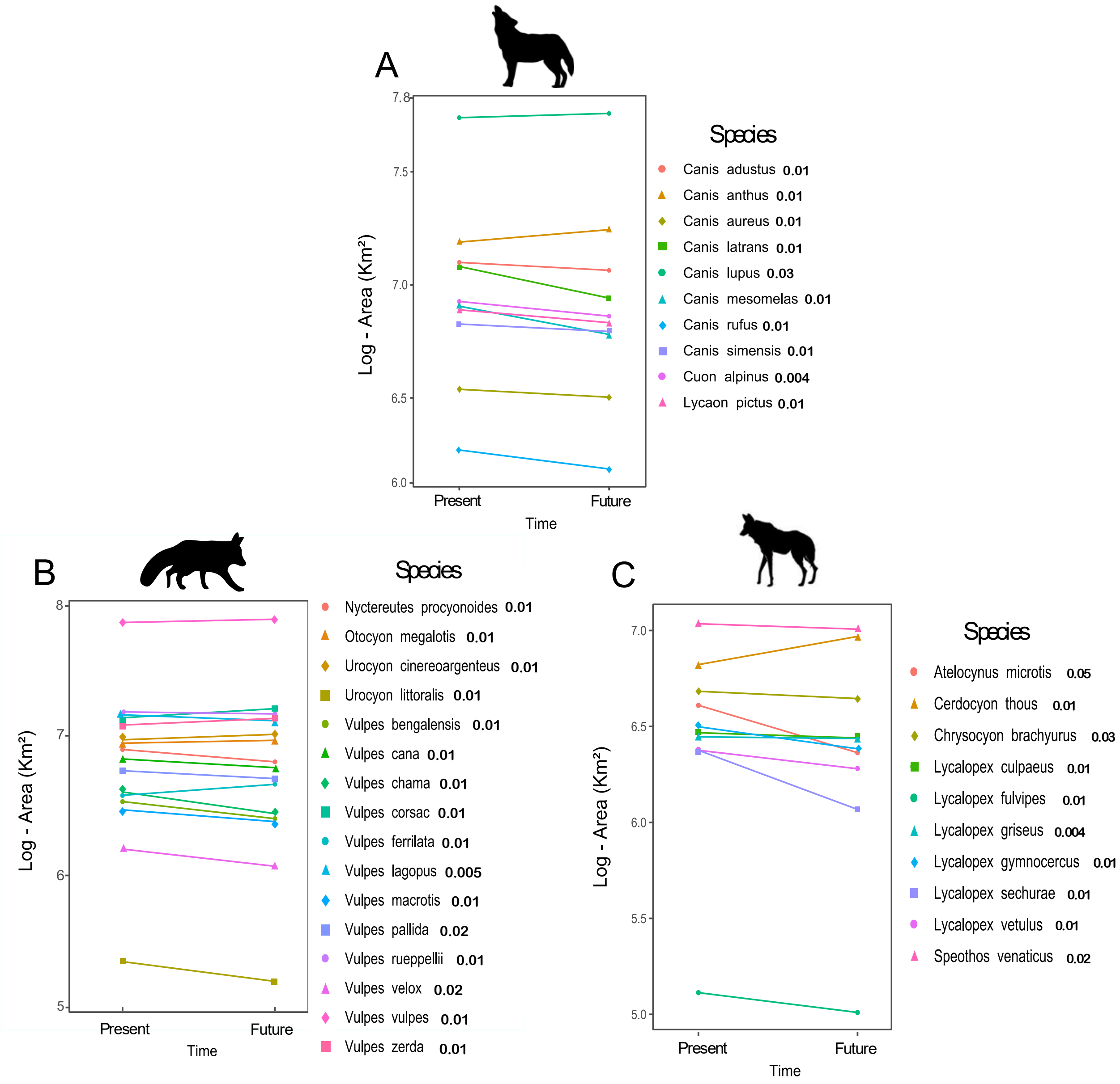

Figure S38. Plot representation, on logarithmic scale, of range expansion or contraction over time for the clades of wolves (A), foxes (B), and South American canids (C). *H* values for each species are indicated next to each species name.

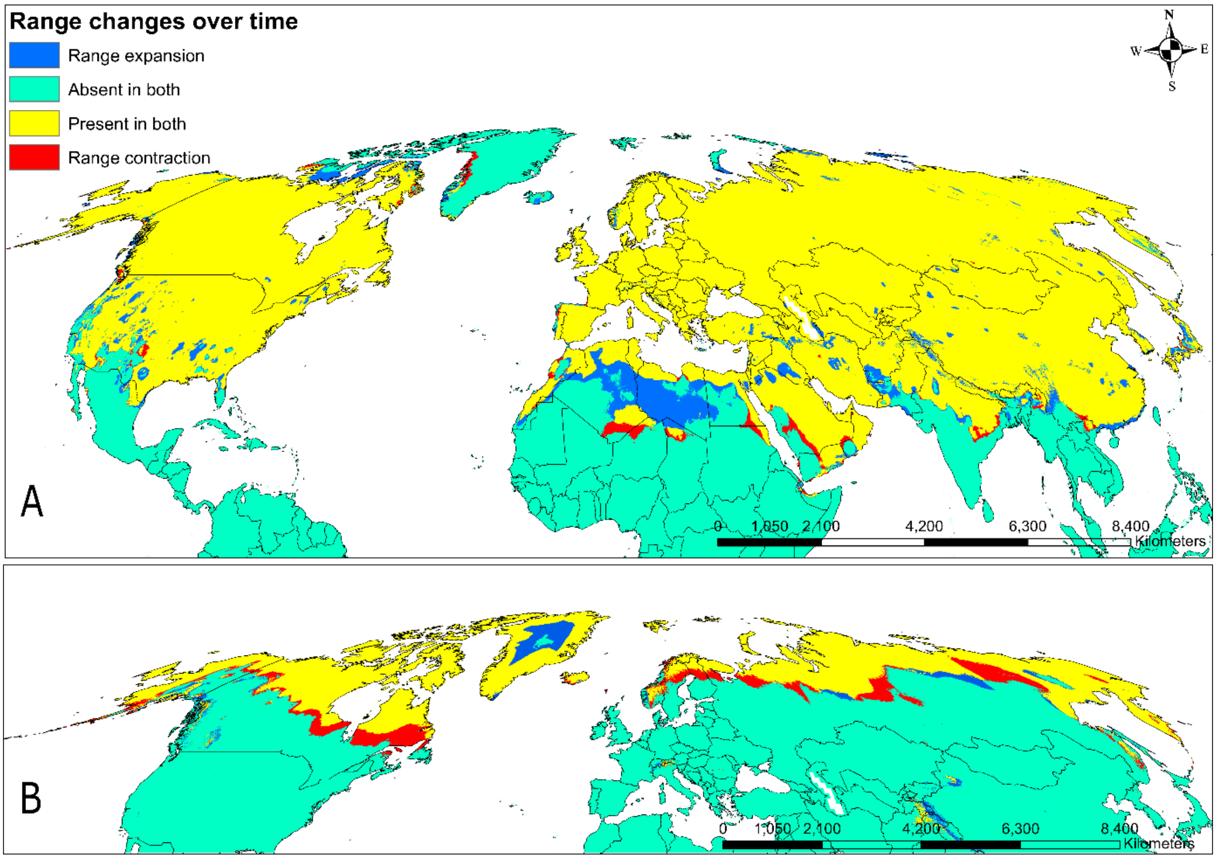

Figure S51. Comparison of present and future suitable areas of *Vulpes vulpes* (A) and *Vulpes lagopus* (B). The image shows regions where loss is expected to occur (red) and regions where the species will increase their distributions (blue).

Tables

Table S1. List of the 36 species of Canidae included in our study. Age of sexual maturity of females (years), the number of generations until 2075, the number of occurrence points for each species, and the source of the original description are indicated here.

Species	Sexual maturity of females	Number of generations	Number of occurrence points	Descriptor
Canis adustus	0.75	100	1.028	Sundevall, 1847
Canis aureus	1	75	2.769	Linnaeus, 1758
Canis anthus	1	75	1.536	Cuvier, 1820
Canis lupus	2.5	25	8.490	Linnaeus, 1758
Canis latrans	0.84	89.3	2.402	Say, 1823
Canis mesomelas	0.84	89.3	645	Schreber, 1775
Canis rufus	1	75	30	Audubon & Bachman, 1851
Canis simensis	2	37.5	12	Rüppell, 1840
Cuon alpinus	1	75	507	Pallas, 1811
Lycaon pictus	1.23	60.4	281	Temminck, 1820
Nyctereutes procyonoides	0.82	91.5	846	Gray, 1834

Vulpes bengalensis	1.5	50	327	Shaw, 1800
Vulpes cana	0.82	91.5	396	Blanford, 1877
Vulpes chama	0.75	100	229	A. Smith, 1833
Vulpes corsac	1.38	54.3	1.193	Linnaeus, 1768
Vulpes ferrilata	1.15	65.2	264	Hodgson, 1842
Vulpes macrotis	0.82	91.5	229	Merriam, 1888
Vulpes pallida	1	75	406	Cretzschmar, 1826
Vulpes rueppellii	1	75	1.299	Schinz, 1825
Vulpes velox	1	75	88	Say, 1823
Vulpes vulpes	0.83	90.4	9.457	Linnaeus, 1758
Vulpes zerda	0.49	153.1	850	Zimmermann, 1780
Vulpes lagopus	0.83	90.4	3.468	Linnaeus, 1758
Urocyon cinereoargenteus	0.95	78.7	1.089	Schreber, 1775
Urocyon littoralis	1	75	30	Baird, 1857
Otocyon megalotis	0.61	122.6	515	Desmarest, 1822
Atelocynus microtis	1	75	238	Sclater, 1883
Cerdocyon thous	0.76	98.7	864	Linnaeus, 1766
Chrysocyon brachyurus	2	37.5	457	Illiger, 1815
Lycalopex culpaeus	1	75	345	Molina, 1782
Lycalopex fulvipes	1	75	8	Martin, 1837
Lycalopex griseus	1	75	255	Gray, 1837
Lycalopex gymnocercus	1	75	312	G. Fischer, 1814
Lycalopex sechurae	1	75	24	Thomas, 1900
Lycalopex vetulus	1	75	183	Lund, 1842
Speothos venaticus	0.83	90.4	1.076	Lund, 1842

Table S2. Area difference in species distributions for present and future, showing expansion or retraction of canids' geographical distributions. *H* values are also indicated.

Species	Present area (Km²)	Future area (Km²)	*H*
Atelocynus microtis	4.379.627	2.438.970	0,047520
Canis anthus	15.472.384	17.583.018	0,013342
Canis aureus	3.448.559	3.187.594	0,008698
Canis latrans	12.065.866	8.749.988	0,006891
Canis lupus	55.058.863	57.577.546	0,02551
Canis mesomelas	7.840.423	6.214.900	0,009592
Canis rufus	1.858.413	1.529.932	0,012079
Canis simensis	6.707.343	6.227.124	0,012671
Canis adustus	12.577.073	11.623.101	0,011225
Cerdocyon thous	7.224.726	10.225.538	0,011357
Chrysocyon brachyurus	5.202.737	4.755.462	0,027895
Cuon alpinus	7.757.856	6.803.830	0,004926
Lycalopex culpaeus	3.121.231	2.923.795	0,006086
Lycalopex fulvipes	126.236	98.762	0,009984

Lycalopex vetulus	2.539.881	2.040.550	0,012808
Lycalopex griseus	2.961.540	2.903.216	0,004344
Lycalopex gymnocercus	3.354.884	2.561.320	0,005269
Lycalopex sechurae	2.514.432	1.209.669	0,006207
Lycaon pictus	8.445.869	7.276.908	0,014579
Nyctereutes procyonoides	7.413.459	6.018.161	0,006262
Otocyon megalotis	8.251.366	8.676.914	0,007170
Speothos venaticus	11.953.879	11.185.765	0,016549
Urocyon cinereoargenteus	8.757.468	9.595.434	0,011490
Urocyon littoralis	200.615	143.194	0,011346
Vulpes bengalensis	3.053.463	2.287.423	0,014108
Vulpes cana	6.315.447	5.439.834	0,005072
Vulpes chama	3.594.029	2.487.370	0,008272
Vulpes corsac	13.114.501	14.423.740	0,012275
Vulpes ferrilata	3.502.426	3.977.712	0,008895
Vulpes lagopus	13.405.437	12.101.093	0,004969
Vulpes macrotis	2.651.764	2.171.680	0,011933
Vulpes pallida	5.164.447	4.518.576	0,023281
Vulpes velox	1.360.294	1.016.829	0,022411
Vulpes vulpes	64.415.599	68.080.936	0,005214
Vulpes zerda	11.242.325	12.574.885	0,007949
Vulpes rueppellii	14.074.266	13.588.853	0,013633

CHAPTER 4

The influence of biogeographic regions on the evolution of Canidae

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Abstract

The Canidae are an ecologically important group of dog-like carnivores that arose in North America and spread across the planet around 10 million years ago. The distribution patterns of species at present, together with the phylogenetic structure of the group, suggest that Canidae diversification may have had a different pace in different biogeographic areas. This hypothesis can be tested by applying existing methods involving State-dependent Speciation and Extinction (SSE) models to phylogenies of extant species and their distribution patterns. However, these models are often parameter-rich which hinders reliable application to relatively small clades such as the Caninae (the only extant subclade of the Canidae consisting of 36 extant species). Here we extend the methods to phylogenies with extinct species as well (111 species) and compare the results to those of analyses with the extant-species-only phylogeny. The results on the extant-species tree suggest that distinct diversification patterns are related to geographic areas, but the results on the complete tree do not support this conclusion. This suggests that these contrasting findings have resulted from information carried by the extinct species being different from information carried by extant species. Extinct species, by their very nature of being extinct, may have characteristics that caused their extinction, which may be different from the characteristics of extant species that caused them to be extant. However, we note that our extant-species analysis yielded an unrealistically low estimate of the extinction rate. Hence, we conclude that differences in biogeographic areas probably did not contribute much to the variation in diversification rates in Caninae.

Keywords: diversification rates, fossil information, lineage dispersal, species selection, trait inheritance.

Introduction

From a single ancestor around 40 million years ago (Mya), the Canidae family became one of the most widespread and ecologically diverse groups among Carnivora, inhabiting several distinct environments, and being present in all continents, except in Antarctica (Wang and Tedford 2008; Prothero 2013). Canids originated in North America, where successive radiation events gave rise to three subfamilies, Hesperocyoninae, Borophaginae and Caninae (Wang et al. 2004). The first two subfamilies were endemic to North America, and went extinct without reaching other continents, before the geological events that connected N. America to Eurasia and South America around 11 Mya (Geffen et al. 1996; Cox 2000; Macdonald, D.W & Sillero-Zubiri 2004; Wang and Tedford 2008; Potter and Szatmari 2009), i.e. the uplifts of the Bering Strait and the Isthmus of Panama (MacNeil 1965; Hopkins 1967; Montes et al. 2015). Caninae was the only subfamily that managed to cross the land bridges and disperse from North America, producing more than a hundred species, of which 36 are still extant today (Porto et al. 2019).

Although Canidae have a rich fossil history, raw fossil locations paint a limited picture of biogeographic events. Most of what we know is related to the geographic location from which lineages originated (both fossil and extant species), and the most likely routes that canids used to disperse (Wang and Tedford 2008; Porto et al. 2021). Our understanding on how biogeographic events shaped the evolutionary dynamics of canids is therefore still limited. More precisely, we still lack a complete understanding of how dispersal events to new continents affected Canidae diversification rates. Pires et al. (2015) demonstrated how continental dispersals affected the evolution of carnivores in general, but focused only on dispersal between Eurasia and North America, disregarding the rest of the planet. If invasions of new areas have an impact on canid diversification rates, we might expect a scenario of ecological opportunity (EO) upon the arrival in a new continent lacking competitors (Simpson 1953).

Several studies have indicated that dispersal events to new regions can trigger exceptional shifts in species diversification by EO (Mahler and Losos 2010; Mahler et al. 2010; Yoder et al. 2010; Algar and Mahler 2016). Geographic colonization of new areas will lead to range expansion and establishment of new populations, which is likely to increase the rate of speciation (Cardillo et al. 2005; Rabosky and Glor 2010; Uribe-Convers and Tank 2015; Kennedy et al. 2017). Local extinction, however, leads to range contraction implying that the greater the range, the smaller the chance of complete extinction of the species (McKinney 1997). It is evident that species diversification can be linked to distinct factors, however it is not always clear how speciation, extinction and dispersal can be disentangled. Over the last few years, several studies have attempt to fully integrate phylogenetic comparative methods together with ecologically relevant traits to understand how biodiversity can be generated (Mairal et al. 2015; Pires et al. 2015, 2017; Herrera-Alsina et al. 2018; O'Donovan et al. 2018). A promising way to such integration is through diversification methods that estimate rates of speciation, extinction and dispersal, detailed below.

The state-dependent speciation and extinction (SSE) family of models (Maddison 2006; FitzJohn 2010, 2012) was developed to elucidate the impact that trait changes have on patterns of lineage diversification. In an explicit geographical scenario, the geosse (geographic state-dependent speciation and extinction) model (Goldberg et al. 2011) would be ideal to test the influence of geographic distribution on Canidae diversification, but it was recently found that the initial SSE models have a high Type I error in detecting the influence of traits on diversification rates, as they attribute rate variation directly to trait influences without allowing for rate variation being due to hidden factors (i.e. a null model) (Fitzjohn 2012; Machac 2014; Rabosky and Goldberg 2015). To avoid false positives, Beaulieu and O'Meara (2016) proposed the hisse model (hidden-state-dependent speciation and extinction), which can be used to detect if diversification events are more related to an unknown hidden trait than to the observed character. Geohisse (Caetano et al. 2018), a combination between geosse and hisse models, focused on geographical state dependence in particular. However, hisse and geohisse can only deal with a small number of hidden states and have some inconsistencies in the computation of conditional probabilities (Herrera-Alsina et al. (2019). The secsse model (several examined and concealed states-dependent speciation and extinction (Herrera-Alsina et al. (2019), which combines the features of hisse with the musse model for multiple states (Fitzjohn 2012), solved the limitations of previous SSE models. Moreover, secsse can also consider trait changes (here changes in biogeographical state) during speciation, as in the geosse and classe (Goldberg and Igić 2012) models (see e.g. Aduse-Poku et al. 2021).

The inferences that can be made with SSE models heavily rely on the quality of the data, but few biological groups have well-resolved phylogenies and complete trait-datasets. One such group is the Canidae family, which have a well-resolved tree (Porto et al. 2019) and an incredibly detailed fossil record (Wang et al. 2004; Wang and Tedford 2008; Tedford et al. 2009). The rich and well-identified records of extinct Canidae species offer a unique opportunity to study the processes and mechanisms of their worldwide diversification when lineages reached new continents. Here, we first extend the secsse model (Herrera-Alsina et al. 2019; Aduse-Poku et al. 2021) to complete phylogenies (with all extinct species). This new secsse version is the first SSE model able to work with hidden states and fossils species, being a great advance in the field. We then apply this new version to a complete tree of Caninae to study the effects of biogeographic states on canid rates of diversification and dispersal. We expected to find different speciation rates in South America and Africa due to the very distinct environments that both continents had in comparison with North America (Zachos et al. 2001; Strömberg 2011; Zhang et al. 2014), and also due to the absence of competitors in South America (Wang and Tedford 2008), which could be indicative of ecological opportunity. Furthermore, we expected extinction rates to be higher in Eurasia than elsewhere due to encounters with other groups of carnivores as Felidae (Wang and Tedford 2008; Pires et al. 2015, 2017). However, our results do not support either scenario. Interestingly, our findings based on the complete tree for Canidae are very different from what we find if we only use extant species. This demonstrates the importance of using fossil information when available and being cautious in interpreting results when it is not available.

Materials and Methods

Formulation

The secsse model assumes that speciation (λ_i) and extinction rates (μ_i) depend on the trait state *i* of the lineage. This trait is a combination of an observed trait and a hidden or concealed trait that can take discrete states which can change from state *i* to state *j* with a rate q_{ij}. During speciation, the daughter species usually inherit the trait from the parent species, but secsse also allows the daughter species to have different trait states than the parent. In our implementation of secsse the trait is the biogeographic state which can take the following eight values: North America (NAM), South America (SAM), Eurasia (EUR), Africa (AFR), NAM + SAM, NAM + EUR, EUR + AFR, and NAM + EUR + AFR (Figure 1A). Speciation in a species that is present in only one continent is always sympatric, which means that daughter species inherit the parent's state. Speciation in a species that is present in multiple continents is always allopatric (vicariant), which means that the daughter species each inherit part of the range of the parent. Species can disperse to other continents thereby extending their ranges, and they can contract their ranges by going locally extinct. Note that species in states comprising multiple continents cannot become extinct in a single step. They first need to contract their range, i.e., undergo a local extinction in one of the continents. Figures S1-S23 show the states and transitions in the models.

Because the available version of the R package secsse only considered reconstructed trees without extinct species, we extended the package so it can be applied to complete trees (with all extinct species). For reconstructed trees, Goldberg and Igić (2012) provided equations to compute the likelihood $D_i(t)$ of the phylogeny subtending from a lineage at time *t* and the trait states at the present given trait state *i* at time *t*. By computing these probabilities backward in time (from tips to crown), and combining probabilities at the nodes, one can obtain the likelihood of the entire tree given the trait state at the crown. The equations also involve the extinction probability $E_i(t)$ which is the probability of the lineage at time *t* not having any descendants at the present. These formulas have been implemented in various packages including *secsse*. However, the mathematical formulation for complete trees is in fact much simpler as we no longer need to track the extinction probability because we observe all extinctions in the complete tree (but note that we need it still to condition on survival of the process). The equation for $D_i(t)$ becomes:

$$\frac{dD_i}{dt} = -\left(\sum_{j,k} \lambda_{ijk} + \mu_i + \sum_j q_{ij}\right) D_i + \sum_j q_{ij} D_j$$

where we use, for the tree tips at the present, the initial condition $D_i = 0$ when the species is in state *i* at the tip and 0 otherwise, and for the extinct species $D_i = \mu_i$ when the species is in state *i* at the tip and 0 otherwise.

Phylogenetic tree and distribution data

The phylogeny produced by Porto et al. (2019) for the Canidae family was used here as the basis for our tree. Their phylogeny, constructed with molecular and osteological data through Bayesian inference, has all the 36 extant canids in the world, plus the recently extinct (1876) *Dusicyon australis*. We added all the other 74 extinct species described for Caninae following (Wang and Tedford 2008), generating a complete tree for the subfamily. A literature review was performed in the digital paleobiology dataset Fossilworks (Alroy 1998) in order to define the most likely phylogenetic positions that each extinct species would take. This resulted in the phylogeny used in this study with 36 extant and 75 extinct species (Figure 1B) (Table S1).

The complete Caninae tree was time-calibrated using the fossil information of the 74 extinct species obtained from Fossilworks, as well as the fossil ages used by Porto et al. (2019). This analysis was performed in *R* 4.0-2. (R Development Core Team 2020) using the *chronos* function of the ape 5.4-1 package (Paradis and Schliep 2019).

We divided the world into eight biogeographic regions (trait states) (Figure 1A). We categorized all canids into the eight previously mentioned biogeographical regions based on the distribution information for the 111 species obtained from IUCN (2020) and from Fossilworks (Table S1).

Secsse models

We considered several models differing in whether observed (biogeography - i.e., presence in a biogeographic area) or hidden traits affect speciation and/or extinction rates or not, and whether transition rates (in our case range expansion and contraction) differ or not. Each model has one or several hypotheses being tested (Figures S1 – S23). We fitted 45 state-dependent speciation and extinction models. Among these models, 22 are ETD (Examined Trait-Dependent) models, 22 are CTD (Concealed-Trait-Dependent) models with the same set up as the ETD models, and one is a CR (Constant-Rate) model. In ETD models, the diversification rates depend on the trait of interest, i.e., the geographic range. In CTD models, the diversification rates depend on a hidden trait that we are not analyzing. In the CR model, rates are homogeneous across states. The full set of models and all their rate parameters are detailed in the supplementary material (Figures S1 – S23). Note that we allowed the same number of hidden and observed states (8), meaning that our models have 64 possible combinations of examined and concealed states.

Speciation (λ_i) matrices were set to only accommodate dual inheritance or dual symmetric transition scenarios by sympatric and allopatric speciation, respectively. Dual inheritance scenarios reflect that during speciation the trait state from the ancestor is perfectly inherited by both daughter species which in our case occurs for sympatric speciation. Dual symmetric transitions reflect that daughter species can inherit any state; in our case they inherit non-overlapping parts of the parental range (allopatric speciation). All 45 models have the same speciation matrix setup, but they vary in the number of different speciation parameters estimated (Figures S1 – S23). The various models consider 1) distinct rates for sympatric and allopatric speciation; 2) distinct rates for sympatric and allopatric speciation and a third rate for speciation in South America to study whether the endemic clade on this continent has a different diversification than the other continents; 3) a model with five speciation rates, two for sympatric and allopatric speciation in the new world (NAM and SAM and NAM+SAM), two for sympatric and allopatric speciation in the old world (EUR and AFR and EUR+AFR), and one for allopatric speciation among new and old world (for EUR+NAM and EUR+NAM+AFR). We refer to the supplementary material for a complete description of the models.

Extinction rates (μ_i) were set for extinctions in the single-area states (NAM, SAM, EUR, and AFR). For the other four states (multiple-area states) extinction rates were fixed to zero; species in these states first have to contract their ranges to a single-area state before they can become extinct. We set models with a distinct rate for one of the four single-area states while the other three had the same rate. Variations of this model were created for each one of the four single-area states to test if extinction was higher or lower in any of them compared to the others. Another model had four different rates for each one of the single-area states. We also had a model with two distinct extinction rates, one for old world states and another for new world states.

For the transition rates (q_{ij}), we set constrained matrices for all the models, meaning that there are rules prohibiting some transitions. Transition rates from multiple-area states to single-area states are in fact extinction rates because this transition means a local extinction in one of the areas that form the multiple-area state. The models considered here are: 1) distinct transition rates among new and old world; 2) distinct rates among states within new and old world; 3) rates for each one of the possible transitions among areas; 4) and several models with two rates, one for one of the states and another rate for all others.

To run the models, we used the *cla_secsse_ml* function from the extended secsse 2.3.1 package. The best model was selected by AIC after we ran our maximum likelihood inference with CR, ETD and CTD models.

Initial values of the parameter estimation procedure were estimated from the phylogeny through the function *bd_ML* from the DDD 4.3 package (Etienne et al. 2016). To lower chances of ending up in local optima, we set each optimization in the optimize function of the DDD package to have 10 cycles (i.e., optimization starts again from the optimal parameters).

To test how much the interpretation of the evolutionary history of a group can change depending on the presence or absence of extinct species in phylogenies, we applied the 45 models not only to the complete phylogeny of Caninae (111 species), but also to the extant-species tree + one recently extinct (37 species) from Porto et al. (2019). Thus, the total number of analyses doubled to 90.

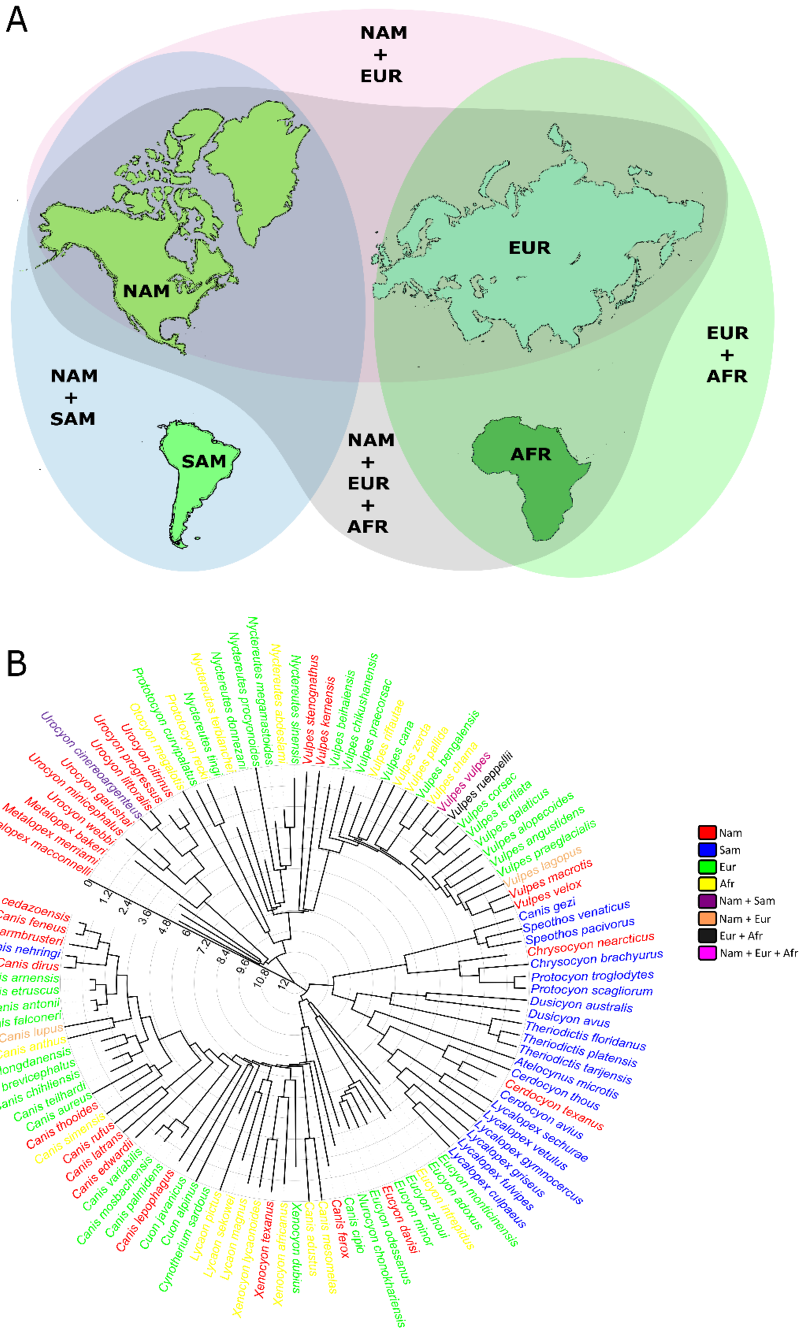

Figure 1. Trait states and phylogenetic tree used here; A) the four single states and their four combinations that we used to classify Canidae distribution patterns; B) the complete phylogenetic tree used here containing 111 species (75 extinct and 36 extant). The tips of the tree are colored based on their distributions.

Results

For the complete tree, we found that a CTD null model had the highest support (model 17 – AIC weight = 0.999 – Figure 2A), in which rates of diversification are allowed to vary across lineages but independently of the areas (Table 1 - see Table S2 for the complete model comparison, and see Figure S9 for the setup of the best-performing model – model 17 has the same setup as the ETD model 16 in Figure S9, but focuses on variation in speciation rates in the concealed states). Model 17 has three distinct speciation rates which were estimated as λ_1 = 2.70E-15, λ_2 = 3.92E-15, and λ_3 = 0.344. This model has one μ for extinctions in all states (μ_1 = 0.297). Although we find no effect of biogeographic areas on rates of diversification, we found substantial differences in rates of area expansion (q_1 = 0.055) and contraction ($q_2 = \mu_1$ = 0.297) (Table S3).

For the complete tree, CTD models had a better performance when compared to ETDs.

Table 1. Model comparison based on AIC for the 10 best performing models tested with the complete tree. Models differ in what state changes are allowed, and whether state changes occur during speciation. CR = Constant Rates; CTD = Concealed trait-dependent; ETD = Examined trait-dependent; K = number of free parameters. The highest supported model (model 17) is the CTD version of the ETD model 16, which has three speciation rates and one extinction rate, plus a single transition rate (area expansion) between all states. The area contraction rate is the same as μ_1. Model 17 assumes that lineages have distinct rates of diversification that are not correlated with areas.

Models	Trait-dependence	Likelihood	K	AIC	ΔAIC	AICw
17	CTD	-599.464	5	1208.928	0	0.9999999990
19	CTD	-619.506	6	1251.012	42.084	7.27E-10
9	CTD	-621.335	7	1256.67	47.742	4.29E-11
5	CTD	-629.585	4	1267.169	58.242	2.25E-13
13	CTD	-632.153	4	1272.306	63.379	1.73E-14
15	CTD	-633.217	4	1274.434	65.507	5.96E-15
21	CTD	-632.285	5	1274.569	65.642	5.57E-15
23	CTD	-632.209	6	1276.418	67.49	2.21E-15
28	ETD	-642.022	7	1298.045	89.117	4.45E-20
33	CTD	-642.931	7	1299.862	90.934	1.79E-20

Among the 45 models we compared for the extant-species tree, we found the highest support for an ETD model (model 38 – AIC weight = 0.275 – Figure 2B) that assumes differential speciation rates for the historical hotspots of diversification for canids, i.e. Africa (fox clade) and South America (S. American clade) based on Wang and Tedford (2008) and Porto et al. (2021) (See Table S4 for the model comparison, and see Figure S20 for the setup of the best-fitting model). Model 38 has three distinct speciation rates: λ_1 for sympatric speciation in North America and Eurasia, and also for the four allopatric speciation events; λ_2 for sympatric speciation in South America; and λ_3 for sympatric speciation in Africa. The estimated speciation rates were λ_1 = 0.199, λ_2 = 0.136, and λ_3 = 0.021 (Table S5). Model 38 had only one μ estimated that represented extinctions in all the single-area states and also area contraction (μ_1 = 3.09E-15). This model assumes three transitions rates: $q_{SAM,SAM+NAM} = q_2$ = 3.02E-16 for the transition from South America to N. America + S. America; $q_{AFR,AFR+EUR} = q_3$ = 6.35E-15 for the transition from Africa to Eurasia + Africa; and q_1 = 0.113 for transitions among all other combinations of areas.

The second-best model for the extant-species tree was also an ETD model, i.e., model 36, with a ΔAIC = 0.171 (Table S4). This model has a very similar setup as model

38, only differing in the λ matrix. Model 36 focuses on Africa and S. America, like model 38 does, but assumes the same speciation rates for both biogeographic regions. Together, the models present an Akaike weight of 0.53.

Support for ETD models was generally high, regardless of the setup of each model, summing up to an AIC weight of 0.73 (note that our set of models is balanced; for every ETD model there is a corresponding CTD model).

Models 40, 42 and 44 that were set up to test whether the centers of origin of the three major clades of Canidae (South America, North America, and Africa) have different speciation rates than the other regions did not perform better than models that assumed these rates were identical, such as models 32 and 36. In addition, models with region-dependent extinction did not perform better than models with region-dependent speciation.

Looking at the rates of speciation and extinction among all the 45 models for the extant-species tree, we found that rates of allopatric speciation have a very wide range of values, from 0.06 to 0.6, but most of the estimations are around 0.4 (Figure 3A). The sympatric speciation rate was lower than the allopatric speciation rate across the 45 models, with a median of 0.12.

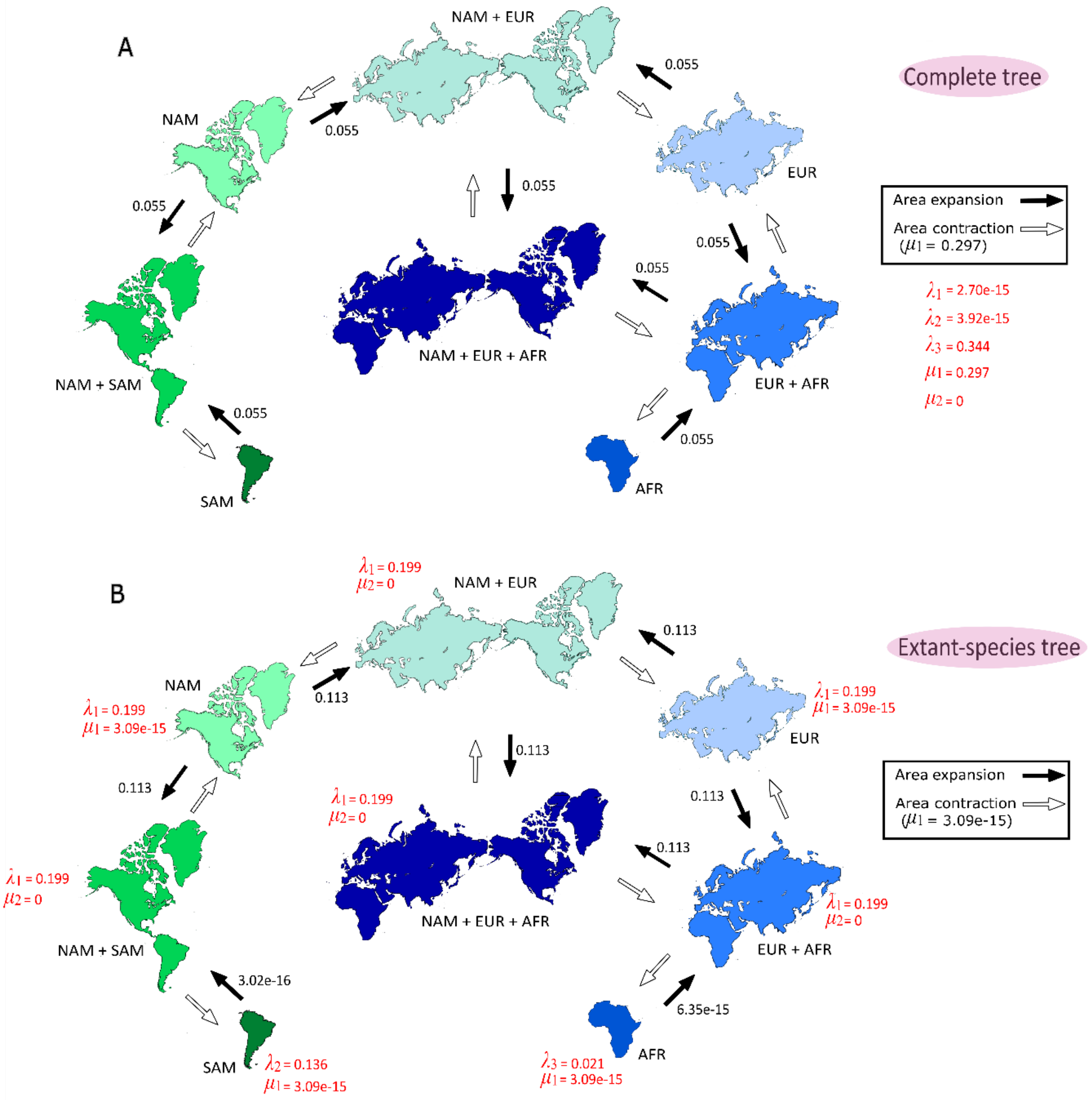

Figure 2. Estimates of rates of speciation (λ), extinction (μ) and transition across states (q_{ij}) for the best supported models (see Tables S2 – S5). A) In the scenario where we assessed the complete tree, CTD models had better results, which suggests that other factors than biogeographic areas cause variation in diversification rates. B) For the extant-species tree, ETD models performed better, suggesting that the geographic distribution partly drives Canidae diversification.

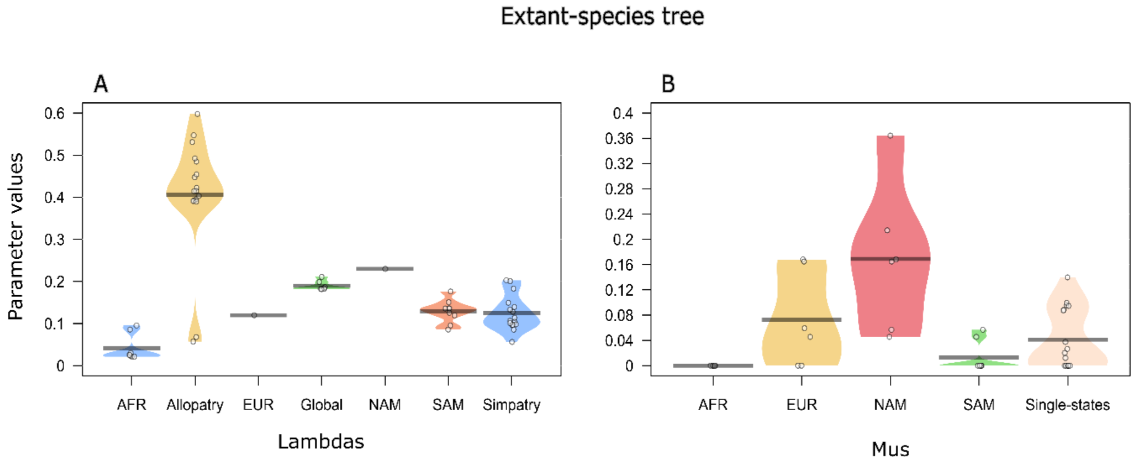

Figure 3. Comparison among all the diversification rates estimated across the 45 models tested here for the extant-species tree. On the left (A) the speciation rates, and on the right (B) the extinction rates. “EUR”, “AFR”, “NAM” and “SAM” mean a separate λ or μ for each of these continents; “allopatry” and “sympatry” mean a separate λ for these speciation events; and “single-states” means one single λ or μ for NAM + SAM + EUR + AFR.

Discussion

Our analyses, carried out separately for the reconstructed as well as the complete phylogeny, showed that taking into account fossil information in secsse models substantially changed the interpretation of how biogeographic areas influenced the diversification rates of Canidae lineages. In the scenario with only extant species, we found better performance of ETD models, suggesting that the distinct diversification patterns that we see on the phylogeny of extant canids are related to geographic areas. By contrast, when extinct species were incorporated into the phylogeny, we detected that CTD models performed much better than ETD models. This indicates that the rates of diversification for all known Caninae species cannot be explained by continent-related biogeographic events.

The disagreement in the results for complete and extant-species tree is unlikely due to a lower statistical power, as biogeographic areas had a prominent effect on diversification rates on the analyses with a lower number of species, so it would be expected that with more information available, the patterns would at least be maintained.

The incorporation of fossils in the analysis led to rates of speciation/extinction being roughly similar among biogeographic regions, suggesting similar diversification dynamics all over the world. However, this pattern is masked when we consider extant species only.

A possible explanation for this discrepancy is that when we use SSE frameworks to understand the effect of geographic range on evolution, we can end up overloading models of our examined trait when comparing them to null ones that account for a concealed variation among observed states (Caetano et al. 2018). This problem arises due to the need for accommodating a wide range of geographical variation into discrete areas. This culminates in the loss of some information about the heterogeneous features within the areas, strongly impacting parameter estimates. The studies from Rolland et al. (2014)

and van Els et al. (2021) are good examples of this potential for hidden variation within latitudinal and elevation gradients, respectively. Such categorizations overlook the distinct environmental conditions in the tropics or along mountains. And this turns out to be very compatible with the scenario we have here, as 67% of the species in our complete tree are extinct. This leads us to hypothesize that extinct species may have different factors determining their (absence of) diversification than extant species. Furthermore, unlike extant species, which have well-known distribution limits, fossil species have much more uncertain information in this regard. Even though there is a lot of knowledge about the number of extinct lineages in Canidae, this is due to specific regions spread across the planet where fossil preservation is ideal, but the real distributions may be larger. Hence, the analysis on the complete tree, even though it incorporated more data, also contains more uncertain data (including those on the actual branching times) which may have biased our results.

The best scenario for the extant-species tree shows very appealing results as lineages are more unlikely to expand their ranges and move out of Africa and South America rather than they did over the rest of the planet. The transition rates for the extant-species tree actually go in line with a scenario of incumbency effect, similar to what is likely to have happened in Beringia (Rosenzweig and Mccord 1991) due to the presence of other carnivores, as Felidae, hindering the passage of competing lineages, which might have been the case along the Isthmus of Panama and North Africa. However, as tempting as this idea is, the extinction rates for all continents are very low, and we know from the observation of 75 species, that this value cannot be correct. Therefore, the low extinction rate for the extant-species phylogeny together with the CTD model being chosen for the complete tree practically disqualifies any interpretation we can get from the extant-species tree analyses. Thus, it is important to point out how our interpretations of the evolution of whole groups can radically change when fossil information is incorporated.

With respect to the models with the complete tree, no effect of biogeographic areas on rates of diversification was found, but there were differences in rates of transitions. According to the best supported model, the estimated per-lineage rate of area contraction was 0.297 per Myr, substantially faster than area expansion 0.055 per Myr. Model 17 also shows globally homogeneous rates of transition, and this model is much more supported than alternative expansion–contraction scenarios, in which transition rates differ among regions, like other CTD models 21, 31 and 37. The incumbency effect can be a good explanation for these low values of area expansion. To be able to disperse into new continents, Canidae lineages needed to pass through very narrow land areas such as the Bering Strait, the Isthmus of Panama and portions of land that connect Africa with Eurasia. These places probably had the presence of other carnivores that would hinder the passage of canids. For example, it was suggested by Silvestro et al. (2015) that Felidae might have contributed to increase the extinction rate in North American canids.

There are many possibilities why geographic areas are not important to explain the diversification of canids in our complete tree scenario. It is very unlikely that major events of dispersal around the world did not have a large impact on lineages (Porto et al. 2021), but probably there is one or there are a few traits that these fossil species carry with them, and are essential for a complete understanding of Canidae. The influence of an attribute such as "biogeographic area" on group diversification can be much more complex than what we have studied here, because at our continental scales a trait state can offer several ecological opportunities for the colonizing lineages. Two traits present themselves as potential candidates: 1) diet variation, such as omnivory, can be a strategy for surviving based on resource availability (Ingram et al. 2009) and, if lineages shift to omnivorous habits during moments of environmental perturbation, this may lead to low diversification (Van Valkenburgh et al. 2004). This could explain diversification of the South American clade, which contains several species with omnivorous diets; 2) body size is generally believed to contribute to diversification, because smaller species of mammals tend to have higher speciation rates, while larger species tend to have larger extinction probabilities (Liow et al. 2008).

In summary, our findings suggest that even though there is heterogeneity in rates of diversification for canids, the biogeographic region where the species occurs does not seem to drive this heterogeneity when we incorporate fossil species in our analyses. Thus, we highlight the effect that the inclusion of fossil information in our models has on our understanding about the evolution of Canidae, but we caution that the fossil information contains uncertainty that may bias results. In addition, we propose that more complex models can help our understanding about evolutionary dynamics. As lineages disperse to new continents, other traits (e.g., diet and body size) may have played prominent roles in the evolution of species and, together with distribution patterns, could bring a more complete scenario about diversification events through time.

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Supplementary Material

Table List

Table S1. List of the 111 species of Caninae included in our study with the distribution areas that they belong based on our eight biogeographical regions used here. Species marked with (*) are the extinct canids include in the tree of Porto et al. (2019).

Species	State
Canis lupus	NAM+EUR
Canis anthus	AFR
Canis aureus	EUR
Canis simensis	AFR
Canis rufus	NAM
Canis latrans	NAM
Cuon alpinus	EUR
Lycaon pictus	AFR
Canis adustus	AFR
Canis mesomelas	AFR
Lycalopex vetulus	SAM
Lycalopex sechurae	SAM
Lycalopex gymnocercus	SAM
Lycalopex culpaeus	SAM
Lycalopex fulvipes	SAM
Lycalopex griseus	SAM
Cerdocyon thous	SAM
Atelocynus microtis	SAM
Dusicyon australis	SAM
Chrysocyon brachyurus	SAM
Speothos venaticus	SAM
Vulpes rueppellii	EUR+AFR
Vulpes vulpes	NAM+EUR+AFR
Vulpes ferrilata	EUR
Vulpes corsac	EUR
Vulpes velox	NAM
Vulpes macrotis	NAM
Vulpes lagopus	NAM+EUR
Vulpes chama	AFR
Vulpes bengalensis	EUR
Vulpes pallida	AFR
Vulpes zerda	AFR
Vulpes cana	EUR

Nyctereutes procyonoides	EUR
Otocyon megalotis	AFR
Urocyon littoralis	NAM
Urocyon cinereoargenteus	NAM
*Canis dirus**	NAM+SAM
*Canis armbrusteri**	NAM
*Cuon javanicus**	EUR
*Canis ferox**	NAM
*Canis edwardii**	NAM
*Lycaon magnus**	AFR
*Canis lepophagus**	NAM
*Vulpes riffautae**	AFR
*Cerdocyon avius**	NAM+SAM
*Chrysocyon nearcticus**	NAM
*Dusicyon avus**	SAM
*Canis nehringi**	SAM
*Protocyon troglodytes**	SAM
*Protocyon scagliorum**	SAM
*Nyctereutes donnezani**	EUR
*Nyctereutes megamastoides**	EUR
*Speothos pacivorus**	SAM
*Vulpes stenognathus**	NAM
*Vulpes kernensis**	NAM
*Vulpes alopecoides**	EUR
*Vulpes praecorsac**	EUR
*Vulpes angustidens**	EUR
*Vulpes galaticus**	EUR
*Vulpes chikushanensis**	EUR
*Vulpes beihaiensis**	EUR
*Vulpes praeglacialis**	EUR
*Metalopex bakeri**	NAM
*Metalopex merriami**	NAM
*Metalopex macconnelli**	NAM
*Urocyon citrinus**	NAM
*Urocyon progressus**	NAM
*Urocyon galushai**	NAM
*Urocyon minicephalus**	NAM
*Prototocyon recki**	AFR
*Prototocyon curvipalatus**	EUR
*Nyctereutes tingi**	EUR
*Nyctereutes sinensis**	EUR
*Nyctereutes abdeslami**	AFR
*Nyctereutes terblanchei**	AFR
*Theriodictis floridanus**	NAM+SAM

*Theriodictis tarijensis**	SAM
*Theriodictis platensis**	SAM
*Eucyon intrepidus**	AFR
*Eucyon minor**	EUR
*Eucyon davisi**	NAM+EUR
*Eucyon zhoui**	EUR
*Eucyon monticinensis**	EUR
*Eucyon adoxus**	EUR
*Eucyon odessanus**	EUR
*Nurocyon chonokhariensis**	EUR
*Canis cipio**	EUR
*Canis etruscus**	EUR
*Canis falconeri**	EUR
*Canis arnensis**	EUR
*Canis antonii**	EUR
*Canis chihliensis**	EUR
*Canis palmidens**	EUR
*Canis variabilis**	EUR
*Canis teilhardi**	EUR
*Canis longdanensis**	EUR
*Canis brevicephalus**	EUR
*Cynotherium sardous**	EUR
*Canis cedazoensis**	NAM
*Canis gezi**	SAM
*Canis mosbachensis**	EUR
*Xenocyon africanus**	AFR
*Lycaon sekowei**	AFR
*Xenocyon dubius**	EUR
*Xenocyon texanus**	NAM
*Xenocyon lycaonoides**	NAM+EUR+AFR
*Cerdocyon texanus**	NAM
*Canis feneus**	NAM
*Canis thöoides**	NAM
*Urocyon webbi**	NAM

Table S2. Model comparison based on AIC for the models tested with the complete tree. Models differ in what state changes are allowed, and whether state changes occur during speciation. CR = Constant Rates; CTD = Concealed trait-dependent; ETD = Examined trait-dependent; K = number of free parameters.

Model	Trait-dependence	loglikelihood	K	AIC	ΔAIC	AICw
17	CTD	-599.464	5	1208.928	0	0.999999999
19	CTD	-619.506	6	1251.012	42.084	7.27E-10
9	CTD	-621.335	7	1256.67	47.742	4.29E-11
5	CTD	-629.585	4	1267.169	58.242	2.25E-13
13	CTD	-632.153	4	1272.306	63.379	1.73E-14
15	CTD	-633.217	4	1274.434	65.507	5.96E-15
21	CTD	-632.285	5	1274.569	65.642	5.57E-15
23	CTD	-632.209	6	1276.418	67.49	2.21E-15
28	ETD	-642.022	7	1298.045	89.117	4.45E-20
33	CTD	-642.931	7	1299.862	90.934	1.79E-20
26	ETD	-644.158	6	1300.316	91.388	1.43E-20
38	ETD	-644.049	7	1302.097	93.17	5.87E-21
24	ETD	-647.521	5	1305.043	96.115	1.35E-21
43	CTD	-645.696	7	1305.391	96.463	1.13E-21
4	ETD	-649.686	4	1307.373	98.445	4.20E-22
18	ETD	-648.877	6	1309.754	100.826	1.28E-22
44	ETD	-648.301	7	1310.602	101.674	8.35E-23
16	ETD	-650.392	5	1310.784	101.857	7.62E-23
22	ETD	-649.54	6	1311.08	102.152	6.58E-23
31	CTD	-815.176	7	1311.471	102.544	5.41E-23
32	ETD	-648.736	7	1311.471	102.544	5.41E-23
6	ETD	-651.016	5	1312.032	103.104	4.09E-23
1	CR	-653.137	3	1312.273	103.345	3.62E-23
30	ETD	-649.358	7	1312.717	103.789	2.90E-23
12	ETD	-652.404	4	1312.808	103.881	2.77E-23
20	ETD	-651.779	5	1313.558	104.631	1.90E-23
10	ETD	-652.998	4	1313.996	105.069	1.53E-23
14	ETD	-653.079	4	1314.157	105.229	1.41E-23
2	ETD	-653.7	4	1315.401	106.473	7.58E-24
11	CTD	-653.924	4	1315.847	106.919	6.06E-24
42	ETD	-651.471	7	1316.941	108.014	3.51E-24
7	CTD	-653.796	5	1317.591	108.664	2.54E-24
8	ETD	-652.052	7	1318.104	109.177	1.96E-24
36	ETD	-652.148	7	1318.296	109.369	1.78E-24
34	ETD	-652.511	7	1319.022	110.094	1.24E-24
40	ETD	-653.623	6	1319.246	110.318	1.11E-24
3	CTD	-657.714	4	1323.427	114.5	1.37E-25
37	CTD	-663.628	7	1341.256	132.329	1.84E-29
29	CTD	-998.813	7	2011.625	802.698	4.97E-175
35	CTD	-1139.602	7	2293.204	1084.277	3.57E-236
27	CTD	-1880.189	6	3772.378	2563.45	0
39	CTD	-3167.797	7	6349.595	5140.667	0
25	CTD	-3400.495	5	6810.99	5602.062	0
45	CTD	-5559.671	7	11133.343	9924.415	0
41	CTD	-11952.555	6	23917.11	22708.183	0

Table S3. Estimates of all the parameters used in each model for the complete tree. Models are ordered from best fitted model to the worst.

Model	λ_1	λ_2	λ_3	λ_4	λ_5	μ_1	μ_2	μ_3	μ_4	q_1	q_2	q_3	q_4
17	2.70E-15	3.92E-15	0.344	-	-	0.297	0	-	-	0.055	-	-	-
19	0.004	0.429	-	-	-	0.188	0	5.36E-46	0.359	0.033	-	-	-
9	2.77E-71	0.34	0	-	-	0.302	0	6.89E-48	-	0.063	3.42E-07	-	-
5	0.175	-	-	-	-	0.266	0	-	-	0.062	1.01E-15	-	-
13	0.175	-	-	-	-	0.264	0	1.033	-	0.057	-	-	-
15	0.175	-	-	-	-	0.266	0	-	-	0.057	0.041	-	-
21	0.174	-	-	-	-	0.268	0	-	-	0.024	0.042	0.062	-
23	0.175	2.68E-15	-	-	-	0.269	0	-	-	0.024	0.042	0.062	-
28	0.153	0.033	0.208	0.291	0.014	0.199	0	-	-	0.09	-	-	-
33	2.18E-32	5.39E-56	0.197	1.23E-53	-	0.709	0	0.139	-	0.069	-	-	-
26	0.25	0.035	0.207	0.014	-	0.197	0	-	-	0.088	-	-	-
38	0.187	0.188	0.014	-	-	0.168	0	-	-	0.071	0.02	1.06E-16	-
24	0.186	0.191	0.019	-	-	0.17	0	-	-	0.062	-	-	-
43	9.32E-25	7.51E-08	0.258	-	-	0.68	0	0.191	-	0.088	0.018	-	-
4	0.17	-	-	-	-	0.169	0	-	-	0.068	2.07E-15	-	-
18	0.225	0.021	-	-	-	0.306	0	0.171	0.186	0.093	-	-	-
44	0.157	1.253	0.03	-	-	0.147	0	0.105	-	0.049	1.58E-14	-	-
16	0.183	0.236	0.032	-	-	0.195	0	-	-	0.083	-	-	-
22	0.214	0.034	-	-	-	0.195	0	-	-	0.03	0.067	0.092	-
31	2.75E-17	62.694	-	-	-	0.713	0	-	-	1.262	0.564	0.836	0.446
32	0.142	1.878	0.182	0.043	-	0.154	0	0.106	-	0.046	-	-	-
6	0.131	2.334	-	-	-	0.137	0	-	-	0.054	1.03E-14	-	-
1	0.17	-	-	-	-	0.169	0	-	-	0.061	-	-	-
30	0.217	0.029	-	-	-	0.196	0	-	-	0.081	0.112	0.071	0.03

12	0.17	-	-	-	-	0.179	0	0.125	-	0.061	-	-	-
20	0.17	-	-	-	-	0.169	0	-	-	0.021	0.052	0.068	-
10	0.166	0.191	-	-	-	0.17	0	-	-	0.061	-	-	-
14	0.17	-	-	-	-	0.169	0	-	-	0.062	0.051	-	-
2	0.131	2.055	-	-	-	0.137	0	-	-	0.046	-	-	-
11	3.15E-15	0.223	-	-	-	0.188	0	-	-	0.066	-	-	-
42	0.102	2.108	0.142	-	-	0.16	0	0.13	-	0.056	0.022	-	-
7	0.226	0	-	-	-	0.206	0	-	-	0.071	1.53E-17	-	-
8	0.118	2.308	0.183	-	-	0.142	0	0.113	-	0.051	0.028	-	-
36	0.145	1.774	0.115	-	-	0.136	0	-	-	0.052	0.013	0.015	-
34	0.138	1.978	0.122	-	-	0.153	0	0.117	0.093	0.046	-	-	-
40	0.137	2.095	0.126	-	-	0.141	0	0.134	-	0.046	-	-	-
3	0.22	0	-	-	-	0.2	0	-	-	0.062	-	-	-
37	3.03E-18	4.59E-41	0.172	-	-	0.153	0	-	-	0.068	3.90E-40	1.07E-32	-
29	0.04	0.365	2.53E-15	3.41E-13	7.28E-13	0.241	0	-	-	4.05E-07	-	-	-
35	6.47E-61	1.54E-51	0.178	-	-	0	0	6.78E-39	0.095	1.15E-07	-	-	-
27	9.12E-16	0.344	1.41E-19	6.40E-15	-	0.297	0	-	-	0.055	-	-	-
39	3.05E-16	0.001	6.69E-37	-	-	9.18E-10	0	-	-	6.42E-09	0.288	5.09E-10	-
25	0.217	5.40E-08	4.81	-	-	9.07E-17	0	-	-	1.78E-05	-	-	-
45	1.16E-28	1.57E-26	7.32E-28	-	-	0.635	0	2.14E-43	-	9.34E-07	1.64E-08	-	-
41	1.18E-66	3.39E-36	1.86E-28	-	-	8.66E-72	0	1.32E-25	-	1.02E-08	-	-	-

Table S4. Model comparison based on AIC for the models tested with the extant-species tree. Models differ in what state changes are allowed, and whether state changes occur during speciation. CR = Constant Rates; CTD = Concealed trait-dependent; ETD = Examined trait-dependent; K = number of free parameters.

Model	Trait-dependence	loglikelihood	K	AIC	ΔAIC	AICw
38	ETD	-146.305	7	306.61	0	0.27574
36	ETD	-146.39	7	306.781	0.171	0.25319
22	ETD	-148.533	6	309.066	2.455	0.08078
13	CTD	-150.673	4	309.346	2.735	0.07022
21	CTD	-149.711	5	309.422	2.811	0.06761
30	ETD	-147.964	7	309.928	3.318	0.05249
39	CTD	-148.252	7	310.504	3.894	0.03934
23	CTD	-149.701	6	311.401	4.791	0.02513
19	CTD	-149.72	6	311.439	4.829	0.02466
31	CTD	-173.311	7	311.686	5.075	0.0218
32	ETD	-148.843	7	311.686	5.075	0.0218
37	CTD	-149.218	7	312.436	5.826	0.01498
18	ETD	-150.444	6	312.889	6.279	0.01194
42	ETD	-149.807	7	313.614	7.004	0.00831
44	ETD	-149.943	7	313.886	7.276	0.00725
20	ETD	-152.133	5	314.266	7.655	0.006
34	ETD	-150.464	7	314.928	8.318	0.00431
3	CTD	-153.968	4	315.935	9.325	0.0026
2	ETD	-154.14	4	316.281	9.671	0.00219
16	ETD	-153.48	5	316.96	10.35	0.00156
26	ETD	-152.495	6	316.991	10.381	0.00154
40	ETD	-152.602	6	317.203	10.593	0.00138
6	ETD	-153.936	5	317.871	11.261	0.00099
17	CTD	-153.962	5	317.923	11.313	0.00096
11	CTD	-155.259	4	318.517	11.907	0.00072
28	ETD	-152.484	7	318.967	12.357	0.00057
5	CTD	-155.674	4	319.348	12.738	0.00047
12	ETD	-155.809	4	319.619	13.008	0.00041
24	ETD	-155.098	5	320.195	13.585	0.00031
9	CTD	-153.236	7	320.472	13.862	0.00027
7	CTD	-155.602	5	321.204	14.593	0.00019
1	CR	-157.936	3	321.872	15.262	0.00013
4	ETD	-157.372	4	322.743	16.133	0.00009
10	ETD	-157.966	4	323.933	17.322	0.00005
15	CTD	-158.863	4	325.726	19.116	0.00002
41	CTD	-157.852	6	327.703	21.093	0.00001
8	ETD	-157.73	7	329.459	22.849	0
14	ETD	-160.762	4	329.523	22.913	0
29	CTD	-159.369	7	332.738	26.128	0
33	CTD	-159.369	7	332.738	26.128	0
35	CTD	-234.67	7	483.339	176.729	0
25	CTD	-915.007	5	1840.014	1533.404	0
27	CTD	-1734.635	6	3481.269	3174.659	0
45	CTD	-1771.978	7	3557.957	3251.347	0
43	CTD	-1827.683	7	3669.366	3362.756	0

Table S5. Estimates of all the parameters used in each model for the extant-species tree. Models are ordered from best fitted model to the worst.

Model	λ_1	λ_2	λ_3	λ_4	λ_5	μ_1	μ_2	μ_3	μ_4	q_1	q_2	q_3	q_4
38	0.199	0.136	0.021	-	-	3.09E-15	0	-	-	0.113	3.02E-16	6.35E-15	-
36	0.133	0.403	0.095	-	-	0.012	0	-	-	0.117	1.87E-15	3.27E-16	-
22	0.097	0.414	-	-	-	1.48E-16	0	-	-	6.68E-18	0.064	0.108	-
13	0.139	-	-	-	-	0.885	0	7.26E-18	-	0.186	-	-	-
21	0.166	-	-	-	-	0.178	0	-	-	1.71E-16	0.116	0.165	-
30	0.096	0.415	-	-	-	9.46E-18	0	-	-	0.126	0.065	0.063	7.73E-17
39	0.174	1.57E-28	3.94E-20	-	-	0.149	0	-	-	0.155	3.17E-21	2.71E-42	-
23	0.168	0.062	-	-	-	0.179	0	-	-	8.40E-16	0.12	0.162	-
19	6.10E-11	0.227	-	-	-	0.721	0	1.50E-19	0.309	0.122	-	-	-
31	1.73E-29	4.169	-	-	-	0.719	0	-	-	1.163	1.579	0.582	4.21E-43
32	0.203	0.447	0.125	0.024	-	0.165	0	2.83E-15	-	0.087	-	-	-
37	0.327	1.19E-58	4.11E-38	-	-	0.148	0	-	-	0.138	2.84E-42	1.63E-20	-
18	0.101	0.547	-	-	-	0.214	0	1.80E-15	0.059	0.102	-	-	-
42	0.23	0.598	0.085	-	-	0.364	0	1.08E-15	-	0.115	0.06	-	-
44	0.149	0.422	0.021	-	-	0.046	0	1.40E-13	-	0.087	2.98E-15	-	-
20	0.184	-	-	-	-	0.095	0	-	-	1.63E-16	0.102	0.126	-
34	0.201	0.454	0.086	-	-	0.168	0	4.01E-15	4.78E-15	0.089	-	-	-
3	0.005	0.229	-	-	-	0.206	0	-	-	0.105	-	-	-
2	0.104	0.485	-	-	-	0.026	0	-	-	0.082	-	-	-
16	0.128	0.068	0.492	-	-	0.02	0	-	-	0.083	-	-	-
26	0.114	0.391	0.136	0.026	-	1.19E-17	0	-	-	0.073	-	-	-
40	0.139	0.531	0.057	-	-	0.057	0	2.79E-16	-	0.086	-	-	-
6	0.098	0.392	-	-	-	1.43E-14	0	-	-	0.066	0.154	-	-
17	4.93E-14	0.011	0.229	-	-	0.206	0	-	-	0.105	-	-	-
11	0.036	0.258	-	-	-	0.127	0	-	-	0.11	-	-	-

28	0.106	0.39	0.136	0.12	0.025	2.91E-13	0	-	-	0.073	-	-	-
5	0.165	-	-	-	-	0.156	0	-	-	0.096	0.252	-	-
12	0.183	-	-	-	-	0.14	0	1.01E-14	-	0.098	-	-	-
24	0.211	0.15	0.03	-	-	0.037	0	-	-	0.077	-	-	-
9	7.72E-12	0.244	2.11E-24	-	-	0.413	0	1.64E-24	-	0.21	2.12E-14	-	-
7	0.255	0.038	-	-	-	0.114	0	-	-	0.095	0.192	-	-
1	0.182	-	-	-	-	0.088	0	-	-	0.087	-	-	-
4	0.186	-	-	-	-	0.096	0	-	-	0.098	1.71E-15	-	-
10	0.183	0.176	-	-	-	0.088	0	-	-	0.088	-	-	-
15	0.163	-	-	-	-	0.164	0	-	-	0.141	2.35E-17	-	-
41	3.99E-22	1.78E-42	0.23	-	-	6.55E-14	0	0.096	-	0.086	-	-	-
8	0.056	0.395	0.119	-	-	1.66E-37	0	1.69E-24	-	0.099	3.27E-18	-	-
14	0.182	-	-	-	-	0.099	0	-	-	0.117	3.57E-15	-	-
29	7.71E-28	4.09E-17	0.172	1.49E-28	1.49E-29	3.33E-16	0	-	-	0.068	-	-	-
33	3.25E-10	3.28E-34	0.172	9.78E-22	-	2.65E-28	0	1.07E-50	-	0.068	-	-	-
35	1.03E-80	1.17E-61	0.152	-	-	7.38E-82	0	7.46E-43	1.48E-62	0	-	-	-
25	7.73E-13	3.33E-14	0	-	-	4.95E-24	0	-	-	6.16E-08	-	-	-
27	1.24E-20	3.61E-24	2.58E-23	1.44E-18	-	1.18E-33	0	-	-	3.98E-08	-	-	-
45	1.27E-34	2.37E-33	0.143	-	-	4.56E-19	0	1.38E-15	-	0.081	7.48E-40	-	-
43	4.68E-25	6.28E-18	6.74E-26	-	-	1.80E-36	0	1.97E-22	-	1.98E-11	3.43E-12	-	-

Figure List

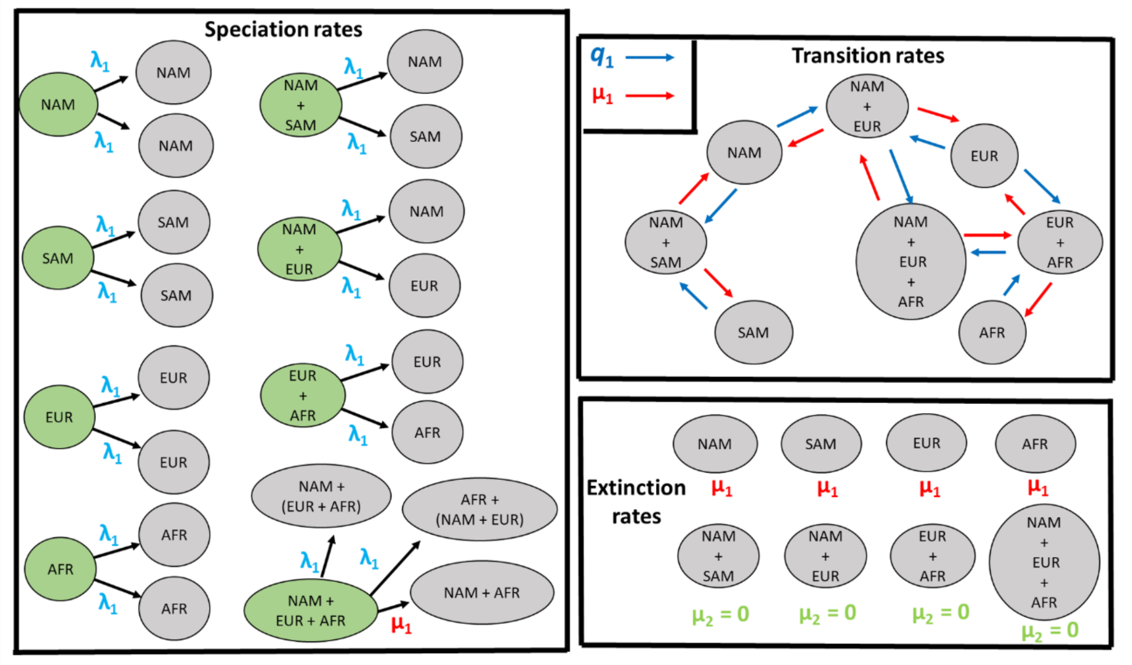

Figure S1. Diagram representing the Constant-Rate model (model 1). This model has 3 free parameters to be estimated (λ_1, μ_1 and q_1). Transitions from multiple-area states to single-area states were regarded as extinctions (μ_1). In the CR model, all species have the same speciation rate regardless of their trait state (e.g., $\lambda_{1A} = \lambda_{1B} = \lambda_{1C}$), where the numbers refer to the observed and examined biogeographic state and the letter to the unknown hidden trait. For all models, the extinction rate for multiple-area states was fixed to zero ($\mu_2 = 0$), and transitions from multiple-area states to single-area states were regarded as extinctions (μ_1).

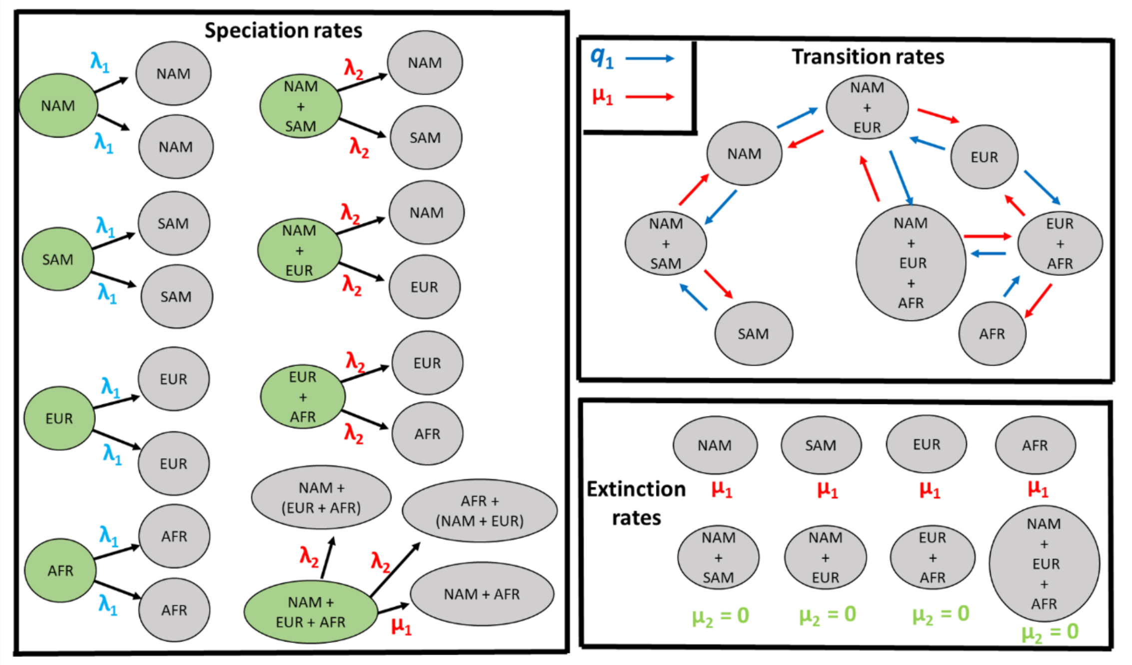

Figure S2. Diagram representing the model 2. This ETD model has 4 free parameters to be estimated (λ_1, λ_2, μ_1 and q_1). Transitions from multiple-area states to single-area states were regarded as extinctions (μ_1). In this ETD model, speciation rates are allowed to vary only for the examined states, and then only between sympatric and allopatric speciation. This model assumes that there is a difference between sympatric and allopatric speciation in canid diversification.

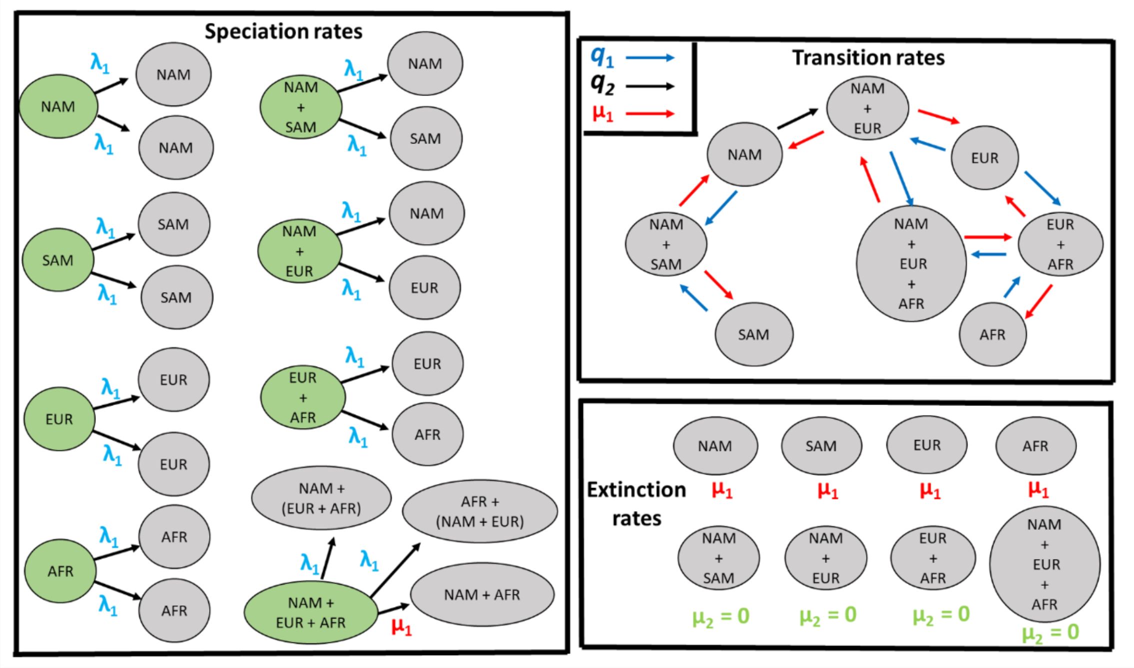

Figure S3. Diagram representing model 4. This ETD model has 4 free parameters to be estimated (λ_1, μ_1, q_1 and q_2). It is a generalization of the CR model (model 1) with one more transition rate. This model tests if transitions among new and old world were lower or higher than transitions within old world and new world. Here we are interested if crossing the Bering land-bridge was more difficult than crossing to areas within new and old world. Some evidence suggests that crossing from North America to Eurasia was difficult for some lineages due the felines in Siberia (incumbency effect).

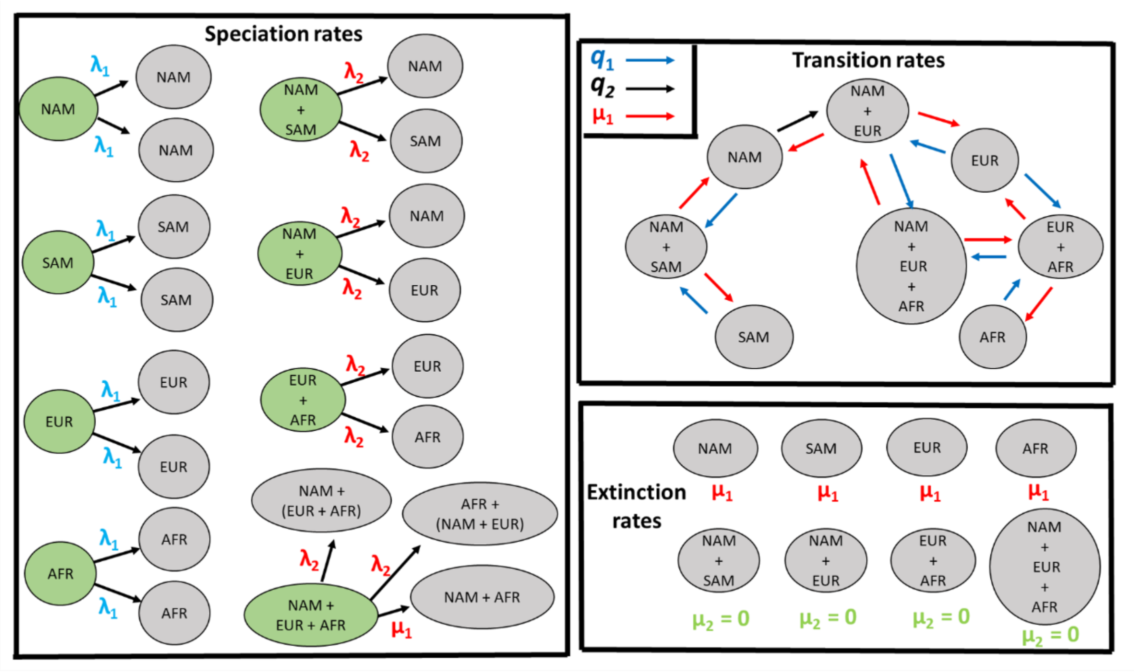

Figure S4. Diagram representing model 6. This ETD model is similar to model 2, but with one more transition rate (5 free parameters - λ_1, λ_2, μ_1, q_1 and q_2). Here assume that there is a difference between sympatric and allopatric speciation in canid diversification, and we test if transitions among new and old world were lower or higher than transitions within old world and new world (we are interested if crossing the Bering land-bridge was more difficult than crossing to areas within new and old world). Some evidence suggests that crossing from North America to Eurasia was difficult for some lineages due the felines in Siberia (incumbency effect).

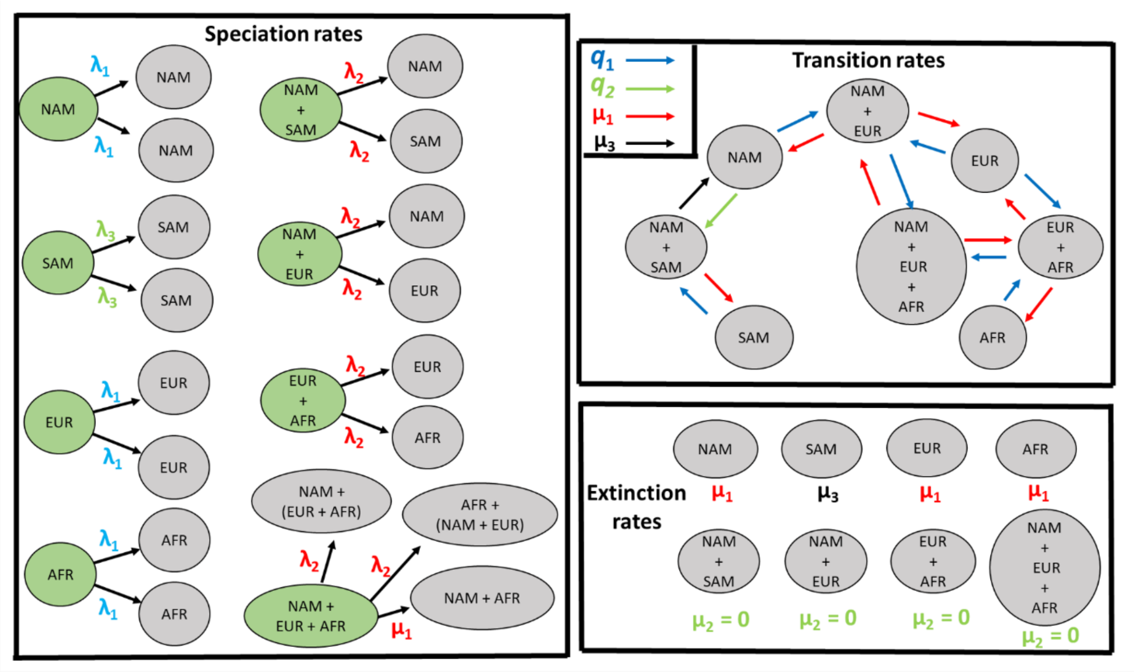

Figure S5. Diagram representing model 8. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, μ_3, q_1 and q_2). Transitions from multiple-area states to single-area states were regarded as extinctions (μ_1). This model tests for 1) a difference between sympatric and allopatric speciation in canid diversification; 2) distinct speciation and extinction rates in S. America.

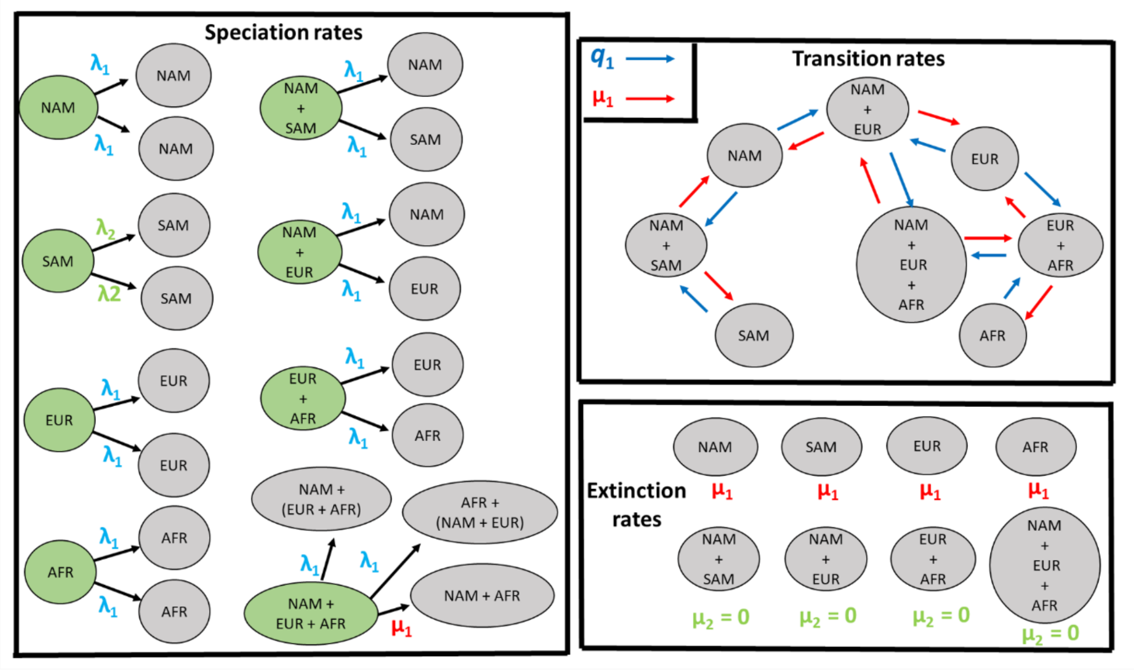

Figure S6. Diagram representing model 10. This ETD model has 4 free parameters to be estimated (λ_1, λ_2, μ_1 and q_1). This model tests fora distinct speciation rate of S. America compared to the rest of the world.

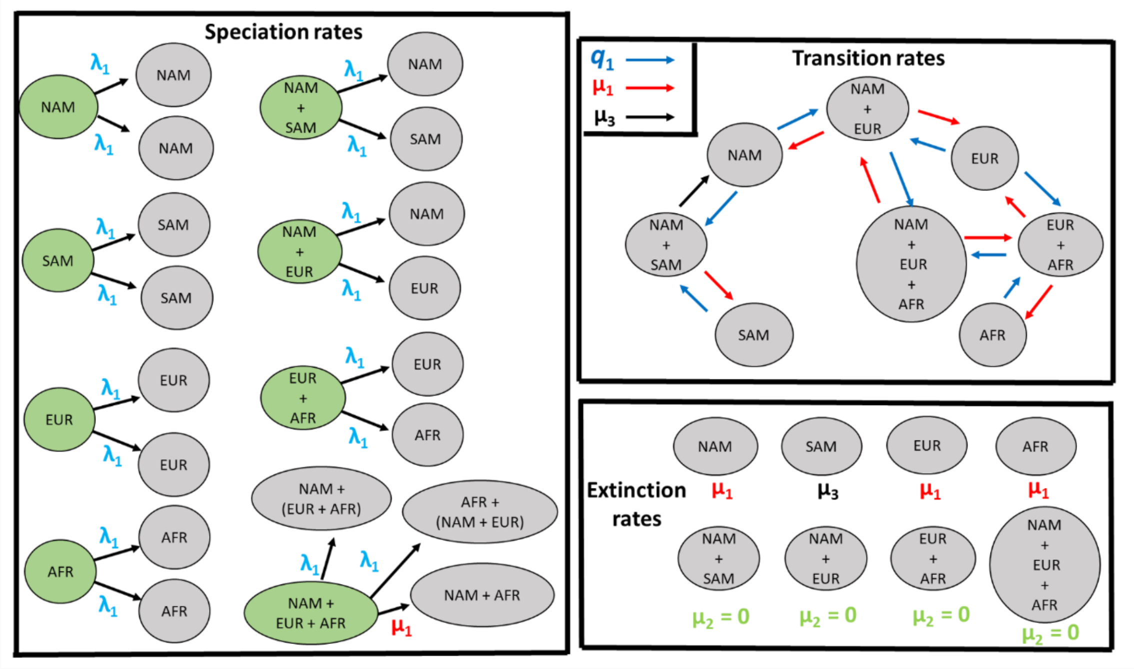

Figure S7. Diagram representing model 12. This ETD model has 4 free parameters to be estimated (λ_1, μ_1, μ_3 and q_1). This model assumes a distinct speciation rate for S. America compared to the rest of the world and a specific rate of extinction in S. America.

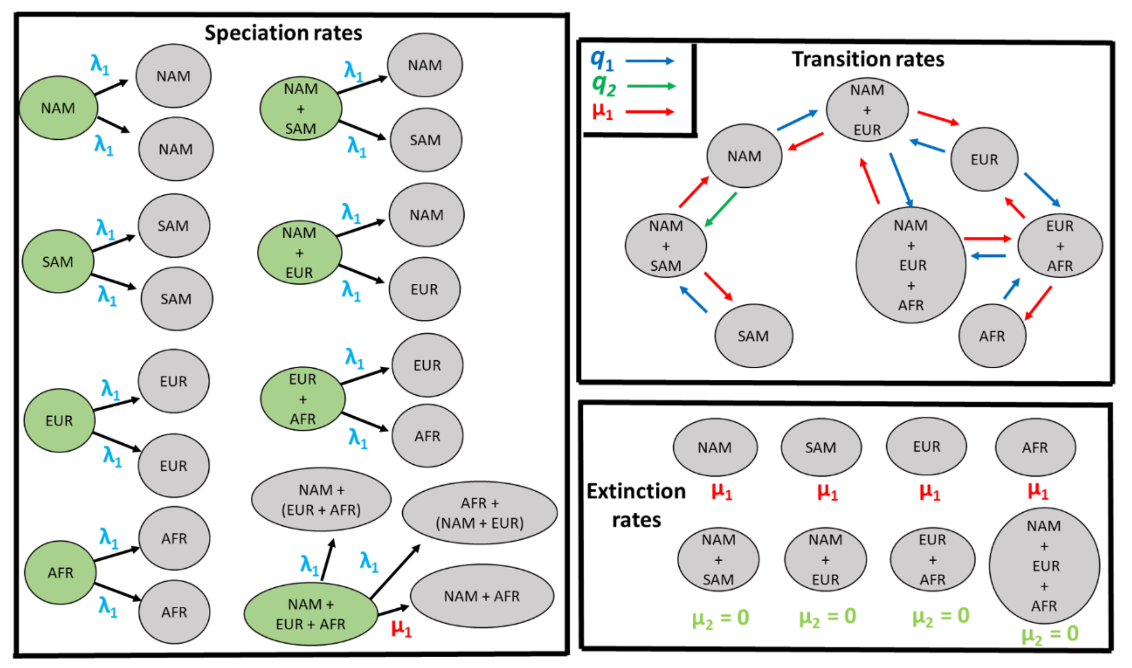

Figure S8. Diagram representing model 14. This ETD model has 4 free parameters to be estimated) (λ_1, μ_1, q_1 and q_2). This model assumes distinct speciation and extinction rates for old and new world and a distinct transition rate to South America.

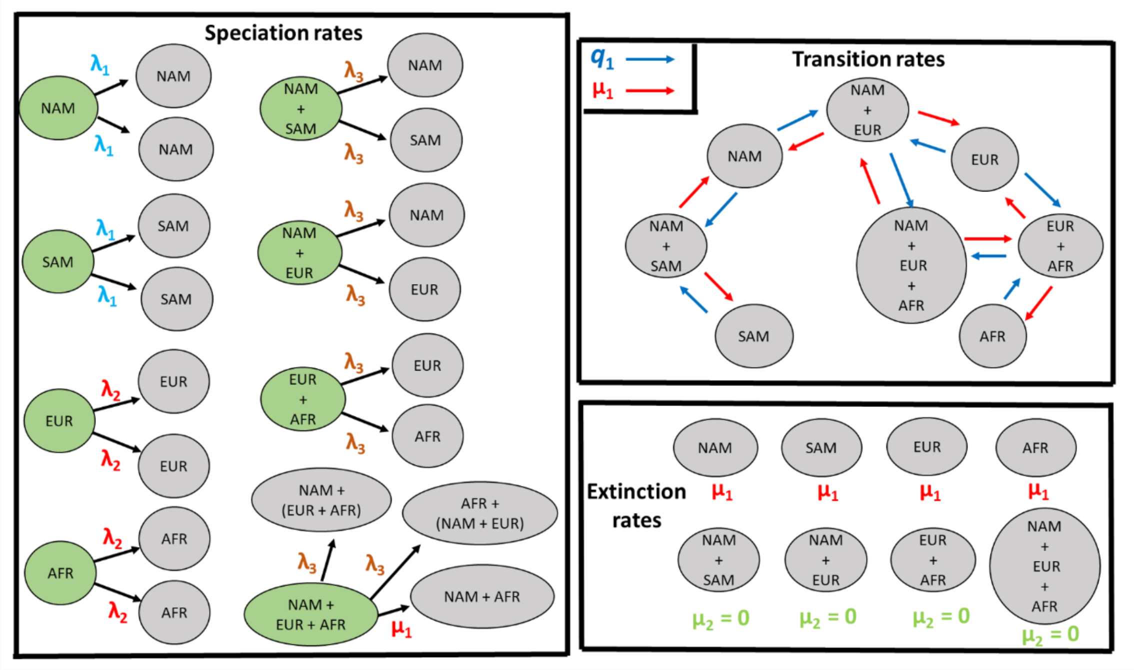

Figure S9. Diagram representing model 16. This ETD model has 5 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1 and q_1). This model tests for distinct speciation rates for sympatric speciation in new and old worlds, and a third rate for allopatric speciation. The justification for exploration of this model is that North American lineages of carnivores invading Eurasia underwent explosive radiations, whereas lineages invading North America maintained uniform diversification dynamics.

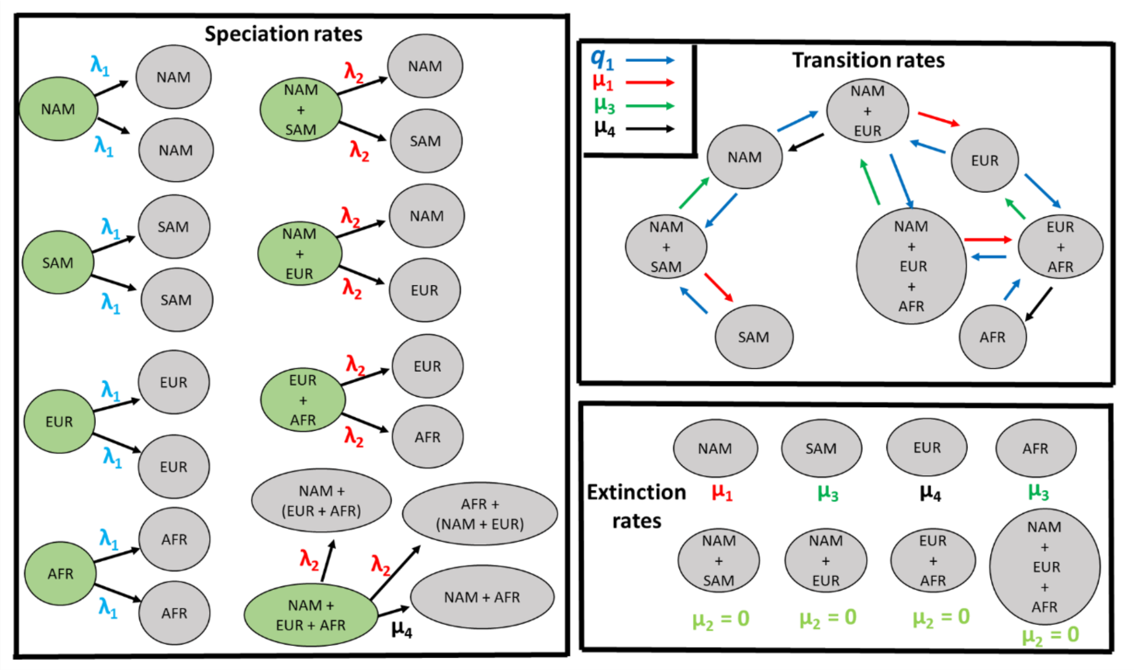

Figure S10. Diagram representing model 18. This ETD model has 6 free parameters to be estimated (λ_1, λ_2, μ_1, μ_3, μ_4 and q_1). Here we test if extinction rates were higher in North America, because Pires et al. (2015) suggest that diversification rates of carnivores in this continent were lower than in Eurasia, which could be due to the entrance of felines from Eurasia hunting for and competing with canids.

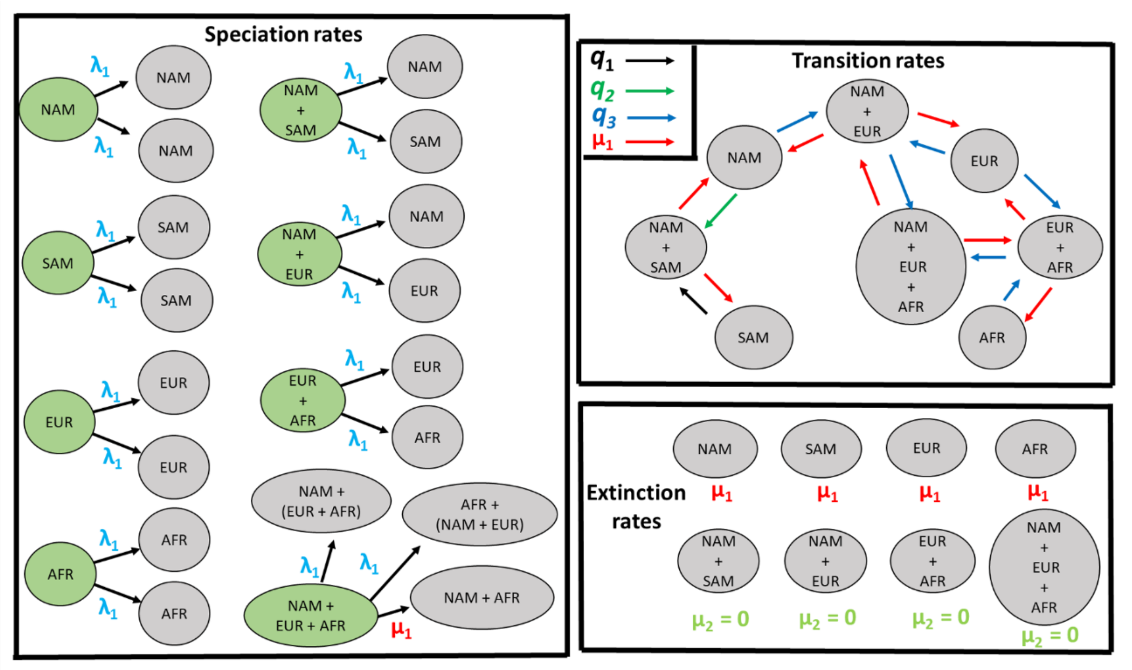

Figure S11. Diagram representing model 20. This ETD model has 5 free parameters to be estimated (λ_1, μ_1, q_1, q_2, and q_3). This model tests if South American lineages expanded more their distributions to North America or if North American lineages expanded more to the south. This explores how strong the Panama land-bridge was as a filter for the lineages in both regions.

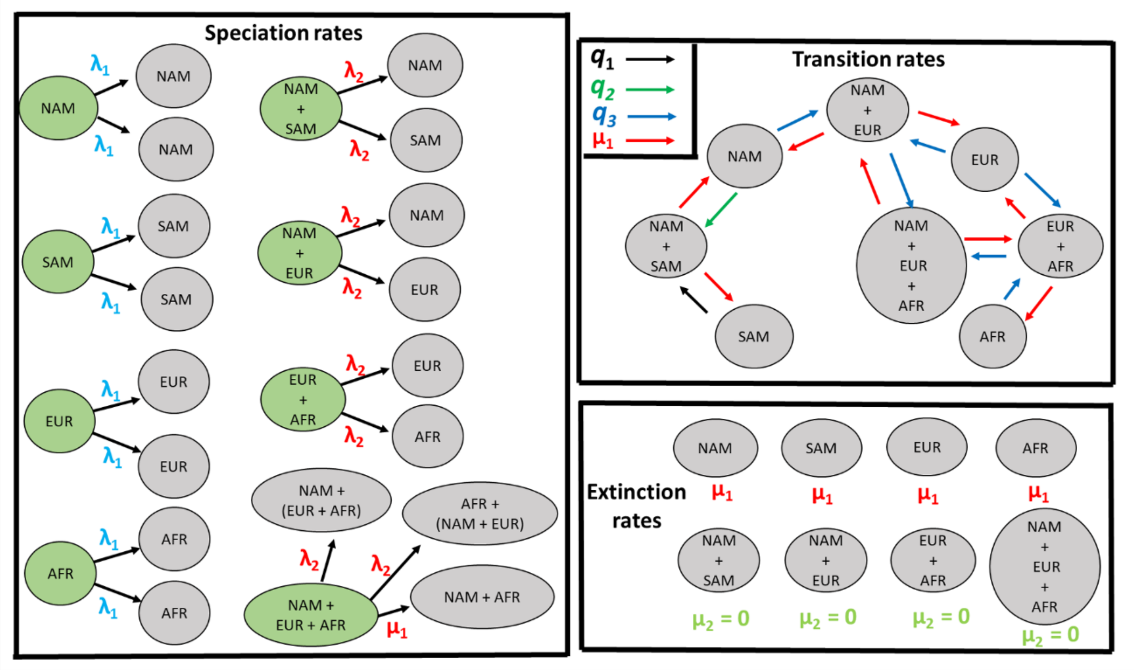

Figure S12. Diagram representing model 22. This ETD model has 6 free parameters to be estimated (λ₁, λ₂, μ₁, q_1, q_2, and q_3). This model assumes distinct speciation rates for sympatric and allopatric speciation, and explores if South American lineages expanded more their distributions to North America or if North American lineages expanded more to the south. This explores how strong the Panama land-bridge was as a filter for the lineages in regions.

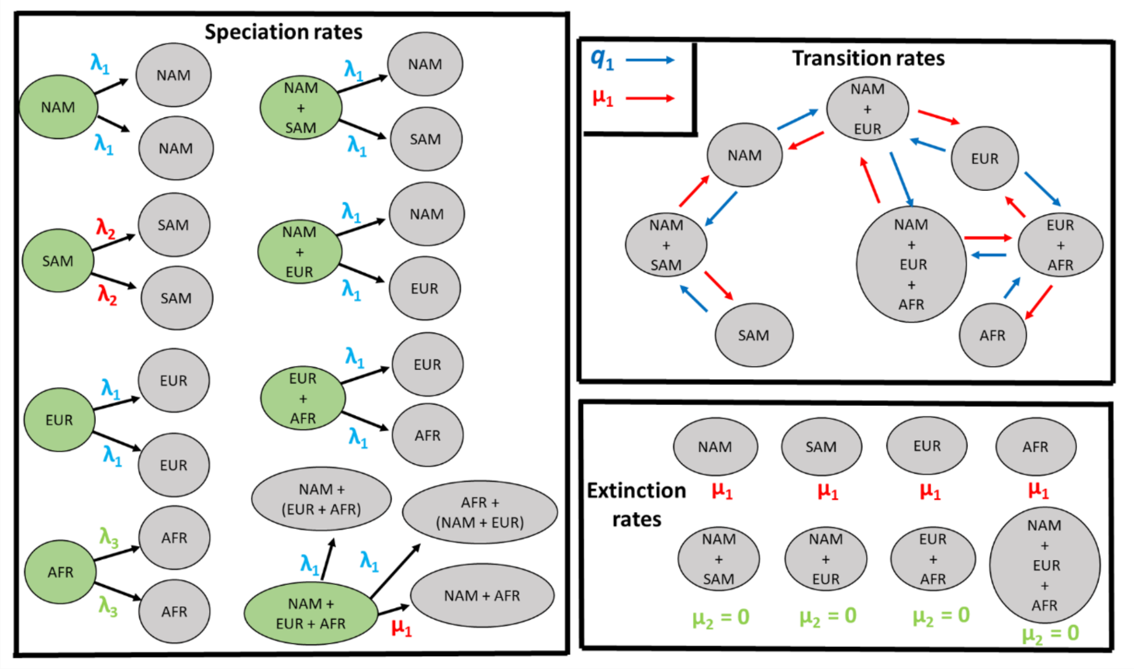

Figure S13. Diagram representing model 24. This ETD model has 5 free parameters to be estimated (λ₁, λ₂, λ₃, μ₁, and q_1). This model assumes the same speciation rate for sympatric and allopatric speciation, and two distinct speciation rates for Africa and S. America. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

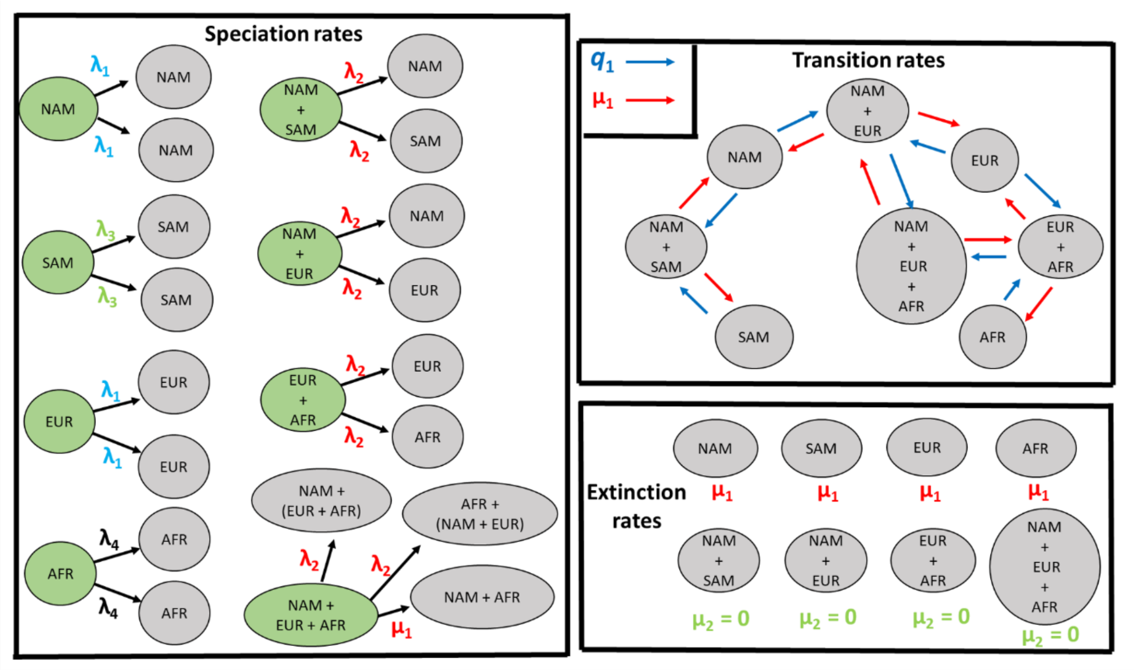

Figure S14. Diagram representing model 26. This ETD model has 6 free parameters to be estimated (λ_1, λ_2, λ_3, λ_4, μ_1, and q_1). This model assumes distinct speciation rates for sympatric and allopatric speciation, and distinct speciation rates for Africa and S. America. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

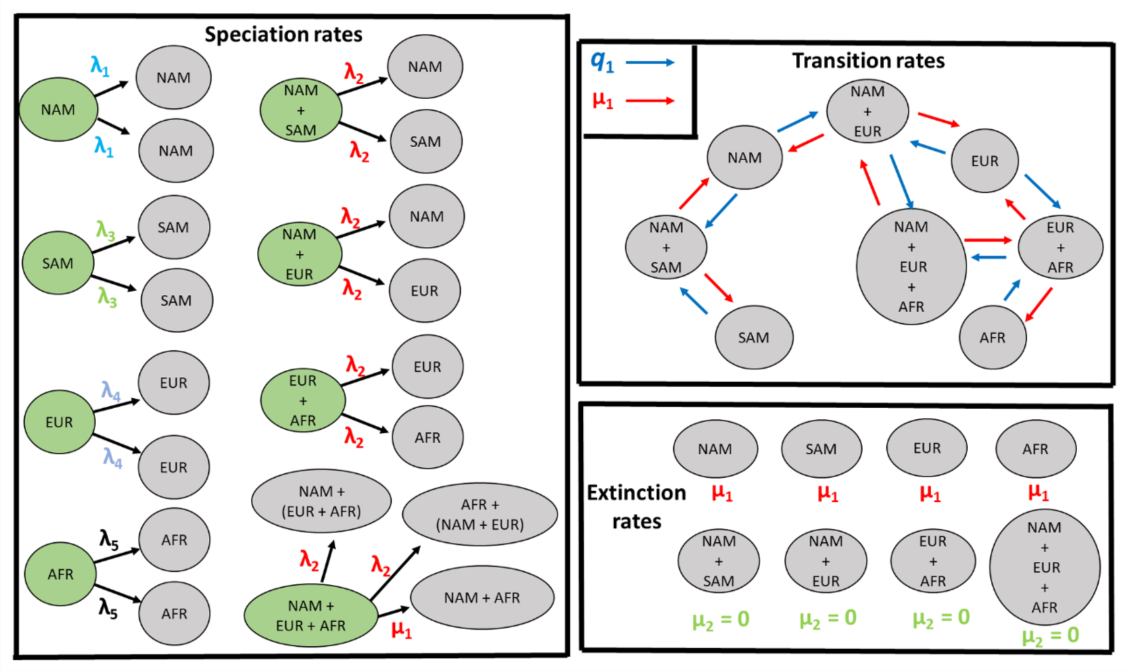

Figure S15. Diagram representing model 28. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, λ_4, λ_5, μ_1, and q_1). This model assumes distinct speciation rates for sympatric and allopatric speciation, and distinct dynamics of sympatric speciation in 4 areas.

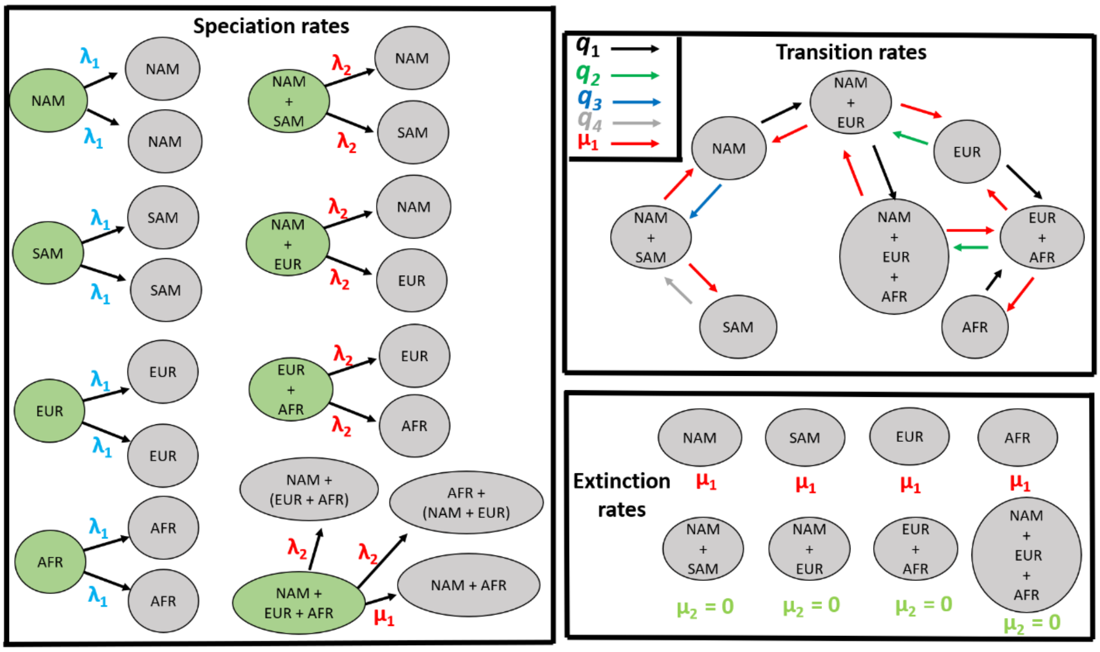

Figure S16. Diagram representing model 30. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, μ_1, q_1, q_2, q_3, and q_4). This model assumes distinct speciation rates for sympatric and allopatric speciation, and explores if Eurasian lineages expanded more their distributions to North America or North American lineages expanded more to Eurasia (if there is a higher transition to N. America from Eurasia than the other way around, this could suggest that Felidae really imposed an incumbent effect on Canids throughout Beringia). The model also explores how strong the Panama bridge was as a filter for N. American lineages and S. American lineages that tried to cross it.

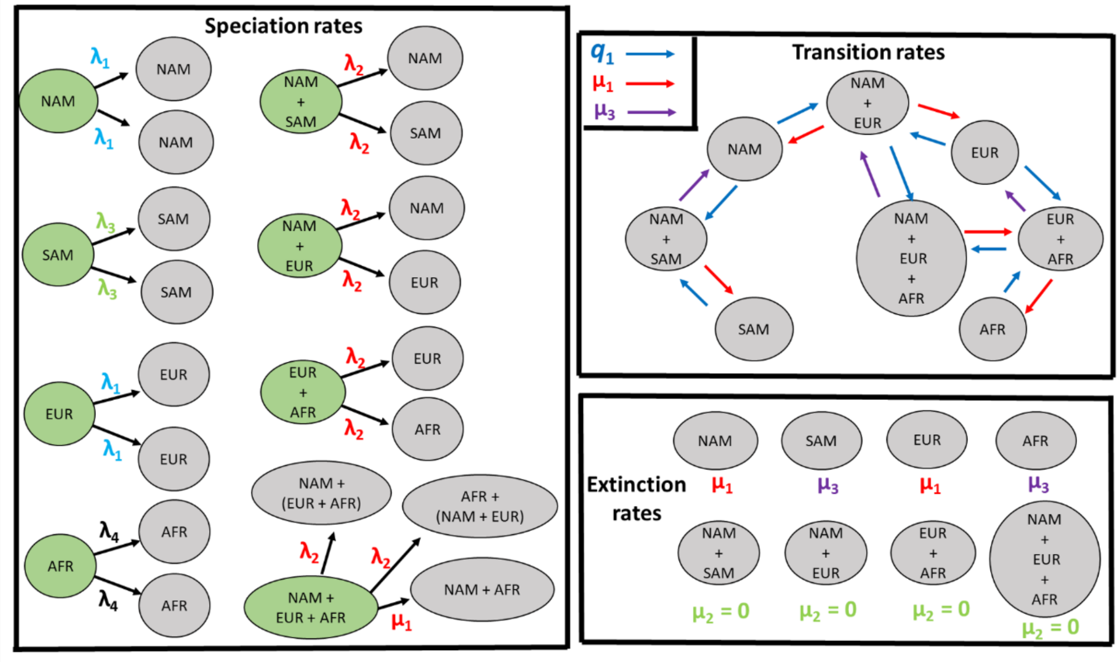

Figure S17. Diagram representing model 32. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, λ_4, μ_1, μ_3, and q_1). This model assumes distinct speciation rates for sympatric and allopatric speciation, and assumes one speciation rate for S. America and another for Africa. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

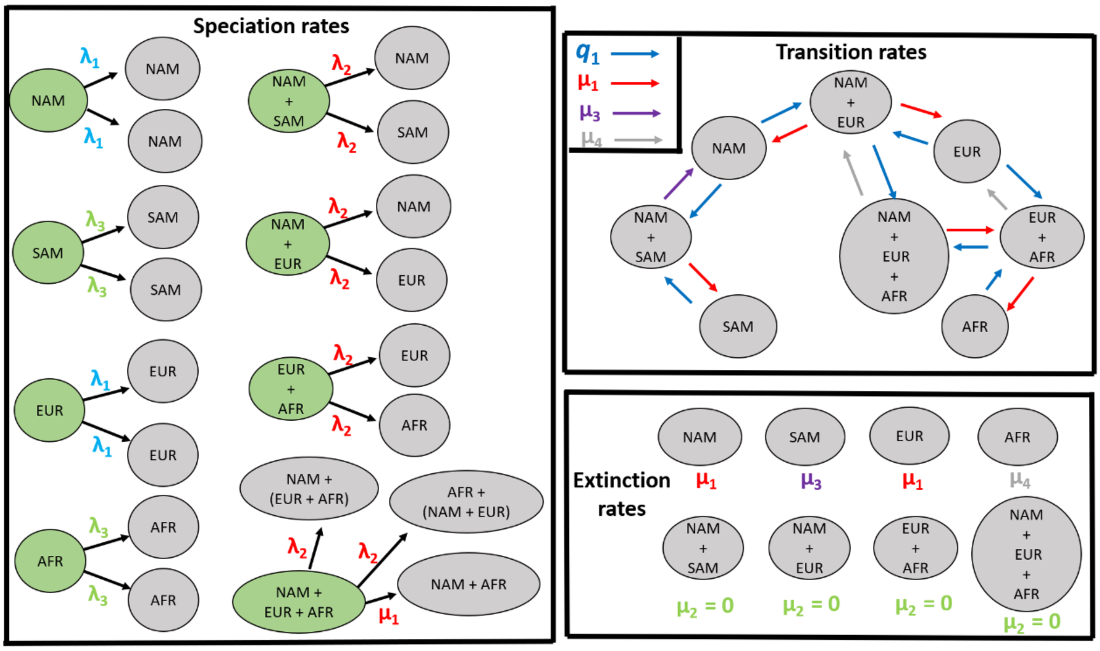

Figure S18. Diagram representing model 34. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, μ_3, μ_4, and q_1). This model assumes distinct speciation rates for sympatric and allopatric speciation, and the same speciation rate for S. America and Africa. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

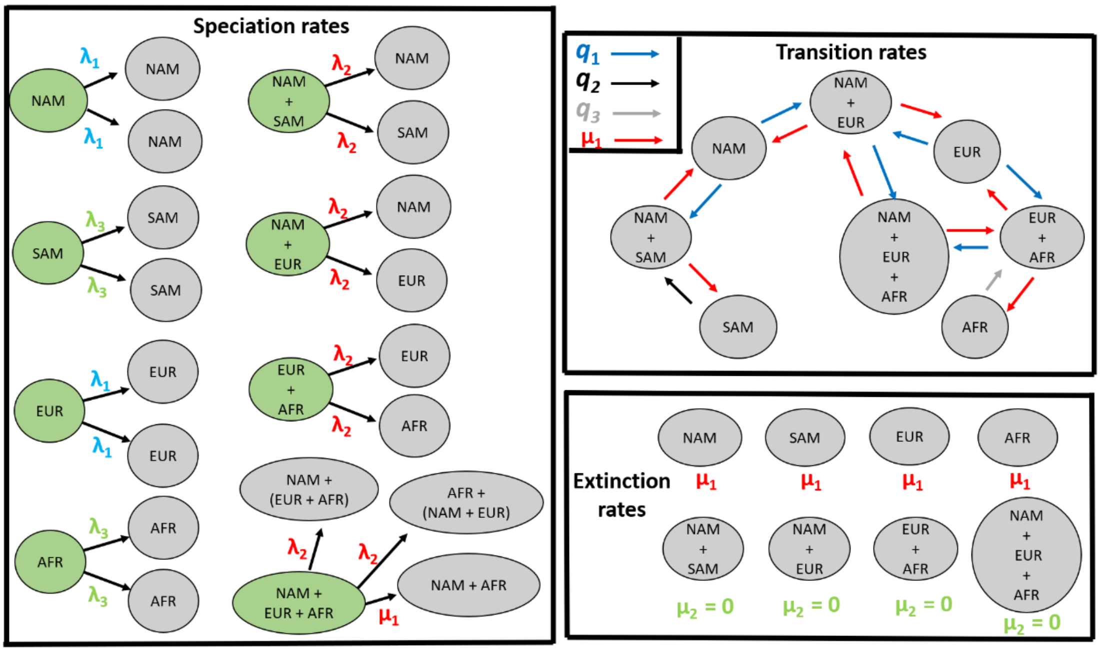

Figure S19. Diagram representing model 36. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, q_1, q_2, and q_3). This model assumes distinct speciation rates for sympatric and allopatric speciation, and the same speciation rate for S. America and Africa, and assumes three distinct transitions, one for transitions from S. America, another for transitions from Africa, and one for the rest of the continents. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

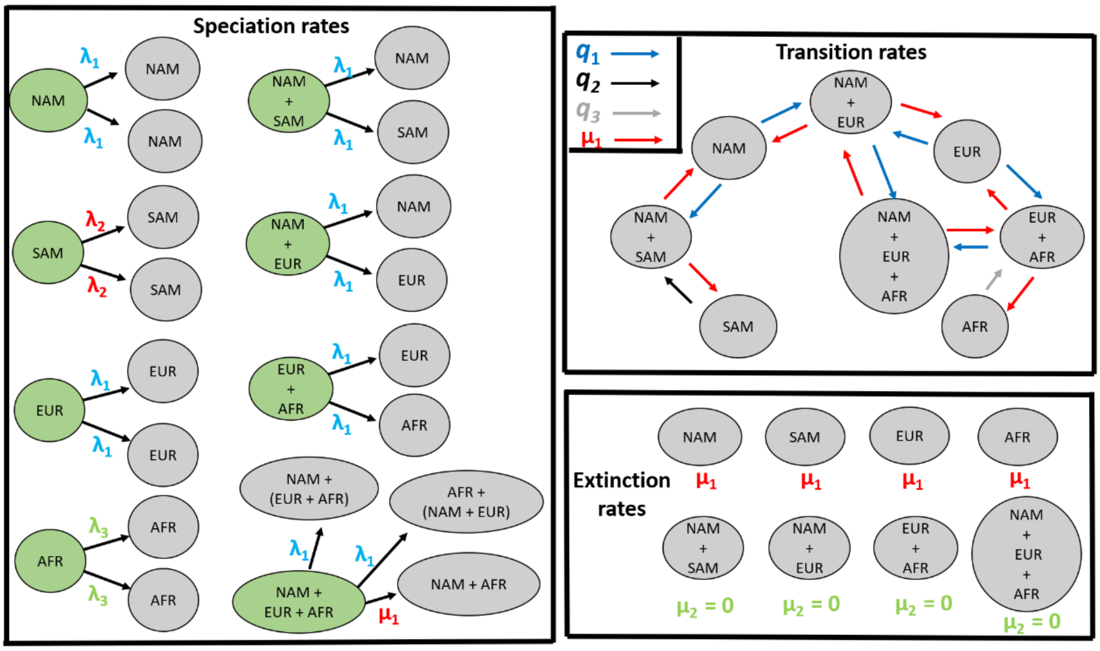

Figure S20. Diagram representing model 38. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, q_1, q_2, and q_3). This model assumes the same speciation rate for sympatric and allopatric speciation, and two distinct speciation rates for S. America and Africa, and assumes three transitions, one for transitions from S. America, another for transitions from Africa, and one for the rest of the continents. Both regions seem to be hotspots of diversification – Africa (fox clade) and S. America (S. American clade).

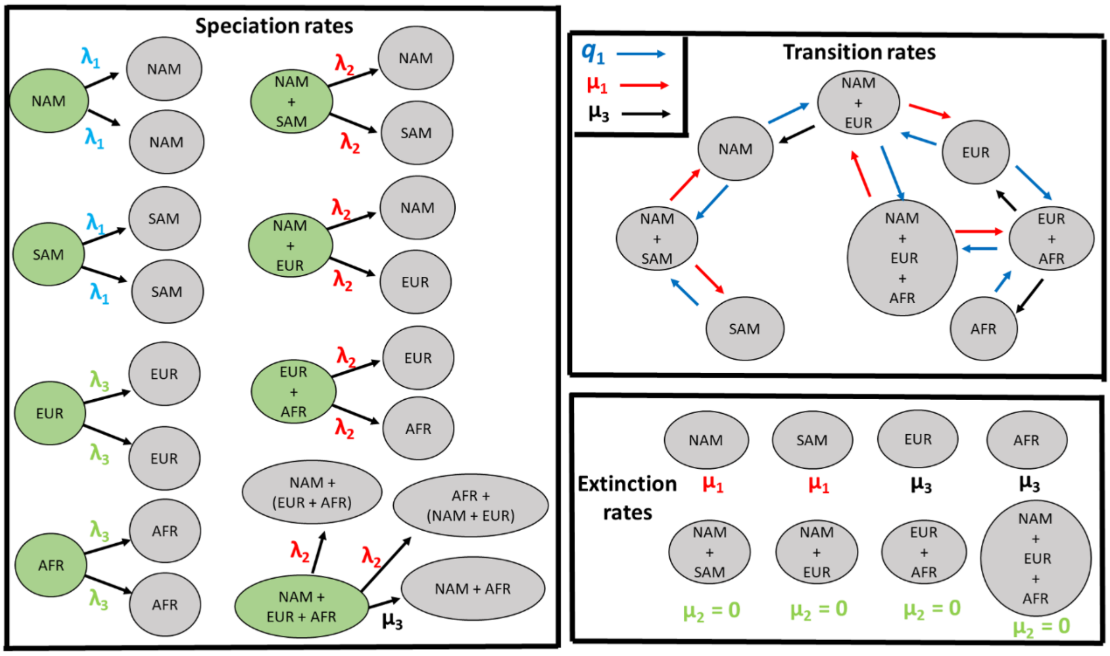

Figure S21. Diagram representing model 40. This ETD model has 6 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, μ_3, and q_1). This model assumes distinct speciation rates for sympatric speciation in new and old worlds, and another rate for allopatric speciation, and two distinct extinction rates for new and old worlds.

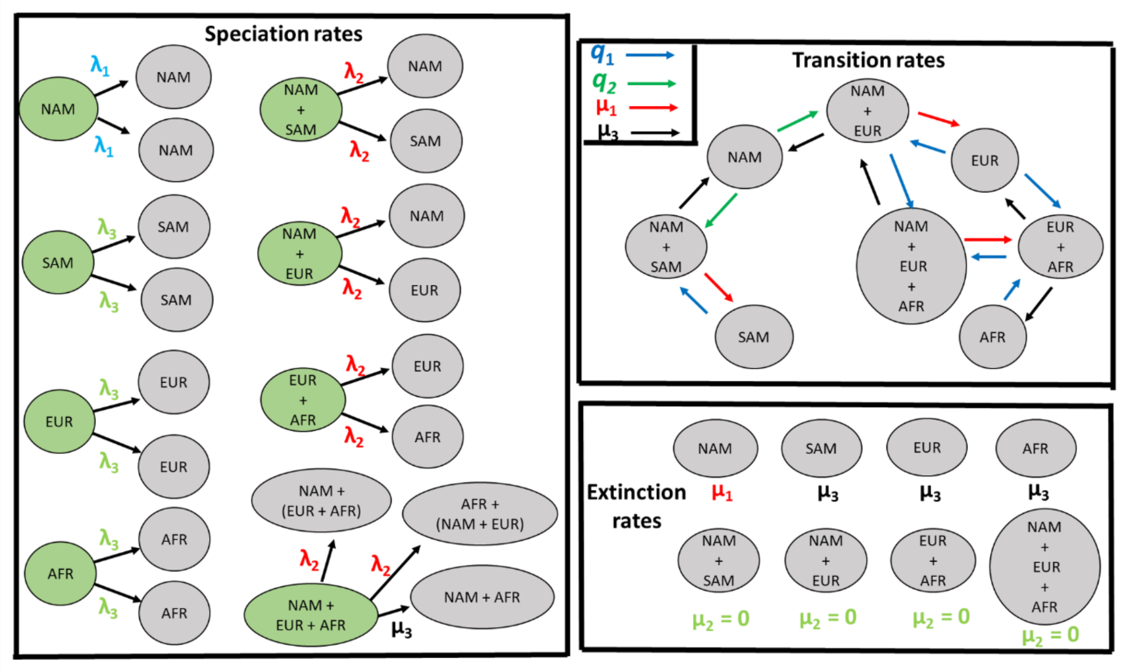

Figure S22. Diagram representing model 42. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, μ_3, q_1, and q_2). This model assumes distinct speciation rates for sympatric and for allopatric speciation, a distinct rate of speciation for N. America, two distinct extinction rates, one for N. America and the other for the rest of the single-area states, and one transition rate from N. America and another for transitions between the other regions. We explore distinct dynamics for N. America, because canids originated here, so the diversification may have been different.

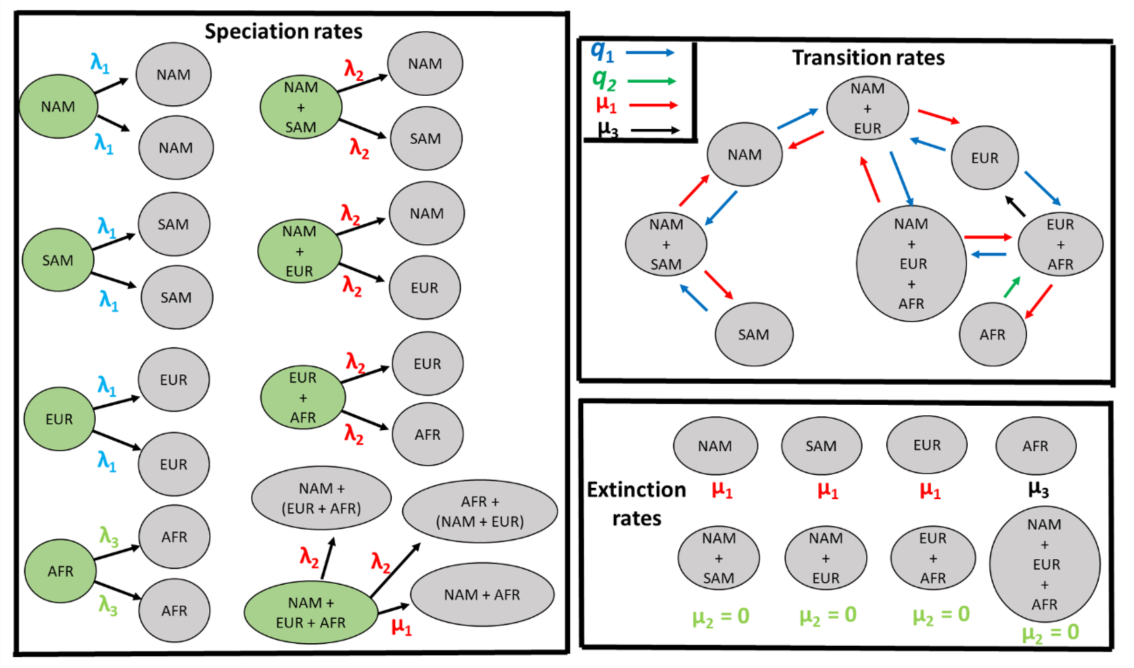

Figure S23. Diagram representing model 44. This ETD model has 7 free parameters to be estimated (λ_1, λ_2, λ_3, μ_1, μ_3, q_1, and q_2). This model assumes distinct speciation rates for sympatric and for allopatric speciation, a distinct rate of speciation for Africa, two distinct extinction rates, one for Africa and the other for the rest of the single-area states, and one transition rate from Africa and another for transitions between the rest of the regions. We explore distinct dynamics for N. America, because canids originated here, so the diversification may have been different.

SYNTHESIS

A short recap

The main intention of this thesis was to bring a broader view on distinct aspects of the distribution patterns of Canidae, and thereby elucidate many points that are not yet very well understood about this group. In short, the dispersal of an organism to new environments occurs when the benefits of moving outweigh the costs. The reasons for organisms to disperse can be many, including finding new resources, environmental stochasticity, or avoiding competition. However, moving to new environments can also generate risks, such as greater mortality due to the energy spent, unfamiliar habitat, or predation. Many of these aspects, which influence species both over their evolutionary histories and at the present, end up leaving traces that we can identify from phylogenies and from patterns of geographic distribution.

Using phylogenetic trees and paleontological data, I was able to demonstrate which were the main continental dispersal events over the last 13 million years in Canidae, and how these events shaped the diversification patterns of this clade (Chapters 1 and 4). Then, in Chapter 2, I used a phylogenetic tree and geographic distribution patterns to show that environmental factors are more important than species interactions to explain how Canidae assemblages are structured spatially at the present. And in Chapter 3, I used environmental data to demonstrate how canids are facing climate change, and what are going to be their potential new distributions in the future.

It is important to clarify that Chapters 2 and 4 discuss how Canidae are distributed across the planet in different time scales. Chapter 4 argues that diversity is determined by diversification rates, while Chapter 2 argues that it is environmental factors and biotic interactions that determine diversity (but not diversification). However, both chapters do not contradict each other, as there is diversity-dependence in both diversification and colonization. This diversity-dependence (i.e., the carrying capacity) is set by environmental factors and biotic interactions. Herrera-alsina et al. (2018) explored more this idea by developing a stochastic, spatially explicit simulation model of speciation, colonization, and local extinction, where they show how large- and small-scale events unite evolutionary and ecological mechanisms for understanding patterns of species diversity.

Puzzles of the past

Canidae family has more than two-thirds of its history only in North America, where this group originated. Among the three Canidae subfamilies, only Caninae managed to leave its home continent and remain extant until the present. But canids had some opportunities to cross Beringia, a periodic land bridge between eastern Siberia and Alaska that is called the Bering Strait today, and expand to the Old World. In fact, over the last 40 Mya several other lineages of carnivores did just that. Afterwards, the Isthmus of Panama, a land bridge connecting the Americas, also presented a great opportunity for Caninae to cross it (Wang & Tedford, 2008).

Until now, we still do not know completely how this Caninae dispersal over the globe unfolded, and this was a problem that I wanted to tackle during this thesis. As much as canids are a group that gets a lot of our attention for being close to humans due to domestication of wolves, what made them live into our houses, most studies dealing with their evolution focus on specific lineages and/or on relatively short geological time scales (Koepfli et al. 2015; Bubadué et al. 2016; Viranta et al. 2017; Plassais et al. 2019). When looking at the evolutionary history of Canidae, much of what is known about the origin of the lineages is still only from the fossil record. However, relying only on fossil data to study the evolutionary history of a group falls short of painting a complete picture about past processes such as dispersal events, mainly because fossil records are highly biased. The greatest archaeological sites about Canidae are located in the United States and China. Furthermore, tropical forest environments, like in South America, Africa and Asia, do not preserve fossils very well, or if they do, the sediments that trap the fossils are often poorly exposed, and in high latitudes the continental ice sheets from the Pleistocene damaged many of the sediments on top that were deposited in the late Cenozoic (Wang & Tedford, 2008). Thus, we have a dearth of knowledge about fossils in these several parts of the globe, leaving us a biased view about immigration events.

The main contribution of Chapter 1 was to shed light on some of these aspects that are still not so well understood about the past history of Canidae, bringing some interesting insights about the diversification of the three major clades of Caninae, and elucidating events that have occurred on continents where fossil records in large quantities are scarce.

The idea of an explosive diversification after the arrival in new continents, that I explored here, had already been suggested before by Wang & Tedford (2008) to explain, for example, the endemic clade in South America (Cerdocyonina), but was not actually tested with phylogenetic data. With very poor fossil records in South America, and a relatively short timespan since the arrival of canids in that continent, the idea of an explosive diversification was very appealing to explain an endemic clade with several species. We showed here that the speciation rate for the clade, even with a certain increase right after canids' arrival to this region, did not show the characteristic peak of an explosive radiation. However, the extinction rate of this endemic clade was low and constant over time, what is also shown in Chapter 4, which probably explains much better the success of canids in South America.

Shortly after North America's connection with the rest of the planet was complete, Canidae lineages dispersed to South America, Eurasia and Africa, generating a peak in the diversification rate of the clade. Explosive radiations are often interpreted as a consequence of the availability of unexplored ecological opportunities (Schluter, 2000; Simpson, 1953). I cannot say that this condition happened without testing it properly with ecological data, but the scenario that Chapter 1 presented suggests that it happened in canids. Therefore, the use of the trait "geographic distribution" does not mean only the area in which the species is found, but all the aspects that compose it and that might generate an opportunity for the lineages to diversify. As such, I believe that geographical distributions present a good proxy for all these aspects, similar to how a phylogenetic tree reflects all factors that played a role in the evolution of a clade.

Overall, this thesis brings a new perspective on the way in which canids dispersed across the planet, describing the routes by which the lineages used, and showing how they behaved when arriving in new regions. This turns out to be something valuable for a new phase on the Canidae research, where efforts can be concentrated to understand, in a more detailed way, the fauna and flora conditions that the Canidae lineages faced in different regions of the planet, something that it is still largely based on conjectures.

Did dispersal events among continents really affect Canidae diversification rates?

As stated earlier, most of what we know about how biogeographic events shaped the evolutionary dynamics of canids is very limited, as a great part is based on biased and incomplete fossil records. More precisely, we still lack a complete understanding of how dispersal events to new continents affected Canidae diversification rates. Chapter 4 was designed to explore this, and although its idea resembles Chapter one, both differ in the way they tackle these problems. While the first Chapter focuses more on the routes canids used to disperse, the fourth Chapter aims to understand, through a new approach, how these dispersal events might have influence diversification patterns around the world.

In the parts of the thesis where I focus on the Canidae past (Chapters 1 and 4), the use of geographic areas was very prominent, not only shedding light on different aspects of the origin of different lineages, but mainly demonstrating that the use of complete phylogenies can change our interpretation of diversification process. Part of my results in Chapter 4 suggest that dispersal events across continents were important in explaining the patterns of diversification in extant Canidae, which goes in line with what I found in Chapter 1. However, in Chapter 4 I also explored how including extinct species in the Canidae phylogeny may change our interpretation about their evolutionary processes. This approach, focusing on a complete phylogeny, showed that Canidae diversification cannot be explained by continent-related biogeographic events, at least with the information we have.

As puzzling as this inconsistency between our results in Chapter 4 is, there are many possibilities why geographic areas are not important to explain the diversification of canids in our complete tree scenario. It is very unlikely that major events of dispersal around the world did not have a large impact on lineages (Porto et al. 2021), but probably there is one or there are a few traits that these fossil species carry with them, and are essential for a complete understanding of Canidae. The influence of an attribute such as "biogeographic area" on group diversification can be much more complex than what we have studied here, because at our continental scales a trait state can offer several ecological opportunities for the colonizing lineages. In addition, the scenario shown for the complete tree in Chapter 4 brings a different interpretation than we had in Chapter 1, but it is important to note that the first Chapter used only half of the species used in the fourth Chapter, besides having a much greater refinement in their geographic distributions, which probably influenced so that Chapter 4 presented this inconsistency.

Nevertheless, chapter 4 makes some interesting contributions on diversification events. We must highlight the effect that the inclusion of fossil information in our models had on our understanding about the evolution of Canidae, as incomplete taxon sampling affects our ability to infer phylogenetic relationships and macroevolutionary processes (Nee et al. 1994; Rabosky 2015).

Canids and their environment

Canidae zoogeography provides insights into the intricate relationships among canid species around the world and their environments. For many years, there was an intense debate about environmental filters and interactions among species acting on the assembly of ecological communities (Leibold, 1998; Webb et al., 2002; Cavender-Bares et al., 2004; Kraft et al., 2007). With greater availability of phylogenies and advances in phylogenetic methods, we already know that biotic and abiotic forces influence the phylogenetic structure of assemblages generating clustered and overdispersed patterns, as several studies already found (Cadotte and Tucker, 2017; Zhang et al., 2018; Kusumoto et al., 2019).

Unfortunately, patterns of phylogenetic structure are not always easy to interpret as they can be generated by distinct forces. Besides, many studies end up addressing biotic and abiotic factors separately and this has become a big problem as it is likely that most observational data reported as evidence for environmental filtering, in fact, reflects the combined effects of the environment and local competition (Cadotte & Tucker, 2017). My Chapter 2 brings, as a contribution to the literature, a new point of view on the assembly of communities, not just for Canidae, showing that clustered and overdispersed patterns can indeed be generated together by different forces along the distribution of a clade. In natural communities, both environmental filtering and competitive interactions co-occur (Ackerly, 2003), but so far, the majority of studies of the phylogenetic structure within communities have demonstrated contrasting patterns of phylogenetic composition, where either competition or environmental filters dominated the communities.

Overall, Chapter 2 agrees with the points brought up by Chapter 1 on the origin and dispersal of the Canidae lineages. Highly phylogenetically clustered communities, such as South America, the Middle East, and South Asia, present several lineages that originated within these regions, as is pointed out in the first Chapter. South America, for example, is inhabited only by species of a single clade — endemic to this continent. Furthermore, highly overdispersed regions, such as North America, Europe and South Africa, are inhabited by lineages of distinct clades, where many have their origins outside these regions. This shows that if we use an approach that focuses on several distinct angles, rather than just one, like the method I applied here, we are able to identify traces that the evolutionary history of entire clades can leave, helping to elucidate its current distribution patterns.

Can I predict where canids will be?

For the first time in human history, there are more people living in cities than in rural areas, and this is expected to continue to increase (United Nations, 2014). Related to this, we know that currently the main cause of species loss on the planet is due to the conversion of natural landscapes into cities (Nogeire et al. 2013), and as cities are constantly growing across the planet, the impacts of this trend on wildlife species are more evident every year.

Species distributions are determined by a variety of ecological factors, such as biotic interactions and abiotic conditions. Throughout Chapter 2, I realized that, although it was not the most important factor to explain the distribution of canids, the anthropic impact still had a great influence on the structure of Canidae communities, as well as on temperature and vegetation cover in the assemblages that I sampled. Studies indicate that some species of canids are able to adapt and enter urban areas, such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and grey foxes (*Urocyon cinereoargenteus*) (Nagy et al. 2016; Lombardi et al. 2017), but it is evident that living within cities reduce the size of populations that once lived in their natural habitat. Few other species of canids have similarly detailed studies, leaving us with almost no clue about how the environmental changes affect canids.

Chapter 3 indicates that global warming will affect canids differently. But another contribution from this chapter is to enrich the debate about the importance of looking from different angles on the impacts that climate change can impose on species. Being able to see a broader picture about the difficulties that species are going through should be valuable information for conservation strategies. The attempt to predict responses of species to climate change is further limited by uncertainties surrounding climatic predictions (Synes & Osborne, 2011), and it is becoming more evident every year that in order to make really robust inferences we need to evaluate others species' niche dimensions and the effects of several intricate mechanisms (Diniz-Filho et al., 2019).

Chapter 3 agrees with the recent publication of the IPCC report (IPCC, 2021), which shows that the most pessimistic future climate scenario that we used during the niche modeling is actually the most realistic one. The IPCC report highlights that the changes which have already started, such as the rise in sea level, are irreversible and that it will still take 20 to 30 years for temperatures to stabilize, even with significant reductions in carbon emissions, which is unlikely to occur given the pace of our constant globalization. Moreover, these changes are already affecting canids as many will lose a large part of their ranges, but also most Canidae hotspot regions are outside protected areas, and this is an alert for decision-makers to act and identify key areas for conservation, because, as described previously, canids are very important for the ecosystems they inhabit.

Concluding remarks

In summary, I hope that the results from this thesis have contributed with new insights about the patterns of Canidae distribution, the mechanisms that drive them, and how they influenced the diversification rates of the group over the last 13 Mya. The understanding of distribution patterns throughout the past, present, and future of Canidae proved to be a complex process, where there is no one-explanation-fits-all. Actually, it was necessary to integrate phylogenetic information, ecology, and biogeographic history of canids to explain the biodiversity patters described here, which suggests that the knowledge on the life history of canids was fundamental to formulate the ecological and evolutionary hypotheses presented over the chapters.

Although I have managed here to address distinct aspects of Canidae, it is just a glimpse of what still needs to be discovered. One important underexplored aspect is how past competition between canid lineages and with lineages of other carnivores has shaped current distributions and affected diversification. Silvestro et al. (2015) already suggested that Felidae might have contributed to increase the extinction rate in North American canids. The scenarios that are presented by Chapters 1 and 4 suggest that these interactions could explain many aspects about patterns of diversification around the world for canids. The presence of other carnivore lineages, as Felidae, along narrow land bridges between continents, may have created an incumbency effect (Rosenzweig and Mccord 1991), making it difficult for other competing lineages to cross these connections.

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- **Porto, L.M.V.**, Etienne, R.S., Maestri, R. 2021. Competition and environmental gradients structure Canidae assemblages across the planet. https://www.biorxiv.org/content/10.1101/2021.01.09.426069v1.full

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