



Research

Cite this article: Pires MM, Silvestro D, Quental TB. 2015 Continental faunal exchange and the asymmetrical radiation of carnivores. *Proc. R. Soc. B* **282**: 20151952. <http://dx.doi.org/10.1098/rspb.2015.1952>

Received: 12 August 2015

Accepted: 21 September 2015

Subject Areas:

evolution, palaeontology, ecology

Keywords:

ecological opportunity, extinction, mammals, macroevolution, speciation

Authors for correspondence:

Mathias M. Pires

e-mail: mathiaspires@gmail.com

Tiago B. Quental

e-mail: tbquental@usp.br

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1952> or via <http://rspb.royalsocietypublishing.org>.

Continental faunal exchange and the asymmetrical radiation of carnivores

Mathias M. Pires¹, Daniele Silvestro^{2,3} and Tiago B. Quental¹

¹Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 11294, 05422–970 São Paulo, Brazil

²Department of Evolution and Environmental Sciences, University of Gothenburg, Carl Skottsbergs gata 22B, 413 19 Gothenburg, Sweden

³Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

Lineages arriving on islands may undergo explosive evolutionary radiations owing to the wealth of ecological opportunities. Although studies on insular taxa have improved our understanding of macroevolutionary phenomena, we know little about the macroevolutionary dynamics of continental exchanges. Here we study the evolution of eight Carnivora families that have migrated across the Northern Hemisphere to investigate if continental invasions also result in explosive diversification dynamics. We used a Bayesian approach to estimate speciation and extinction rates from a substantial dataset of fossil occurrences while accounting for the incompleteness of the fossil record. Our analyses revealed a strongly asymmetrical pattern in which North American lineages invading Eurasia underwent explosive radiations, whereas lineages invading North America maintained uniform diversification dynamics. These invasions into Eurasia were characterized by high rates of speciation and extinction. The radiation of the arriving lineages in Eurasia coincide with the decline of established lineages or phases of climate change, suggesting differences in the ecological settings between the continents may be responsible for the disparity in diversification dynamics. These results reveal long-term outcomes of biological invasions and show that the importance of explosive radiations in shaping diversity extends beyond insular systems and have significant impact at continental scales.

1. Introduction

When a lineage colonizes a new environment it may initiate an explosive evolutionary radiation characterized by an accelerated accumulation of species and a burst in ecological diversification [1,2]. This phenomenon is particularly well documented for insular vertebrates [3,4]. An iconic example is the radiation of finches in the Galapagos archipelago where all 15 species of finches descend from a single migrant species and today use a suite of different food resources that is comparable with what is used by several different bird families in the mainland [5]. Anoles of the Greater Antilles are another well-studied case. In this lineage the radiation occurred independently in each island with similar ecomorphs arising after each colonization by different ancestral species [6]. These early bursts of diversification, sometimes referred to as adaptive radiations [2], are recurrently found in many other insular groups such as the Hawaiian honeycreepers [7] and lobeliads [8], the Gulf of Guinea white-eyes [9] and Madagascan vangids [4].

The explosive dynamics of evolutionary radiations are often interpreted as a consequence of the availability of unexplored ecological opportunities [1–3]. When arriving in an island with low diversity, a given species may find itself in a scenario where the evolutionary constraints imposed by biotic interactions (e.g. competition, predation) are weak in comparison to the mainland [10]. This ecological release allows the niche of the immigrant species to broaden and species with different ecologies might emerge from a single lineage [3,10]. As diversity increases, ecological opportunities lessen, speciation rate declines and the net diversification rate levels off [11]. The levelling-off of diversification

can also derive from increased extinction as population sizes diminish thus increasing the likelihood of extinction due to stochastic effects [12]. In this sense, islands can be seen as macroevolutionary test tubes where evolution, from the perspective of a given migrant lineage, can experiment with different forms and functions.

On continents, the diversification dynamics of a lineage may be constrained by the dynamics of multiple co-occurring clades [13]. However, as with island radiations, an immigrant lineage may undergo an evolutionary radiation when arriving in a new continent. According to the ecological opportunity hypothesis, this will be more likely if the immigrant has a substantially different ecology (e.g. using otherwise unexploited resources), or if the continent is poor of species with similar ecologies. For instance, a phylogenetic study suggests that rat snakes (Colubridae: tribe Lampropeltini) underwent an explosive diversification in North America after migrating from Eurasia through the Bering land bridge [14]. This pattern is interpreted as the outcome of the colonization of a continent where ecological opportunities were plentiful, since the existing diversity of snakes in North America at the time of immigration was relatively low [14]. Likewise, a phylogeny of muroid rodents suggests that a rapid radiation characterized by a burst in speciation rates, followed the arrival to South America [15]. Muroid rodents originated in Eurasia during the Eocene but only invaded South America later in the Miocene after colonizing and dispersing through North America. Thus, intercontinental migrations may also provide the opportunity for lineages to flourish in new ecological settings.

The connections between continents changed over time creating new routes for biotic exchange [13]. The fossil record suggests faunal exchanges between North America and Eurasia were particularly important in shaping mammalian faunas in both continents through the whole Cenozoic [16–19]. Yet, our understanding on the evolutionary dynamics of such large-scale invasions is still elusive. Here we focus on eight families of Carnivora with a history of migration and diversification across the Northern Hemisphere [17,20] and investigate the macroevolutionary dynamics involved in such exchanges. We use the fossil record of North American and Eurasian carnivorans and a Bayesian approach that jointly estimates speciation and extinction rates and their temporal variation, while incorporating the fossilization and sampling processes [21]. We analysed the dynamics of each family separately given that, in general, families represent evolutionary lineages with species that tend to share similar ecologies. We expected to find an explosive radiation when a given family established itself in a continent for the first time.

2. Methods

(a) Dataset

We compiled information on fossil occurrences of carnivores in North America and Eurasia from the Paleobiology database (PBDB: <http://paleobiodb.org>) and NOW database (Fortelius, M.: Coordinator, 2014, New and Old Worlds database of fossils: www.helsinki.fi/science/now/; data downloaded between April and May 2014). We included only fossil occurrences identified at the species level and we adopted a conservative measure and excluded all occurrences where uncertainty about taxonomy was explicit in the database, i.e. those occurrences where species or genus were marked with qualifiers such as sp., cf., aff., and '?',

which code different degrees of taxonomic uncertainty [22]. The same occurrence may be registered in both PBDB and NOW databases. To avoid including duplicates when merging datasets from both databases, when the same occurrences of a given species were present in both datasets we excluded one of the duplicates. To identify potential duplicated occurrences, we first checked species identity and whether the estimated time range for the occurrences were similar. Then, if latitude/longitude estimates also matched for similar occurrences in different databases we discarded one of the occurrences. We adopted a threshold of 0.1 decimal degrees of latitude and longitude as an indicator that occurrences registered in both databases were from the same locality. Because latitude/longitude values assigned to some occurrences were allegedly approximate based on nearby reference locations, we also double-checked those occurrences and removed potential duplicates when the formation, age estimates and location were similar enough so occurrences could be considered the same. The NOW database focuses on Eurasian Neogene occurrences whereas the mammal dataset of PBDB includes preferentially North American occurrences. For this reason the databases were complementary and the number of duplicates was only high for Eurasian Neogene occurrences but proportionally low for the overall dataset, which includes many occurrences from the Palaeogene and Quaternary (see the electronic supplementary material, data S1 and S2).

Because the method we used to estimate speciation and extinction rates requires the ages of fossil occurrences (see below), we also excluded from the analyses the occurrences with very poor temporal resolution, here defined as occurrences with temporal range larger than 15 Myr. After the initial filters, these occurrences corresponded to less than 1% of the occurrences of each family. We checked our merged dataset for synonyms using the most recent taxonomic reviews of each family or subfamily published in the literature (see refs [5–15] in the electronic supplementary material) and other sources such as recent papers on the diversification of carnivorans that also used both databases [23]. All the raw data are accessible from PBDB and NOW database, but the final revised dataset with the removed duplicates can be found in the electronic supplementary material, data S1–S2.

Given our interest in diversification dynamics of families that occur in both North America and Europe, we split the full dataset containing all Carnivora lineages at the family level at each continent. The main dataset included the following families within order Carnivora: Amphicyonidae, Ursidae, Canidae, Mustelidae, Mephitidae, Procyonidae, Felidae, Barbouroufelidae. We adopted a minimum of five species as a threshold for the analysis, resulting in the exclusion of families Ailuridae and Hyaenidae in North America and Nimravidae in Eurasia, which had a total diversity smaller than five species in our dataset. To get a better sense of the ecological settings in both continents, we also analysed the fossil occurrences of hyaendontid Creodonta and families that were present preferentially in one continent such as Hyaenidae, Percrocutidae and Viverridae in Eurasia and Nimravidae in North America. We did not analyse other earlier groups such as oxyaenid Creodonta as they had little temporal overlap with the carnivorans we focus on here. A list with the number of species and occurrences of each family can be found in the electronic supplementary material, table S1.

Because there is a lot of uncertainty on the taxonomy of early musteloids [24–27], we analysed the crown group of Mustelidae, sometimes referred as 'neomustelids' [24]. In the baseline analysis, we followed the classification scheme proposed by Finarelli [24] and removed all early musteloids assigned to Mustelidae in the PBDB and NOW databases. To test the sensitivity of our results to the different taxonomic schemes proposed for Mustelidae, we repeated the analysis excluding early North American fossils, often grouped together in subfamily Oligobuninae [25], following recent assessments on the taxonomy of the group [26,27]. We also

split Mustelidae and Mephitidae, which are not classified as separate families in the original databases, but are separate monophyletic groups according to the most recent studies [24,28]. Additionally, to further check the influence of Mustelidae taxonomy in our estimates, we analysed the whole clade Musteloidea, which includes families Mustelidae, Procyonidae, Ailuridae and Mephitidae.

The method we used to infer diversification dynamics also requires information on the number of extant species within each lineage. We obtained these estimates from the International Union for Conservation of Nature database (<http://www.iucn-redlist.org/> accessed between April and May 2014). The number of extant species was considered separately for each continent. Thus, for instance, if a species is extant, but locally extinct in Eurasia, it was not listed as an extant species when analysing the diversification of its lineage in Eurasia.

(b) Estimating diversification rates

To assess diversification dynamics of each lineage in each continent we used a hierarchical Bayesian approach [29] in which fossil occurrences are modelled as the result of two processes: preservation and diversification. This method, implemented as an open-source PYTHON program (PYRATE [21]), uses all fossil occurrences of a given taxon to estimate the parameters of the preservation processes, the times of speciation and extinction, the speciation and extinction rates and rate shifts through time. Assuming preservation is a stochastic process, it can be modelled as a non-homogeneous Poisson process in which the rate parameter is a function of time and the expected number of fossil occurrences per lineage per million years (Myr) is given by the preservation rate q , which is estimated from the data [21]. Thus, times of speciation and extinction are estimated while taking the preservation process into account, instead of assuming that first and last appearances in the fossil record represent the true speciation and extinction times. A birth–death process (with constant or variable rates) is set as a prior on the times of speciation and extinction of all taxa and is itself estimated from the data.

The PyRate method has been fully tested with simulations and shown to provide accurate estimates of preservation, speciation, and extinction rates under a range of diversification scenarios and preservation regimes [29]. It is robust against incomplete taxon sampling and variations of the preservation process across lineages and through time [29]. However, as currently implemented, PYRATE cannot distinguish between *in situ* speciation and immigration, thus estimates of speciation time and speciation rates may include both speciation and immigration events. This limitation is also imposed by the fact that very few species (between zero and 3% of all species considering each family separately) have occurrences in both Eurasia and North America, making it difficult to assign the first occurrence of a species to a speciation or a migration event. We note that for the sake of our argument this limitation is not severe, as the addition of a new species either by *in situ* speciation or by immigration represents a change in the dynamics at the initial stage of colonization of a continent.

PYRATE jointly estimates all model parameters, including the number of temporal rate shifts, using a birth–death Markov chain Monte Carlo algorithm (BDMCMC) [21,29]. For each family in each continent we ran 10 000 000 BDMCMC iterations, discarded the first 1 000 000 as burn-in, and sampled every 1000 iterations to obtain posterior parameter estimates. We used TRACER [30] to monitor chain mixing and effective sample sizes. Fossil occurrences in the raw data are often assigned a temporal range, which depicts the uncertainty on their age. To account for this uncertainty, we randomly drew ages within the range of each occurrence, generated 100 randomized datasets for each family in each continent and replicated the analyses on the randomized datasets [29].

We generated rates through time (RTT) plots to summarize the results on diversity dynamics. The significance of the differences

between rates can be inferred from the overlap between the posterior credible intervals and posterior point estimates [31] and the support for a given number of rate shifts can be assessed from BDMCMC sampling frequencies. Using the estimated times of speciation and extinction we also computed the number of living species through time to infer range-through diversity trajectories of each family in Eurasia and North America. To infer the direction of migration, we used the estimated age of origin in each continent.

3. Results

Of the eight Carnivora families analysed, four seem to have appeared earlier in North America and the other four in Eurasia (figure 1). Root age estimates unambiguously suggest Canidae, Amphicyonidae, Ursidae and Mustelidae migrated from North America to Eurasia whereas Mephitidae and Procyonidae went in the opposite direction (figure 1). Those estimates also suggest Barbourfelidae and Felidae moved from Eurasia to North America. Although root age posteriors for these two families overlap, the best estimates (maximum *a posteriori*) are significantly younger for North America (figure 1).

Our results on the diversification history of Carnivora lineages indicate a strong asymmetry in the dynamics of lineages invading North America and Eurasia. Lineages migrating into Eurasia—Amphicyonidae, Ursidae, Mustelidae and Canidae—invariably experienced an early burst in diversification. Diversification of Amphicyonidae and Ursidae rose sharply in Eurasia during the Oligocene after a short period of low diversification (figure 2) produced by the interplay of both high speciation (and potentially immigration, but see Discussion) and extinction rates (figures 3 and 4 and the electronic supplementary material, figures S1 and S2). As extinction decelerated (figure 4), diversification reached its peak before the drop in speciation, which reduced the net diversification. The diversification rate of Mustelidae peaked roughly at the same time (approx. 24–20 Myr) due to high initial speciation and low extinction rates (figures 3 and 4 and the electronic supplementary material, figure S3). By contrast, changes in the diversification dynamics of Amphicyonidae, Ursidae and Mustelidae were less pronounced in North America, where they first appeared, showing no evidence of radiation bursts nor an increase in rates at the same geological time those lineages show a burst in Eurasia (figure 2 and the electronic supplementary material, figures S1–S3).

Canidae invaded Eurasia at a later time (approx. 10–7 Myr), in the Late Miocene, and also underwent a burst of diversification (figure 2 and the electronic supplementary material, figure S4). When compared with the dynamics in North America, the radiation of Canidae in Eurasia is characterized not only by higher speciation but also higher extinction rates (figures 3 and 4). Canidae also experienced an initial burst of diversification in North America during the Eocene when they originated (approx. 40 Myr; figure 2 and the electronic supplementary material, figure S4), presumably from another North American ancestral Carnivora lineage [32].

A model with one or more shifts in speciation rates is statistically supported for all the lineages invading Eurasia (electronic supplementary material, table S2). By contrast, the lineages that migrated from Eurasia to North America—Procyonidae, Mephitidae, Felidae and Barbourfelidae—showed more uniform diversification dynamics, without rate shifts (electronic supplementary material, table S2) and no evidence for initial

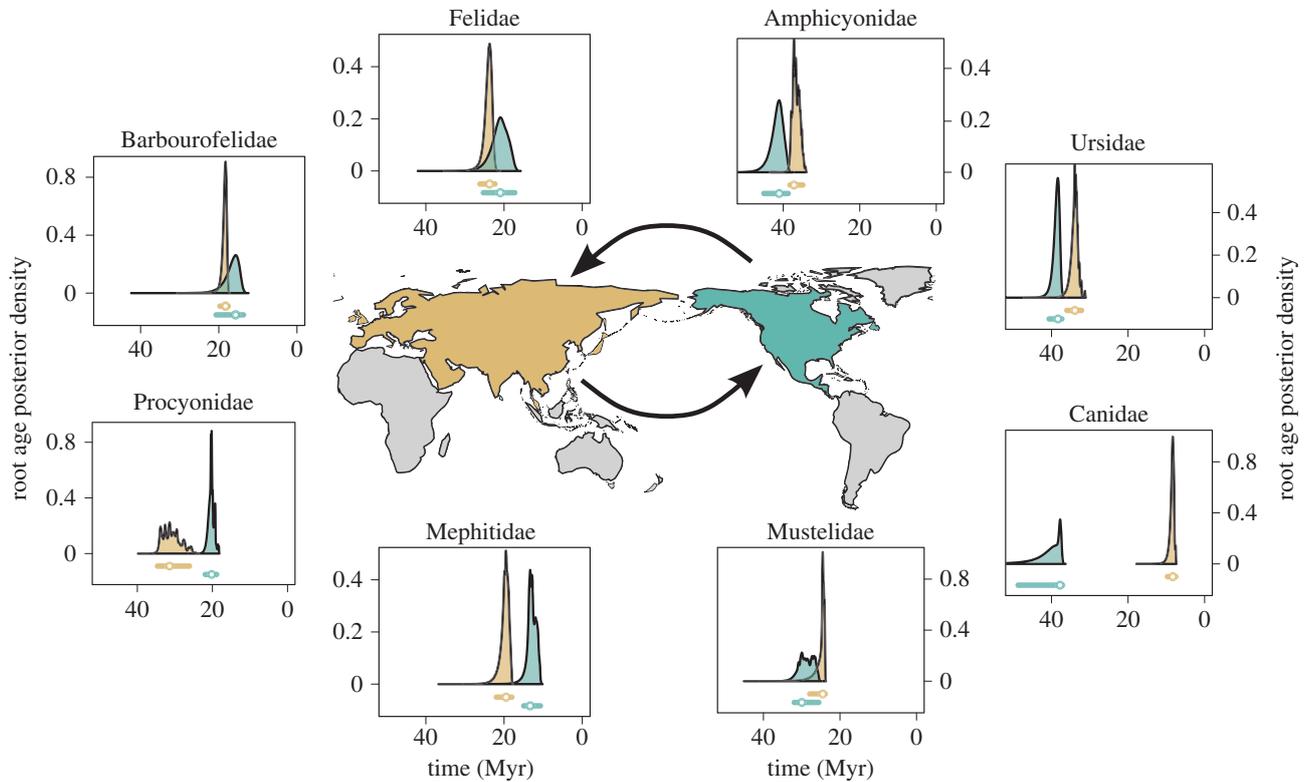


Figure 1. Lineage first time of occurrence and direction of migration. Panels show the estimated posterior densities of root ages for each Carnivora family in Eurasia and North America. The bars depict the 95% highest posterior density (HPD) and circles represent the maximum *a posteriori* probabilities (MAP). Panels on the left represent families that migrated into North America and panels on the right represent families that migrated into Eurasia. (Online version in colour.)

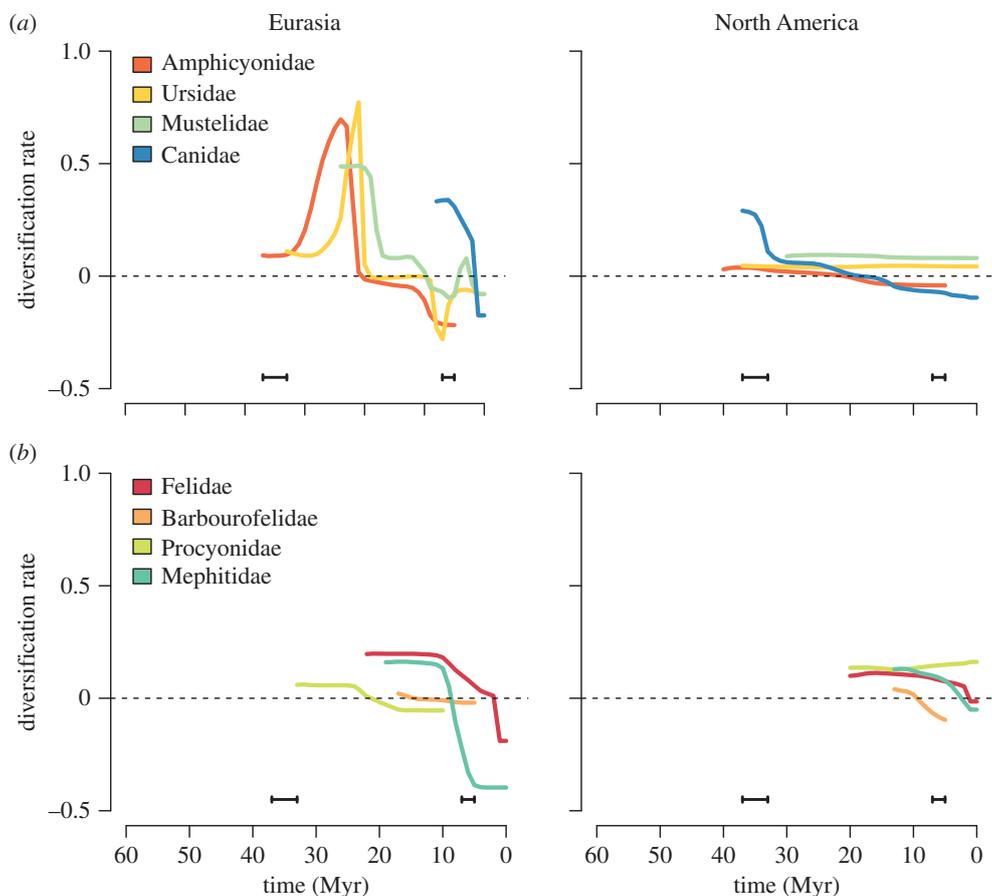


Figure 2. Diversification rate of Carnivora families in each continent. Solid lines represent the medians considering all BDMCMC iterations from all 100 replicates. (a) Rates for lineages that migrated into Eurasia; (b) rates for lineages that migrated into North America. Black bars indicate the two major climatic (Eocene–Oligocene cooling and Messinian crisis) events discussed in the text. Rate-through-time (RTT) plots of net diversification rate with 95% HPD can be found in the electronic supplementary material, figures S1–S8.

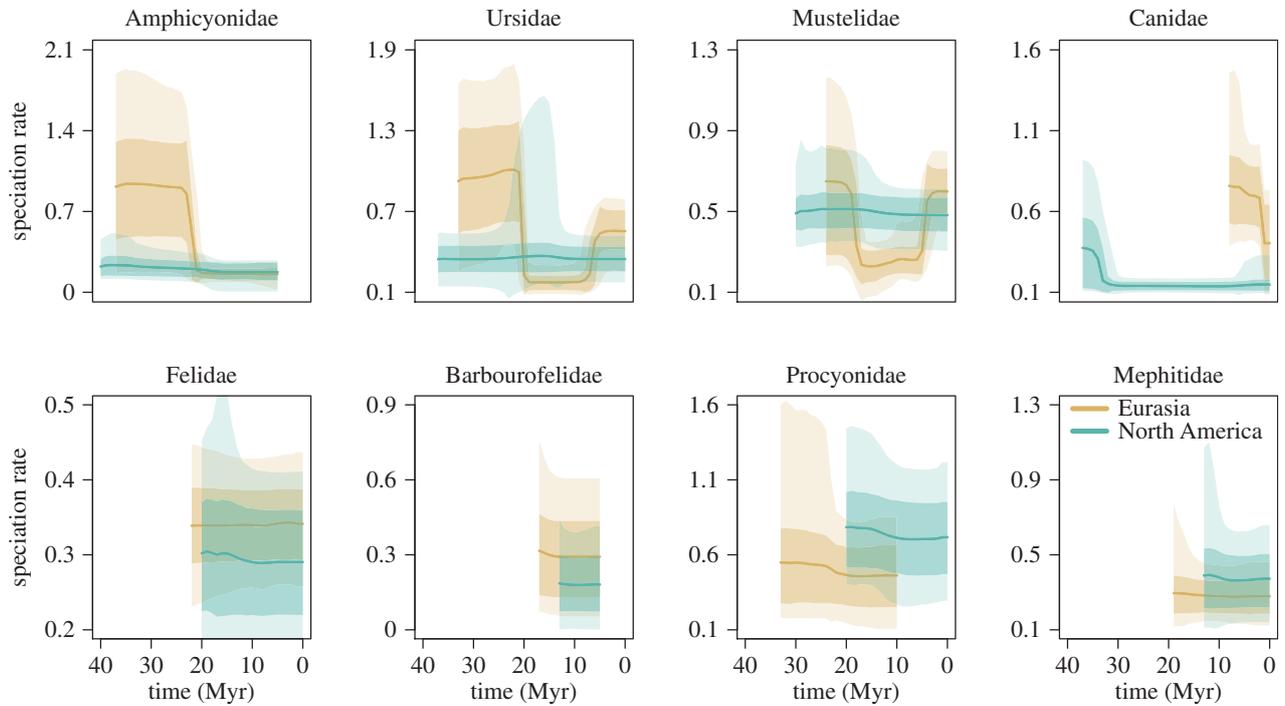


Figure 3. Rate-through-time (RTT) plots showing marginal rates of speciation of each Carnivora family in each continent. Solid lines represent the median considering all BDMCMC iterations for 100 replicates. Shaded areas display the range of the 75% and 95% credibility intervals. (Online version in colour.)

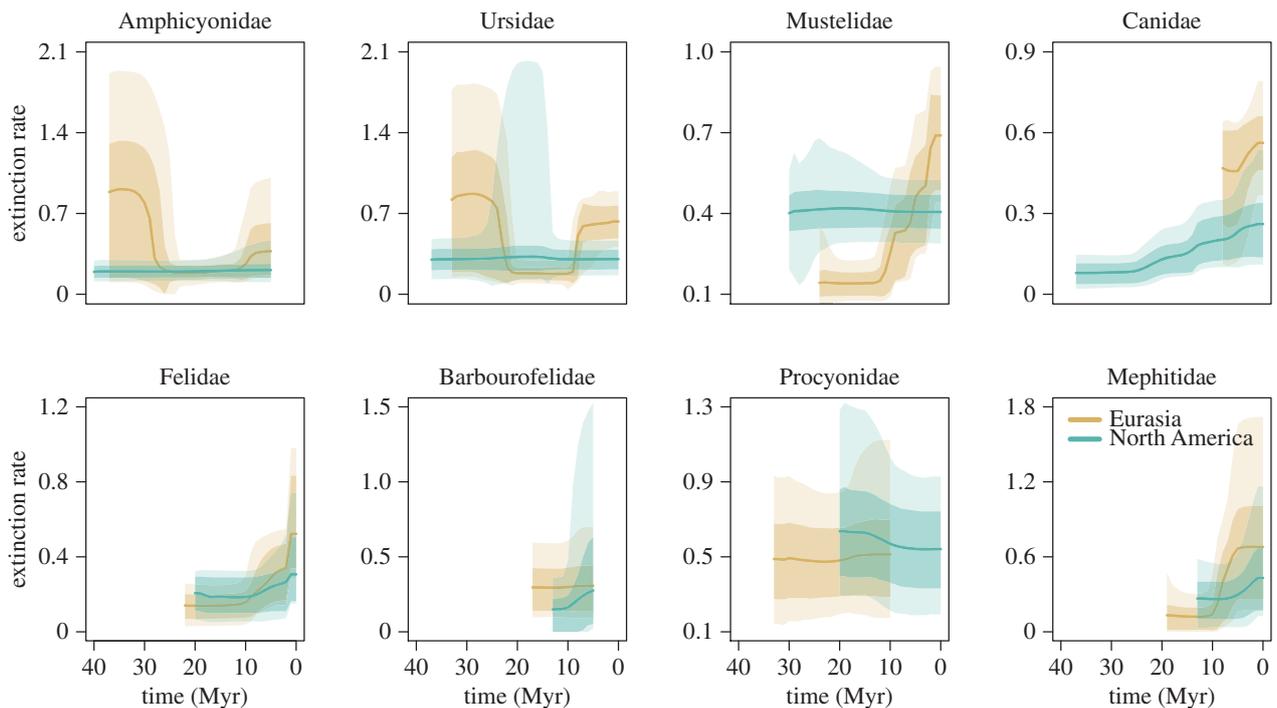


Figure 4. Rate-through-time (RTT) plots showing marginal rates of extinction of each Carnivora family in each continent. Solid lines represent the median considering all BDMCMC iterations for 100 replicates. Shaded areas display the range of the 75% and 95% credibility intervals. (Online version in colour.)

bursts in speciation after migration into North America or during their evolutionary history in Eurasia (figures 2 and 3 and the electronic supplementary material, figures S5–S8). Similarly, other Eurasian lineages that did not establish in North America, such as Viverridae and Hyaenidae did not undergo diversification bursts (electronic supplementary material, figure S9). Diversity trajectories reflect the two opposing dynamics described above. For lineages that invaded Eurasia we see a sharp increase in diversity while those lineages that invade North America show less pronounced changes in diversity (electronic supplementary material, figures S10–S12).

For most lineages, in both continents, the net diversification rates dropped below zero during the Miocene (23–5.3 Myr) or close to the Miocene–Pliocene transition (approx. 5 Myr; figure 2). In general, this negative diversification occurred in response to increased extinction rates, but the shifts in extinction rates were more pronounced in Eurasia than in North America (figure 4). The decline of Procyonidae in Eurasia [33] and Amphicyonidae in North America [34], are owing to a decrease in speciation rather than increase in extinction rates (figure 3).

Because Amphicyonidae and Ursidae invaded Eurasia during the Palaeogene, which has a poorer fossil record

[23], we questioned whether the early bursts in speciation found for these lineages could artificially derive from the differences in preservation through time. Therefore, we performed a sensitivity analysis by simulating datasets under constant rates and strongly biased preservation rates to test whether such biases could result in the erroneous estimation of shifts in speciation rates (see the electronic supplementary material, text S1). These analyses show that the inferred early bursts in speciation found for Amphicyonidae and Ursidae are very unlikely to derive from preservation biases (electronic supplementary material, text S1 and figure S13). Additionally, we found no evidence that preservation rate differences between North America and Eurasia could bias our results (electronic supplementary material, text S2).

4. Discussion

We showed here that the faunal exchanges of carnivorans between North America and Eurasia resulted in asymmetrical macroevolutionary dynamics, with explosive radiations of immigrant lineages when entering Eurasia and more constrained dynamics after invading North America. We also found that at the time of faunal exchange the dynamics of the immigrant lineages show no sign of burst in diversification in their continent of origin (figure 2). Although recent work [23] indicated that diversification of carnivorans throughout the Neogene was globally stable, by looking at finer taxonomic and spatial scale (family level and separate continents) and at a longer time span we show diversity dynamics were more variable. We hypothesize differences in the ecological settings between Eurasia and North America can explain the macroevolutionary patterns unclosed here.

The method we use to estimate speciation and extinction rates cannot distinguish between *in situ* speciation and immigration events. We emphasize, however, that from the perspective of species accumulation at a new continent, the distinction between speciation and immigration is not relevant to our argument, as both contribute to the rapid accumulation of species at the inception of the colonization process. Moreover, the low proportion of shared species between continents (see Methods), unless resulting from differences in taxonomic practices, suggests that at the continental scale the diversification dynamics estimated here is largely driven by *in situ* diversification.

The early bursts in diversification of Amphicyonidae, Ursidae, Mustelidae and Canidae after invading Eurasia are characterized by initially large speciation rates that decelerate through time, one of the key components of adaptive radiations [35]. In general, our results agree with the palaeontological interpretation of the earliest records assigned to Amphicyonidae and Ursidae, suggesting both families originated in North America but invaded Eurasia soon after [20,34,36]. Our estimates also suggest that this period is characterized by high extinction rates in Eurasia. The high extinction rates seen in this period might be owing to an unsuccessful initial establishment of Amphicyonidae and Ursidae in Eurasia. Speciation rates corroborate the notion that Amphicyonidae expanded rapidly [18], especially after establishing in Eurasia. Similarly, the earlier taxa recognized as true ursids, grouped in the subfamily Amphicyonodontinae seem to have evolved in North America and reached Eurasia in the Early Oligocene (approx. 34 Myr). The other two subfamilies Hemicyoninae and Ursinae only radiated during the Late

Oligocene and Early Miocene (approx. 23 Myr) [33]. We identified an explosive radiation following the appearance of Hemicyoninae bears, which are thought to have evolved in Eurasia and reinvaded North America [20,36]. Phylogenetic studies using mitochondrial genomes suggest an explosive radiation of Ursinae close to the Miocene–Pliocene boundary (approx. 5 Myr) [37]. Our analyses separating Eurasian and North American taxa and including all Ursidae suggests this radiation extends far back to the Early Miocene (approx. 23 Myr) with the rise of Hemicyoninae ursids in Eurasia.

The details of Mustelidae radiation are poorly resolved owing to taxonomic uncertainty of the earliest occurrences [24,26,27,38]. These earliest forms appear in North America in the Early Miocene (approx. 23 Myr; [24]). Yet, depending on the taxonomic scheme, the origin of Mustelidae may be traced to Eurasia [27,39]. Irrespective of the taxonomic scheme, we found an explosive radiation of Mustelidae in Eurasia that is not present in the North American record (electronic supplementary material, figure S14). This agrees with previous results based on a phylogeny of extant taxa, which suggest mustelids preferentially diversified in Eurasia [26,40].

Amphicyonidae and Ursidae first appear in Eurasia around the Eocene–Oligocene boundary (approx. 34 Myr), but only radiate and accumulate species in Eurasia at approximately the same time as the first occurrences of Mustelidae, close to the boundary between the Oligocene and Miocene (approx. 23 Myr). At this time the diversity of the main Eurasian carnivores, the hyaenodontid Creodonta, a sister clade of Carnivora was in steady decline [17] (electronic supplementary material, figures S12 and S15). The demise of creodonts, may have allowed immigrant lineages to flourish in face of the wealth of ecological opportunities. Alternatively, it has been suggested that amphicyonids and hemicyonine ursids could have actively displaced creodonts [17].

History repeated itself close to the Miocene–Pliocene boundary when Canidae invaded Eurasia. Although other Canidae subfamilies were present in North America during the Cenozoic, only Caninae established and radiated in Eurasia in the Late Miocene (approx. 10–7 Myr) starting an explosive radiation that decelerated over time. The rapid radiation of Eurasian Canidae is also supported by phylogenetic studies [41]. Ecological opportunity may also explain the burst in Canidae diversification after invading Eurasia. Eurasia experienced massive losses of terrestrial mammals during the Late Miocene (approx. 11–5.3 Myr) [17,42], most likely owing to the climatic events related to the Messinian crisis, broadly characterized by an increase in aridity that resulted in a decrease in forest cover and the expansion of grasslands [43–45]. The fossil record suggests that most carnivore lineages declined in diversity during this period [17]. Our results show these declines were mainly because of increased extinction rates. Yet, this is the time when Canidae invade Eurasia and diversify rapidly with an early peak in speciation rates followed by a decline phase. We hypothesize the radiation of Canidae in Eurasia was also bolstered by the decline of other carnivorans such as hyaenids [17]. The fact that in many cases the taxa that replace those from declining lineages are morphologically similar to the deceased [17] advocates the role of ecological opportunity in shaping radiations.

Our estimates suggest that the radiation of Amphicyonidae, Ursidae and Canidae are characterized by initially high speciation and extinction rates. The invasion of Mustelidae in Eurasia does not result in high extinction rates, but if we look at the dynamics of Musteloidea (electronic

supplementary material, figure S16) a similar pattern of high initial extinction rate is present. Most work on evolutionary radiations is based on neontological data and molecular phylogenies [35], which tend to underestimate extinction [46]. Our findings highlight that explosive radiations may be a period of evolutionary turmoil where both speciation and extinction rates are initially high.

The instances of migration from Eurasia to North America are not followed by bursts in diversification as seen for immigrant lineages going in the opposite direction. Palaeontologists generally agree that Procyonidae, Mephitidae, Barbourfelidae and Felidae migrated from Eurasia to North America [16,20], as reconstructed in our analysis. Our results indicate that the diversification dynamics of these four lineages were similar in North America and Eurasia, with roughly constant speciation rates.

Although some lineages, mainly ungulates, appear to have undergone radiations in North America, the diversity of mammals over the Cenozoic in North America seem to have been relatively stable [47]. Yet, North America also had its own explosive radiation of carnivorans. Canidae emerged in the Eocene [48] and underwent an explosive radiation between 37 and 34 Myr that was similar to those of the lineages that immigrated into Eurasia. The rise of North American early canids also happened while the hyaenodontid creodonts declined and the cat-like nimravids had low diversity [16,17] (electronic supplementary material, figures S11 and S15). Current evidence suggests that the 'double-wedge' pattern involving creodonts and carnivorans was more likely a case of incumbent replacement rather than active displacement [49]. Assuming biotic interactions such as competition and predation can indeed constrain evolutionary dynamics, the early rise of Canidae may have constrained the radiation of other lineages that originated in North America such as Amphicyonidae, Ursidae and Mustelidae. Although later forms of amphicyonids and ursids were large-bodied, the earliest forms were smaller and morphologically similar to contemporaneous canids [34,36,50,51]. Thus, constraints imposed by small-sized Canidae over those groups are conceivable. Together, these early North American carnivorans may have limited the diversification of immigrant lineages from Eurasia through incumbency effects [13,52]. At a later phase, the invasion of Eurasian lineages such as Felidae and to a less extent Barbourfelidae might have contributed to increase the extinction rate in North American canids [53].

Here we focused on lineages present in both North America and Eurasia, but there are also lineages that, although diverse in Eurasia never established in North America, namely Viverridae and Hyaenidae. The reason is elusive, but it might be the case that the incumbent North American carnivores (as well as established immigrant lineages) not only limited diversification, but also impeded some lineages to establish, so putative invasions were never successful. Interestingly, although many of the extinct hyaenids were bone-crackers, the only hyaenid known to have reached North America is *Chasmaporthetes*, a cursorial hunter [54]. The failure of hyaenids to thrive in North America could be related to incumbency effects by the bone-cracking borophagine canids, which were diverse during the Miocene (23–5.3 Myr).

Our results suggest the establishment of Carnivora families in Eurasia and the rise of Canidae in North America happened through explosive radiations that coincide with a time when other lineages of carnivores declined [17,49]. Yet, the two main episodes of carnivorans radiation in Eurasia also occur after two major climate change events [45,55]. The Eocene–

Oligocene boundary (approx. 34 Myr), which saw the radiation of Canidae in North America and the establishment of amphicyonids and ursids in Eurasia, marks the shift from the 'greenhouse' to the 'icehouse' phase after the onset of the Late Eocene global climate cooling (figure 2 [56–58]). By contrast, the radiation of Eurasian canids followed the global warming and aridification episodes of the Miocene–Pliocene boundary (approx. 7 Myr; figure 2 [59,60]). Climatic changes may be responsible for triggering intercontinental dispersal events [61]. Besides that, the vegetation changes associated with these events [19,45,62] may have played a direct role in the radiation of Eurasian immigrants by providing new ecological opportunities for arriving lineages. The interplay between migrations and climatic events was determinant for the diversification of other terrestrial mammals in Eurasia such as ungulates [42,62]. For instance, in Eurasia, taxa adapted to open habitats such as equids and giraffids benefited from the expansion of grasslands in the Late Miocene [42]. The radiation of Caninae, which were well adapted to hunting in open habitats in North America [63], might have been favoured by such climatic and vegetation changes also in Eurasia [48].

The timing of radiations supports the role of ecological opportunity in shaping the asymmetry in macroevolutionary patterns between North America and Eurasia. However, geographical differences between Eurasia and North America may also have played a role in these diversification dynamics. Eurasia occupies a larger area comprising different biomes. Such differences in area were already in place at the time Carnivora lineages diversified and might also have contributed to shape macroevolutionary patterns by generating more opportunities for speciation events [64].

Here we focus on one component of adaptive radiations, the rapid accumulation of species [35]. As more information on morphological traits of extinct taxa is gathered we might be able to test whether the explosive radiations we unveiled here were accompanied by increased ecological diversity [65]. Our findings indicate that the interplay between intercontinental migrations and ecological opportunity played an important role in the diversification of Carnivora, allowing speciation bursts of invading lineages in Eurasia while limiting the diversification of immigrants in North America. These results reveal the long-term outcomes of biological invasions and migrations and show explosive radiations might not only be important in insular systems, but also shape diversity at a continental scale.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. M.M.P., D.S. and T.B.Q. conceived and designed the study and analyses. M.M.P. and D.S. performed the analyses. M.M.P., D.S. and T.B.Q. wrote the manuscript.

Competing interests. We have no competing interests.

Funding. M.M.P. and T.B.Q. are supported by São Paulo Research Foundation (FAPESP grants nos. 2013/22016–6; 2012/04072–3). D.S. received funding from Carl Tryggers stiftelse and Wenner-Gren Foundation (Sweden).

Acknowledgements. We thank Lars Werdelin for helping us with the taxonomy of Hyaenidae. We also thank John Alroy and Mark Uhen who contributed the bulk of the data we used from PBDB and Mikael Fortelius and other organizers for running the NOW database. This publication is PBDB publication no. 243. We ran part of the analyses at the high-performance computing centre Vital-IT of the Swiss Institute of Bioinformatics (Lausanne, Switzerland) and at the LCCA-Laboratory of Advanced Scientific Computation of the University of São Paulo (São Paulo, Brazil).

References

- Simpson GG. 1953 *The major features of evolution*. New York, NY: Columbia University Press.
- Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Losos JB, Mahler DL. 2010 Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In *Evolution since Darwin: the first 150 years* (eds MA Bell, DJ Futuyma, WF Eanes, JS Levinton), pp. 381–420. Sunderland, MA: Sinauer Associates.
- Jonsson KA *et al.* 2012 Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proc. Natl Acad. Sci. USA* **109**, 6620–6625. (doi:10.1073/pnas.1115835109)
- Grant PR, Grant BR. 2014 *40 years of evolution: Darwin's finches on Daphne Major Island*. Princeton, NJ: Princeton University Press.
- Losos JB. 2010 A tale of two radiations: similarities and differences in the evolutionary diversification of Darwin's finches and Greater Antillean Anolis lizards. In *Search of the causes of evolution from field observations to mechanisms* (eds PR Grant, BR Grant), pp. 309–331. Princeton, NJ: Princeton University Press.
- Pratt HD. 2005 *The Hawaiian honeycreepers*. Oxford, UK: Oxford University Press.
- Givnish TJ *et al.* 2009 Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proc. R. Soc. B* **276**, 407–416. (doi:10.1098/rspb.2008.1204)
- Melo M, Warren BH, Jones PJ. 2011 Rapid parallel evolution of aberrant traits in the diversification of the Gulf of Guinea white-eyes (Aves, Zosteropidae). *Mol. Ecol.* **20**, 4953–4967. (doi:10.1111/j.1365-294X.2011.05099.x)
- Yoder JB *et al.* 2010 Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* **23**, 1581–1596. (doi:10.1111/j.1420-9101.2010.02029.x)
- Rabosky DL, Lovette IJ. 2008 Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* **62**, 1866–1875. (doi:10.1111/j.1558-5646.2008.00409.x)
- Levinton JS. 1979 Theory of diversity equilibrium and morphological evolution. *Science* **204**, 335–336. (doi:10.1126/science.204.4390.335)
- Jablonski D, Sepkoski JJ. 1996 Paleobiology, community ecology and scales of ecological pattern. *Ecology* **77**, 1367–1378. (doi:10.2307/2265534)
- Burbrink FT, Pyron RA. 2010 How does ecological opportunity influence rates of speciation, extinction, and morphological diversification in New World ratsnakes (tribe Lamproleptini)? *Evolution* **64**, 934–943. (doi:10.1111/j.1558-5646.2009.00888.x)
- Schenk JJ, Rowe KC, Steppan SJ. 2013 Ecological opportunity and incumbency in the diversification of repeated continental colonizations by Muroid rodents. *Syst. Biol.* **62**, 837–864. (doi:10.1093/sysbio/syt050)
- Hunt RM. 2004 Global climate and the evolution of large mammalian carnivores during the later Cenozoic in North America. *Bull. Am. Mus. Nat. Hist.* **285**, 139–156. (doi:10.1206/0003-0090(2004)285<0139:C>2.0.CO;2)
- Van Valkenburgh B. 1999 Major patterns in the history of carnivorous mammals. *Annu. Rev. Earth Planet. Sci.* **27**, 463–493. (doi:10.1146/annurev.earth.27.1.463)
- Rose KD. 2006 *The beginning of the age of mammals*. Baltimore, MA: The Johns Hopkins University Press.
- Figueirido B, Janis CM, Perez-Claros JA, De Renzi M, Palmqvist P. 2012 Cenozoic climate change influences mammalian evolutionary dynamics. *Proc. Natl Acad. Sci. USA* **109**, 722–727. (doi:10.1073/pnas.1110246108)
- Goswami A, Friscia A. 2010 *Carnivoran evolution*. Cambridge, UK: Cambridge University Press.
- Silvestro D, Salamin N, Schnitzler J. 2014 PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods Ecol. Evol.* **5**, 1126–1131. (doi:10.1111/2041-210X.12263)
- Bengtson P. 1988 Open nomenclatures. *Palaeontology* **31**, 223–227.
- Liow LH, Finarelli JA. 2014 A dynamic global equilibrium in carnivoran diversification over 20 million years. *Proc. R. Soc. B* **281**, 20132312. (doi:10.1098/rspb.2013.2312)
- Finarelli JA. 2008 A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia): relationships among basal taxa. *J. Mamm. Evol.* **15**, 231–259. (doi:10.1007/s10914-008-9074-x)
- Wang X, McKenna MC, Dashzeveg D. 2005 *Amphicticeps* and *Amphicyonodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, Central Mongolia and phylogeny of basal arctoids with comments on zoogeography. *Am. Mus. Novit.* **3483**, 1–57. (doi:10.1206/0003-0082(2005)483[0001:AAAACF]2.0.CO;2)
- Sato JJ, Wolsan M, Minami S, Hosoda T, Sinaga MH, Hiyama K, Yamaguchi Y, Suzuki H. 2009 Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. *Mol. Phylogenet. Evol.* **53**, 907–922. (doi:10.1016/j.ympev.2009.08.019)
- Sato JJ, Wolsan M, Prevosti FJ, D'Elia G, Begg C, Beeg K, Hosoda T, Campbell KL, Suzuki H. 2012 Evolutionary and biogeographic history of weasel-like carnivores (Musteloidea). *Mol. Phylogenet. Evol.* **63**, 745–757. (doi:10.1016/j.ympev.2012.02.025)
- Flynn JJ, Finarelli JA, Zehr S, Hsu J, Nedbal MA. 2005 Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Syst. Biol.* **54**, 317–337. (doi:10.1080/10635150590923326)
- Silvestro D, Schnitzler J, Liow LH, Antonelli A, Salamin N. 2014 Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. *Syst. Biol.* **63**, 349–367. (doi:10.1093/sysbio/syu006)
- Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014 Tracer v1.6. See <http://beast.bio.ed.ac.uk/Tracer>.
- Silvestro D, Cascales-Miñana B, Bacon CD, Antonelli A. 2015 Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol.* **207**, 425–436. (doi:10.1111/nph.13247)
- Wesley-Hunt GD, Flynn JL. 2005 Phylogeny of the Carnivora: basal relationships among the Carnivoramorphans, and assessment of the position of 'Miacoidea' relative to Carnivora. *J. Syst. Palaeontol.* **3**, 1–28. (doi:10.1017/S1477201904001518)
- McKenna MC, Bell SK. 1997 *Classification of the mammals above the species level*. New York, NY: Columbia University Press.
- Hunt RM. 2005 Amphicyonidae. In *Evolution of tertiary mammals of North America* (eds CM Janis, KM Scott, L Jacobs), pp. 196–227. Cambridge, UK: Cambridge University Press.
- Gavrillets S, Losos JB. 2009 Adaptive radiation: contrasting theory with data. *Nature* **323**, 732–737. (doi:10.1126/science.1157966)
- Hunt RM. 2005 Ursidae. In *Evolution of tertiary mammals of North America* (eds CM Janis, KM Scott, L Jacobs), pp. 174–195. Cambridge, UK: Cambridge University Press.
- Krause J *et al.* 2008 Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. *BMC Evol. Biol.* **8**, 220. (doi:10.1186/1471-2148-8-220)
- Yonezawa T, Nikaido M, Kohno N, Fukumoto Y, Okada N, Hasegawa M. 2007 Molecular phylogenetic study on the origin and evolution of Mustelidae. *Gene* **396**, 1–12. (doi:10.1016/j.gene.2006.12.040)
- Wolsan M. 1993 Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). *Acta Theriol.* **38**, 345–384. (doi:10.4098/AT.arch.93-29)
- Koepfli K, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK. 2008 Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biol.* **6**, 10. (doi:10.1186/1741-7007-6-10)
- Tedford RH, Wang X, Taylor BE. 2009 Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). *Bull. Am. Mus. Nat. Hist.* **325**, 1–218. (doi:10.1206/574.1)
- Costeur L, Legendre S. 2008 Spatial and temporal variation in European Neogene large mammals diversity. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **261**, 127–144. (doi:10.1016/j.palaeo.2008.01.011)
- Janis CM. 1993 Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu. Rev. Ecol. Syst.* **24**, 467–500. (doi:10.1146/annurev.es.24.110193.002343)

44. Cerling TE, Ehleringer JR, Harris JM. 2008 Carbon dioxide starvation, the development of C4 ecosystems, and mammalian evolution. *Phil. Trans. R. Soc. B* **353**, 159–171. (doi:10.1098/rstb.1998.0198)
45. Fortelius M, Eronen J, Liu L, Pushkina D, Tesakov A, Vislobokova I, Zhang Z. 2006 Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **238**, 219–227. (doi:10.1016/j.palaeo.2006.03.042)
46. Quental TB, Marshall CR. 2010 Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* **25**, 434–441. (doi:10.1016/j.tree.2010.05.002)
47. Stucky RK. 1990 Evolution of land mammal diversity in North America during the Cenozoic. In *Current mammalogy*, vol. 2 (ed. HH Genoways), pp. 375–432. New York, NY: Plenum Press.
48. Wang X, Tedford RH. 2008 *Dogs: their fossil relatives and evolutionary history*. New York, NY: Columbia University Press.
49. Friscia AR, Van Valkenburgh B. 2010 Ecomorphology of North American Eocene carnivores: evidence for competition between carnivorans and creodonts. In *Carnivoran evolution: new views on phylogeny, form, and function* (eds A Goswami, AR Friscia), pp. 311–341. Cambridge, UK: Cambridge University Press.
50. Finarelli JA, Flynn JJ. 2006 Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Syst. Biol.* **55**, 301–313. (doi:10.1080/10635150500541698)
51. Figueirido B, Pérez-Claros JA, Hunt RM, Palmqvist P. 2011 Body mass estimation in amphicyonid carnivoran mammals: a multiple regression approach from the skull and skeleton. *Acta Palaeontol. Pol.* **56**, 225–246. (doi:10.4202/app.2010.0005)
52. Rosenzweig ML, Mccord RD. 1991 Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* **17**, 202–213.
53. Silvestro D, Antonelli A, Salamin N, Quental TB. 2015 The role of clade competition in the diversification of North American canids. *Proc. Natl Acad. Sci. USA* **112**, 8684–8689. (doi:10.1073/pnas.1502803112)
54. Berta A. 1981 The Plio-Pleistocene hyaena *Chasmaporthetes ossifragus* from Florida. *J. Vertebr. Paleontol.* **1**, 341–356. (doi:10.1080/02724634.1981.10011905)
55. Prothero DR. 1994 The late Eocene-Oligocene extinctions. *Annu. Rev. Earth Planet. Sci.* **22**, 145–165. (doi:10.1146/annurev.ea.22.050194.001045)
56. Francis JE *et al.* 2009 The Eocene/Oligocene in Antarctica. In *Developments in earth and environmental sciences* (eds F Florindo, M Siebert), pp. 309–368. Amsterdam, The Netherlands: Elsevier.
57. Hren MT, Sheldon ND, Grimesd ST, Collinsone ME, Hooker JJ, Buglerd M, Lohmann KC. 2013 Terrestrial cooling in Northern Europe during the Eocene–Oligocene transition. *Proc. Natl Acad. Sci. USA* **110**, 7562–7567. (doi:10.1073/pnas.1210930110)
58. Woodburne MO, Gunnell GF, Stucky RK. 2009 Climate directly influences Eocene mammal faunal dynamics in North America. *Proc. Natl Acad. Sci. USA* **106**, 13 399–13 403. (doi:10.1073/pnas.0906802106)
59. Duggen S, Hoernie K, van den Bogaard P, Rüpke L, Morgan JP. 2003 Deep roots of the Messinian salinity crisis. *Nature* **422**, 602–606. (doi:10.1038/nature01553)
60. Whybrow PJ, Andrews P. 2004 Response of Old World terrestrial vertebrate biotas to Neogene climate change. In *Biotic response to global change: the last 145 million years* (eds SJ Culver, PF Rawson), pp. 350–366. Cambridge, UK: Cambridge University Press.
61. Blois JL, Hadly EA. 2009 Mammalian response to Cenozoic climatic change. *Annu. Rev. Earth Planet. Sci.* **37**, 181–208. (doi:10.1146/annurev.earth.031208.100055)
62. Fortelius M, Eronen JT, Kaya F, Tang H, Raia P, Puolamäki K. 2014 Evolution of Neogene mammals in Eurasia: environmental forcing and biotic interactions. *Annu. Rev. Earth Planet. Sci.* **42**, 579–604. (doi:10.1146/annurev-earth-050212-124030)
63. Figueirido B, Martín-Serra A, Tseng ZI, Janis CM. 2015 Habitat changes and changing predatory habits in North American fossil canids. *Nat. Comm.* **6**, 7976. (doi:10.1038/ncomms8976)
64. Losos JB, Schluter D. 2000 Analysis of an evolutionary species-area relationship. *Nature* **408**, 847–850. (doi:10.1038/35048558)
65. Slater GJ. 2015 Iterative adaptive radiations of fossil canids show no evidence for diversity-dependent trait evolution. *Proc. Natl Acad. Sci. USA* **112**, 4897–4902. (doi:10.1073/pnas.1403666111)