A Journal of Macroecology

Global Ecology and Biogeography

RESEARCH PAPER

Dispersal is a major driver of the latitudinal diversity gradient of Carnivora

Jonathan Rolland[1]*, Fabien L. Condamine[2], Champak R. Beeravolu[3], Frédéric Jiguet[4] and Hélène Morlon[5]

[1]*Department of Ecology and Evolution, Biophore, University of Lausanne, Lausanne, 1015, Switzerland,* [2]*UMR 7641 Centre de Mathématiques Appliquées (Ecole Polytechnique), CNRS, Route de Saclay, 91128 Palaiseau, France,* [3]*UMR 1041 Centre de Biologie pour la Gestion des Populations, INRA, Campus international de Baillarguet CS30016, 34988 Montferrier-sur-Lez, France,* [4]*Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-UPMC, Muséum National d'Histoire Naturelle, CP51, 55 rue Buffon, 75005 Paris, France,* [5]*UMR 8197 Institut de Biologie de l'Ecole Normale Supérieure, CNRS, 46 rue d'Ulm, 75005 Paris, France*

*Correspondence: Jonathan Rolland, Department of Ecology and Evolution, Biophore, University of Lausanne, Lausanne, 1015, Switzerland.
E-mail: jonathan.rolland@yahoo.fr

ABSTRACT

Aim Understanding the relative contribution of diversification rates (speciation and extinction) and dispersal in the formation of the latitudinal diversity gradient – the decrease in species richness with increasing latitude – is a main goal of biogeography. The mammalian order Carnivora, which comprises 286 species, displays the traditional latitudinal diversity gradient seen in almost all mammalian orders. Yet the processes driving high species richness in the tropics may be fundamentally different in this group from that in other mammalian groups. Indeed, a recent study suggested that in Carnivora, unlike in all other major mammalian orders, net diversification rates are not higher in the tropics than in temperate regions. Our goal was thus to understand the reasons why there are more species of Carnivora in the tropics.

Location World-wide.

Methods We reconstructed the biogeographical history of Carnivora using a time-calibrated phylogeny of the clade comprising all terrestrial species and dispersal–extinction–cladogenesis models. We also analysed a fossil dataset of carnivoran genera to examine how the latitudinal distribution of Carnivora varied through time.

Results Our biogeographical analyses suggest that Carnivora originated in the East Palaearctic (i.e. Central Asia, China) in the early Palaeogene. Multiple independent lineages dispersed to low latitudes following three main paths: toward Africa, toward India/Southeast Asia and toward South America via the Bering Strait. These dispersal events were probably associated with local extinctions at high latitudes. Fossil data corroborate a high-latitude origin of the group, followed by late dispersal events toward lower latitudes in the Neogene.

Main conclusions Unlike most other mammalian orders, which originated and diversified at low latitudes and dispersed 'out of the tropics', Carnivora originated at high latitudes, and subsequently dispersed southward. Our study provides an example of combining phylogenetic and fossil data to understand the generation and maintenance of global-scale geographical variations in species richness.

Keywords
Biogeographical history, Carnivora origin, dispersal–extinction–cladogenesis, diversification, out of the tropics, tropical niche conservatism.

INTRODUCTION

Species diversity is not homogeneously distributed on Earth (Pianka, 1966; Rohde, 1992). The increase in species richness with decreasing latitude, called the latitudinal diversity gradient, is one of the most striking patterns in ecology and biogeography, with examples in various forms of organisms from micro-organisms (Fuhrman *et al.*, 2008) to macro-organisms

(Jablonski *et al.*, 2006; Weir & Schluter, 2007; Wiens *et al.*, 2009; Condamine *et al.*, 2012). Many hypotheses have been formulated to explain why there are so many species in the tropics (Hillebrand, 2004; Mittelbach *et al.*, 2007). One of the main hypotheses is that the high species richness observed in the tropics may be due to a higher net diversification rate (speciation rate minus extinction rate; Jablonski *et al.*, 2006; Pyron & Wiens, 2013, Rolland *et al.*, 2014), itself potentially driven by increased biotic interactions (Schemske *et al.*, 2009), temperature (Allen *et al.*, 2006) and climatic stability (Dynesius & Jansson, 2000).

The contribution of diversification rates to the mammalian latitudinal diversity gradient (the evolutionary speed hypothesis) is highly debated (Weir & Schluter, 2007; Soria-Carrasco & Castresana, 2012; Rolland *et al.*, 2014). A recent study based on state speciation extinction (SSE) models found a striking correspondence between latitudinal patterns in diversification rates and species richness in all the main mammalian orders except Carnivora (Rolland *et al.*, 2014). Although the confidence we can have in the results of a single SSE analysis is currently debated, consistent results across phylogenies suggest a 'real' trend across mammalian groups (Rabosky & Goldberg, 2015), and contrasting results in Carnivora suggest that something different is happening in this group. Keeping in mind the limitations of SSE models, the SSE analyses suggested that in Carnivora, net diversification rates were similar in tropical and temperate regions (Fig. 2 in Rolland *et al.*, 2014) or slightly higher in temperate regions (Fig. S3 in Rolland *et al.*, 2014), depending on the constraints imposed on dispersal. Despite these trends in diversification rates, species richness in Carnivora is higher in the tropics than in temperate regions (see Fig. 2 in Rolland *et al.*, 2014). If the net diversification rate is not higher for Carnivora in the tropics, why are there more tropical than temperate species in this group?

Apart from hypotheses involving differences in diversification rates, two main hypotheses can explain high tropical species richness. The first, known as the 'time and area' hypothesis, stipulates that there might be more species in the tropics because (1) tropical lineages are older than temperate ones, meaning that tropical lineages have had more time to diversify (Stephens & Wiens, 2003; Wiens & Donoghue, 2004) and (2) tropical areas were probably more widespread than temperate areas in Earth's history (Fine, 2015). Alternatively, the higher species richness of carnivores in the tropics could be due to differential dispersal from high latitudes to low latitudes, coupled with range contraction ('extinction') at high latitudes. This scenario – whereby lineages originate and diversify at high latitudes, after which they disperse into lower latitudes and contract their range – could explain the latitudinal diversity gradient without invoking the 'diversification rate' or 'time and area' hypotheses (Kennedy *et al.*, 2014). However, this latter possibility has rarely been considered in the literature (but see Darlington, 1959; Condamine *et al.*, 2012). High-latitude regions are only rarely considered as a source of diversity and/or a centre of origin. A notable exception is the study by Condamine *et al.* (2012), which highlights the case for a high-latitude origin for swallowtail butterflies.

The two main hypotheses involving dispersal rates assume a tropical origin of clades: the 'out of the tropics' hypothesis stipulates that the tropics act as a cradle of biodiversity, whereby tropical regions subtend high speciation rates and 'export' species to temperate regions through dispersal and range expansion (Jablonski *et al.*, 2006, 2013). The 'tropical niche conservatism' hypothesis instead proposes that tropical species have difficulties in adapting to and dispersing into temperate regions, such that they accumulate in the tropics (Wiens & Donoghue, 2004). No major hypothesis proposes that diversity could originate in temperate regions and disperse 'into the tropics' by repeated range expansions/range contraction events (but see Darlington, 1959; Condamine *et al.*, 2012). To see that this 'into the tropics' scenario can result in a higher tropical species richness, let's imagine an (unrealistic) extreme case where lineages: (1) originate in temperate regions, (2) diversify only in temperate regions, and (3) all follow a cycle of range expansion/contraction events into the tropics after their origination. Such a process would result in a high tropical richness equal to the number of origination events. While this particular scenario is unrealistic, a more moderate scenario combining temperate origins and massive expansion into the tropics followed by contraction in the temperate regions could in theory explain higher tropical than temperate species richness, even with similar net diversification rates between temperate and tropical regions (or even slightly higher net diversification rates in temperate than in tropical regions).

Within Carnivora, results from previous studies could be consistent with our 'into the tropics' hypothesis. We do not know with precision the relative ratio of tropical to temperate species richness for this group in the Cenozoic, but the fossil record suggests that high latitudes (probably supporting temperate biomes even at this period of Earth history; Chaboureau *et al.*, 2014) might have been rich in the past (Hunt, 1996). The formation of refugia during periods of strong climatic oscillations and glaciations at high latitudes (Dynesius & Jansson, 2000) could have increased the speciation rate in temperate regions, and therefore temperate species richness (Weir & Schluter, 2007). If temperate regions were rich early in the history of the Carnivora, dispersal to tropical areas may have significantly contributed to the accumulation of species in the tropics. Historical reconstructions for Felidae (Johnson *et al.*, 2006) and high estimates of temperate to tropical dispersal rates for the whole group (Fig. S3 in Rolland *et al.*, 2014) are consistent with this hypothesis. There is also evidence from the fossil record that frequent southward dispersal events occurred, such as dispersal events from Eurasia and North America toward Africa, Southeast Asia/India and South America in Ursidae, Procyonidae, Amphicionidae (now extinct), Mustelidae, Canidae, Viverridae, Herpestidae, Hyaenidae and Felidae (Hunt, 1996).

Here, we use a recent phylogeny of Carnivora (Nyakatura & Bininda-Emonds, 2012) and fossil data from the Paleobiology Database (https://www.paleobiodb.org/) to test the hypothesis that frequent dispersal from higher latitudes (temperate) to lower latitudes (tropical) could be responsible for the latitudinal diversity gradient in this group. We first confirm earlier results

from character-dependent diversification models (Goldberg *et al.*, 2011) suggesting that the higher tropical species richness of Carnivora is not explained by high tropical diversification rates but is instead more likely due to frequent dispersal events from temperate to tropical regions (Rolland *et al.*, 2014). Given the limitations of these models, in terms of both power (in particular for a phylogeny of that size; Davis *et al.*, 2013) and type I error rates (Rabosky & Goldberg, 2015), we then approach the question from another angle, by reconstructing the biogeographical history of the group to estimate ancestral areas of origin and major dispersal events. Finally, we use fossils and the palaeo-reconstruction of their latitudes to analyse how the latitudinal distribution of Carnivora varied through time.

METHODS

Time-calibrated phylogenies

We used the most recent time-calibrated complete phylogeny of Carnivora (Nyakatura & Bininda-Emonds, 2012) for diversification analyses and biogeographical reconstruction. Because diversification in marine environments may be governed by different rules from that in terrestrial environments and because we wanted to study diversification of Carnivora in a biogeographical context (with continental splits across time), we removed marine Carnivora from the analyses (i.e. 36 species in the families Odobenidae, Otariidae and Phocidae). After this procedure, the phylogeny contained all the 250 terrestrial Carnivora species currently recognized in the most recent taxonomical revision (Wilson & Reeder, 2005), corresponding to 87% of the 286 total carnivoran species.

Testing the diversification rates hypothesis

We checked that the results concerning diversification and dispersal rates found with a previously proposed phylogeny of Carnivora (Bininda-Emonds *et al.*, 2007; see Fig. S3 in Rolland *et al.*, 2014) held when using the more recent phylogeny of Nyakatura & Bininda-Emonds (2012). We followed the same methodological pipeline used in Rolland *et al.* (2014), detailed here in Appendix S1 in the Supporting Information. In short, we assigned each species to the tropical biome (between 23.4° S and 23.4° N latitude), the temperate biome (below 23.4° S or above 23.4° N) or both biomes, using minimum and maximum latitude data from Jones *et al.* (2009). We then used the combined phylogenetic and biome data to compare the maximum likelihood fit of eight scenarios within the Geographical State Speciation and Extinction model (GeoSSE; Goldberg *et al.*, 2011). We estimated speciation, extinction and dispersal rates associated with the best-fitting model and obtained credibility intervals around these estimates from Markov chain Monte Carlo (MCMC) analyses.

Estimation of historical biogeography

Ancestral areas were estimated using LAGRANGE and the dispersal–extinction–cladogenesis model (DEC; Ree & Smith,

2008). This model estimates which evolutionary scenario including expansions (dispersals) and contractions (extinctions) of the ancestral range is the most likely given a phylogeny and the current spatial distribution of extant species; it also estimates ancestral areas on each node of the phylogeny. We fixed minor bugs and used the new LAGRANGE C++ version (https://github.com/champost/lagrange, last accessed 16 October 2013) that allows one to infer ancestral areas for large trees (Smith, 2009). These models are now implemented in the BIOGEOBEARS package, along with other models accounting for founder speciation events that would have been particularly interesting to evaluate (Matzke, 2014). However, the size of our dataset and the number of areas studied did not allow the use of BIOGEOBEARS. We instead had to use the newest C++ version of LAGRANGE that does not account for founder events.

The DEC approach relies on a time-calibrated tree, the current spatial distribution of species, a geographical model (i.e. the number of geographical areas considered), an adjacency matrix (i.e. a matrix setting the hypothesized connectivity among areas), and a stratified model (i.e. a set of matrices of dispersal rates, each corresponding to a time slice). The spatial distribution of extant Carnivora species was taken from the literature (Holden & Musser, 2005; Jones *et al.*, 2009) and the IUCN Red List (http://www.iucnredlist.org/, accessed September 2013). We used the geographical model of Condamine *et al.* (2012). This model comprises 11 areas delineated using palaeogeographical criteria (e.g. Blakey, 2008) and taking into account the updated Wallacean zoogeographical regions (Holt *et al.*, 2013): West Palaearctic (temperate), East Palaearctic (temperate), Africa (mostly tropical), Madagascar (tropical), India (mostly tropical), Southeast Asia (tropical), Australia (tropical and temperate), West Nearctic (temperate), East Nearctic (temperate), Central America (tropical) and South America (tropical and temperate). Although there are not any Carnivora species in Australia, the model can infer the presence of ancient lineages in geographical regions where extant species are absent (see, e.g., Kambysellis *et al.*, 1995; Lapoint *et al.*, 2013).

Without imposing any constraint, there would be $2^{11} - 1 = 2047$ possible geographical ranges (subsets of areas occupied by the species, each area can be either occupied or not). However, many of these ranges are unrealistic, such as a range that would comprise the Western Nearctic and Madagascar. The adjacency matrix allows us to take into account that some of the possible ranges are biologically implausible based on their past and present spatial configurations and can thus be excluded from consideration, which considerably reduces computation time. For each couple of areas, we set a value of 1 if these areas are currently adjacent or have been adjacent in the past, and 0 otherwise. This defines sets of areas that are or have been connected and thus are possible geographical ranges. In our case, the adjacency matrix defined 91 possible geographical ranges.

We built a stratified model with time slices that add temporal constraints on dispersal rates between areas according to palaeogeographical reconstructions (Blakey, 2008). We considered six time slices of 10 Myr each (except the last one that goes

up to the Cretaceous) covering the 65 Myr of Carnivora evolution. For each time slice, we constructed a matrix of dispersal rates among areas (taking values between 0 and 0.5) according to their geographical position and geographical barriers (e.g. sea straits, mountain chains): dispersal rates were lower for areas that were separated by large distances or by significant geographical barriers. We applied the rules usually used in biogeographical studies (e.g. Buerki *et al.*, 2011; Couvreur *et al.*, 2011; Condamine *et al.*, 2012) to set the dispersal rate between areas: the dispersal rate between adjacent areas was fixed to 0.5 (absence of any barrier) and the dispersal rate was penalized to 0.25 when a geographical barrier had to be crossed (e.g. between Africa and Madagascar). For geographical areas separated by only one area, the dispersal rate was calculated as the product of two dispersal rates: for example in the Miocene, dispersing from the Eastern Palaearctic to Australia implies a passage through Southeast Asia; the corresponding dispersal rate was set to 0.125 as a result of the product of the dispersal rate between the Eastern Palaearctic and Southeast Asia (0.5, which does not imply the crossing of a barrier) and the dispersal rate between the Southeast Asia and Australia (0.25, which implies crossing the sea strait separating Australia from Southeast Asia at that time). Finally, for geographical areas separated by two or more areas, the dispersal rate was set to 0.01 in order to account for long-distance dispersal (e.g. between the Western Palaearctic and Madagascar).

We defined two DEC models with increasing complexity: M1, comprising the geographical model, the adjacency matrix and no stratified model; and M2, comprising the geographical model, the adjacency matrix and the stratified model. We first computed the likelihood of the two models and selected the best model, using no constraint at the root. Given that these models have the same number of parameters (two parameters corresponding to mean rates of dispersal and extinction), a model was considered to be significantly better when it outperformed another model by two log-likelihood units (Ree & Smith, 2008). We then used the best model to reconstruct ancestral areas. We started by assigning one area at the root and estimated the likelihood associated with this area. We repeated this analysis for each area and ranked the associated likelihoods. If there was no single area that was significantly better supported than all the others, we performed new analyses with all combinations of two adjacent areas at the root. We repeated this process with increasingly many areas at the root until a significant area or combination of areas was found.

We counted expansions and extinction (range contraction) events directly on the DEC figure displaying the historical reconstruction. Central America, South America, Africa, Madagascar, Southeast Asia and India were considered as low-latitude regions and East/West Nearctic, East/West Palaearctic were considered as high-latitude regions. For example, an expansion event toward low-latitude regions was a gain of a low-latitude region in a lineage distributed only in high-latitude regions and a high-latitude extinction event was the loss of the high-latitude region in a lineage distributed in both high- and low-latitude regions. This procedure only accounts for events that happened

on lineages that survived to the present, and therefore largely underestimates the total number of events that actually occurred. However, it provides a good idea of the relative occurrence of expansion and extinction events in the low- versus high-latitude regions.

Palaeo-reconstruction of past latitudes and the fossil record

We downloaded a large dataset of 4341 fossil occurrences of 381 fossil genera of Carnivora from the Paleobiology Database (accessed in May 2015), and examined whether the pattern of colonization found with our phylogenetic reconstruction was consistent with past fossil diversity. We took the palaeogeographical coordinates of each fossil from the Paleobiology Database; these were reconstructed according to the age of the fossil, its present-day coordinates and the geological reconstruction of the position of each continent in the past (GPLATES; Wright *et al.*, 2013). Then, we used linear models to test whether palaeolatitudes of all fossil occurrences tend to vary through time. In order to test if the trend observed for all fossils was consistent across genera, we selected genera with at least four fossil occurrences and looked at the variation of palaeolatitudes through time for each genus independently.

RESULTS

Testing the diversification rate hypothesis

Distributional data confirmed that the diversity of carnivoran species followed a striking latitudinal gradient: 75 species were considered as tropical, 48 as temperate and 127 were distributed in both regions (Fig. 1). Results from the GeoSSE analyses suggested that Carnivora experienced slightly higher net diversification rates in temperate regions due to higher temperate speciation rates (Appendices S2 & S3), and that they dispersed more from temperate regions to the tropics than the other way around. These results found using Nyakatura's phylogeny were very similar to those found with a previous phylogeny (Fig. S3 from Rolland *et al.*, 2014).

Historical biogeography

Model M2 (with both the adjacency matrix and the stratified model) fitted the data better than the simpler model M1 with no stratification (log-likelihood = −826 for the best M2 model, and −850 for the best M1 model; Table 1, Appendix S4). In addition, the inclusion of a time-stratified model makes the biogeographical analyses more realistic by taking into account the tectonic history of Earth during the Cenozoic. We therefore present results from model M2 (Table 1). Model M1 provided a similar biogeographical scenario (Appendix S4).

The best DEC model supported an origin of Carnivora at high latitude in the Eastern Palaearctic. In general, an origin at low latitude (Africa, Australia, Madagascar, Central America, South America and Southeast Asia) was less likely than an origin
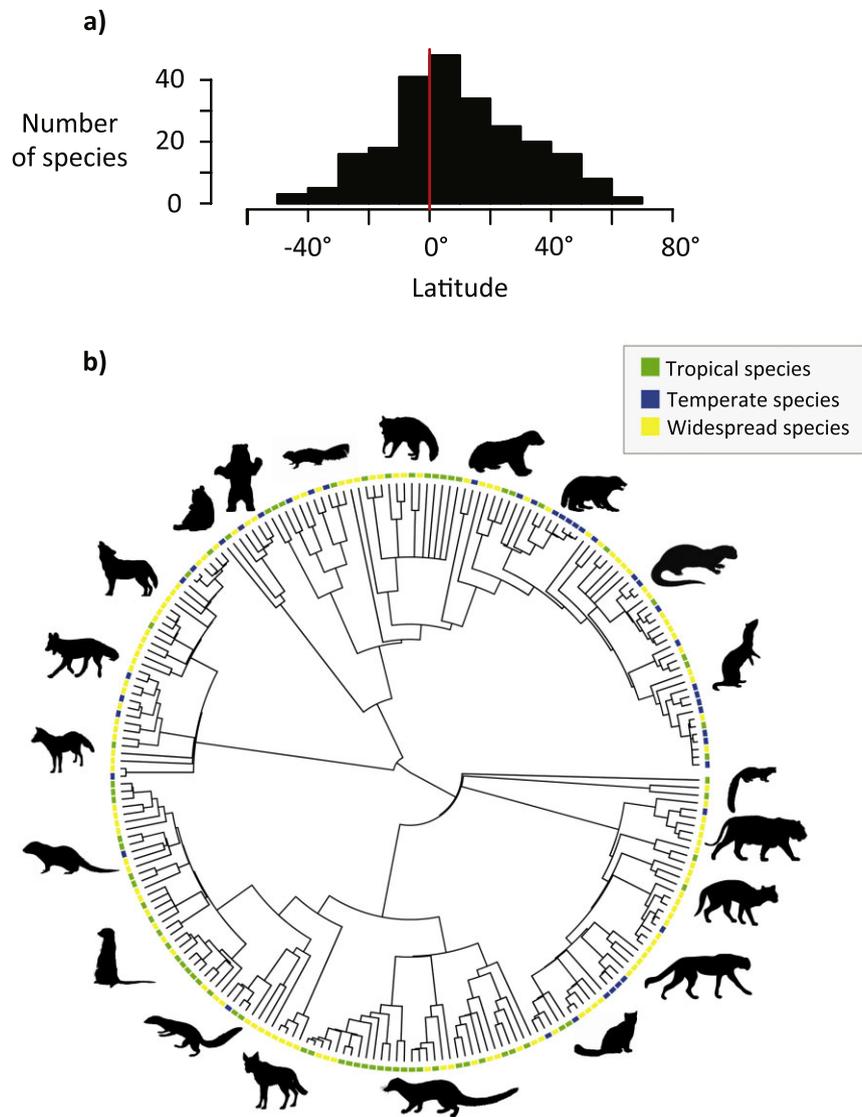
Figure 1 Latitudinal diversity gradient of Carnivora and the distribution of each species (tropical, temperate and widespread) mapped upon the phylogeny.

at high latitude (East and West Palaearctic, or East and West Nearctic; Table 1). With this model, we detected multiple dispersal events from the Eastern Palaearctic toward the south following three main routes: towards Africa, Southeast Asia (and India) and South America via the Bering Strait in North America and the Isthmus of Panama in Central America. The two suborders Feliformia and Caniformia show similar dispersal patterns, with frequent ancient southward dispersal events through these three routes, and some recent recolonizations of high-latitude regions (Figs 2 & 3). We found more range expansion events into low-latitude than high-latitude regions, as well as more range contractions in high- than in low-elevation regions (Fig. 4). We did not find any ancestral areas in Australia, suggesting that Carnivora never colonized Australia (except for recent human-mediated introductions not considered here, e.g. *Canis lupus dingo*).

Among the suborder Feliformia (Fig. 2), the majority of groups have moved southward: toward Africa for Nandinidae, Herpestidae (even if some species secondarily colonized India

and Southeast Asia), Viverridae (mostly *Genetta* + *Poiana*), Hyenidae and Felidae (mostly *Felis*). For example in the Felidae our reconstruction suggests that Africa has been colonized four times independently: for *Panthera*, for the group *Leptailurus* + *Caracal* + *Profelis*, for *Acinonyx* and for the genus *Felis*. Our results suggest that Eupleridae reached Madagascar only once from an African ancestor *c.* 20 Ma (Fig. 2). We also detected dispersal from East Palaearctic to Southeast Asia and India in *Prionodon*, Felidae, Viverridae, Hyaenidae and Herpestidae. Finally, one lineage of Felidae seemed to have crossed the Bering Strait *c.* 20 Ma and gave rise to two lineages that reached South America independently: the genera *Leopardus* and *Puma*. More recently, few species that are currently distributed in large areas secondarily colonized temperate regions from the tropics, such as, for example *Hyaena hyaena*, *Prionodon pardicolor*, *Prionailurus bengalensis* and *Paguma larvata*.

We estimated a similar dispersal pattern for the suborder Caniformia (Fig. 3): Africa has been colonized several times

Table 1 Comparison between the likelihoods and the dispersal and extinction rates for the models with different origins at the root. These models are all M2 models comprising the geographical model, the adjacency matrix and the stratified model. Likelihoods shown are –log-likelihood. When likelihoods were not significantly different, we chose the model with the best likelihood and the smallest number of areas at the root. Bolded rows correspond to the best fitting models with one, two, three or four areas at the root.

Area of origin	Dispersal rate	Extinction rate	Likelihood (–log-likelihood)
EP	**0.151**	**0.024**	**826.156**
IN	0.154	0.023	827.154
WN	0.153	0.025	827.697
WA	0.154	0.024	827.898
WP	0.154	0.025	827.947
AF	0.154	0.024	828.919
EN	0.155	0.026	829.336
MD	0.158	0.026	833.907
AU	0.159	0.022	836.588
SA	0.161	0.023	839.031
CA	0.165	0.029	866.519
EP_WN	**0.152**	**0.024**	**826.187**
EP_WA	0.152	0.024	826.558
WP_AF	0.153	0.024	826.646
WP_EP	0.152	0.025	826.675
WP_EN	0.154	0.025	827.534
WN_EN	0.154	0.026	828.224
WN_CA	0.153	0.025	829.012
AF_MD	0.155	0.025	830.565
EN_CA	0.155	0.026	830.724
SA_AU	0.159	0.022	836.804
SA_CA	0.157	0.024	837.245
WP_EN_AF	**0.153**	**0.024**	**825.835**
WP_EP_AF	0.152	0.024	825.842
EP_WN_WA	0.152	0.024	826.164
EP_WN_CA	0.151	0.023	826.376
WP_EP_WN	0.152	0.025	826.503
EP_WN_EN	0.152	0.025	826.552
WP_EP_EN	0.152	0.025	826.598
WP_EP_WA	0.152	0.024	826.648
WP_WN_EN	0.153	0.025	827.422
WP_AF_MD	0.154	0.025	827.566
WP_EN_CA	0.153	0.024	827.750
WN_EN_CA	0.153	0.025	828.755
WN_SA_CA	0.153	0.024	829.311
EN_SA_CA	0.155	0.025	831.122
SA_CA_AU	0.156	0.023	834.369
WP_EN_AF_CA	**0.152**	**0.023**	**825.014**
WP_EP_WN_AF	0.151	0.024	825.615
WP_WN_EN_AF	0.152	0.024	825.877
WP_EP_EN_AF	0.152	0.024	825.887
EP_WN_SA_CA	0.150	0.022	825.988
WP_EP_AF_WA	0.152	0.024	826.087
EP_WN_CA_WA	0.151	0.023	826.149
WP_EP_WN_WA	0.152	0.025	826.386
WP_EP_AF_MD	0.152	0.025	826.425
EP_WN_EN_CA	0.151	0.023	826.452
WP_EP_EN_CA	0.151	0.024	826.479
EP_WN_EN_WA	0.152	0.025	826.496
WP_EN_AF_MD	0.153	0.025	826.528
WP_EP_EN_WA	0.152	0.025	826.532
WP_EP_WN_CA	0.151	0.023	826.565
WP_EP_WN_EN	0.152	0.025	826.760
WP_WN_EN_CA	0.152	0.024	827.380
WP_EN_SA_CA	0.154	0.024	827.835
WN_EN_SA_CA	0.153	0.024	828.855
WN_SA_CA_AU	0.153	0.024	829.938
EN_SA_CA_AU	0.156	0.025	831.526

EP, Eastern Palaearctic; IN, India; WN, West Nearctic; WA, Wallacea; WP, Western Palaearctic; AF, Africa; EN, Eastern Nearctic; MD, Madagascar; AU, Australia; SA, South America; CA, Central America and Caribbean Islands.

independently in the history of Canidae and Mustelidae. Numerous dispersals are inferred from the East Palaearctic towards India or Southeast Asia in Canidae, Ursidae, Ailuridae and Mustelidae. The Bering Strait has also often been crossed in the history of Caniformia (at least 10 times). Our best model suggests that it has been crossed by the major lineages of Ursidae, Canidae and Musteloidea independently between 20 and 30 Ma. Some of the lineages stayed in the Nearctic, such as *Vulpes* (*Vulpes vulpes*, *Vulpes lagopus*, *Vulpes velox* and *Vulpes macrotis*), *Canis lupus*, *Urocyon littoralis*, *Ursus* (*Ursus arctos*, *Ursus maritimu*s and *Ursus americanus*), *Spilogale*, *Mephitis*, *Taxidea taxus*, *Procyon lotor*, *Lontra canadensis*, *Lynx* (*Lynx rufus* and *Lynx canadensis*), *Gulo gulo* and *Martes* (*Martes pennanti* and *Martes americana*), but most of them reached South America, via the Isthmus of Panama, in massive waves of independent colonizations that started 20 Ma (e.g. the Procyonidae) and continued until the last few million years, such as in the case of the three species of *Lontra* (*Lontra longicaudis*, *Lontra feline* and *Lontra provocax*) which arrived in South America between 2 and 3 Ma.

Palaeo-reconstruction of past latitudes and the fossil record

We found that the occurrences of fossil Carnivora were mostly restricted to high latitude in the first half of the history of the group (i.e. the Palaeogene, 66–23 Ma) and then progressively reached lower latitudes and the Southern Hemisphere (Fig. 5). Linear regression on all occurrences of fossil Carnivora showed that palaeolatitudes decreased significantly through time ($\beta = -0.722°$ Myr^{-1}, $P < 0.0001$; Fig. 5). This decrease was particularly strong between 20 Ma and the present day (Fig. 5). We fitted one linear regression for each genus with at least four occurrences (77 out of 381 genera; Appendix S5), and found that in 61% of them (47 genera) â was negative, indicating southward dispersal. The decrease in the mean latitude of Carnivora is thus probably due to several independent southward dispersals (Appendix S5).

DISCUSSION

Despite the considerable interest in the last decades in identifying why diversity varies spatially, no consensus has emerged on a single major hypothesis to explain the latitudinal diversity gradient across groups (Jablonski *et al.*, 2006; Weir & Schluter, 2007; Wiens *et al.*, 2009; Condamine *et al.*, 2012). Two recent studies have highlighted the importance of latitudinal difference in diversification rates in amphibians (Pyron & Wiens, 2013) and mammals (Rolland *et al.*, 2014). Here we show that in Carnivora, unlike in other mammalian orders, the latitudinal diversity gradient does not seem to be explained by the diversification rates hypothesis; rather, the high species richness of Carnivora in the tropics could be explained by successive waves of colonization southward from the Eastern Palaearctic, followed by range contractions in high-latitude regions.
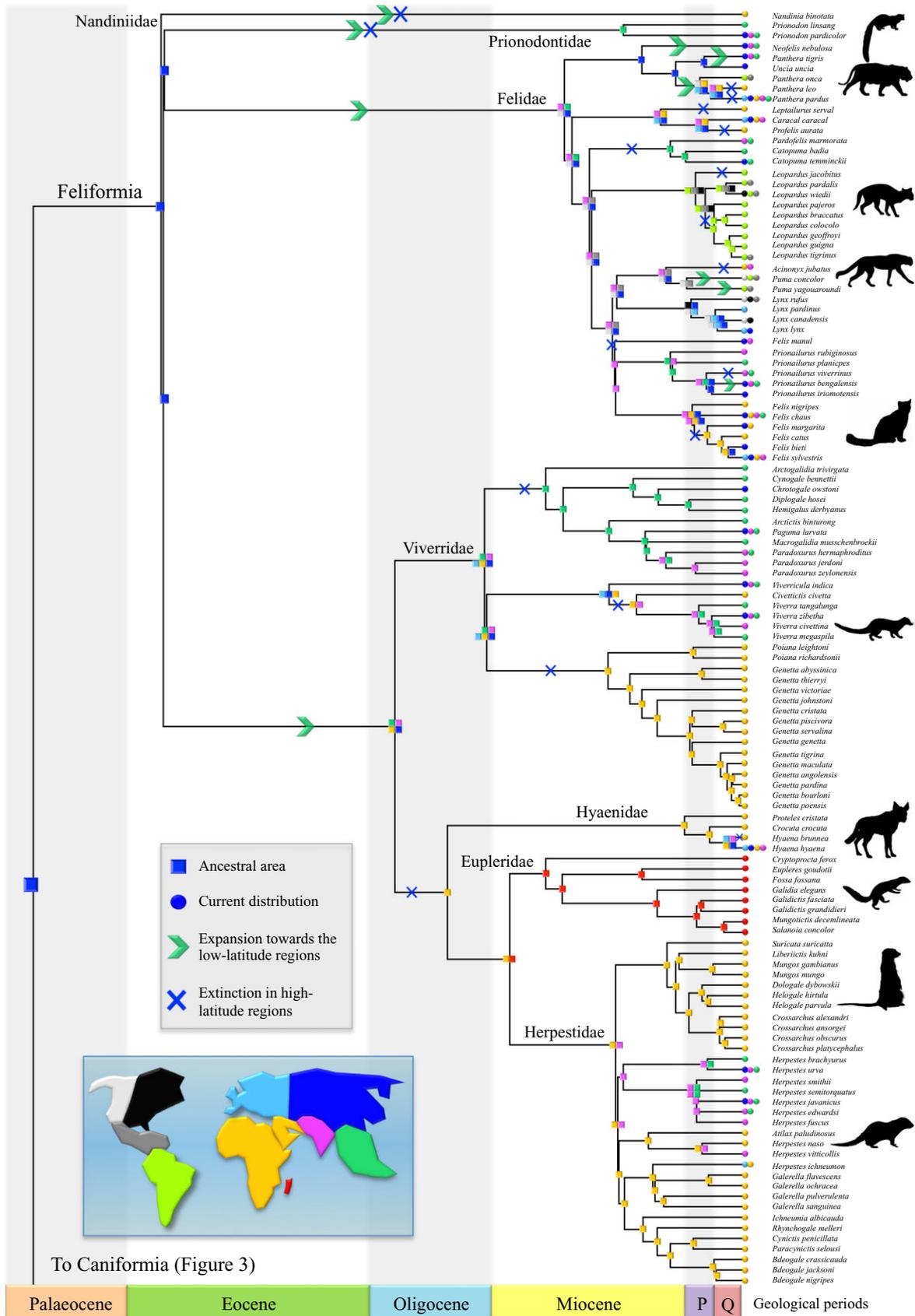
Figure 2 Historical reconstruction of the biogeography of Feliformia. Green arrows show major southward dispersal events (toward South America, Africa, Southeast Asia or India) and blue crosses are temperate range contractions.
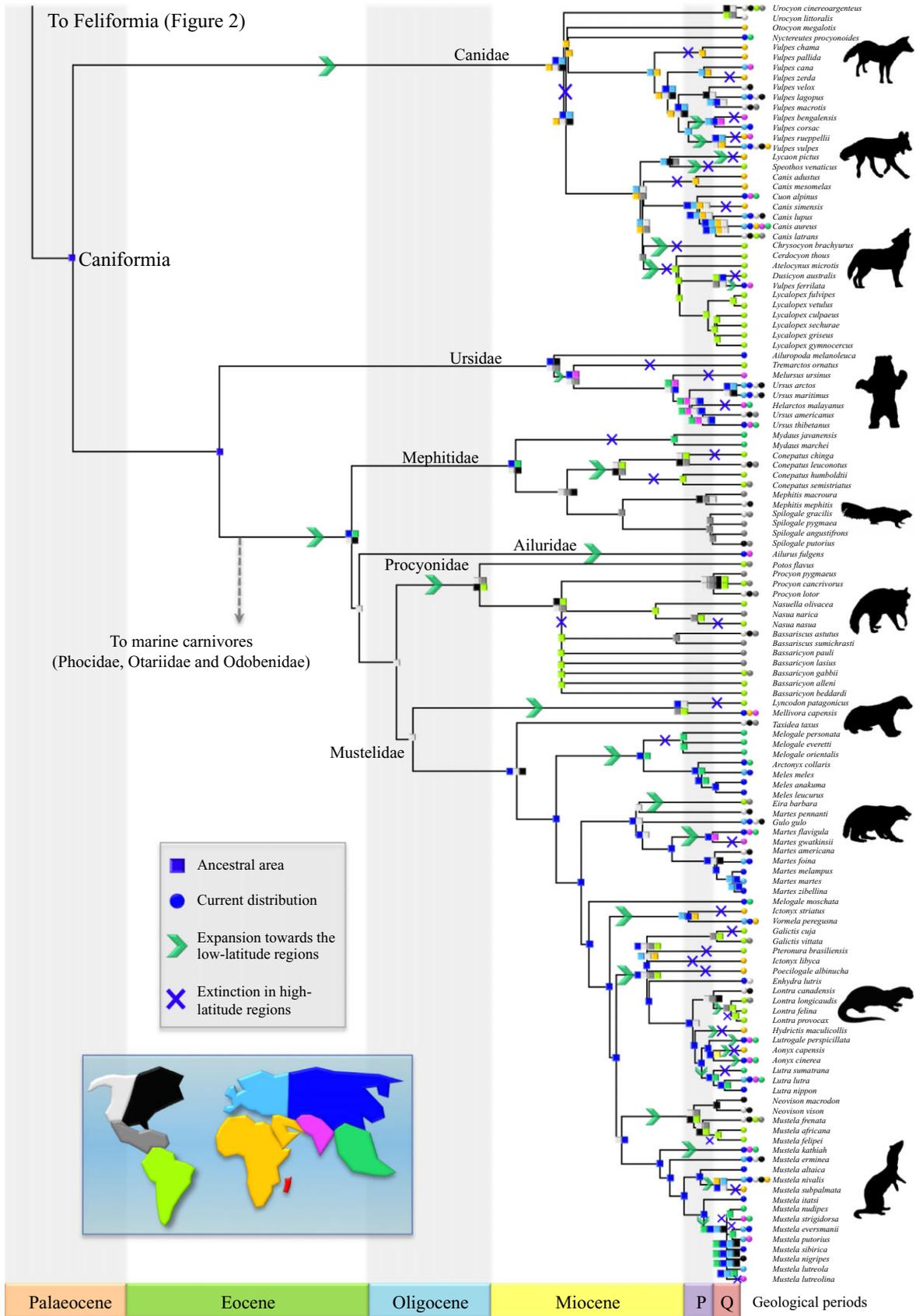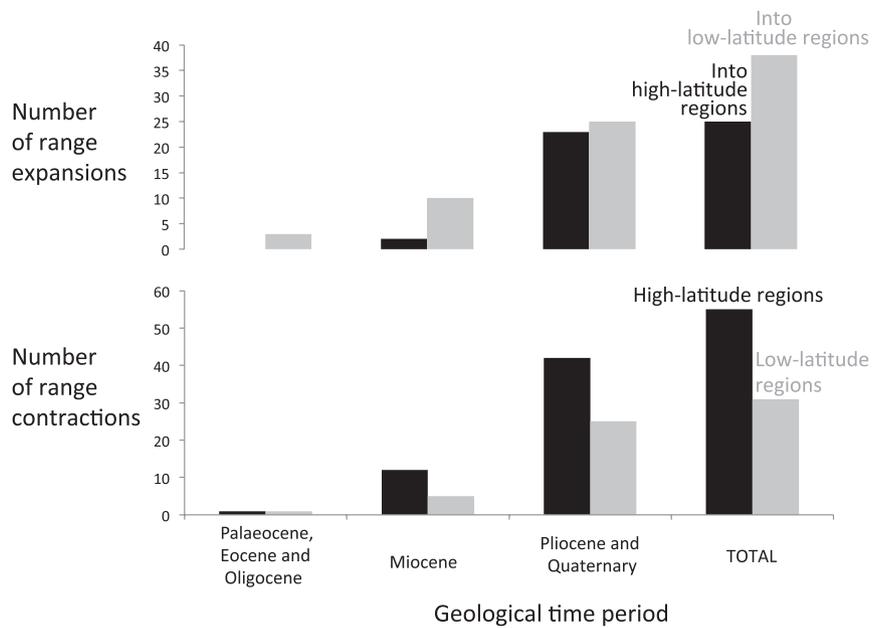
Figure 3 Historical reconstruction of the biogeography of Caniformia. Green arrows show major southward dispersal events (toward South America, Africa, Southeast Asia or India) and blue crosses are temperate range contractions.

Figure 4 Summary statistics of the number of range expansions and number of extinctions in high- and low-latitude regions obtained from our biogeographical reconstruction. Expansions and extinction events are counted directly in Figs 2 & 3, considering that Central America, South America, Africa, Madagascar, Southeast Asia and India were tropical and that East and West Nearctic, and East and West Palaearctic were temperate.
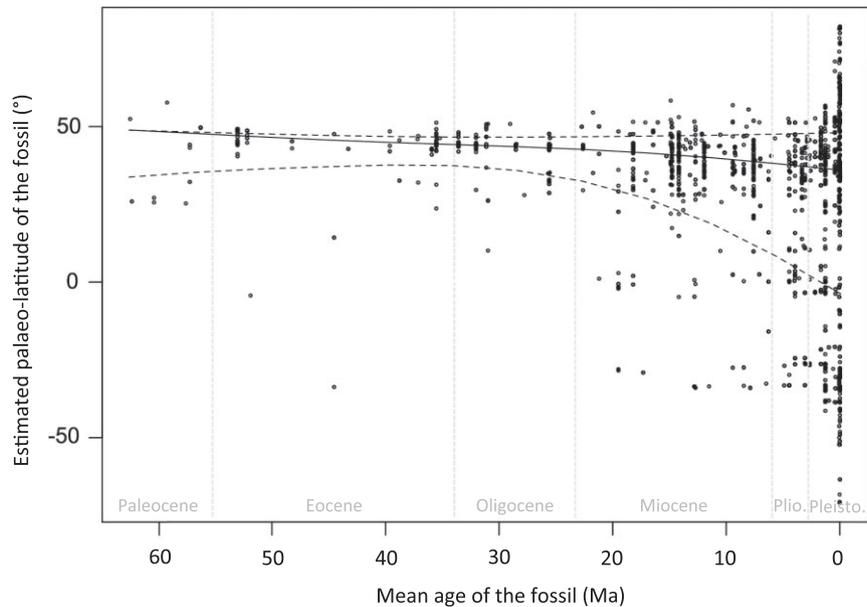

Figure 5 Palaeolatitudes of the 4341 fossils occurrences of 381 genera of Carnivora. Carnivora originations at high latitudes and palaeolatitudes tend to decrease through time. The solid line shows the median through time, and the dashed lines show the 90% and the 10% quantiles. Quantiles and median were first computed from time bins of 10 Myr and were then smoothed to obtain the curves shown here.

Comparing results from state-dependent diversification, ancestral area reconstruction models and the fossil record

Our independent analyses made with the phylogenetic data (using the DEC model) and with the fossil record are consistent in that they both suggest a high-latitude origin of Carnivora and a high dispersal rate from high to low latitudes. An uncertainty remains concerning the biome of origin (temperate or tropical): the latitudinal border of the tropical biome was much higher in the early Cenozoic than it is today, but it is difficult to know how much higher it was at any given time in the past because the cooling of the planet during the Cenozoic has been progressive (Zachos *et al.*, 2001). There is the possibility that the region was

boreotropical, composed of tropical and temperate floras during the Palaeogene (Wolfe, 1975). At the same time, the most recent palaeoclimatic reconstructions suggest that the Eastern Palaearctic was mostly temperate at 70 Ma around the time when carnivores originated (Chaboureau *et al.*, 2014). Hence results from the ancestral reconstruction analyses and the analyses of fossils corroborate the idea suggested by GeoSSE (here and in Rolland *et al.*, 2014) that high dispersal rates from temperate to tropical biomes – and not differences in diversification rates – explain the latitudinal diversity gradient in Carnivora.

To be fully consistent with our biogeographical analyses, and provide a wholly convincing explanation for the latitudinal diversity gradient, the GeoSSE analyses should also show higher extinction rates in temperate regions corresponding to range

contraction into the tropics (as shown in Fig. 4). Although we detected such a pattern for a model constraining dispersal (Fig. 2 in Rolland *et al.*, 2014), we no longer detected it with a more complex model accounting for differential dispersal (Fig. S3 in Rolland *et al.*, 2014). Extinction is notoriously hard to estimate from molecular phylogenies (Rabosky, 2010; see also a discussion of this issue in Morlon, 2014) and it is possible that we lack the power to detect differential extinction in the relatively small phylogeny of Carnivora (there is a high proportion of type II errors for phylogenies with fewer than 300 tips; FitzJohn, 2010; Davis *et al.*, 2013). Hence, we trust the ancestral reconstruction analyses detecting range expansions into low-latitude regions followed by range contraction in high-latitude regions. Interestingly, we found that these multiple range expansion into low latitudes and range contraction from high latitudes were also strongly consistent with the fossil record and the palaeolatitude reconstructions (Fig. 5; Hunt, 1996).

The 'into the tropics' hypothesis

We found that the low-latitude tropical regions may not act as a source of diversity and as the centre of origin of Carnivora. These results contradict the 'out of the tropics' hypothesis proposed by Jablonski *et al.* (2006) in bivalves and supported in several other groups (see the meta-analysis of Jansson *et al.*, 2013), such as mammals (Rolland *et al.*, 2014). We found few dispersal events from low-latitude to high-latitude regions (at least in the early history of the group); this supports part of the 'tropical niche conservatism' hypothesis (Wiens & Donoghue, 2004), by which adaptation to temperate conditions might be difficult. However, in contrary to the tropical niche conservatism hypothesis, we do not find evidence for a tropical origin of diversity. Our results instead provide support for a hypothesis that is only rarely considered in the literature (but see Condamine *et al.*, 2012), which we call the 'into the tropics' hypothesis by analogy with Jablonski *et al.*'s formulation. This hypothesis stipulates that a latitudinal diversity gradient, with more species at low latitudes, can result from frequent dispersal from high- to low-latitude regions. Such frequent dispersal events, associated with extirpation from high-latitude regions, can over-compensate for a high-latitude origin and similar diversification rates between low- and high-latitude regions (or slightly higher in high-latitude regions). We indeed found a high-latitude origin of Carnivora and slightly higher speciation rates in temperate regions. Such temperate speciation rates (if we can trust them, given the high type I error rate of SSE models; Rabosky & Goldberg) may be linked to climatic oscillations and geological changes in the Northern Hemisphere (Dynesius & Jansson, 2000), which may have promoted diversification by vicariance, either by forcing species to move south or by restricting them to refugia separated by unsuitable habitats (Weir & Schluter, 2007). Higher dispersal from temperate regions to the tropics may also be promoted by climatic oscillations (Weir & Schluter, 2007): during glacial periods, ice caps and an unfavourable climate may have obliged species to escape temperate regions.

A temperate origin and southward colonizations

Our results suggest that the order Carnivora originated in the Eastern Palaearctic just after the Cretaceous–Palaeogene boundary (66 Ma). The literature describes the Palaearctic region as a boreotropical climate during the Palaeocene and Eocene (Sanmartín *et al.*, 2001; Condamine *et al.*, 2012). It is thus difficult to invalidate the 'time-for-speciation' hypothesis (Stephens & Wiens, 2003; Wiens & Donoghue, 2004), which stipulates that Carnivora are richer in the tropical biome because they originated there and therefore had more time to diversify in the tropics. Southward dispersals may thus have been triggered by the contraction of the tropical biome to low latitudes. Nonetheless, both the origin of Carnivora and the patterns of colonization are consistent with the fossil record (Fig. 5; Hunt, 1996) and with phylogenetic studies obtained in smaller clades: Felidae (Johnson *et al.*, 2006) and Mustelidae (Koepfli *et al.*, 2008). Carnivora have followed three main pathways to colonize low latitudes: (1) Africa when the Tethys Sea closed around 30–20 Ma (Rosenbaum *et al.*, 2002); (2) Southeast Asia/India since the collision of the Indian Plate about 40 Ma (Bouilhol *et al.*, 2013), and (3) South America during intermittent connections between the Nearctic and Neotropics via the GAARlandia land bridge (35–30 Ma; Ali, 2012) or the Isthmus of Panama (15–3.5 Ma; Iturralde-Vinent, 2006, Montes *et al.*, 2015). Dispersal events via the Bering Strait, a climatically regulated pathway for biological dispersal (Sanmartín *et al.*, 2001), were an important driver of geographical diversification because we found numerous ancestral areas comprising the East Palaearctic + Western Nearctic (see also Condamine *et al.*, 2012). These dispersal routes are also highly consistent with the fossil record (Hunt, 1996). For example, we found, in agreement with the literature, that Procyonidae radiated extensively in America, that *Genetta* + *Poiana* (Viverridae) radiated in Africa and that Eupleridae colonized Madagascar only once (20 Ma; Yoder *et al.*, 2003). We did not account for founder speciation events in our biogeographical reconstruction (Matzke, 2014) because of computational limitations. Further studies applying these models to Carnivora will be helpful for explaining rare long-distance dispersals, such as the colonization of Madagascar by Eupleridae.

Integrating information from the fossil record

Although the Carnivora fossil record is one of the richest among vertebrates, it also has weaknesses. In particular, it has been shown that fossilization can be poor in tropical areas (Hunt, 1996) and this may bias the reconstruction of the palaeolatitude of the origination of Carnivora toward higher latitudes. However, we have two main reasons to think that this bias does not substantially affect our results. First, we found very few Carnivora fossils (only one occurrence) in the temperate regions of the Southern Hemisphere during the first 40 Myr of carnivoran history. If tropical areas were rich in this period, it is very unlikely that no species dispersed toward the Southern Hemisphere. The second reason is that the palaeolatitudes

reconstructed from the fossil record are strikingly consistent with our ancestral area reconstruction (and our GeoSSE analysis).

Previous analyses of the carnivoran fossil record have shown that Carnivora had a sister group, the Creodonta, which is now extinct. This group was a rich clade of about 50 genera occupying North America, Eurasia and Africa from 55 to 11 Ma (Gunnell, 1998). Occupying the same geographical area at high latitudes, the creodonts probably influenced the distributional evolution of Carnivora, as the two groups were probably in competition for resources at the same trophic level. The inferred southward dispersals within Carnivora may have been favoured by the decline of creodonts in the Late Cenozoic.

CONCLUSION

The high species richness of Carnivora in the tropics is not explained by high net diversification rates in the tropics, unlike in other mammalian orders. Rather, this group follows a 'into the tropics' model with a boreotropical origin and multiple range expansion/contraction events toward low-latitude regions. This model should be considered more systematically in studies testing alternative explanations for the latitudinal diversity gradient; it is a plausible scenario that receives empirical support from fossil and phylogenetic data.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Expanded methods and results.
Appendix S2 Model selection of the 16 GeoSSE models.
Appendix S3 Posterior distributions of diversification and dispersal parameters of the best-fitting GeoSSE model obtained from the Markov chain Monte Carlo analyses.

Appendix S4 Comparison between the likelihoods, the dispersal and the extinction rates for dispersal–extinction–cladogenesis models with different origins at the root.
Appendix S5 Trajectories of the palaeo-latitudes through time for the 77 fossil genera of Carnivora for which we found at least four occurrences.

BIOSKETCH

Jonathan Rolland is now a post-doctoral researcher in the University of Lausanne, Switzerland. He took his PhD in Paris (France) at the Ecole Polytechnique and at the Museum of Natural History, supervised by Hélène Morlon and Frédéric Jiguet. His interests cover a wide range of areas in ecology and evolution, including population genetics, niche modelling, phylogenetics, biogeography, macroevolution and conservation. His PhD research was focused on explaining the emergence of diversity patterns such as the latitudinal diversity gradient.

Author contributions: J.R., F.L.C. and H.M. conceived the ideas. J.R., F.L.C. and C.R.B. collected and analysed the data. J.R. wrote the first draft. F.L.C., H.M. and F.J. revised and corrected the manuscript.

Editor: Gary Mittelbach