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 carnivores 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 data 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 hyaenodontid Creodonta and families that were present preferentially in one continent such as Hyaenidae, Perccocutidae 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.iucnredlist.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 (P-Rate) [21], uses all fossil occurrences of a given taxon to estimate the parameters of the preservation process, 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, 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 P-Rate 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, P-Rate 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.

P-Rate 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 Barbourofelidae 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—invarily 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 Barbourofelidae—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 BDMMCMC 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.
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 asymmetric 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 species accumulation at a new continent, the distinction between events. We emphasize, however, that from the perspective of 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 owning 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 carnivores 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, Barbourofelidae 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 seems to have been relatively stable [47]. Yet, North America also had its own explosive radiation of carnivoraes. 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 carnivores 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 Barbourofelidae 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 constraints were never successful. Interestingly, although many of the extinct hyaenids were bone-crackers, the only hyaenid 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 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.

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