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“Deep into the past
Follow the aeon path
Greet a blade of grass
Every endless form most beautiful
Alive, aware, in awe
Before the grandeur of it all
Our floating pale blue ark
Of endless forms most beautiful”

Tuomas Holopainen em: *Endless Forms Most Beautiful*

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Contents

1 Introduction

Understanding the patterns and processes that promote biodiversity is a key goal in ecological and macroevolutionary studies. As a first order approach to diversity, one can measure how the number of species vary whether across different regions, different communities, or even how the number of species vary through time. Macroevolutionary questions are often directed towards understanding how patterns of species diversity changed in deep time, a multimillion-year time scale, as well as what are the processes governing these patterns. Traditional views on the controls of diversity through time often antagonize the roles of the abiotic environment and the biotic interactions between species, however those different approaches are not self-excluding (Benton, 2009). In fact, Benton (2009) proposes that the so-called abiotic and biotic factors act on different scales, where species interactions would be relevant at local shallow time scales, and extrinsic factors would preferentially operate on a regional/global deep time scale.

Much of the ongoing debate regarding abiotic and biotic factors as drivers of species diversity revolve around the interplay between these factors and how they affect diversification dynamics (Ezard et al., 2011). Diversification rates are described as the balance between the processes of speciation and extinction, and many authors have tried to disentangle how abiotic and biotic factors may affect the underlying diversification dynamics. The role of species interactions in shaping diversification dynamics remain far from fully understood (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). This topic has attracted great interest in the paleontological/macroevolutionary community, with special interest on how interspecific competition, and to lesser extent, predation, might regulate biodiversity dynamics (Sepkoski et al., 2000; Van Valkenburgh, 2007; Vermeij, 1987). Recent studies (Pires et al., 2017) have shown that speciation may be driven by competitive interactions between species. The idea that competitive interactions may be a driving force in speciation or extinction is central to the theory of diversity-dependence mechanisms of diversification (Rabosky, 2013). Diversity-dependence theory proposes that species diversity might be self-regulated at large continental scales in an observed feedback between species richness and macroevolutionary rates (Rabosky, 2013; Rabosky & Hurlbert, 2015; Sepkoski, 1996). Drawing from the theoretical concept of competitive exclusion (Gause, 1935) and Hutchinsonian niche concepts (Hutchinson, 1959), Hermoyian et al. (2002) hypothesized that in the absence of disturbing factors, “species that are too morphologically similar […] experience interspecific competition sufficient to drive one of the species locally extinct”. Although these ideas date back to Darwin (1859), it is still difficult to understand how competition scale up to higher hierarchical levels of diversity (Marshall & Quental, 2016; Sepkoski, 1996). Although most theory in diversity-dependence has been centered on how species within a given clade regulate the dynamics of such focal clade, it has also been proposed that clades might in fact regulate and even drive other clades to extinction. This mechanisms have been termed “clade competition” (Sepkoski, 1996; Sepkoski et al., 2000).

Two main mechanisms of clade competition are said to influence species diversity trajectories. In the first, one clade prevents another competing clade to radiate and its replacement can only happen due to its extinction (the incumbent clade) driven by mechanisms other than the clades interaction. Such process is termed passive replacement or incumbent replacement (Rosenzweig & McCord, 1991). In the second (active displacement), the appearance of a new competing clade might actively outcompete the former, leading to its demise (Sepkoski, 1996). Although passive replacement has been considered to be prevalent, there is a growing number of examples that seem to be congruent with active displacement (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 2007). The fossil record (as opposed to molecular phylogenies) might be particularly relevant to study diversity-dependence because it allows not only a direct inference of diversity trajectories, but also to directly estimate speciation and extinction rates (Quental & Marshall, 2010). In fact, inferences about diversity-dependence, either within or between clades have moved beyond the study of diversity curves, e.g., fitting logistic models to diversity trajectories or contrasting diversity curves of potential competitor clades (Sepkoski, 1996), to directly investigate the effect of diversity on the dynamics of speciation and extinction separately (Alroy, 1996; Foote et al., 2018; Pires et al., 2017).

Diversity-dependence has been interpreted as being produced by competition between species that overlap in space and time (Sepkoski, 1978, 1996), through mechanisms such as competitive exclusion acting on extinction, or limited resources acting on suppressing speciation (Rabosky, 2009, 2013; Sepkoski, 1978, 1996). Only a handful few different clades have been investigated at the species level, so it is an open question if different lineages might be more or less prone to such diversity-dependence mechanisms driven by competition. Although seemly relevant, it is possible that our perception of the prevalence of such mechanism might be driven by our study systems. Studies on carnivorous mammals have demonstrated the importance of competition in diversification dynamics (Silvestro et al., 2015; Van Valkenburgh, 1988, 1999). Large predatory mammals are expected to present intense competitive interaction, both in modern and fossil faunas (Van Valkenburgh, 1985, 1988). In fact, competition might indeed have shaped diversification of Canidae species in North America during the Cenozoic (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 1999), and it might have acted differently in speciation and extinction dynamics (Pires et al., 2017; Silvestro et al., 2015).

Canidae is a family of predatory mammals comprising both extant and extinct lineages, with its origins in the Paleogene of North America, having existed for some 40 million years until the present day (Wang & Tedford, 2008). The Canidae fossil record of North America is considerably well documented in both its taxonomic diversity and sampling

(Tedford et al., 2009; Wang, 1994; Wang et al., 1999), and eco-morphological characterization (Balisi et al., 2018; Balisi & Van Valkenburgh, 2020; Janis et al., 1998; Slater, 2015; Van Valkenburgh et al., 2004). Extinct canid species display a wide array in both body size and diet, ranging from small predators of small prey and plant matter (hypocarnivory), to large-bodied bone-crushing or hypercarnivore (whose diet is almost entirely composed of meat) dogs (Van Valkenburgh, 1991; Wang & Tedford, 2008). The succession of canid sub clades in the fossil record also suggests repeated patterns of increase in species diversity, followed by stability and subsequent demise of at least two extinct subfamilies (Silvestro et al., 2015; Van Valkenburgh, 1999; Van Valkenburgh et al., 2004; Wang & Tedford, 2008). The extinction of both Hesperocyoninae and Borophaginae subfamilies seems to be driven by the expansion of the next subfamily, as well as by other Carnivora clades, in a pattern congruent with active displacement (Silvestro et al., 2015). This pattern is also repeatedly observed in other Carnivora clades, and it is argued that the large predator adaptive zone remained fairly unchanged in the Cenozoic, promoting intense competition of Carnivora (Van Valkenburgh, 1999).

Many studies concerning macroevolutionary competitive dynamics of canids (as well as on other lineages) have focused either on diversity-dependence diversification dynamics (Silvestro et al., 2015), or morphological evolution of species traits (Slater, 2015), or on the implications of such morphological evolution on species survival and extinction risk (Balisi et al., 2018; Balisi & Van Valkenburgh, 2020; Van Valkenburgh et al., 2004). The effect of competition on diversification dynamics has been tested fairly indirectly and relied on the assumption that an increase in diversity implies in stronger competition, which would lead to a drop in speciation or rise in extinction rates. Although a reasonable interpretation, to better understand the effect of competition on diversification dynamics it might be more interesting to explore how the occupancy of morphospace might be linked to speciation and extinction dynamics. Canidae exhibit a trend of increasing body size as lineages evolve over time (Van Valkenburgh et al., 2004), a pattern known as Cope's Rule (Hone & Benton, 2005). Such increase in body size seems to be correlated with increasing adaptations to hypercarnivory, an ecological specialization towards large prey consumption (Van Valkenburgh et al., 2004). Specialization to extreme morphologies (either small hypocarnivores or larger hypercarnivores) seems to lead to short living species (Balisi et al., 2018), but hypercarnivory *per se* seems to imply an extinction selective regime only at certain time periods and do not seem correlated to extinction dynamics as a whole (Balisi & Van Valkenburgh, 2020). Slater (2015) has argued that the evolution of canid morphological traits followed patterns of repeated ecological radiations in a bounded morphospace of restricted diet categories. Thus, suggesting that morphospace is rapidly saturated and paving the way to better understanding the complex interactions between the evolution of body size, diet ecology and diversification dynamics. We therefore argue that the role of resource mediated competition in diversification dynamics still remains to be explicitly investigated, as studies mentioned earlier have focused either on diversity-dependence mechanisms assuming that all species coexist with no information regarding ecological overlap; or in studies that investigated the rates of morphological evolution without a direct relationship to diversification dynamics.

2 Objectives

In this study, we intended to develop an approach that more explicitly incorporates ecological mechanisms of competition such as niche overlap in shaping macroevolutionary dynamics. We used canids as a model group to test hypotheses on the role of competition in macroevolutionary dynamics, while taking into account different aspects of species ecology and the incompleteness of the fossil record. Going beyond usual measures of the number of coexisting species through time, we also tried to incorporate aspects of species coexistence in geographical and ecological space, rather than assuming that all species coexisting in a given moment overlap in both space and ecology. To attain these goals, we described competition using different time series designed to measure niche and geographical overlap metrics using the available eco-morphological characterization data for the clade.

We asked the following questions: i) How are speciation and extinction dynamics influenced by competition measured by spatial and niche overlap? ii) How different metrics of niche overlap describe competition dynamics? iii) How comparable are our inferences of the aforementioned effects when using different approaches to describe species coexistence in space and ecology? We hypothesize that if diversity-dependence mechanisms reflect competition mediated by resource acquisition, we expect to find a negative association between speciation dynamics and our measure of intensity of competition: as competition increases and niche space becomes saturated, speciation rates should decrease. The opposite should hold true for extinction, as competitive pressure increases, extinction rates should increase as species might be driven to extinction by local scale dynamics. We retrieved fossil occurrences from the widely used Paleobiology Database (PBDB <https://paleobiodb.org/>), and analyzed data in a Bayesian framework to test these hypotheses while incorporating the incompleteness of the fossil record (Silvestro et al., 2014, 2019). The framework estimates i) true times of speciation and extinction of species; ii) preservation rate and how it changes through time and among species; iii) speciation and extinction rates; and iv) correlation parameters that measures if changes in a time series of interest (here, our different metrics to measure competition intensity) are associated with changes in speciation and extinction rates.

3 Material and Methods

1 Data acquisition

In this section we summarize the primary data used in this study, regarding the origin of the data, whether from compiled literature or online databases.

1.1 Fossil occurrences

We retrieved fossil occurrences from Paleobiology Database (PBDB), a non-governmental, non-profit organization that compiles fossil occurrences from museums and the primary literature, which is readily accessible to researchers. We restricted our analyses to include only North American canids, as most of the clade evolutionary history was confined in this continent (Wang & Tedford, 2008). Curatorial work followed Pires et al. (2015), adopting a conservative measure regarding species taxonomic uncertainty. First, we filtered occurrences incorrectly identified to the species level by removing those with markers of taxonomic uncertainty (Bengtson, 1988; Sigovini et al., 2016): “indet.”, “sp.”, “?”, “aff.”, “cf.”; but kept newly described species identified with “n. sp.”. We followed Canidae taxonomic revisions of experts to recombine subjective synonyms and subspecies (Tedford et al., 2009; Wang, 1994; Wang et al., 1999; Wang & Tedford, 2008), and a recently published phylogeny of the Caninae subfamily (Zrzavý et al., 2018).

To amend the effect of uncertainty in occurrences temporal resolution, we also followed Pires et al. (2015) by removing all occurrences with a temporal range estimated to be larger than 15 million years (Figure S1). This was done to prevent overestimating species true times of speciation and extinction in the following Bayesian framework. Our original dataset comprised 2210 occurrences and after our successive curatorial work, we ended up with 1555 occurrences of 138 species. From PBDB we also retrieved information regarding geographical location of fossil occurrences, as each occurrence is identified with a “collection” flag that associates it to a specific locality from where each specimen was retrieved, allowing grouping multiple occurrences that were found together. Each occurrence is also georeferenced with latitude and longitude coordinates, sometimes approximated to nearest fossil quarry or county. Both aspects of geographical information allowed us to reconstruct some aspects of species distribution in the fossil record (see section 2.2.2).

1.2 Ecomorphological data

We described each species in a two-dimensional morphospace that encompasses two important morphological proxies for species niche: body size and diet (level of carnivory). Body size is widely regarded as a good variable to describe species ecology, as it is known to correlate with several aspects of morphology, physiology and resource use by a species (Bonner, 2006). In a recently published paper, Balisi et al (2018) reviewed aspects of how body size and specialization of canid diet evolved over time and its consequences to the risk of extinction, in fashion with a “macroevolutionary ratchet” (Van Valkenburgh et al., 2004). The specialization of canid diet towards either consumption of large prey (hypercarnivory) or small prey mixed with plant material (hypocarnivory) imposes a series of morphological restrictions and supposedly “bounds” canids in certain optima of phenotypes (Slater, 2015).

Body size measurements of fossil species are not readily available in the fossil record, and must be inferred from surrogate data. Mammalian teeth is usually more well-preserved in the fossil record than post-cranial skeleton, and a series of regression equations are available to estimate body size from teeth data, based on living organisms (Van Valkenburgh, 1990). We used Balisi et al. (2018) published dataset of canid body size, derived from such regression equations, and included two extant species from another dataset (Finarelli, 2008); with a total species summing up to 123 species out of our total of 138 species with fossil occurrence data. See section 2.2.3.1 on how we treated missing data. Both datasets described body mass in kilogram units, and we took the natural logarithm to represent the data.

The interplay between canid body size and dietary evolution led us to also incorporate measurements used to categorize diet. We compiled results of a Linear Discriminant Analysis (LDA) from Slater (2015), a multivariate analysis of several craniodental variables with 21 extant canids and a few other extant Carnivora species as training data. Linear Discriminant Analyses are commonly used to reduce dimensionality of data and later classification into discrete categories, separating between groups. Slater (2015) used such results to classify Canidae species in discrete diet categories of hypercarnivory, mesocarnivory and hypocarnivory. We describe Canidae carnivory using such discrete categories, while also describing carnivory in a continuous variable, the first axis of LDA (LD1) in a manner analogous to using the first Principal Component axis of a PCA. From Slater (2015) data we classified 97 out of 138 species with occurrence data. See section 2.2.3.1 on missing data.

2 Analyses

We proceed our analyses in a three-step framework: first, we analyzed occurrence data in a Bayesian framework to estimate properties of the Canidae fossil record regarding “true” times of origin and extinction of species, preservation and diversification rates. Second, we implemented a modular framework to describe different aspects of species coexistence and the potential for competition by implementing different metrics of morphospace disparity to capture different aspects of competition intensity. Finally, to investigate the potential effects of biotic interactions on macroevolutionary dynamics, we performed a Bayesian analysis to investigate if changes in speciation and extinction rates are associated with changes in our metrics used to describe species coexistence and competition intensity through time.

2.1 ***PyRate*** **framework**

We analyzed fossil occurrences in *PyRate*, a hierarchical Bayesian framework that jointly estimates preservation and diversification processes, while explicitly incorporating different aspects of the incompleteness of the fossil record, using all known occurrences of a given lineage (Silvestro et al., 2014, 2019). *PyRate* works on a fully probabilistic Bayesian paradigm, allowing us to quantify the levels of uncertainty of such estimates. Based on stochastic models of fossilization and sampling, *PyRate* is able to model fossil preservation in different ways. In its latest implementation (Silvestro et al., 2019), such preservation processes can be modeled to simultaneously allow heterogeneity both through-time (using a Time-variable Poisson Process - TPP) and across lineages, an approach deemed more realistic to describe varying patterns of fossil preservation (the mG + qShift model in *PyRate* notation). Instead of relying on the assumption that the oldest occurrence describes the time of origin of a clade, and its latest occurrence describes its extinction; drawing from expectations of the preservation models, *PyRate* estimates the species "true" times of speciation and extinction. Finally, using an algorithm known as Reversible Jump Birth-Death Markov Chain Monte Carlo (RJBDMCMC), *PyRate* draws from the distribution of speciation and extinction times to jointly infer the rate at which such events occur, while also estimating the number of rate shifts from the data. All these estimates are done jointly in the Bayesian framework.

We utilized all our occurrences of Canidae North American fossil record to estimate species times of speciation and extinction, and speciation and extinction rates. We set our analyses using the mG + qShfit model, running 30000000 RJBDMCMC iterations, sampling every 10000 iterations to obtain the posterior estimates of the parameters, discarding the first 10% as burn-in. Additional information on the number of living species and the geological stages which we allowed preservation to differ were set as follows. As most of Canidae fossil occurrences are associated to the North American Land Mammal Ages (NALMAs), we grouped some of these stages to define the time windows where preservation could vary: we set the boundaries at 37.2, 30.8, 20.43, 15.97, 13.6, 10.3, 4.9, 1.8, 0.3 and 0 Million years ago (Ma). We utilized such times frames to accommodate a roughly homogeneous number of occurrences among intervals across the whole time frame (Figure S2). We set the number of living species to be 7 given that this is the number of Canids seem today in North America.

We declared *Cuon alpinus*, an extant species in Eurasia but not currently present in North America to be extinct in our dataset.

To account for the uncertainty associated with the age of each fossil occurrence, we randomly drew ages within each occurrence timespan, generating 50 different temporal replicates and conducted *PyRate* analyses on each of these replicated datasets. For such random drawing of ages, we restricted fossil occurrences found in the same assemblage to be assigned the exactly same age, as they may represent the same fossilizing event and could induce pseudo-replicates if not taken into account. We identified occurrences of the same assemblage with the "collection number" identifier from PBDB data, which also served as the basis for one of the analyses of species distribution (see section 2.2.2). From these analyses we described the general trend in speciation and extinction rates, as well as the times of origin ad extinction of each species, and hence their longevities, which were then used as inputs in the step used to define coexistence in time described in the next sections.

2.2 **Modular framework**

In our attempt to better describe competition dynamics, we developed a modular approach to capture different levels of complexity of species interaction in the fossil record. We designed and explored four different scenarios that could be used as proxies for detecting competition:

a) competition intensity is described by the variation in the absolute number of species coexisting through time, a classic diversity-dependence original scenario, where all species that coexist in time are considered potential competitors, irrespective of their ecology or spatial distribution;
b) competition intensity is described by the variation in the number of species co-occurring in time and space, where not all species (those that do not coexist in time and space) are potential competitors;
c) competition is described by how disparity metrics of morphospace density change through time, without considering if they coexist in space. Here, all species coexisting through time are potential competitors and competition intensity is measured by species distance in the morphospace;
d) competition is described by how the disparity metrics of morphospace density change through time, modulated by temporal and spatial coexistence, hence not all species are considered potential competitors. This is the metric we think better represents the intensity of competition regarding resource use and spatial coexistence.

To describe coexistence in space, time and morphospace, species were grouped in pairwise symmetrical matrices, with each cell representing a species pair. We then simply filled the matrices in a binary fashion for space and time and a morphospace distance for the morphological matrix. In space and time matrices, a value of 0 represents pairs of non-coexisting/competitor species, and 1 represents pairs of coexisting/competitor species. We combined hierarchically such matrices as we increased the complexity of the competition scenario by multiplying the matrices elementwise. The final product of each step was then resumed in a time series as an input to the correlation analyses described in section 2.3. We described each of these time series in a scale of 0.1 million years. We devised such modular framework to be easily interchangeable as we explored new metrics of either spatial coexistence or morphospace occupation, and to be also possible to extract the intermediate steps as we described the different scenarios of competition.

2.2.1 **Temporal coexistence**

The first and foremost aspect of species coexistence needed to describe was the species coexistence through time. We extracted the true times of speciation and extinction from each of the 50 *PyRate* replicas derived from the analyses described in section 2.1 to define the species longevity, by extracting the mean values from the posterior distributions of speciation and extinction times for each species. We then superimposed all individual species longevities and extracted, at each 0.1 million-year discrete time interval, the number of species present at that point for each of the 50 replicas separately. We used those diversity trajectories to create 50 time series and used it as the first metric to investigate potential effects of competition as the classic scenario of diversity-dependence. We also stored the temporal coexistence information in the pairwise symmetrical matrices, that were later used in combination with the following metrics of spatial coexistence. We created 373 matrices (one for each time point interval of 0.1 million years) representing the time-span of Canidae fossil record, starting from 37.2 million years ago to the present (0), for each of the 50 replicas separately. We fixed 37.2, the base of Chadronian NALMA as the origin point for all our time series.

2.2.2 **Spatial coexistence**

To describe species coexistence in space, we explored a few different options that took into account properties of the fossil record of Canidae, as well as their biology. Reconstructing patterns of species distribution from fossil data is not an easy task, regardless of the higher taxonomic identity, either plants or animals (Darroch & Saupe, 2018; Kidwell & Flessa, 1996; McLachlan & Clark, 2004). Traditional approaches to infer distribution of fossil species usually describe how much of the area of interest each species occur, and how such area changes through time, a measure of “success” in space (Balisi et al., 2018; Carotenuto et al., 2010). We emphasize that our intention was not to produce precise distribution maps for each species, but to try to use spatial information to describe potential scenarios of species spatial overlap and coexistence. To do so, we developed two different metrics to measure such potential for coexistence, one very conservative, which is likely to underestimate the level of species coexistence, and a more permissive one. Both are described below.

2.2.2.1 **“Reach distance”**

To define spatial coexistence, we used geographical information of each occurrence. From our original dataset compiled from PBDB, we extracted latitude and longitude values for all occurrences. Given the spatial and temporal resolution of the data, we deemed impossible to precisely reconstruct patterns of expanding distributions on the 0.1 million-year scale adopted to the time series of coexistence. We then proceeded to describe species coexistence using some simplifications. Spatial coexistence was determined using all data points found at the stratigraphic level of most occurrences, the North American Land Mammals Ages (NALMAs). Hence, two species were deemed to coexist through the whole NALMA if geographic information at the temporal resolution suggests spatial overlap.

To define spatial coexistence, we used the spatial information (latitude and longitude) of all occurrences for each species at each NALMA separately. For each pair of species, at each NALMA, we estimated the shortest distance between their occurrences and considered them to coexist if they were closer than a certain “threshold distance”. Such “threshold distance” was determined using the geographical data itself and was inspired by the potential for dispersal of each species. The overall idea was to estimate “dispersal potential” (measured as distances in km) for each species and then use this information for each species pair to determine if they were at a reachable distance (hence the name “reach”) among themselves. Thus, the “threshold distance” was different for each pair of species, measured by the sum of both species dispersal potential. This idea was based on the assumptions of how carnivore species geographical ranges increase with its metabolic needs and body size (Gittleman & Harvey, 1982).

Distances on earth surface can be measured from great-circle distances, the shortest path between two points in an ellipsoid. Great-circle distances are considered a reliable measurement to analyze species distribution in the fossil record, using only a few occurrence sites (Darroch & Saupe, 2018). Thus, for each species in each NALMA we estimated the pairwise great-circle distances between all occurrences within a NALMA, and extracted the maximum value. To do so, we used R software (R Core Team, 2018) packages “sp” and “rgeos” (Bivand et al., 2013; Bivand & Rundel, 2019). To define the “dispersal potential” for each species we considered the maximum value ever reached within a NALMA, which describes the longest possible distance that a species could disperse. Then, for each species pair, we determined the potential for spatial coexistence if the sum of each species individual "dispersal potential" was equal or greater than the minimum distance between them; otherwise, they do not coexist. We then stored the coexisting pairs of species in the matrix fashion as described in section 2.2. Such matrices only inform the potential for species spatial coexistence in a given NALMA, as species may originate or go extinct at any point in time inside NALMAs. By multiplying (elementwise) such spatial matrices with the previous matrices of time coexistence, we ascertain for species pairs coexistence to happen only during each species lifespan. The multiplication of those two types of matrices resulted in a series of 373 matrices, which describes our second proxy for competition presented in section 2.2. This was done separately for each of the 50 temporal *PyRate* replicas. Therefore, at each point (0.1 My) in time we have an estimate of how many species each species alive at that time coexists with. From that information, we estimate the mean number of coexisting species at that point in time to create a time series of average number of coexisting species. As this was done separately for each of the 50 temporal replicas, we ended up with 50 different time series used as the input in the correlation analyses described in section 2.3. This method is henceforward referenced as "reach" coexistence.

Given the incompleteness of the fossil record, two relevant observations should be made. The first relates to the fact that longevities estimated from *PyRate* analyses place the "true" times of speciation and extinction to moments in time beyond the first and last occurrences. Hence, such periods have no direct geographical information. The second relates to the empirical finding that some species might present temporal "gaps" in its occurrence, i.e., be absent in a given NALMA, if such species are sparsely sampled during its longevity. These species therefore may lack geographical information between its first and last occurrences. To overcome the lack of information in both ends of species longevities, we simply replicated the geographical positions of occurrences found in its adjacent NALMA. To deal with gaps in geographical information we estimated the union of convex polygons in both adjacent NALMAs, and used the centroid of such union to describe species occurrence. The construction of the convex polygons and their intersection was also done using the R software (R Core Team, 2018) packages "sp" and "rgeos" (Bivand et al., 2013; Bivand & Rundel, 2019).

2.2.2.2 **"Site"**

As a more conservative metric of species spatial coexistence, we used an approach where only species with occurrences found in the same locality (i.e., the same fossil assemblage) are said to coexist. Using the "collection" identifier from PBDB data, we identified all occurrences of different species in the same fossil assemblage. Under this approach, species are said to coexist in space for the whole-time interval defined by the

NALMA each assemblage is associated with if they are found at least once in the same fossil assemblage. Once again, we stored the spatial coexistence information in our matrices approach and multiplied those to the temporal matrices, to define species coexistence in time and space. We extracted the number of species each species coexist at a given point in time and averaged the number of coexisting species to create the time series of this competition scenario. This method is henceforward referenced as “site” coexistence. It is important to note that no correction such as the one applied in “reach” metric is possible, i.e., duplication of occurrence data in adjacent NALMAs; therefore, we are aware that such metric might underestimate levels of coexistence, and is also a more conservative metric compared to the “reach” method.

2.2.3 **Morphospace**

Multidimensional morphospaces are commonly used to describe many aspects of species niche overlap in different guilds (Van Valkenburgh, 1988), to analyze patterns of disparity in fossil data through time (Hughes et al., 2013; Kotrc & Knoll, 2015) and test hypotheses of competitive exclusion (McGowan & Dyke, 2007). Theoretical morphospaces draw from the metaphor of adaptive landscapes (McGhee, 2006), where many aspects of ecomorphological restraints can be explored (Raup, 1966; Raup & Michelson, 1965). Drawing from concepts of competitive exclusion, we hypothesize that species with very similar morphologies are expected to compete. Additionally, as the morphospace becomes saturated, we expect morphospace distances to decrease producing an overall competitive effect that prevents the emergence of new species. Disparity measurements have been used to describe patterns of dissimilarity between species in the morphospace (Ciampaglio et al., 2001), while different measures can capture different aspects of morphospace occupancy through time. By selecting a few measures of disparity associated with morphospace density (Guillerme et al., 2020), i.e., “crowding” of morphospace, we intended to describe the intensity of competition using different time series explained in detail in section 2.2.3.2.

As described in section 1.2, we defined morphospace occupation using two morphological axis, body mass and an index that describes the level of carnivory. Although previous work complied data for most species (Balisi et al., 2018; Slater, 2015), there are some species with missing data, in particular for the index describing carnivory level. Below we describe how we dealt with this missing data, before explaining how the time series measuring competition were calculated.

2.2.3.1 **Data completion**

Given the reasonable completion of the used datasets (Balisi et al., 2018; Finarelli, 2008; Slater, 2015), we designed a data augmentation-approach to complete the morphology of species we had no eco-morphological data. We note that this data augmentation should not generate any bias given that it was a random data input procedure replicated several times to incorporate its uncertainty. If anything, the procedure introduces white noise and hence could be conservative with respect to finding significant patterns. Using the *R* software package "fitdistrplus" (Delignette-Muller & Dutang, 2015), we analyzed the distributions of body mass and LD1 values we had for each Canidae subfamily independently. We first used the function "*descdist*" to help visualize theoretical distributions that could potentially explain our data (Figure S4). We then fitted our empirical distributions to theoretical distributions using the function "*fitdist*", and compared the fit in a likelihood approach, using AIC values. As Borophaginae body mass data was clearly better described by a uniform distribution, no AIC values are reported.

Body mass distributions were better described by a normal distribution, with the exception of Borophaginae, which was clearly better explained by a uniform distribution (Figure S4). LD1 data, as it contains negative values, were approximated using normal distributions for all subfamilies (Supplementary Tables 1 and 2). Based on each theoretical fitted distribution parameters, we then randomly drew values from such fitted distributions and assigned to those species lacking data (Figure S5). Given that Borophaginae body mass was better described by an uniform distribution, to randomly drew values to augment the missing data we needed to define the boundaries of such distribution. Instead of using the same empirical values to define the boundaries, we expanded the empirical minimum (0.51; log scale) and maximum (3.72; log scale) values to allow the possibility that species with missing data could be either smaller or larger than the species from which we had the data. We choose $\log(1.1) \cong 0.09$ as the minimum and $\log(41.49 + 5) \cong 3.83$ as the maximum parameters to estimate Borophaginae missing data. *Canis lupus* body mass was also estimated differently. As one of the most widespread extant mammals of the world, gray wolf exhibit a wide range of body size measures (Macdonald, 2009) making it unrealistic to rely on only one measure to describe the species. We then drew values from a uniform distribution ranging from 25kg ~ 51kg, the minimum value from the Slater (2015) dataset and the maximum from Balisi et al. (2018) dataset. Another particular species we took a different approach was *Paraenhydrocyon josephi*. In Slater (2015) original dataset, one of the cranio-dental variables used in the LDA analyses (RBL) seemed incompatible with other similar species, leading it to be an extreme outlier value of LD1 (-13.139 – see Figure S6). Therefore, we removed this species LD1 value and applied the data augmentation procedure to it.

In our competition analyses using ecological information (section 2.2.3.2) we used information on diet categorization (hypo, meso, hypercarnivore) to restrict potential competitors. Given that some species in our dataset were not previously categorized we also needed to augment this type of missing data. To classify the diet category of those species without such information we used an algorithm of K-Nearest Neighbors (KNN), a non-parametric method widely used to classify data in machine-learning contexts (Altman, 1992; Cover & Hart, 1967; Hall et al., 2008). Using the *R* software package "*neighbr"* (Bolotov, 2020) function "*knn*", we took the species with known values of LD1 and diet category as the training data to estimate diet discrete categories, based on the 8 nearest neighbors, measured using the Euclidean similarity of both LD1 and body mass data. We choose the value of 8 nearest neighbors after repeated iterations with training data to classify known values of diet categorization because this value demonstrated high accuracy. We normalized LD1 and body mass data by rescaling the range in a min-max normalizing approach, before conducting the KNN algorithm. One should also note that the categorization of those species with missing data is done by using the already augmented data for LD1, but given that such procedure is repeated many times, this should not introduce any bias.

We repeated the whole data augmentation process 10 times for each one of the 50 temporal replicas, ending up with 500 different morphological datasets. As mentioned earlier, this procedure only introduces white noise, and hence the analysis is able to incorporate uncertainty without introducing any bias.

2.2.3.2 **Disparity metrics**

Disparity metrics have been used to describe patterns of a clade's morphological and/or ecological diversity through time (Hughes et al., 2013; Kotrc & Knoll, 2015), and are strongly context dependent. One should note that different metrics can capture different aspects of morphospace occupation (Ciampaglio et al., 2001; Guillerme et al., 2020). Given our interest in capturing the potential effect of species competition, we selected two measures deemed to capture density patterns of the morphospace: Mean Pairwise Distance (MPD) and Mean Nearest Neighbor Distance (MNND), explained below. Our expectation is that highly similar, and, therefore, potential competitor species should be closely placed in a multidimensional morphospace. We measured species proximity pairs using the Euclidean distances of both LD1 and body mass axis in our 500 datasets, storing the data in the pairwise matrix fashion. We latter multiply the spatiotemporal matrices described in section 2.2.2, either to the "reach" or "site" metric, to the matrices of ecological similarity to generate time series that describes how the crowding of morphospace changes taking into account only those species that overlap in space and time.

2.2.3.2.1 **Mean Pairwise Distance of Diet classes (MPD_diet)**

According to Ciampaglio et al (2001): “The mean pairwise distance is defined as the sum of the Euclidean distances in morphospace between all possible pairwise combinations divided by the total number of combinations”. We selected such measure because it is robust to sample size and percentage of missing data, providing a reliable estimate of the amount of differences between character states of species in the morphospace (Ciampaglio et al., 2001). We estimated MPD by calculating the mean of species pairwise distances matrices, after removing the upper matrix and diagonal and all pairs of non-coexisting species in a given competition scenario. Given that MPD will assume that every species might interfere with each other (even those at the opposite side of the morphospace), we decided to restrict MPD according to the diet categories. Under this metric, we allowed only species of either the same diet category or the adjacent category in the carnivory spectrum to compete. This was done by simply computing binary pairwise matrices of such interactions. Therefore, hypercarnivorous species did not compete with hypocarnivorous and vice-versa, while mesocarnivorous species (≈ 27% of species) were allowed to compete with itself and both hyper and hypocarnivorous species. Once again, we multiplied such matrices with the Euclidean distances matrices to estimate MPD and stored the metric values in time series. This metric will be henceforward referenced as “MPD_diet” to highlight the incorporation of diet categories competition.

2.2.3.2.2 **Mean Nearest Neighbor Distance (MNND)**

Our second and final metric of disparity used is known as the Mean Nearest Neighbor Distance (MNND). Different to MPD_diet, the only distances that are computed are those of each species to its nearest neighbor i.e., the closest species in the morphospace (Foote, 1990; Guillerme et al., 2020). We can estimate such metric by extracting the shortest distance between species pairs, and averaging such values instead of all pairwise distances in a given moment in time. As only the shortest distances were measured, we do not expect MNND to include the potential competition of species that are unlikely to compete. In this case, the nearest species will most likely be in the same diet category as the focus species (or at most at adjacent diets), hence we did not have to modulate competition based on diet categories as was done to MPD. We expect MNND to capture the effect of the competition imposed by the most likely competitor. We also expect the time series to exhibit an increase in competition intensity as the value of MNND decrease. Once again, MNND values were stored in time series to input in the correlation analyses.

2.2.4 **Time-space ecology**

Summing up our different approaches to model different scenarios of competition, our modular framework allowed us to independently estimate metrics of purely diversity-dependence competition and also incorporate more realistic mechanisms of competition. Such scenarios included either spatiotemporal aspects of coexistence or ecomorphological overlap, or even a combination of both. Time coexistence is the pivotal aspect of coexistence, incorporated across all scenarios by multiplying whatever matrices of interest by temporal coexistence. By successively increasing the complexity of competition scenarios and simultaneously analyzing intermediate steps, we expect to get a better understanding of how competition can be measured and analyzed in the fossil record.

Compiling all intermediate and final steps of our modular framework, we ended up with 3150 time series comprising all different aspects of coexistence, competition and data completion. To discuss such results, we reference all time series according to its competition scenario:

a) "global" number of coexisting species through time, purely diversity-dependence: 50 time series;
b) mean number of spatially coexisting species trough time:
    - "reach" coexistence: 50 time series;
    - "site" coexistence: 50 time series.
c) "global" ecological competition:
    - MPD: 500 time series;
    - MNND: 500 time series.
d) spatiotemporal ecological competition:
    - MPD + "reach": 500 time series;
    - MPD + "site": 500 time series;
    - MNND + "reach": 500 time series;
    - MNND + "site": 500 time series.

2.3 ***PyRateContinuous*** **framework**

We conducted the statistical correlation analyses between each different time series describing competition and diversification dynamics using the *PyRateContinuous* framework. *PyRateContinuous* is an implementation of the original *PyRate* software which explicitly tests if variations in speciation and extinction rates through time are associated with a given time series of a continuous variable (Silvestro et al., 2015). Under this framework, speciation and extinction rates can be associated to the time series either by a linear or exponential function, and such association can be estimated separately for different time windows. The parameter of interest is the correlation parameter, which quantifies the strength of the correlation between changes in birth-death rates and the variable of interest. Traditionally, such variable could represent external factors such as proxies for paleotemperature (Balisi & Van Valkenburgh, 2020; Silvestro et al., 2015), or intrinsic factors as a clade's own diversity (Silvestro et al., 2015).

PyRateContinuous implementation typically does not need to model the preservation process, and uses the "true" times of speciation and extinction derived from a previous *PyRate* analysis. Here we followed this approach and used the species longevities extracted from our preliminary 50 *PyRate* analyses, explained in section 2.1. Here, we assumed an exponential correlation (Lehtonen et al., 2017) between changes in rates and changes in our time series of interest (described in section 2.2.4), comprising all of our competition scenarios. Given that the nature of competition might change in absolute time, due to internal or external factors, we designed our correlation analyses to be structured in different geological periods (see below). We also modeled the potential correlations assuming no temporal changes in the importance of competition and hence analyzed the changes in the whole diversification history of the clade as one process. We therefore ended up with two classes of analyses, namely:

a) correlations estimated across the whole timespan from 37.2 million years ago to the present.
b) correlations split in the Cenozoic epochs of the geologic timescale and NALMAs, i.e., Late Eocene, Oligocene, Miocene, Pliocene and Quaternary, with boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma.

We determined the correlations to be estimated for the Cenozoic epochs after inspections of how rates of speciation and extinction varied through time, capturing intervals of rate shifts in such rates, and also avoiding the risk of overparametrization in selecting too small intervals for correlations to be estimated (this is also why we combined the Pleistocene and Holocene epochs into the Quaternary). We analyzed the correlations between Canidae diversification dynamics and our different 3150 time series fixing the times of speciation and extinction derived from the previous *PyRate* analyses. We ran 30000000 MCMC iterations sampling every 1000 and discarded the first 10% as the burn-in for each analysis, separately for both across the whole timespan and for the epoch-oriented correlations. By default, the time series of interest is rescaled so that its range of values equals 1. We summarized the posterior distributions of correlation parameters of speciation (*Gl*) and extinction (*Gm*) with median values and the 95% Highest Posterior Density (HPD) credibility intervals. We also reported the baseline speciation and extinction rates, which represent the estimated speciation and extinction rates if those rates were not associated with the time series of interest (Supplementary Tables 3, 4, 5). We considered results to show strong evidence if the 95% HPD distributions did not overlap 0, however, we did not discard considerations about weaker signals of correlation, as we interpreted many results under the different temporal replicas lens.

4 Results

1 Canidae diversification dynamics

Our results clearly show that speciation and extinction rates change through time, resulting in a dynamic diversification rate (Figure 1). Diversification rates are strongly positive at first, but around 30 Ma experience a marked deceleration, followed by a long phase where diversification rates were estimated to be very close to zero. Although the median diversification rate from the Late Oligocene until around the Miocene boundary is constant and positive, we should note that the 95% HPD includes zero. Through the whole Miocene, diversification rates remained very close to zero, although now the median was slightly negative. There is evidence that the clade might have experienced a punctual shift in diversification around 22 Ma, and again around 13 Ma. Those shifts in diversification are not ubiquitous because the temporal placement of extinction rate shifts is highly uncertain (Figure 1B). Therefore, after the Late Eocene/Early Oligocene radiation, Canidae diversification experienced phases of either stability or subtle diversity changes with short pulses of diversification drop that might have interrupted this steady decline in diversity (See Figure 2A). In the Quaternary, diversification considerably drops leading the median estimate to be considerably negative, although the 95% HPD still includes zero.

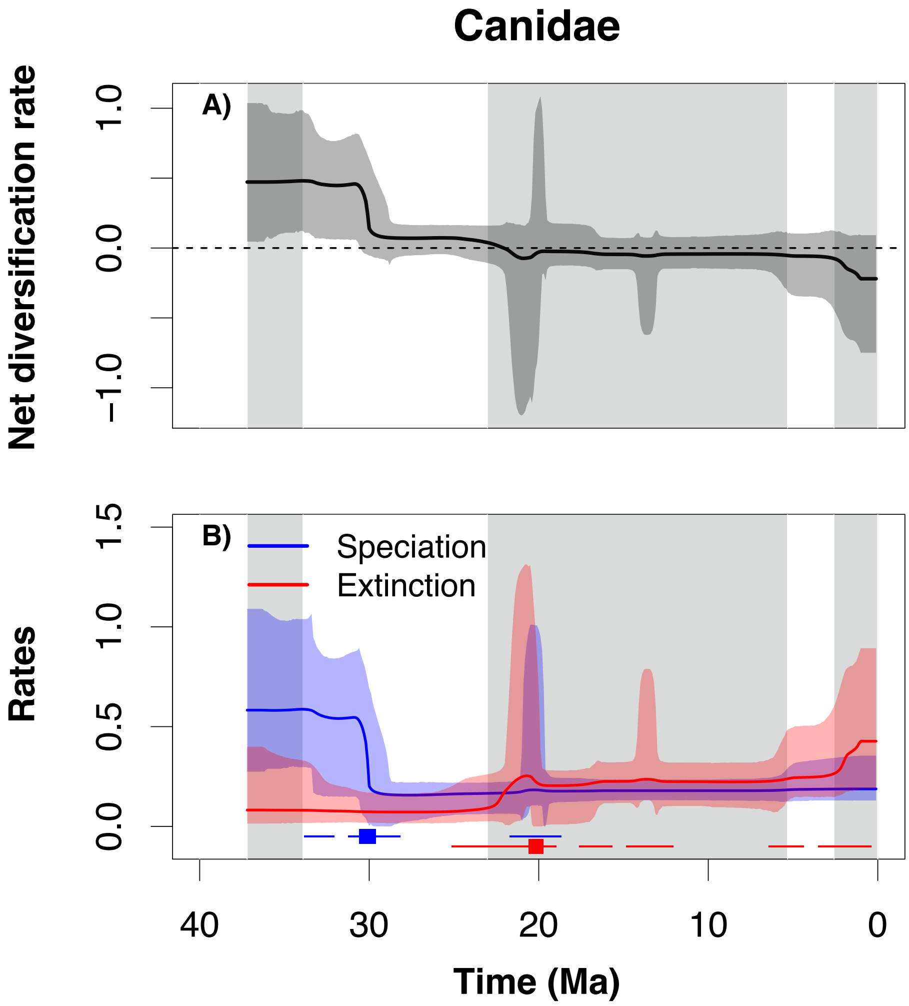

Figure 1: Rates through time plots showing Canidae diversification dynamics. A) Net diversification rates (speciation – extinction). B) Speciation and extinction rates. Diversification, speciation and extinction rates are expressed as the number of events per lineage per million years. Solid lines represent the median of posterior distribution, with shaded areas representing the 95% credible intervals, the Highest Posterior Density (HPD). Solid horizontal lines at the bottom represent the moments of rate shifts with BF > 2, and boxes the moments of rate shifts with BF > 6. Gray and white vertical shaded boxes represent the Cenozoic epoch/mammal age boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma.

When looking at speciation and extinction rates separately (Figure 1B), we notice that the initial decrease in diversification is driven by a strong shift in speciation rates around 30 Ma, with no concomitant changes in extinction. The Bayes Factors (BF) analysis suggested strong support for this rate shift, with a BF value higher than 6 (Silvestro et al., 2019), for the combined posterior (Figure 1B), as well as for the majority of temporal replicates (Figure S3). Speciation then remained lower and constant with no strong rate shifts until the present (Figure 1B). After a period of stability through the Late Eocene and Oligocene, extinction rate increased to become slightly higher than speciation around the Oligocene/Miocene boundary, leading to a negative net diversification. The placement of that extinction shift shows a relative temporal uncertainty, both within and between each replicate (Figure S3). Although several replicates indicates two sequential strong shifts (BF > 6) in extinction, others show a longer uncertainty in placing those shifts, which produced Bayes Factors values smaller than 6, but still higher than 2, denoting relative support (Figure S3). Subsequent pulses in extinction might have occurred throughout the second half of Canidae history, but the support for such events is weaker (Figures 1B and S3). At the Quaternary, we detected an increase in extinction rates, although the temporal uncertainty of such shifts also lead to weaker support ($2 < BF < 6$) in the posterior and in many replicates. We note however, that such extinction shift towards the present is likely to be real given that it is present in virtually all replicates, with some even showing strong support (BF > 6) for such final shift (Figure S3).

2 **Competition scenarios and time series**

We summarize the different time series used as our proxies for competition intensity in Figure 2. Through most of the Late Eocene, only one or very few species were present, leading to estimates that should be taken with caution such as “zero” spatial coexistence or estimates of disparity metrics. The remaining time periods show considerably diversity and we concentrate our results and discussions on those time windows.

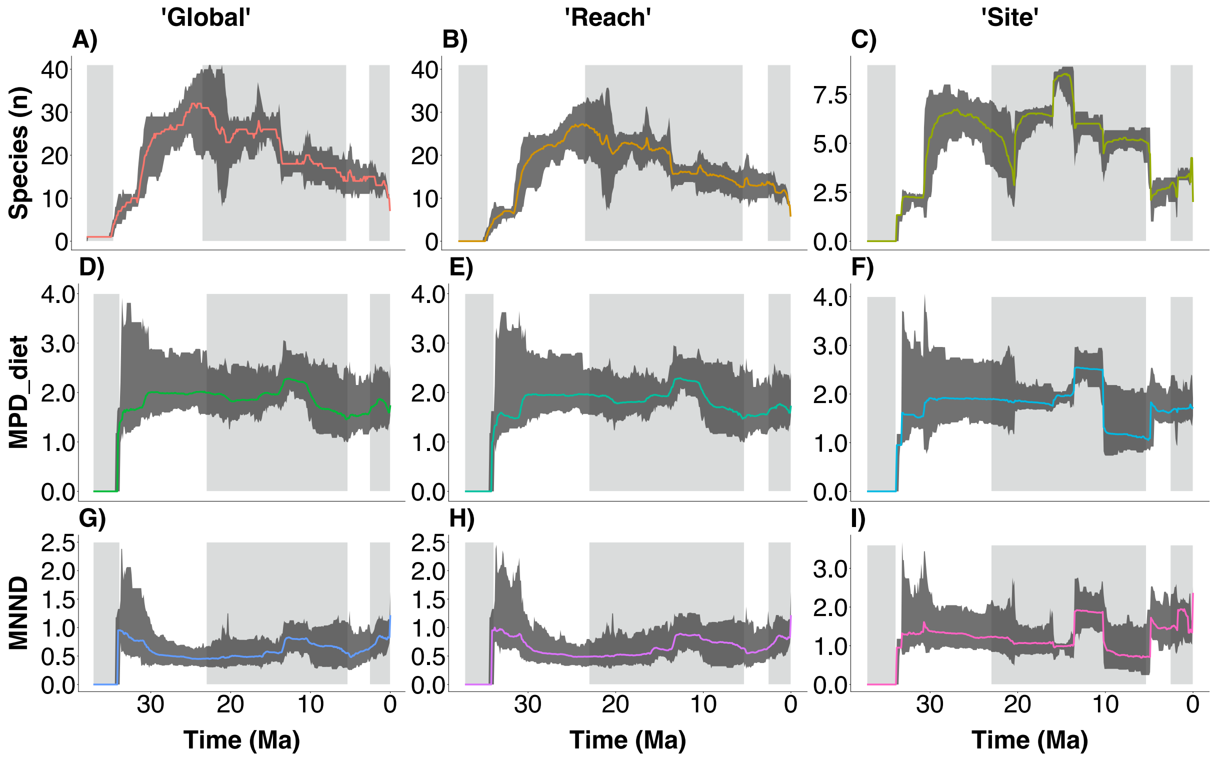

Figure 2: Nine different times series used as proxy for competition intensity. Solid lines represent the median value for each competition scenario, with shaded areas representing the maximum and minimum limits of each metric across the different replicas. Gray and white vertical shaded boxes represent the Cenozoic epoch/mammal age boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma. Rows represent the different metrics used to measure competition intensity in morphospace, while columns represent the different approaches to measure spatial coexistence. In “global”, species numbers are absolute, while the “reach” and “site” time series are expressed in mean number of coexisting species. MPD and MNND are dimensionless measures of Euclidean distances in the morphospace. Notice the difference of scale between metrics of spatial coexistence and MNND.

For the first competition scenario we used “global” diversity trajectory as our proxy for competition intensity, which represents the typical time series used to infer the diversity-dependent diversification dynamics (Figure 2A). Species diversity in the Late Eocene is characterized by either the sole presence of one species, *Hesperocyon gregarius*, or few coexisting Hesperocyoninae species such as *H. coloradensis* and *Osbornodon renjiei*. Species diversity rapidly expands in the Oligocene (Figure 2A), driven by high speciation rates (Figure 1B). The “global” species richness seemed to “overshoot” around the Oligocene/Miocene boundary but remained relatively stable through most of the Oligocene and Miocene until about 15 Million years ago. Diversity then experienced a quick drop, and then a steady and subtle decline throughout the Miocene and Pliocene. Very close to the present, “global” species richness abruptly drops to reach current number of species. The “reach” spatial coexistence scenario (Figure 2B) closely mirrors the “global” diversity pattern, although with slightly lower values (see also Figure S8 showing the correlation of those two time series).

The "site" scenario, on the other hand, displays some striking differences, although it resembles the other two patterns in the general trend of "rise and fall" in the number of coexisting species. The phase of expanding diversity suggests a very abrupt rise in number of coexisting species at the Early Oligocene. The remainder of the period, and part of the Miocene, presents a roughly constant number of coexisting species, punctuated by two events: one showing a dramatic drop and immediate recover in number of coexisting species (around 20 Ma), and another showing a momentary increase in the number of coexisting species (around 13 Ma). Such marked decline and subsequent rise in diversity are not seen in the other diversity time series (Figure 2A, B). Through the rest of the Miocene it follows two short periods of roughly constant numbers of coexisting species interrupted by a stepwise drop. Hence, the most striking differences between the "site" time series and the other measures of spatial coexistence are: i) there are more stepwise changes in diversity throughout time, and ii) the gentle increase in the number of coexisting species throughout most of the Pliocene and Pleistocene (only seen in "site" coexistence).

The different time series depicting changes in Mean Pairwise Distances (MPD) are mostly concordant (Figure 2D, E, F) and show in fact a very strong correlation (Figure S8). Contrary to our expectations, MPD did not change much throughout most of Canidae history. Apart from the first abrupt increase in the Eocene/Oligocene boundary, which is likely an artifact resulting from estimating distances at very low richness in the Eocene, the MPD values remained roughly constant throughout the whole time. The main exceptions were two stepwise changes at the Late Miocene when we used the "site" spatial coexistence metric. During the Canidae radiation (Late Eocene/Early Oligocene) the MPD values, if anything, increases instead of decreasing as expected.

Mean Nearest Neighbor Distances (MNND), showed temporal trends that better corresponded to our expectations of increasing competition, at least when considering the "global" and "reach" approaches. During the expanding phase of diversity, MNND decreases in both "global" and "reach" coexistence (Figure 2G, H). In other words, as more species are added in the morphospace, the distance between a species and its nearest competitor becomes smaller, even at the face of an increase in total morphospace for the same time period (Figure S7). Through the Miocene, MNND values remained constantly low for the "global" and "reach" approaches (Figure 2G, H), but showed an increase during the Pliocene and Quaternary. Such increase in MNND was accompanied by decreases in species diversity/coexistence (Figure 2A, B), and an increase in total morphospace area (Figure S7), suggesting a scenario of less intense competition, where species were more sparsely distributed in the morphospace. However, these patterns were only seen for the "global" and "reach" methods. The "site" MNND time series did not show the steady decrease seen in Canidae radiation during the Oligocene (Figure 2I), nor the steady rise from the Miocene/Pliocene boundary up to the present. Instead, it showed marked stepwise shifts occurring from the second half of the Miocene up to the present.

3 Correlation of macroevolutionary dynamics and competition

When considering only the number of coexisting species (Figure 2A, B, C), all metrics used suggested strong evidence for negative correlation between changes in speciation rate and changes in the diversity/coexistence time series during the Oligocene (Figure 3). For this time interval, the 95% Highest Posterior Density (HPD) interval did not overlap with 0. Such pattern of negative correlation is only present during the phase of diversity expansion (Oligocene), whereas in other time periods, where diversity is roughly constant or decreasing, no evidence for correlation was detected (Figure 3A, B, C). MPD analyses did not show any association between any of the different time series and speciation rates (Figure 3D, E, F). Given the roughly constant value of MPD (Figure 2D, E, F), this is not surprising, but we suspect that such lack of association might have also been affected by a concomitant change in the total morphospace area (Figure S7). During the Oligocene, as the number of species increased, the total morphospace area increased allowing the mean distance between species pairs to either remain constant or even slightly increase.

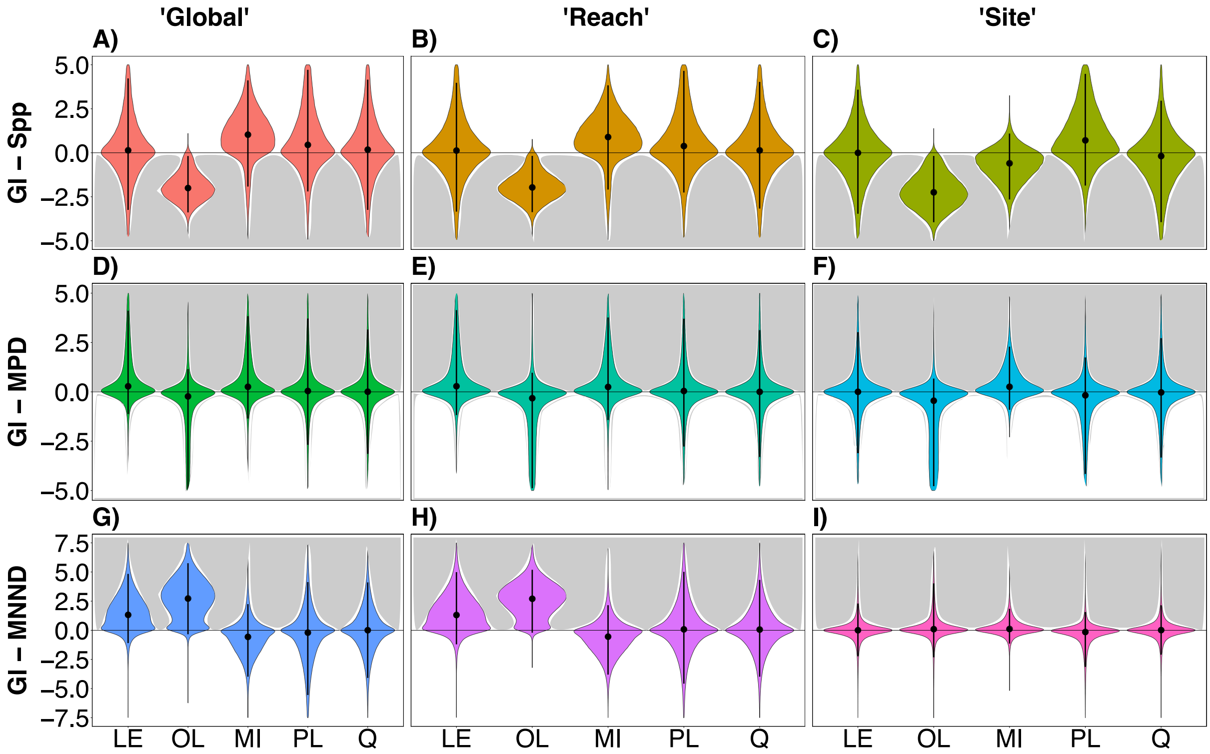

Figure 3: Posterior distributions of speciation correlation parameters (*Gl*) in discrete time windows. LE: Late Eocene, OL: Oligocene, MI: Miocene, PL: Pliocene, Q: Quaternary. Correlation parameters are dimensionless and quantify the amount of change in rates associated with the change in the time series of interest. Rows, columns and color-coding are the same as in Figure 2. Gray shaded areas highlight our expectations for the values of the parameter if speciation rate responded accordingly to what would be expected if competition was a relevant factor, with positive or negative values depending on the metric. The vertical black lines within each violin plot represents the 95% HPD and the dot represent the median of each combined posterior distribution.

During the Late Eocene and Oligocene time windows, the *Gl* 95% HPD describing the potential association between MNND and speciation rate showed evidence for a positive correlation for the “global” and “reach” coexistence scenarios. Although this positive correlation might seem at first counter-intuitive (compared to the negative correlation seen for the number of species) we should note that MNND measures the minimum distance between two neighbor species. Therefore, as MNND increases, species becomes further apart from each other, and we expect the intensity of competition to decrease. Similarly, the positive correlation means that as MNND decreases species becomes closer to each other, and we expect intensity of competition to increase, leading to deceleration in speciation. During the Late Eocene, the rapid expansion of diversity from one to only a few species (Figure 2A) leads to a rapid increase in MNND from 0 to 1 (Figure 2G). Given that such dynamics was measured in a very small interval with very few taxa, we suggest that such correlation must be viewed with caution.

Although we see evidence for correlation between changes in competition intensity and speciation rate during the Oligocene (when using “global” and “reach” MNND), we note that the 95% HPD do cross the value of zero, weakening the evidence for this correlation

(Table S3). In both cases ("global" and "reach" MNND) we see a rather bimodal pattern, where the major mode is clearly offset from the value of zero, but the minor mode is very close to zero (Figure 3G, H, table S3). When we look at the posterior distributions of each replicated dataset independently (Figures S9 and S10), we note that the median of every dataset is offset from the value of zero, but some (less than half) replicates have their 95% HPD crossing the value of zero. This indicates that this uncertainty seen in the combined posterior distribution mostly comes from differences between replicates but also from uncertainty within some replicates. One possible explanation for such signal is the amount of white noise introduced by our conservative approach to augment the missing morphological data (Section 2.2.3.1 in material and methods). The relative uncertainty in the placement of species in the morphospace might have led to different MNND trajectories among the different replicated datasets, which in turn might have produced different correlations among the different replicates, and uncertainty within some replicates. We detect no evidence of correlation between "site" MNND and speciation rate, a result somewhat expected given the trajectories observed in these individual time series (Figures 2I and 3I).

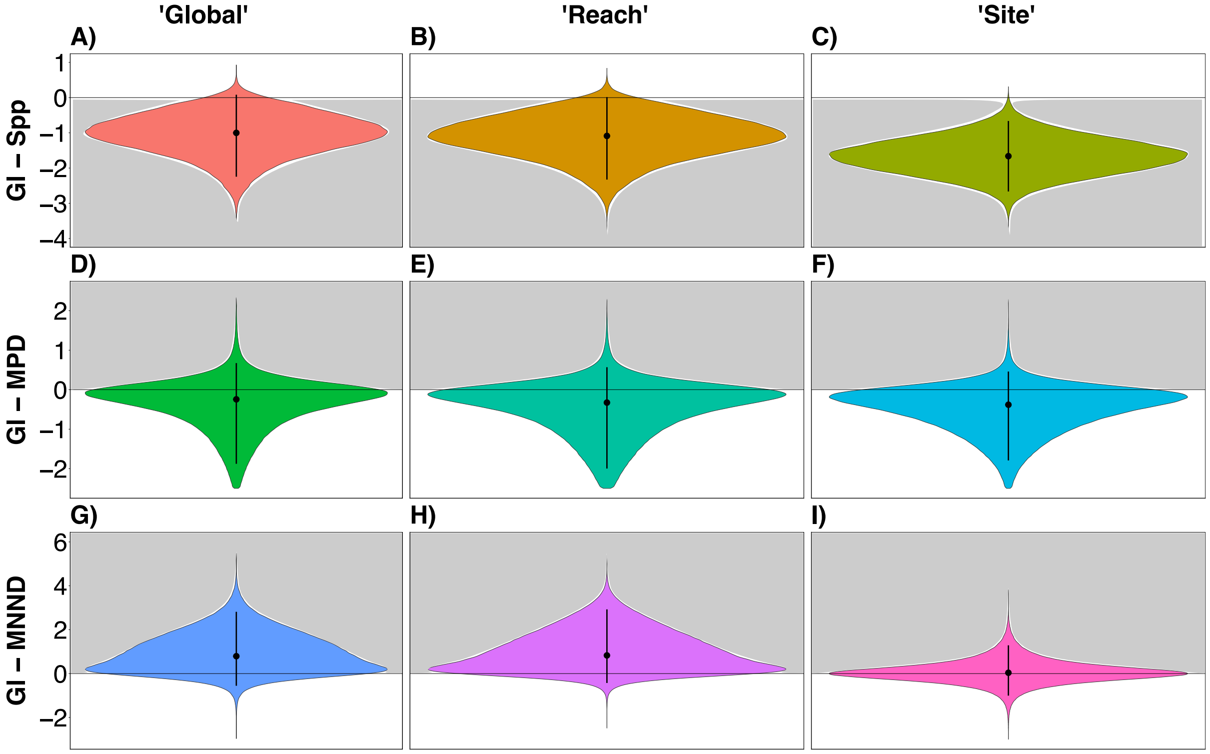

Figure 4: Posterior distributions of speciation correlation parameters (*Gl*) when analyzing the whole Cenozoic. Correlation parameters are dimensionless and quantify the amount of change in rates associated with the change in the time series of interest. Rows, columns, and color-coding are the same as in Figure 2. Gray shades areas highlight our expectations for the values of the parameter if speciation rate corresponded accordingly to what would be expected if competition was a relevant factor, with positive or negative values depending on the metric. The vertical black lines within each violin plot represents the 95% HPD and the dot represent the median of each combined posterior distribution.

When looking at the results where the Cenozoic was analyzed as a whole (Figure 4), we see weaker evidence in favor of a potential association between changes in the number of coexisting species and speciation rate for two of the three metrics, the "global" and "reach" metrics (Figure 4A, B). Although the correlation is negative and the distribution is clearly offset from zero, the 95% HPD upper interval crosses zero (0.078 for "global" and 0.015 for "reach", see Table S5). The "site" MNND on the other hand, still shows strong evidence for an association between changes in the MNND and speciation rate when looking at the Cenozoic as a whole (Figure 5C, Table S5).

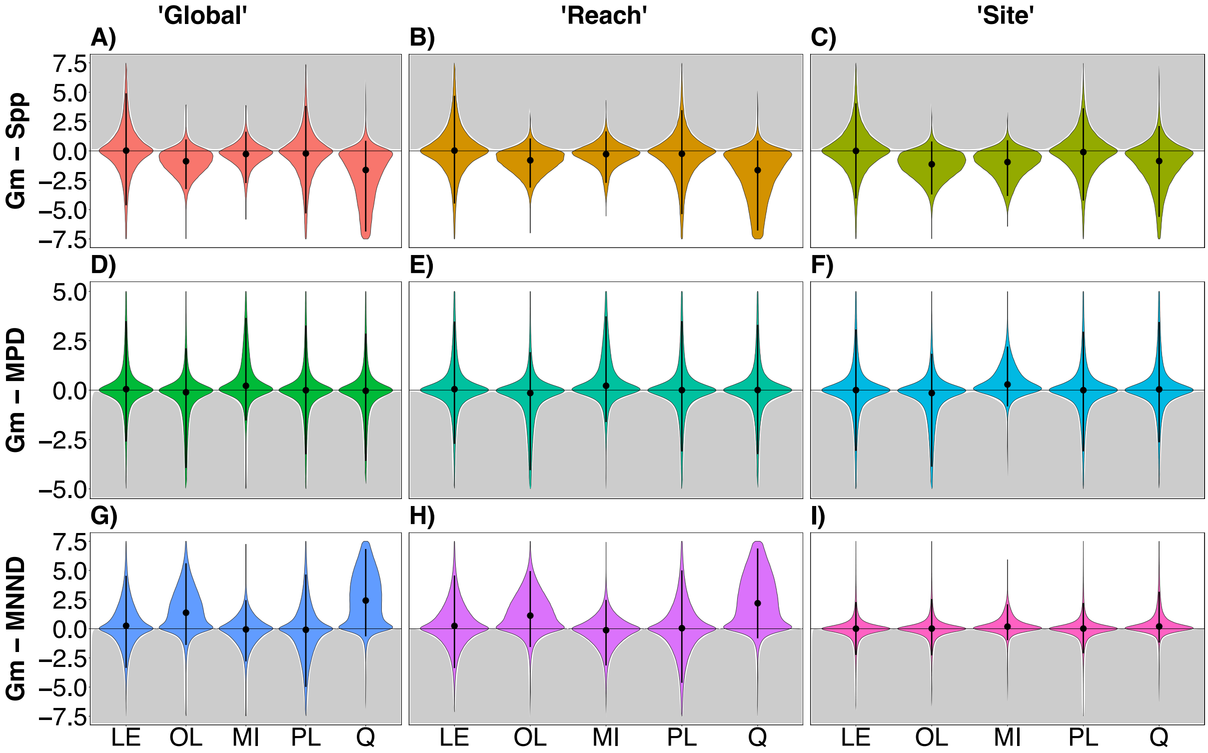

Figure 5: Posterior distributions of extinction correlation parameters (*Gm*) in discrete time windows. LE: Late Eocene, OL: Oligocene, MI: Miocene, PL: Pliocene, Q: Quaternary. Correlation parameters are dimensionless and quantify the amount of change in rates associated with the change in the time series of interest. Rows, columns and color-coding are the same as in Figure 2. Gray shaded areas highlight our expectations for the values of the parameter if extinction rate responded accordingly to what would be expected if competition was a relevant factor, with positive or negative values depending on the metric. The vertical black lines within each violin plot represents the 95% HPD and the dot represent the median of each combined posterior distribution.

The results for the extinction dynamics showed no strong correlation between the different proxies for competition and extinction rates (Figure 5). The *Gm* posterior distributions across all competition scenarios are usually centered at or very close to zero, and in few time windows where this was not the case, the 95% HPD crossed zero, and showed a correlation in the opposite direction as expected (Figure 5). In the only time interval (Quaternary) where we see some reasonable evidence for an association, the evidence was weak and again in favor of a pattern that is also the inverse of what would be expected if competition was relevant. This unexpected association was detected for the "global" and "reach" analyses of species coexistence (Figure 5A, B), and their corresponding MNND analyses at the Quaternary time window (Figure 5G, H). Here, the 95% HPD is off centered towards positive values for the "global" and "reach" coexistence analyses and towards negative values for their corresponding MNND analyses.

When analyzing the extinction dynamics for the Cenozoic as a whole, we only detected strong evidence for an association between the number of coexisting species and extinction rate for the "site" spatial coexistence (Figure 6C), although "global" and "reach" once again did show some weaker evidence of an association (Figure 6A, B). However, these associations are in the opposite direction expected under the competition scenario. Interestingly, the "global" and "reach" species coexistence time series analyzed for the whole Cenozoic shows slightly stronger signal (Figure 6A, B, G, H) when compared to the signal recovered for the individual time windows (Figure 5), but again in the opposite direction we would expect for competition.

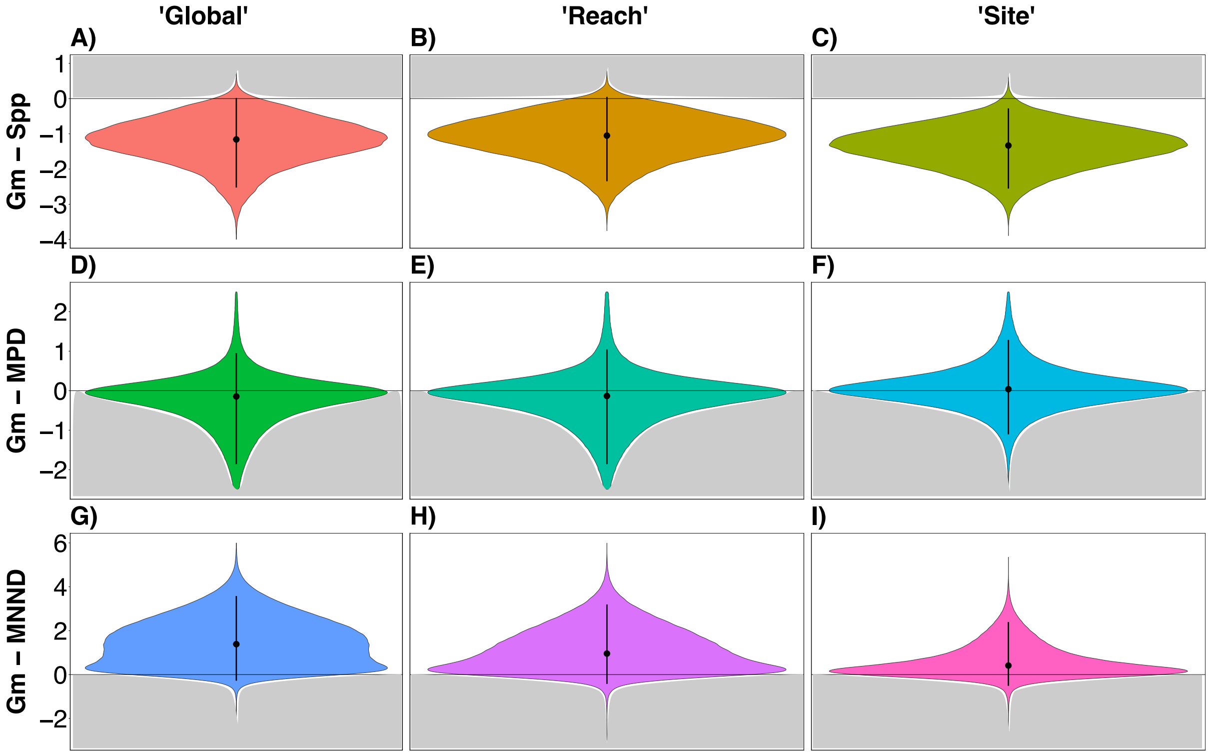

Figure 6: Posterior distributions of extinction correlation parameters (*Gm*) when analyzing the whole Cenozoic. Correlation parameters are dimensionless and quantify the amount of change in rates associated with the change in the time series of interest. Rows, columns, and color-coding are the same as in Figure 2. Gray shades areas highlight our expectations for the values of the parameter if extinction rate corresponded accordingly to what would be expected if competition was a relevant factor, with positive or negative values depending on the metric. The vertical black lines within each violin plot represents the 95% HPD and the dot represent the median of each combined posterior distribution.

5 Discussion

Although diversity-dependence has been previously described for several lineages (Condamine et al., 2019; Foote et al., 2018), including Canidae (Pires et al., 2017; Silvestro et al., 2015), the idea that resource competition is the underlying mechanism is, due to the nature of historical studies, an interpretation. In our study, we could not truly overcome this barrier but we used a more mechanistic approach that measures how the amount of niche and spatial overlap changes through time, to try more directly test the effect of resource competition in diversification dynamics. We have demonstrated that the portrayed diversity-dependence diversification might indeed be linked to resource partitioning in Canidae. However, by analyzing speciation and extinction dynamics separately, we demonstrate that diversity-dependence and resource competition mechanisms might only be relevant through speciation, and when the lineage is initially radiating. Extinction dynamics, on the other hand, do not seem to be correlated with changes in the intensity of competition, nor diversity *per se*.

Studying the effect of species interactions in deep time is not an easy task, given that it is not possible to directly observe the outcome of such interactions (Ezard et al., 2016). Therefore, macroevolutionary studies have relied upon the use of diversity-dependent models to indirectly infer the potential effects of species interactions, in particular competition (Ezard et al., 2016; Marshall & Quental, 2016; Rabosky, 2013; Sepkoski, 1996). Interestingly, there has been a recent accumulation of studies showing the potential relevance of diversity-dependence at macroevolutionary scales (Condamine et al., 2019; Foote et al., 2018; Pires et al., 2017; Silvestro et al., 2015). To some extent, the limitations of not being able to directly measure competition when using diversity-dependent models have been partially overcome by choosing smaller clades where one might expect competition should have acted (Marshall & Quental, 2016).

Our results are in accordance to previous analysis (Pires et al., 2017), which suggested that variations in Canidae diversity are indeed associated with changes in speciation dynamics, confirming the idea that self-diversity-dependence typically operates through speciation rather than extinction dynamics. Although this has been interpreted as evidence in favor of interspecific competition, we note that the use of diversity trajectories implies that all species potentially interfere with each other. In a spatial overlap perspective, this would mean that all species coexisting at a given moment in time also coexist in space, which may not be necessarily true. In fact, our results suggest that not all species coexist in space and time, highlighted when we compare the "site" metric to the other spatial metrics (Figure 2A, B, C). Interestingly, the results from the "reach" and "site" metrics, designed to explicitly incorporate spatial coexistence, also show strong evidence for diversity-dependence. Therefore, by more explicitly taking into account spatial coexistence, we show that such mechanism also acts solely on speciation (Figure 3) and not on extinction (Figure 5), and only at a certain time window. Given that both metrics have shown to capture different aspects of species coexistence (Figure 2B, C), our results suggest diversity-dependence can be captured at different spatial scales.

By directly incorporating eco-morphological information, one can potentially better infer the effect of resource competition on lineages diversification. This can be done by explicitly measuring how species are distributed in the morphospace (Ciampaglio et al., 2001; Foote, 1990; Guillerme et al., 2020; McGowan & Dyke, 2007), presuming that morphology can be translated to ecological function (Van Valkenburgh, 1988, 2007). The initial expansion of Canidae diversity is mostly driven by the appearance of hypo and mesocarnivorous morphologies (Figures S12 and S13), while the hypercarnivorous niche was mostly occupied by other clades such as Hyaenodonts and Nimravids (Van Valkenburgh, 1999). However, right after the initial occupation of the morphospace, when diversity started to rise, many hypercarnivorous forms start to appear roughly at the same time around 30 Ma (Figures S12 and S13; see also Slater 2015). The rapid expansion of early hypercarnivorous Canidae forms is hypothesized to have actively influenced the demise of Hyaenodonts (Van Valkenburgh, 1999), with recent studies demonstrating such displacement (Pires et al., 2017). In the context of competition imposed by species within the family Canidae, this rapid filling of the morphospace translates into a progressive drop in the MNND metric (Figure 2G, H), a concomitant drop in speciation (Figure 1B), and hence a more direct evidence for a role of resource competition on driving the speciation dynamics during the Oligocene (Figure 3G, H).

Interestingly, only when considering one morphospace metric (MNND) we see evidence for an association between changes in speciation rate and changes in the time series measuring competition intensity. We expected that the other metric (MPD) would also have captured the intensity of competition by measuring how the packing of morphospace changed through time. However, our results suggest that MPD might not be the most appropriate metric for competition analyses. We suspect this result was strongly influenced by how the total morphospace area varied through time (Figure S7). As more species were added, the total morphospace area increased during the Oligocene. Hence, by measuring all pairwise distances, the competition effect was diluted when we used MPD metric. Even when restricting competition to take place at the same or adjacent diet categories, we might still average distances of species that are really far apart in the morphospace, and thus are unlikely to interfere with each other.

The most unexpected result was the absence of correlation between changes in MNND and speciation rates when we considered spatial coexistence at the “site” metric (Figure 3I). This was somewhat surprising given that MNND showed evidence for association with speciation dynamics for the other metrics of spatial coexistence (Figure 3G, H), and that the number of coexisting species when using the “site” metric also showed to be correlated with speciation dynamics (Figure 3C). It is worth noticing that through the Oligocene, the moment with a significant strong shift in speciation rates, the MNND at the “global” and “reach” scenarios showed a very different trajectory than MNND at the “site” scenario (Figures 2 and S14). In the “global” and “reach” scenarios, we see a steady drop in MNND values, while in “site” scenario, MNND remains roughly constant (with a sharp peak around 30 Ma) and at a considerable higher value than the others (see Figure S14). This suggests that the species coexisting when using “site” metric were on average further apart in the morphospace than the species that were considered to coexist when using the other spatial metrics.

Extant canids avoid sharing the habitat when competition is intense (Johnson et al., 1996), either by partitioning habitat use or food resource, or by dominant-subordinate dynamics. If we assume such interference/avoidance to have happened in extinct canids (which we do), and that the composition of species might change drastically from one locality to another, we can imagine that coexistence measured when using the “site” metric might not detect all traces of competition in the fossil record (Sepkoski, 1996), at least when measuring distances in the morphospace. We note that our metric of coexistence when using the “site” metric is different than measuring the number of species or the morphospace occupation with each site (each location or fossil assemblage) individually. Here, we measured what was the average number of species that each species potentially coexisted and interacted with. Future work could try to investigate how the identity of interacting species, from the point of view of a focal species, change through space and time (e.g. beta diversity). Unfortunately, our metric is insensitive to changes in species identity, but it is possible that gathering this information might help one understand why we did not detect an association between changes in speciation and changes in MNND when using the “site” spatial coexistence approach. Alternatively, it is possible that the absence of association with MNND when using the “site” spatial approach might be related to differences in the completeness of the fossil record. It is known that the fossil record typically increases in quality both at higher taxonomic and spatial scales. Therefore, it is possible that describing coexistence when using the “site” metrics might underestimate the number of coexisting species and how far apart they are in the morphospace. As mentioned above, our idea to use “site” spatial coexistence was to measure the average number of species each species coexists with, and to also measure the average distance between each focus species and its potential competitors. We see this metric as a minimum estimate of coexistence, rather than assuming speciation occurs at the sites we analyzed. In that sense, we suspect that the incompleteness of the fossil record might perhaps renders the “site” metric not sensitive to fully detect the effects of competition on diversification dynamics. That said, it is an open question if this lack of correlation was simply an artifact of the fossil record, or if different biological information is captured at different scales. In fact, changes in scale have been shown to change the relevance of different mechanisms. For example, Slater & Friscia (2019) have shown that at the Carnivora order level, a model describing the evolution of morphological aspects related to diet supported the classic view of adaptive radiation (early burst in morphological diversification), while such model was not universally adequate at the family level. Future work could try to directly measure how the occupation of each site *per se* happens, a different metric than the one we used here. As such, one can calculate other disparity metrics apart from MNND or MPD for each site, such as the total area occupied in the morphospace.

We have demonstrated that extinction dynamics in Canidae does not seem to be correlated with changing morphospace or species coexistence dynamics, at least as expected by interspecific competition mechanisms. Contrary to the initial propositions of diversity-dependence (Sepkoski, 1996), we see that changes in interspecific competition intensity (measured by changes in diversity or changes in the morphological average distances between spatially coexisting species) did not result in changes in the extinction dynamics. We note that at the moment Canidae family was experiencing its radiation and rise in diversity, extinction remained constant (Figure 1B), even in a progressively more crowded morphospace (measured by changes in MNND – Figure 2G, H). We suggest that the apparent irrelevance of competition on extinction dynamics might be related to the speciation mechanism itself. If ecological speciation (Nosil, 2012) is relatively common, then it is possible that through the process of speciation only those species that became ecologically distinct enough would be produced, at least locally. If this is the case, then this ecological differentiation at the inception of species might ameliorate later effects that competition might have on the survival of species within the clade of interest. Under this logic, interspecific competition would more likely drive species to extinction when those species have not "perceived themselves" during the process of speciation. The observation that diversity-dependence extinction is typically detected among clades (Pires et al., 2017; Silvestro et al., 2015) is in accordance with such reasoning, especially if the competing clade has migrated from another continent. Pires et al (2017) have demonstrated that North American Canidae extinction dynamics is strongly associated with changes in Felidae diversity, which have presumably migrated from Eurasia sometime during the Miocene. We argue that the extinction dynamics of Canidae is more strongly controlled by climate (Balisi & Van Valkenburgh, 2020; Pires et al., 2017), clade competition (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 1999), or to evolutionary ratchet mechanisms (Balisi & Van Valkenburgh, 2020; Van Valkenburgh, 1999; Van Valkenburgh et al., 2004) than by factors related to its own diversity, or morphospace occupation. Some of these external factors (climate and clade competition) are likely to have been more relevant in the second half of Canidae history, when extinction seemed to have played a major role in its diversification dynamics (Figure 1B).

Changing climate shaped much of mammalian diversification in the last 20 Million years (Janis, 1993), driven mostly by the transition to the "Icehouse Earth" in Late Cenozoic (Smith & Pickering, 2003). Cooling climates driven by reconfiguration of oceanic currents and formation of ice caps lead to the turnover of vegetational habitats across the world, with increasing diversity of open grasslands in North America, at the demise of denser forests of the Early Cenozoic (Strömberg, 2002, 2005). Although the transition to Icehouse climates started around the Early Oligocene, no impact on mammalian extinction was observed (Prothero & Heaton, 1996), a pattern similar to what we recovered for Canidae given that extinction rate remained constant throughout the Oligocene (Figure 1B). Early Canidae forms exhibited post-cranial adaptations to savannah-woodland environments, which in turn, are proposed to be correlated with greater species packing and richness (Van Valkenburgh, 1985). The progressively less productive habitats observed through the Late Miocene (Jetz & Fine, 2012) are correlated with greater extinction and demise of smaller forms (Janis, 1993), which we also observe in Canids (Figure S12), with no preferential extinction of hypercarnivorous forms (Figure S13), except perhaps very close to the present (Balisi & Van Valkenburgh, 2020). There is evidence of cooling climate effects on Canidae extinction dynamics in the Late Miocene as well (Balisi & Van Valkenburgh, 2020; Pires et al., 2017; Silvestro et al., 2015) and, although no explicit mechanism that would fit different taxa has been proposed, extinction dynamics driven by climate might be correlated to the potential patterns of periodic extinction events (Raup & Sepkoski, 1984, 1986). We suspect the weak evidence for an inverse correlation between extinction dynamics and changes in diversity and competition metrics during the Quaternary (Figure 5A, B, G, H) might be at least partially explained by the association between extinction and climate, as the correlations observed are opposed to what one would expect under a competition scenario. Pires et al (2017), as well as Balisi & Van Valkenburgh (2020) found an overall (across the whole Cenozoic) negative association between changes in diversity and temperature. During the Quaternary, both temperature and Canidae diversity are dropping (Balisi & Van Valkenburgh, 2020; Pires et al., 2017; Zachos et al., 2001), hence we interpret that the weak evidence for a negative association between richness and extinction rate in the Quaternary (Figure 5A, B) represents that both are responding, at least partially, to a third variable, in this case temperature. Interestingly, when the Cenozoic was analyzed as a whole, we see stronger association between changes in the number of coexisting species and extinction rate, especially when we used the "site" spatial metrics (Figure 6). Similar to the weaker evidence found with the other metrics in the Quaternary (Figure 5A, B), this association is in the opposite direction one would expect from competition. We also interpret this association to represent the effect of temperature on both analyses. We also note that the splitting of time into different time windows might have affected our ability to detect an association between extinction and changes in richness, in particular in the last time window, which we might not have fully captured all changes in extinction dynamics (Figure 1B; uncertainty of the moment of the first rise in extinction). That said, given the direction of evidence in both analysis (splitting time - Figure 5 or not - Figure 6); we are confident that had we chosen other time windows, if we recovered association with extinction dynamics, it would still be on the opposite direction as the one expected under competition.

Another potential external factor affecting Canidae extinction dynamics would be clade competition. Between-clade competition and turnover of faunas have been proposed to be strong drivers of increased extinction rates of North American Carnivora (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 1999). One of the candidates to explain the inverse associations we see between richness/competition and extinction rates for the Quaternary is the interaction between Felidae and Canidae. The intense diversification dynamics observed in those migrating Felidae (Pires et al., 2015) was shown to be correlated with the displacement of North American Canidae throughout the Neogene and Quaternary (Pires et al., 2017; Silvestro et al., 2015). Unfortunately, the previous studies mentioned here that estimated the effect of climate or clade-competition in Canidae have not investigated diversity-dependence or climatic effects at different time windows as we did here. This highlights one relevant advance of the approach proposed in our study, the possibility to localize in time the effect of any potential controller of diversification dynamics.

The framework decision of investigating the effect of competition in different phases of a radiation also made evident that diversity-dependence, and more generally interspecific competition, are not omnipresent mechanisms regulating Canidae diversification dynamics. By incorporating spatial and ecological overlap more explicitly, and discretizing different time windows, we have demonstrated that interspecific competition only took part in suppressing speciation rates in moments of high species diversity, when the diversity was increasing at the initial radiation. Although we did not explicitly test the effects of climate and clade competition, we are compelled to propose that such effects were more relevant at the second half of Canidae history, when diversity-dependence and interspecific competition within the clade itself are unlikely to have played a significant role. We also argue that the shifting dynamics in Late Cenozoic habitats might be more correlated to extinction dynamics, and while body size measures may reflect some level of adaptation to such environments, analyses of post-cranial locomotory adaptations might also be an interesting avenue for testing competition and diversification dynamics (Figueirido et al., 2015). The external factors associated with a declining environment driven by constant cooling and drying, with the expansion of less productive habitats in the latter half of the Cenozoic may have outpaced diversity-dependence mechanisms in Canidae diversification, changing its carrying-capacity (Marshall & Quental, 2016).

Initial debates on whether biotic or abiotic factors might control biodiversity in deep time have played one factor against the other resulting in somewhat artificially dichotomic views on deep time controls of biodiversity. Although there is a growing body of evidence suggesting a role for biotic factors (Foote et al., 2018; Liow et al., 2015), it is well established among paleontologists that, at deep time, abiotic factors are undoubtedly relevant (Barnosky, 2001; Erwin, 2009; Hannisdal & Peters, 2011; Jaramillo et al., 2006; Mayhew et al., 2012; Peters, 2008). More recent and nuanced prepositions have suggested that at local and short temporal scales biotic factors might be relevant, while at deep time and continental scales abiotic factors might be the overwhelming factor (Benton, 2009). Additionally it has been recognized that in fact biotic and abiotic factors might interact to produce changes in biodiversity (e.g. Ezard et al., 2011). Here we propose that the relevance of biotic and abiotic factors might in fact change according to the lineage's "ontogeny". Biotic factors driven by interspecific competition imposed by species of the clade of interest (self-diversity-dependence) might be more relevant at the initial stages of lineages, while external factors such as climate, or clade competition, might be more relevant later on. Hence, although it is clear that in the "ecological theater and evolutionary play" (Hutchinson, 1965) we should not have a monologue of either the Red Queen[1] or the Court Jester, it is still possible that their role as leading actress/actor changes depending on the act.

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[1] We note that even though in his original formulation of the Red Queen hypothesis, Van Valen (1973) gave special attention to biotic factors, he considered changes in a deteriorating environment to be caused by both biotic and abiotic factors. More recently, researchers have restricted the term Red Queen to biotic factors and Court Jester to abiotic factors.

6 Conclusions

1. We developed a new approach to study the potential effects of interspecific competition in diversification dynamics that goes beyond the usual diversity-dependent models.

2. Our new approach takes into account not only temporal coexistence, but also spatial coexistence and ecological overlap in an explicit manner by using geographical information from fossil occurrences and the morphology of fossil and extant species.

3. We recovered the usual signal of diversity-dependence when using “global” diversity trajectories, which do not explicitly account for spatial coexistence; but we show that diversity-dependence is detected even when the spatial distribution of species is explicitly taken into account.

4. We showed that changes in speciation rate were associated with changes in diversity and with changes in different metrics used to describe the intensity of competition, but only at the moment in time when Canidae was expanding its diversity. We found that an increase in extinction rate was not related to an increase in competition intensity or an increase in diversity, as expected by competition models.

5. We hence confirm previous results, which suggested that diversity-dependence imposed by the species within a clade only operate through the speciation dynamics. We expanded this view by showing that mechanistic models of competition also suggest that interactions among species within the focal clade only affect speciation dynamics.

6. We discussed our results in the light of the roles of biotic and abiotic factors on controlling biodiversity in deep time and suggest that, in long-lived clades, self-diversity-dependence and resource competition might preferentially act during the initial radiation phases, while later on their history such effects might be overwhelmed by external factors such as climatic changes or clade competition.

Resumo

Compreender os padrões da biodiversidade e os processos que os geram são objetivos centrais em estudos ecológicos e macroevolutivos. Os efeitos de fatores bióticos e abióticos na geração e manutenção da biodiversidade, incialmente analisados isoladamente, são hoje considerados interligados e importantes em determinar o balanço da diversidade de espécies. Os modelos de diversificação dependente de diversidade postulam que um aumento no número de espécies resultaria em reduções na taxa de especiação e aumentos na taxa de extinção. À essa dinâmica é atribuído o efeito da competição interespecífica, porém de forma indireta e interpretativa, pois os modelos tipicamente carecem de abordagens mais mecanísticas. Neste estudo, incorporamos mais explicitamente aspectos espaciais e eco-morfológicos, construindo métricas que capturam além da coexistência no tempo, coexistência no espaço e interação no morfoespaço. Desta forma, testamos como inferências indiretas se comparam com nossas inferências que utilizam uma abordagem mais mecanística para estudar a competição. Utilizamos o registro fóssil da família Canidae na América do Norte, um grupo amplamente estudado e bem caracterizado do ponto de vista eco-morfológico e paleontológico. Testamos a hipótese de que a intensidade da competição resultaria tanto na diminuição das taxas de especiação quanto no aumento das taxas de extinção. Encontramos que a competição atuou de forma mais intensa durante as fases iniciais da radiação de Canidae, resultando na supressão da taxa de especiação no momento em que o grupo apresentava expansão de diversidade. Entretanto, não detectamos uma associação entre a intensidade da competição e a dinâmica de extinção esperada pelo efeito competitivo. Os resultados sugerem que a queda de diversidade e aumento na extinção próxima do presente estariam relacionadas a fatores externos à competição de espécies de Canidae, como por exemplo mudanças climáticas e competição com outros grupos como Felidae. Nossos resultados estão de acordo com estudos anteriores que apontaram assimetrias no efeito da competição nas taxas de especiação e de extinção. A novidade apresentada aqui foi mostrar que os efeitos da competição interespecífica não se manifestaram ao longo de toda a história evolutiva de Canidae. Também mostramos que modelos mais mecanísticos de fato sugerem que, ao menos parcialmente, os efeitos dependentes de diversidade podem ser influenciados por competição de recursos. Concluímos então que a relevância de fatores bióticos e abióticos na dinâmica de diversificação de um grupo pode se alterar ao longo do tempo, e que não apenas um mecanismo atua em detrimento do outro.

Palavras-chave: Macroevolução. Registro Fóssil. Especiação. Extinção.

Abstract

Understanding biodiversity patterns and the processes that generate them are key goals in ecology and macroevolutionary studies. The deep time effects of biotic and abiotic factors on biodiversity, initially considered in isolation, have been shown to be interconnected and important on determining biodiversity dynamics. Diversity-dependent models of diversification postulate that an increase in diversity should result in a decrease in speciation rate and an increase in extinction rate. Interspecific competition is typically considered to be the underlying mechanism of such dynamics but the evidence is indirect and interpretive as such models typically lack a more mechanistic view of competition. In this study, we more explicitly incorporated spatial and eco-morphological aspects to test how the aforementioned effects manifest in deep time. We built different metrics that capture not only species temporal coexistence, but also their coexistence in space and morphospace. We hence tested how indirect inferences compare with our inferences that use a more mechanistic approach to study competition. We used the North American fossil record of the family Canidae, a group that has been extensively studied and well characterized both from the eco-morphological and paleontological points of view. We tested the hypothesis that an increase in the intensity of competition would result in both a decrease in speciation rate and an increase in extinction rate. We found that interspecific competition only affected diversification dynamics during the early stages of Canidae radiation, resulting only in the suppression of speciation rate at the time the clade was expanding in diversity. On the other hand, we found no association between the intensity of the competition and extinction dynamics as expected by a competitive effect. The results suggest that the decrease in diversity and increase in extinction rate close to the present might be better explained by external factors, such as climate change and competition with other clades such as Felidae, and not by interspecific competition within Canidae. Our results are in line with previous studies that showed asymmetric effects of competition on speciation and extinction dynamics. We have demonstrated that more mechanistic models suggest that diversity-dependence effects could indeed result from resource competition, but these effects are not present throughout the whole evolutionary history of Canidae. We therefore conclude that the relevance of biotic and abiotic factors on driving diversification dynamics changes over time and that neither is likely to be the sole responsible for changes in biodiversity in deep time.

Keywords: Macroevolution. Fossil Record. Speciation. Extinction.

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Appendix A – Supplementary Figures

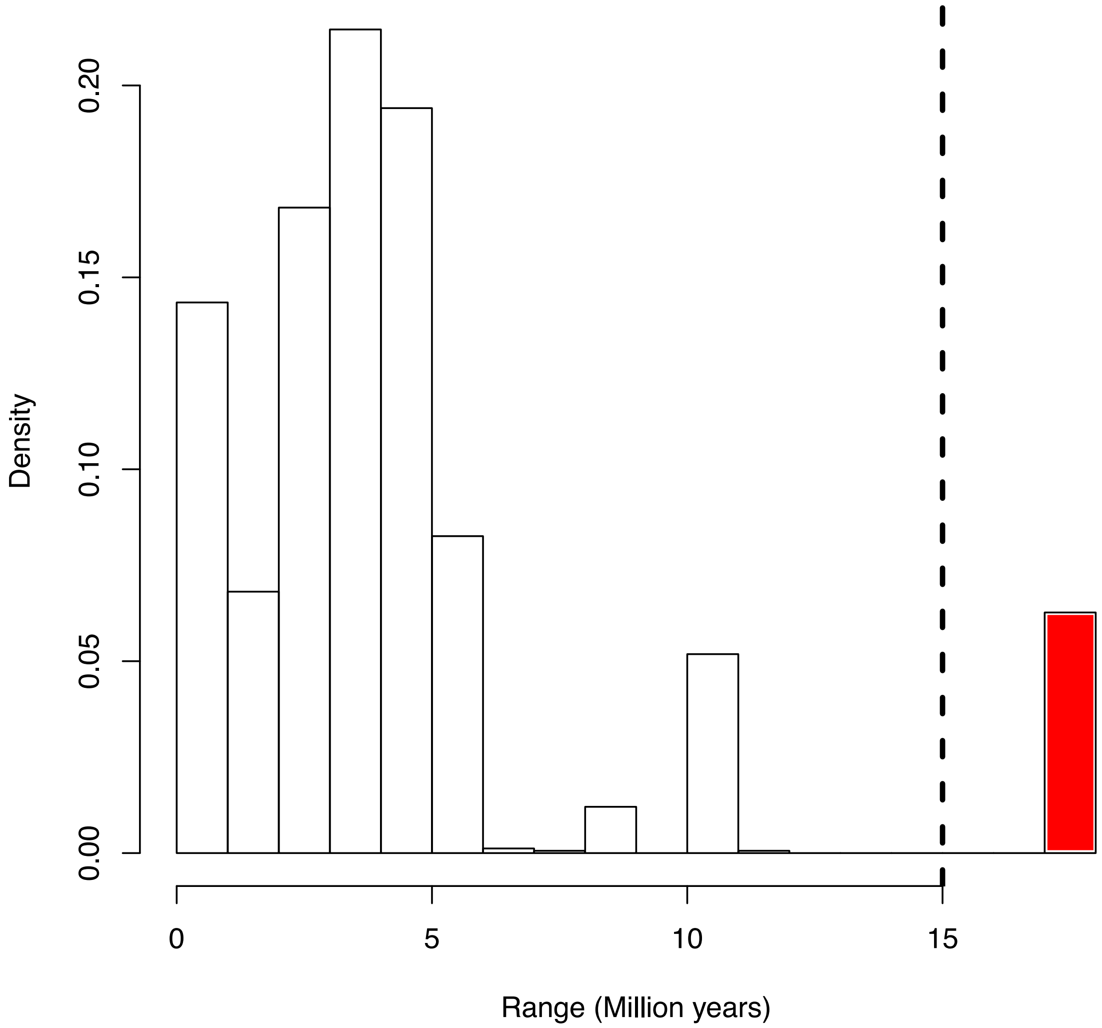

Figure S1: Histogram depicting the resolution of occurrence data. Range is measured as the difference between the date of the base of the interval to the top of the interval for each individual occurrence.

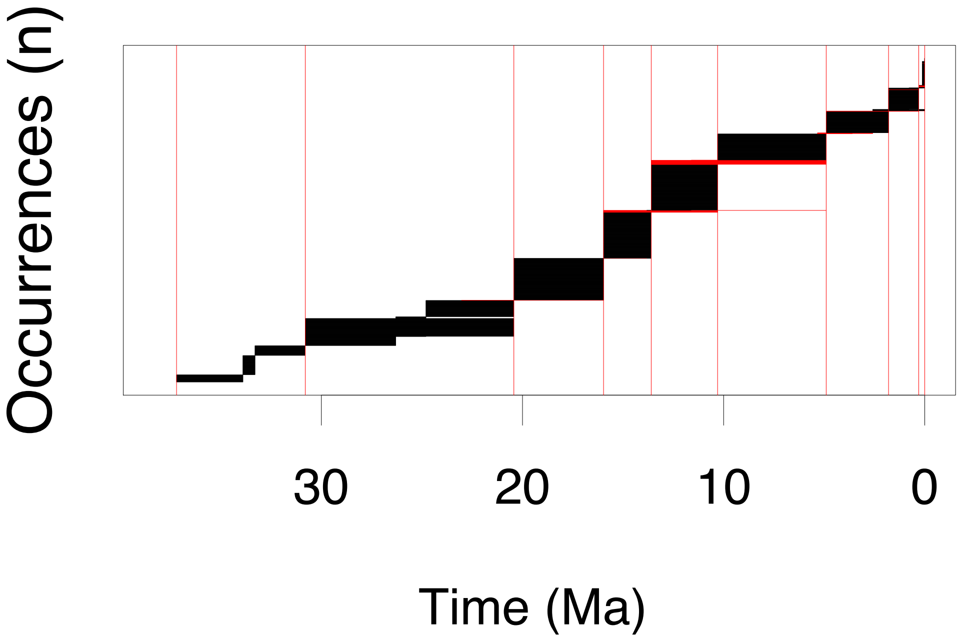

Figure S2: Occurrence temporal distribution and fit to different time windows. Red vertical lines correspond to the grouped NALMA boundaries at 37.2, 30.8, 20.43, 15.97, 13.6, 10.3, 4.9, 1.8, 0.3, and 0 million years. Black bars represent occurrences whose range fits within the intervals described by the boundaries. Red horizontal bars are occurrences whose ranges do not fit any of the grouped NALMA intervals.

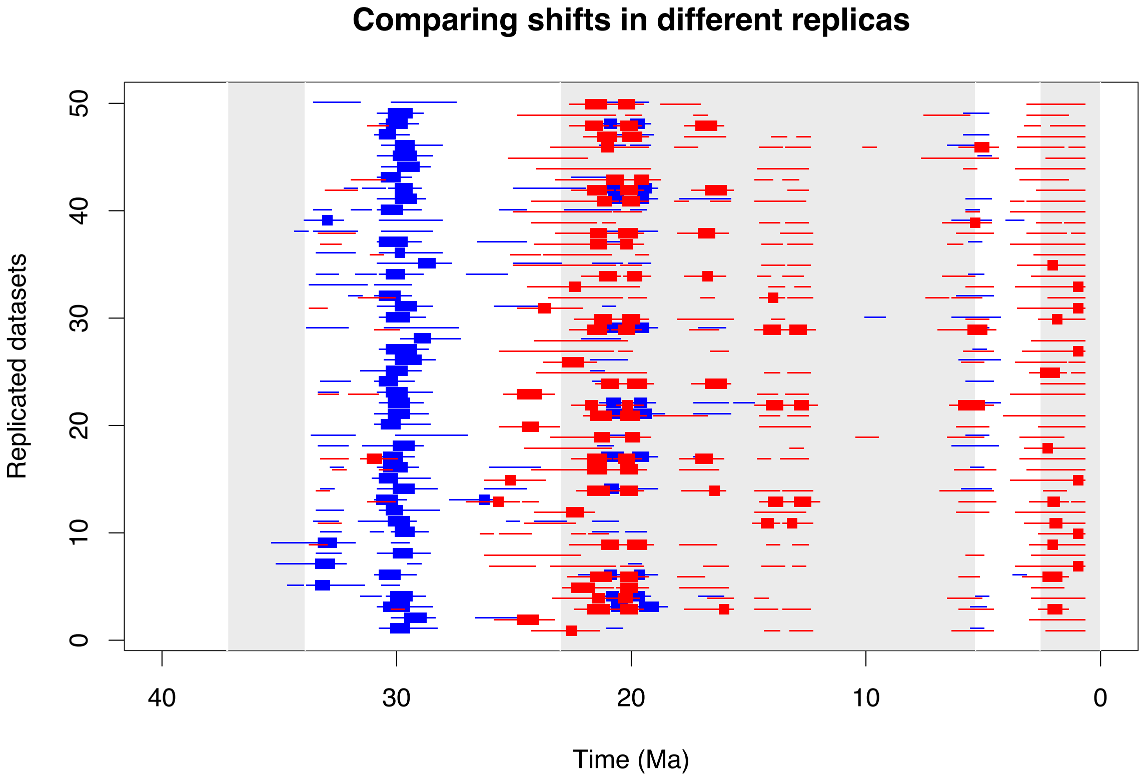

Figure S3: Placement of diversification shifts across the 50 *PyRate* temporal replicates. The horizontal thin lines represent moments of shifts with BF > 2, while boxes represent shifts with BF > 6. Blue lines and boxes represent speciation rate shifts and red lines and boxes extinction rate shifts. Gray and white vertical shaded boxes represent the Cenozoic epoch/NALMA boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma.

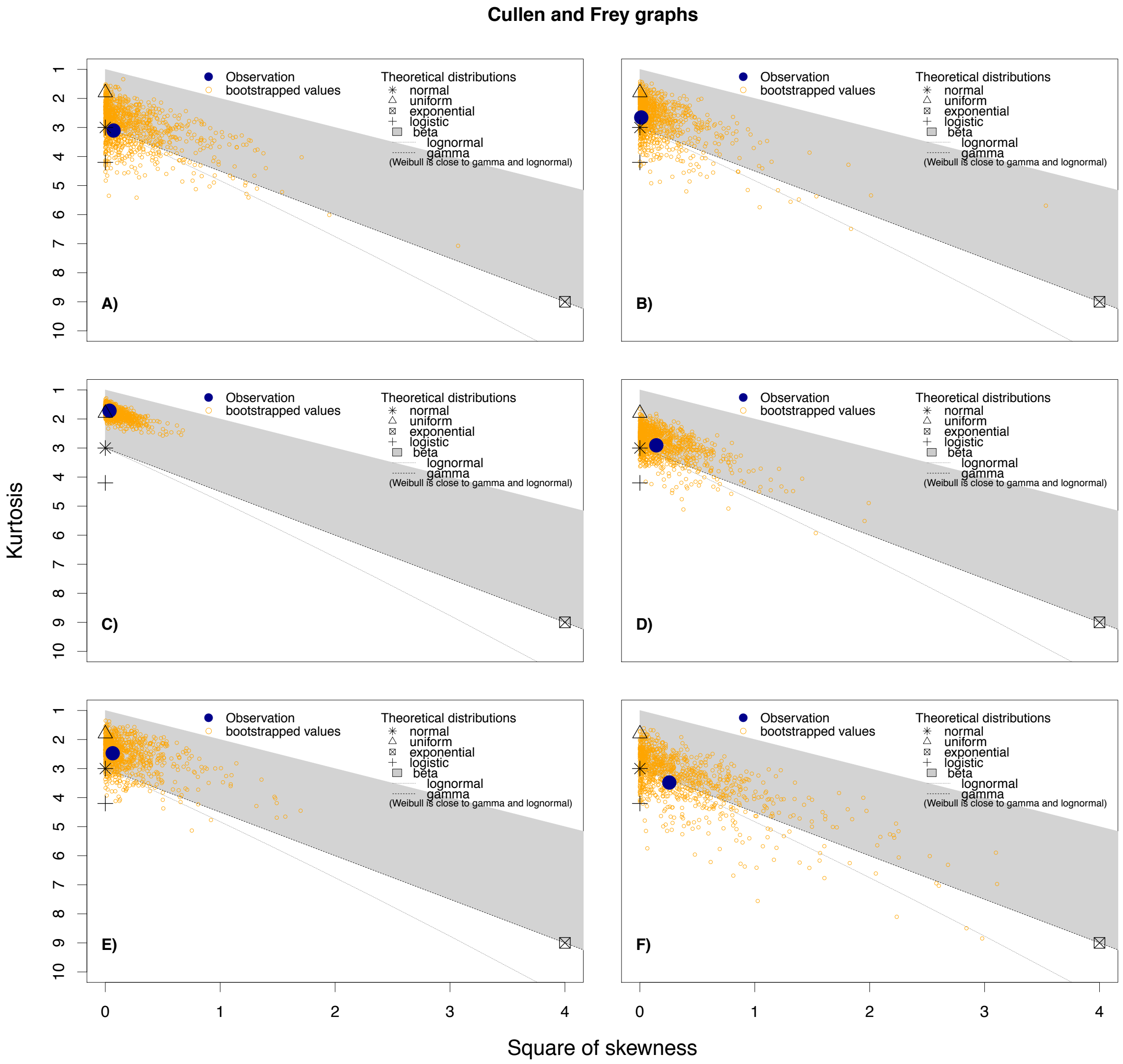

Figure S4: Cullen and Frey graphs for the subfamilies distributions of mass and LD1. Graphical visualization of descriptive parameters of empirical distributions to help guiding the choice of theoretical distributions to fit the data (in a likelihood approach). A – B) Hesperocyoninae, C – D) Borophaginae, E – F) Caninae. A, C, E) Body mass, B, D, F) LD1. See Suplementary Table 1 for the likelihood test.

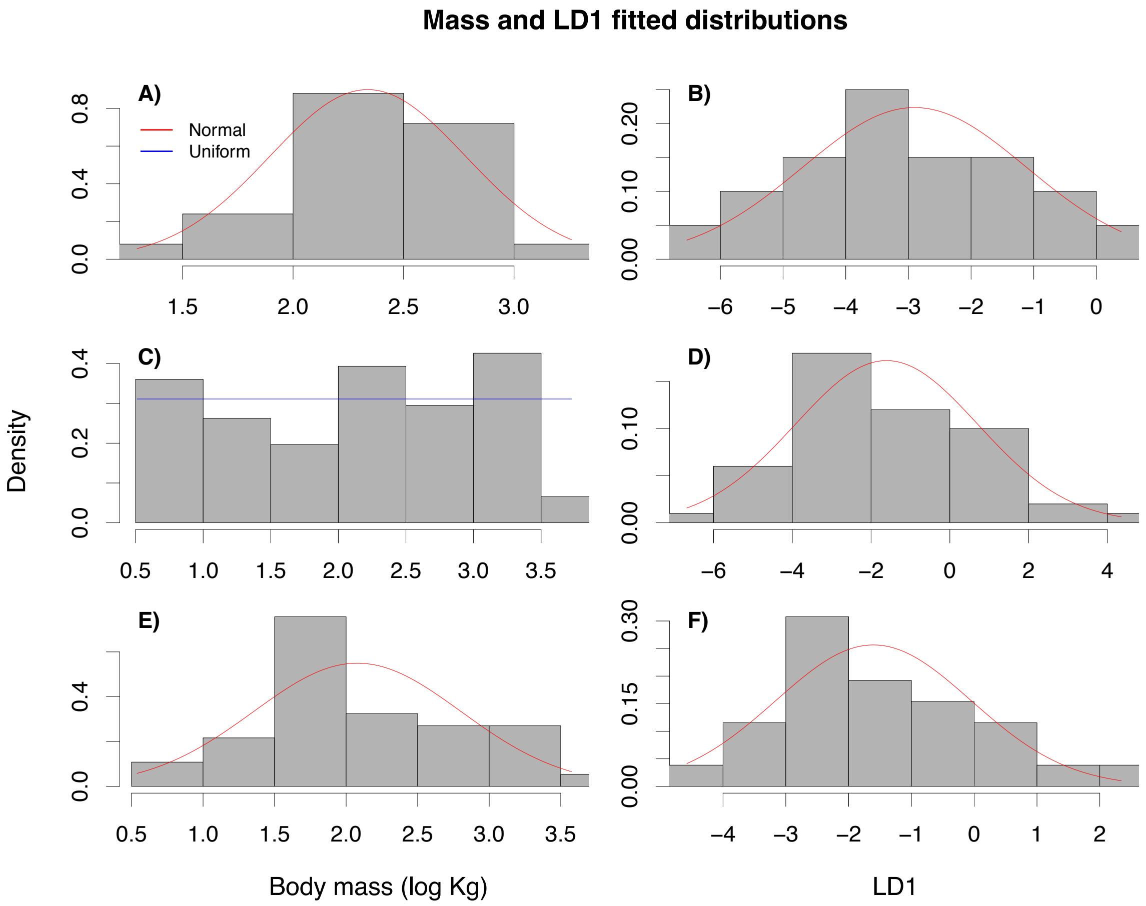

Figure S5: Fitted theoretical and empirical distributions of subfamilies mass and LD1 data. Gray histograms represent the empirical distributions with curves representing the theorical best fitted distributions. A – B) Hesperocyoninae, C – D) Borophaginae, E – F) Caninae. A, C, E) Body mass, B, D, F) LD1. See Supplementary Table 1 for the likelihood test.

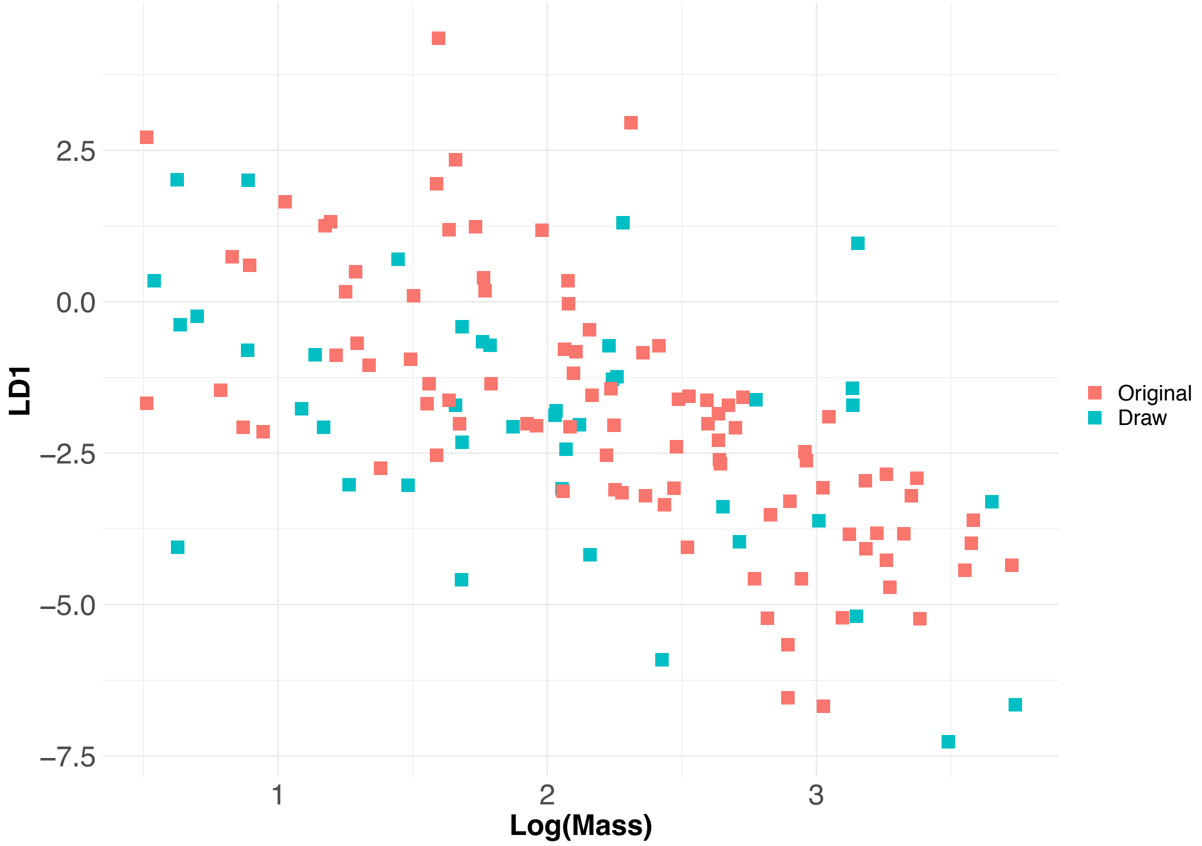

Figure S6: Morphospace example after data augmentation approach. A single dataset is represented, highlighting the amount of data which we had available values from the literature (96 for LD1 and 122 for mass) and species for which we drew values from theoretical distributions (42 for LD1 and 16 for mass).

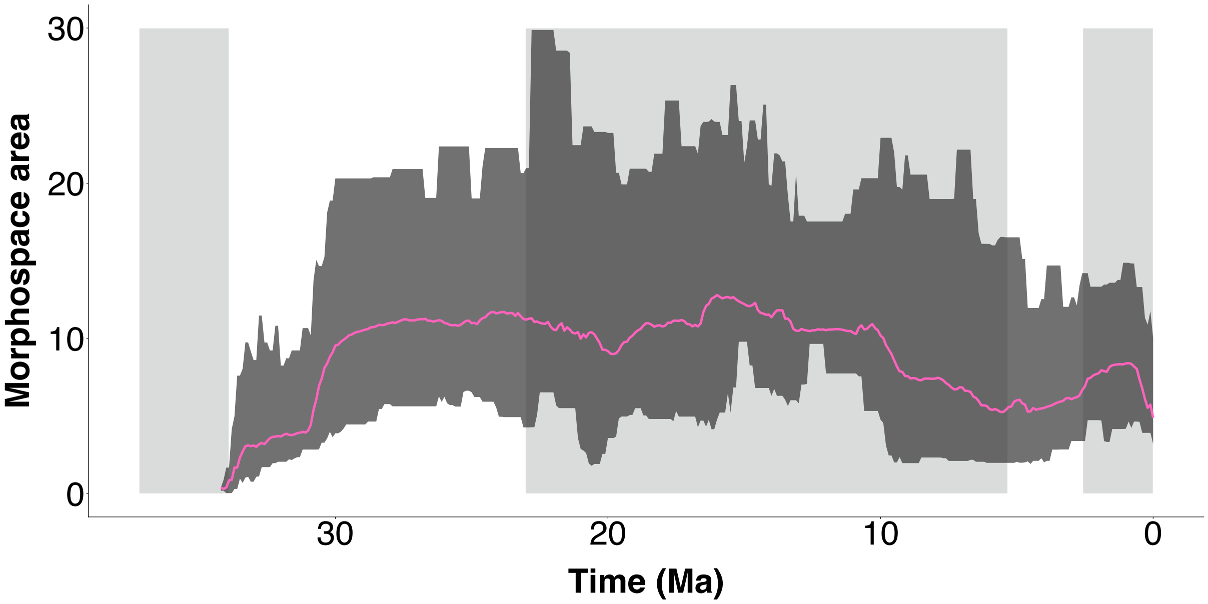

Figure S7: Total Morphospace area through time. Gray and white vertical shaded boxes represent the Cenozoic epoch/NALMA boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma. Pink curve represents the median value, shaded areas representing the maximum and minimum limits across the different replicates.

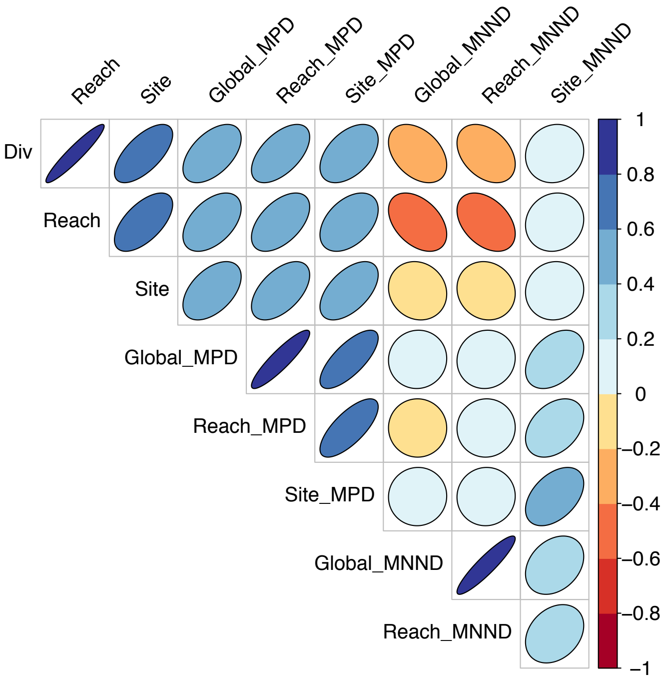

Figure S8: Correlation analyses of the nine time series used to infer the different competition scenarios. Values represent Kendall's τ coefficient.

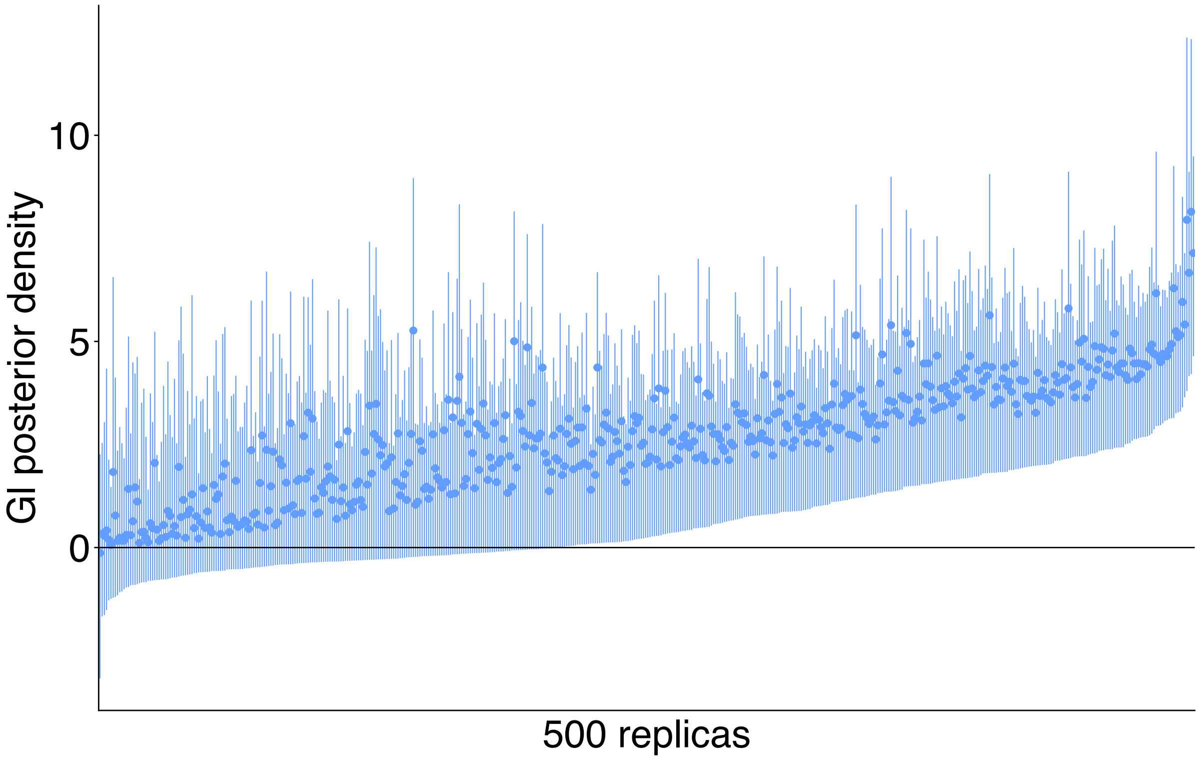

Figure S9: *Gl* posterior distributions across all replicated datasets for global MNND. Colored bars represent the 95% credible intervals (HPD) and the dot the median value. Color code corresponds to Figure 2.

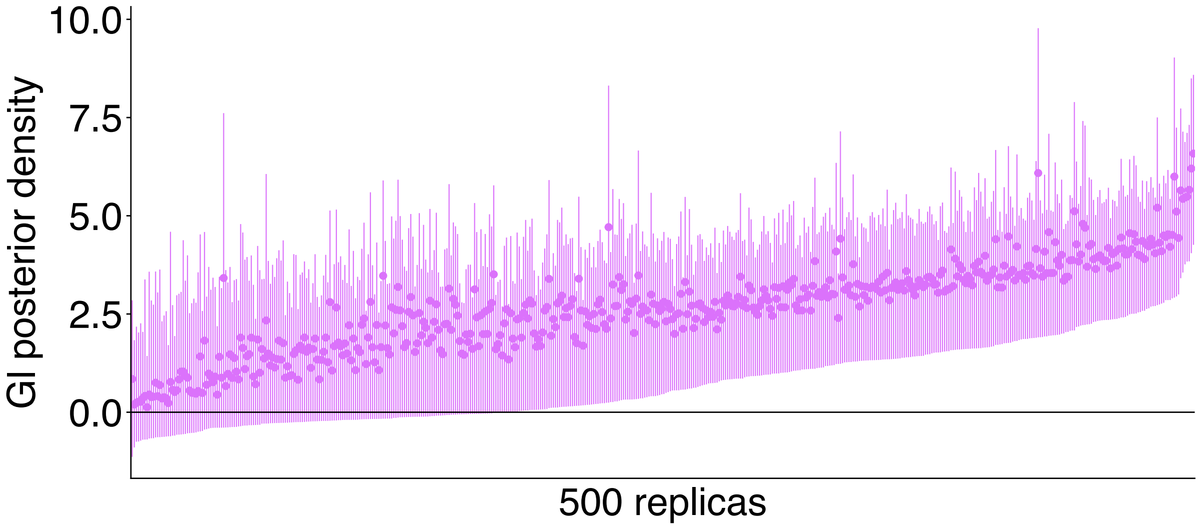

Figure S10: *Gl* posterior distributions across all replicated datasets for reach MNND. Colored bars represent the 95% credible intervals (HPD) and the dot the median value. Color code corresponds to Figure 2.

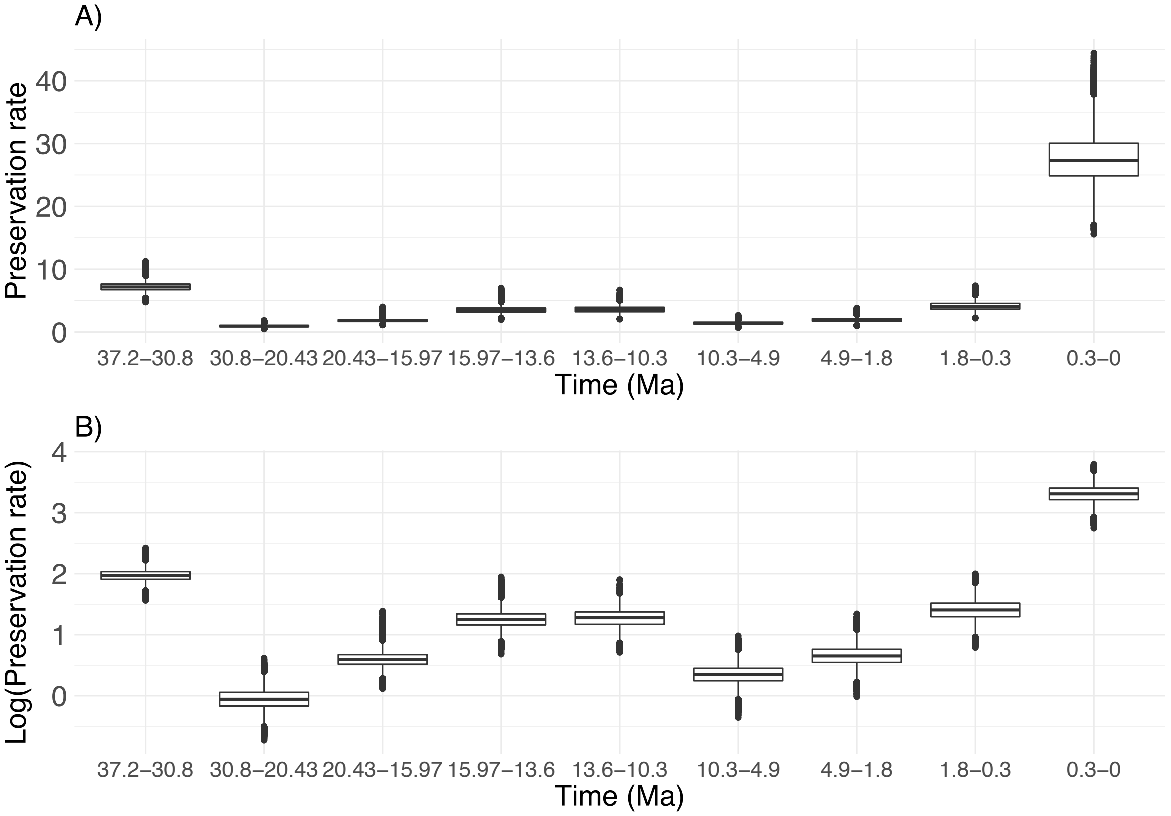

Figure S11: Posterior distribution of preservation parameter for Canidae diversification analyses. Preservation rate is measured as the expected number of occurrences per lineage per million year, estimated in each time window using the mG+qShift preservation model. A) Preservation rates plotted on a linear scale, B) Preservations rates plotted on a log scale to help visualization.

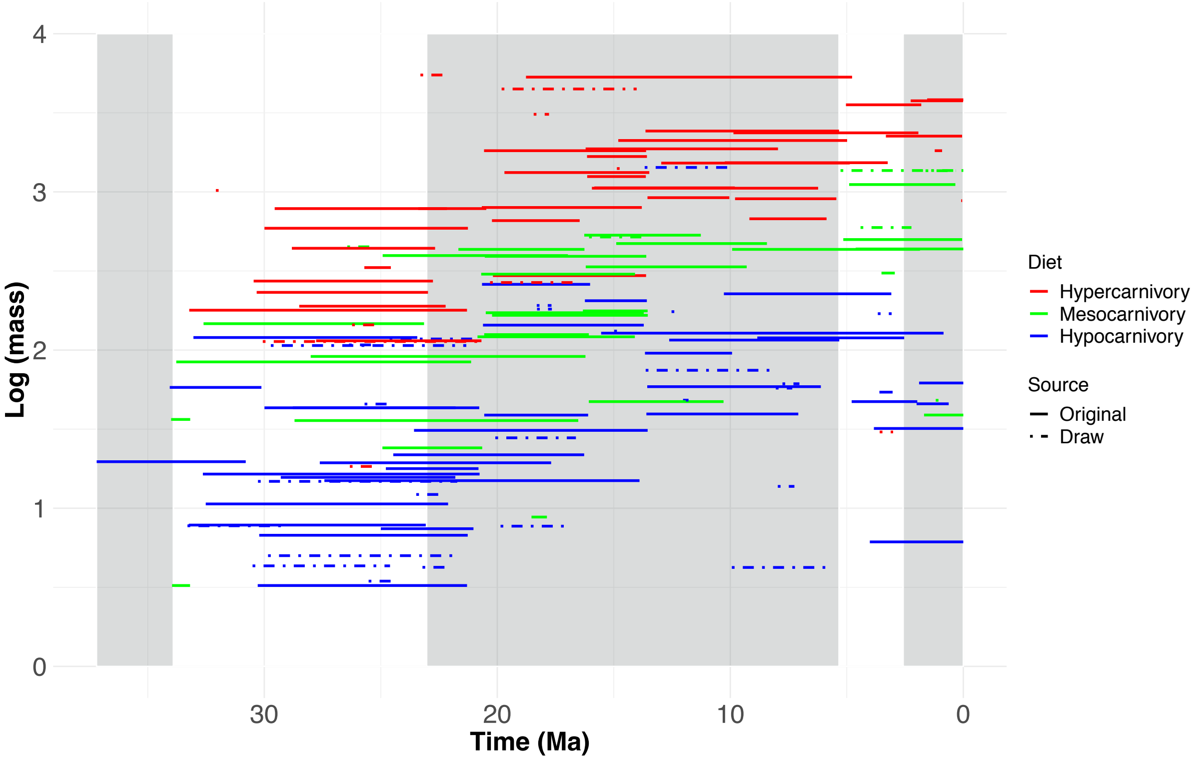

Figure S12: Canidae body mass evolution through time. Species body masses from one exemplar dataset are plotted against mean longevities estimated from the 50 temporal replicates. Gray and white vertical shaded boxes represent the Cenozoic epoch/NALMA boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma. "Draw", shown as dashed-dot lines, represents random values sampled for those species with missing body mass data. "Original" represents species from which we had empirical data.

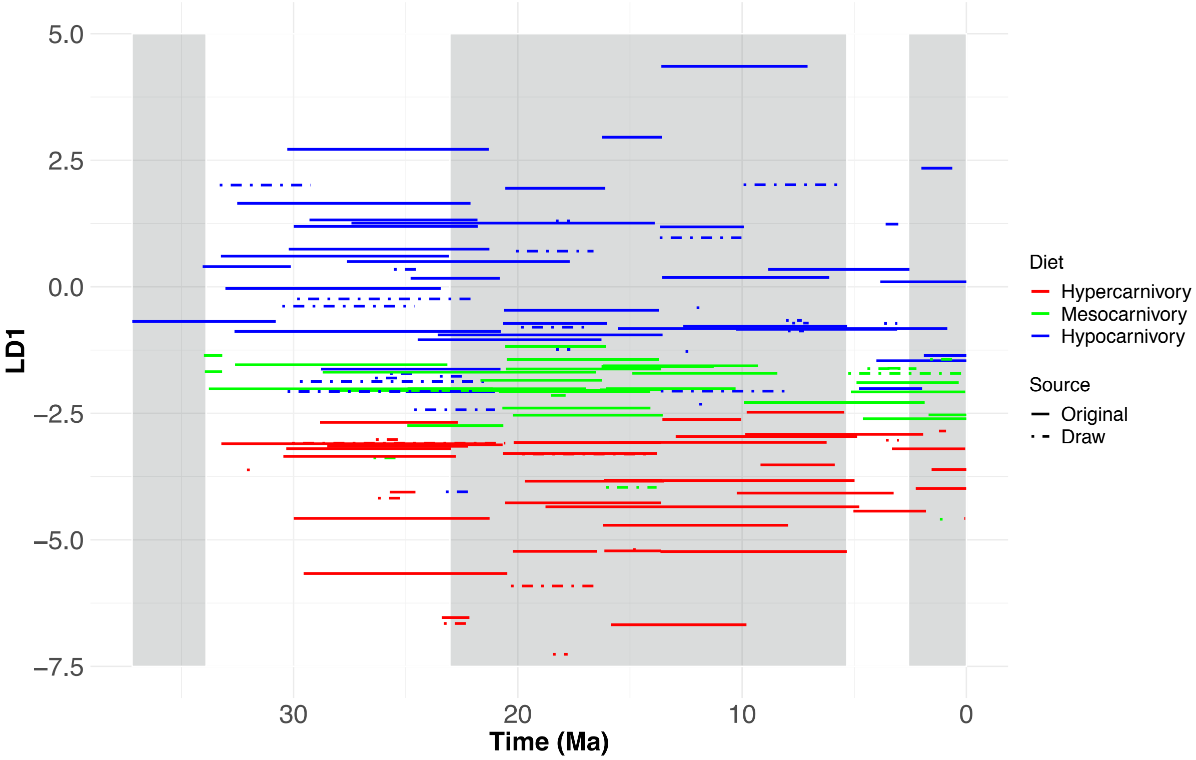

Figure S13: Canidae hypercarnivory index evolution through time. Species LD1 values from one exemplar dataset are plotted against mean longevities estimated from the 50 temporal replicates. Gray and white vertical shaded boxes represent the Cenozoic epoch boundaries at 37.2, 33.9, 23.03, 5.33 and 2.58 Ma. “Draw”, shown as dashed-dot lines, represents random values sampled for those species with missing LD1 data. “Original” represents species from which we had empirical data.

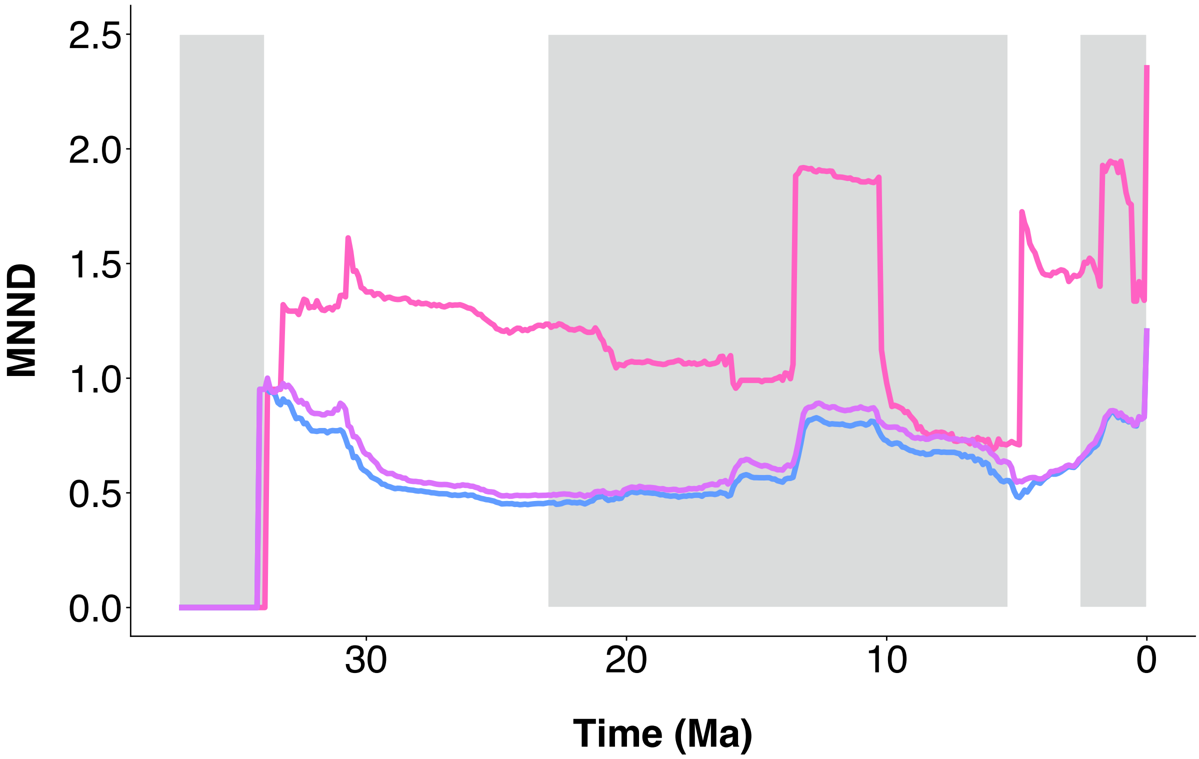

Figure S14: MNND trajectories for "global", "reach" and "site" spatial metrics. Lines represent median values, but see Figure 2 for their maximum and minimum limits across the different replicates. Color-coding corresponds to Figure 2.

Appendix B – Supplementary Tables

	AIC	
	Normal	**Weibull**
Hesperocyoninae	34.283	33.982
Borophaginae	NA	NA
Caninae	85.281	84.646

Supplementary Table 1: AIC values for different distributions used to fit subfamilies body mass empirical distribution (Figure S5). For Hesperocyoninae and Caninae, AIC difference between the two distributions tested is < 2, so we choose normal distributions for both subfamilies for the sake of simplicity. For Borophaginae, however, we did not fit the data given that the distribution is clearly uniform (Figures S4,S5).

		Hesperocyoninae	**Borophaginae**	**Caninae**
Mass	Distribution	Normal	Uniform	Normal
	Parameters	mean = 2.337	min = 0.095	mean = 2.078
		sd = 0.443	max = 3.839	sd = 0.725
LD1	Distribution	Normal	Normal	Normal
	Parameters	mean = -2.901	mean = -1.606	mean = -1.603
		sd = 1.784	sd = 2.317	sd = 1.554

Supplementary Table 2: Parameters estimated for each distribution fit on the empirical distributions used to latter augment the missing data.

	Late Eocene	Oligocene	Miocene	Pliocene	Quaternary
Global (*Gl*)	0.197 (-4.813 6.768)	**-2.007** **(-3.387 -0.185)**	1.036 (-2.034 4.205)	0.631 (-3.374 8.137)	0.211 (-4.422 5.662)
Global (l_0)	0.645 (0.087 1.420)	0.253 (0.166 0.356)	0.166 (0.117 0.220)	0.307 (0.143 0.508)	0.277 (0.107 0.488)
Reach (*Gl*)	0.172 (-4.687 6.223)	**-1.972** **(-3.373 -0.175)**	0.895 (-2.161 3.836)	0.509 (-3.498 7.470)	0.158 (-4.266 5.089)
Reach (l_0)	0.645 (0.091 1.426)	0.252 (0.167 0.350)	0.168 (0.121 0.219)	0.306 (0.144 0.506)	0.278 (0.108 0.491)
Site (*Gl*)	-0.004 (-4.274 4.204)	**-2.249** **(-3.947 -0.168)**	-0.598 (-2.654 1.092)	0.778 (-2.358 5.289)	-0.208 (-4.557 3.681)
Site (l_0)	0.643 (0.095 1.418)	0.266 (0.169 0.383)	0.176 (0.130 0.230)	0.322 (0.145 0.544)	0.283 (0.117 0.487)
Global MPD (*Gl*)	0.310 (-1.419 4.950)	-0.324 (-8.137 2.316)	0.262 (-1.613 4.355)	0.050 (-3.580 4.845)	0.005 (-3.867 3.894)
Global MPD (l_0)	0.654 (0.090 1.466)	0.213 (0.129 0.358)	0.171 (0.121 0.225)	0.306 (0.144 0.506)	0.283 (0.117 0.485)
Reach MPD (*Gl*)	0.321 (-1.501 5.235)	-0.430 (-7.489 1.783)	0.248 (-1.763 4.268)	0.049 (-3.627 4.845)	-0.003 (-4.117 3.987)
Reach MPD (l_0)	0.655 (0.089 1.467)	0.217 (0.128 0.379)	0.172 (0.123 0.227)	0.307 (0.143 0.505)	0.283 (0.119 0.487)
Site MPD (*Gl*)	0.000 (-3.831 3.717)	-0.610 (-6.474 1.004)	0.254 (-0.909 2.290)	-0.200 (-5.137 2.257)	-0.038 (-3.977 3.341)
Site MPD (l_0)	0.640 (0.090 1.413)	0.225 (0.131 0.434)	0.172 (0.128 0.222)	0.311 (0.146 0.513)	0.283 (0.118 0.490)
Global MNND (*Gl*)	1.321 (-1.105 4.896)	2.742 (-0.362 5.897)	-0.573 (-3.985 2.251)	-0.220 (-6.143 4.522)	0.001 (-4.119 4.186)
Global MNND (l_0)	0.676 (0.087 1.533)	0.305 (0.144 0.573)	0.167 (0.115 0.223)	0.303 (0.137 0.505)	0.281 (0.099 0.516)
Reach MNND (*Gl*)	1.314 (-1.228 5.049)	2.705 (-0.210 5.226)	-0.550 (-3.801 2.161)	0.080 (-4.910 5.450)	0.061 (-4.126 4.353)
Reach MNND (l_0)	0.678 (0.094 1.541)	0.321 (0.157 0.576)	0.168 (0.119 0.223)	0.305 (0.139 0.510)	0.284 (0.105 0.519)
Site MNND (*Gl*)	-0.001 (-2.337 2.298)	0.093 (-2.396 4.205)	0.110 (-1.140 1.844)	-0.150 (-3.187 1.672)	0.012 (-2.109 2.147)
Site MNND (l_0)	0.639 (0.092 1.414)	0.205 (0.133 0.299)	0.175 (0.130 0.226)	0.310 (0.144 0.511)	0.282 (0.116 0.489)

Supplementary Table 3: Median and 95% HPD (shown in parenthesis) for the correlation parameters (*Gl*) and the baseline speciation rate (*l0*), for each time windows used to analyze the potential association between changes in speciation rate and thetime series of interest. Strong evidence for correlations (*Gl)* are highlighted in bold.

	Late Eocene	Oligocene	Miocene	Pliocene	Quaternary
Global (Gm)	0.026 (-5.525 6.017)	-0.885 (-3.250 0.977)	-0.269 (-2.737 1.634)	-0.251 (-6.518 4.618)	-2.134 (-11.565 1.359)
Global (m_0)	0.108 (0.000 0.479)	0.089 (0.032 0.155)	0.214 (0.164 0.268)	0.297 (0.119 0.518)	0.562 (0.291 0.895)
Reach (Gm)	0.028 (-5.280 5.541)	-0.806 (-3.125 1.058)	-0.282 (-2.719 1.662)	-0.279 (-6.310 4.120)	-2.051 (-10.762 1.293)
Reach (m_0)	0.109 (0.000 0.480)	0.088 (0.034 0.155)	0.215 (0.165 0.270)	0.296 (0.120 0.516)	0.563 (0.295 0.897)
Site (Gm)	0.000 (-4.386 4.162)	-1.140 (-3.707 0.805)	-0.953 (-3.837 0.904)	-0.107 (-4.217 3.872)	-0.925 (-6.757 2.388)
Site (m_0)	0.108 (0.000 0.478)	0.093 (0.036 0.164)	0.221 (0.166 0.288)	0.289 (0.114 0.514)	0.503 (0.267 0.789)
Global MPD (Gm)	0.054 (-3.199 4.114)	-0.126 (-4.948 2.629)	0.224 (-1.670 3.927)	-0.014 (-4.329 4.480)	-0.040 (-4.552 3.750)
Global MPD (m_0)	0.106 (0.000 0.476)	0.081 (0.030 0.145)	0.213 (0.159 0.272)	0.297 (0.118 0.518)	0.499 (0.271 0.771)
Reach MPD (Gm)	0.053 (-3.384 4.167)	-0.167 (-5.009 2.459)	0.226 (-1.795 3.985)	-0.004 (-4.262 4.690)	0.007 (-4.330 4.383)
Reach MPD (m_0)	0.106 (0.000 0.476)	0.082 (0.030 0.147)	0.214 (0.161 0.272)	0.297 (0.119 0.520)	0.499 (0.269 0.768)
Site MPD (Gm)	0.000 (-3.730 3.842)	-0.163 (-4.488 2.150)	0.288 (-0.824 2.205)	-0.001 (-3.583 3.479)	0.049 (-3.499 4.267)
Site MPD (m_0)	0.108 (0.000 0.476)	0.083 (0.029 0.155)	0.214 (0.165 0.267)	0.296 (0.116 0.521)	0.498 (0.267 0.769)
Global MNND (Gm)	0.253 (-3.411 4.653)	1.382 (-1.441 5.727)	-0.056 (-2.801 2.455)	-0.096 (-5.342 4.963)	2.540 (-0.905 7.482)
Global MNND (m_0)	0.102 (0.000 0.484)	0.102 (0.031 0.210)	0.213 (0.159 0.274)	0.296 (0.114 0.523)	0.594 (0.273 1.047)
Reach MNND (Gm)	0.245 (-3.441 4.693)	1.125 (-1.557 4.992)	-0.129 (-3.163 2.473)	0.046 (-5.071 5.384)	2.339 (-1.183 7.798)
Reach MNND (m_0)	0.104 (0.000 0.486)	0.100 (0.031 0.207)	0.213 (0.159 0.272)	0.298 (0.115 0.528)	0.580 (0.273 1.020)
Site MNND (Gm)	0.000 (-2.338 2.295)	0.012 (-2.355 2.593)	0.181 (-0.984 2.098)	0.011 (-2.094 2.266)	0.198 (-1.217 3.230)
Site MNND (m_0)	0.108 (0.000 0.476)	0.079 (0.031 0.139)	0.219 (0.168 0.274)	0.295 (0.118 0.518)	0.508 (0.270 0.790)

Supplementary Table 4: Median and 95% HPD (shown in parenthesis) for the correlation parameters (Gm) and the baseline extinction rate ($m0$), for each time windows used to analyze the potential association between changes in extinction rate and thetime series of interest. Strong evidence for correlations (Gm) would be highlighted in bold.

Competition scenario	*Gl*	l_0	*Gm*	m_0
Global	-1.001	0.227	-1.159	0.219
	(-2.250 0.078)	(0.177 0.283)	(-2.527 0.018)	(0.168 0.276)
Reach	-1.088	0.231	-1.051	0.218
	(-2.327 0.015)	(0.178 0.291)	(-2.347 0.050)	(0.167 0.276)
Site	**-1.662**	0.237	**-1.332**	0.220
	(-2.665-0.663)	(0.193 0.285)	**(-2.555 -0.277)**	(0.176 0.266)
Global MPD	-0.248	0.216	-0.145	0.198
	(-1.942 0.701)	(0.148 0.329)	(-2.012 1.063)	(0.125 0.309)
Reach MPD	-0.334	0.221	-0.133	0.197
	(-2.083 0.602)	(0.152 0.341)	(-2.045 1.182)	(0.121 0.306)
Site MPD	-0.384	0.215	0.038	0.187
	(-1.842 0.461)	(0.163 0.285)	(-1.105 1.327)	(0.136 0.244)
Global MNND	0.793	0.207	1.386	0.199
	(-0.556 2.815)	(0.163 0.259)	(-0.281 3.581)	(0.154 0.254)
Reach MNND	0.828	0.207	0.957	0.196
	(-0.428 2.926)	(0.159 0.279)	(-0.425 3.196)	(0.150 0.262)
Site MNND	0.038	0.198	0.412	0.186
	(-1.010 1.283)	(0.163 0.237)	(-0.513 2.398)	(0.149 0.225)

Supplementary Table 5: Median and 95% HPD (shown in parenthesis) for the correlation parameters (*Gl*, *Gm*) and baseline rates (*l0*, *m0*) for the analysis considering the whole Cenozoic to analyze the potential association between changes in speciation or extinction and the time series of interest. Strong evidence for correlations (*Gl*, *Gm*) are highlighted in bold.