

# 1 **Dispersal ability predicts evolutionary success among mammalian carnivores**

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## 12 **Abstract**

13 Understanding why some clades contain more species than others is a major challenge in evolutionary  
14 biology, and variation in dispersal ability and its connection to diversification rate may be part of the  
15 explanation. Several studies have suggested a negative relationship between dispersal capacity and  
16 diversification rate among living mammals. However, this pattern may differ when also considering  
17 extinct species, given known extinction biases. The colonization of new areas by various lineages may  
18 be associated with both diversity increases in those colonising lineages and declines in the lineages  
19 already present. Past diversity declines are, however, effectively impossible to infer based on  
20 phylogenies of extant taxa, and the underlying process may, therefore, be difficult to determine. Here  
21 we produce a novel species-level phylogeny of all known extant and extinct species of the order  
22 Carnivora and related extinct groups (1,723 species in total) to show that there is instead a positive  
23 relationship between dispersal rate and diversification rate when all extinct species are included.  
24 Species that disperse between continents leave more descendant species than non-dispersers, and  
25 dispersing species belong to lineages that at the time of dispersal were diversifying faster than the  
26 average non-disperser. Our study showcases the importance of combining fossils and phylogenies to  
27 better understand evolutionary and biogeographic patterns.

28

# 29 **1 Introduction**

30 Clades from across the tree of life vary widely in both diversification rate and in the dispersal capacity  
 31 of the species they comprise, but the extent to which the variation in the two is coupled remains  
 32 unclear. Among extant vertebrates, a limited number of clades show substantially higher  
 33 diversification rates than others (1). The fossil record also shows that vertebrate classes vary widely in  
 34 how many families of equal ages they contain (2). The variation in dispersal capacity among extant  
 35 vertebrates is equally evident. Some species have colonised nearly the entire world. At one extreme,  
 36 the range of the wild horse (*Equus ferus*) spanned five continents including northern Africa, the whole  
 37 of Eurasia and most of the Americas until the end of the last ice age (3). At the other extreme, we find  
 38 the lemur genus *Eulemur* in Madagascar, where even minor rivers have restricted the migration of  
 39 individuals sufficiently to result in individual species that are endemic to small areas between  
 40 neighbouring rivers (4). Interestingly, the clades encompassing these two examples have identical  
 41 numbers of species (12; *sensu* [3]), at least when the extinct Late Pleistocene species of horses are  
 42 included (Equidae: *Equus*, *Haringtonhippus*, and *Hippidion*). These two clades also have similar ages  
 43 (the most recent common ancestor [MRCA] of the lemur genus is ~4.5 million years [My] old  
 44 following (4); the MRCA of the horses is ~6 My following [5]). Taken together, there is thus no  
 45 universal relationship between dispersal rate and diversification rate.

46           There are, however, strong arguments for why a relationship between dispersal rate and  
 47 diversification rate should be expected. A negative correlation between the two rates may be generated  
 48 under purely neutral models (see e.g. [6]). This is because the *in situ* per area speciation rates would  
 49 normally increase with decreasing dispersal rates, since populations of poorly dispersing organisms  
 50 can more readily become isolated from each other and eventually speciate. While a negative  
 51 relationship is most likely based on neutral models, arguments could also be made for a positive  
 52 relationship. Increased dispersal rate could potentially increase diversification rate by increasing the  
 53 total area occupied by the clade, but empirical support for such an effect is limited (7).

54           While neutral models are thus likely to predict a negative relationship, a positive  
 55 relationship between diversification and dispersal rates may be the expected outcome of non-neutral

models based on interspecific competition (hereafter non-neutral models). A common pattern is a wax-and-wane model with increases followed by decreases in diversity within each clade (e.g. 8, 9). If this is driven by competition, it should produce increased diversity for species with higher dispersal rates, both at the time of diversity increase and the time of diversity decline. During the period of increased diversity, species with a higher dispersal rate would be faster at colonizing all the areas formerly occupied by the species of a clade that they are outcompeting. During their global decline, species with a higher dispersal ability would be able to survive in peripheral regions by escaping direct contact with their competitors.

Although the expectations for non-neutral models have not been explicitly tested, there is anecdotal support based on distribution data, at least when fossils are included. The clearest examples come from the isolated archipelago of New Zealand, where both the Tuatara (*Sphenodon* spp.) and the only known non-flying mammal native to those islands (an unnamed Miocene species often referred to as the Saint Bathans mammal) represent the last remnants of formerly far more diverse and widespread clades (1, 10). There is also evidence of large geographic ranges for some rapidly diversifying lineages, presumably in their expanding phase, such as the Pacific flying foxes (*Pteropus* spp.) (11), but the latter pattern could be generated under both a neutral and a non-neutral model. The expectations from these non-neutral models are also seen in macro-evolutionary analyses of the fossil record. Among mammalian carnivores, there is evidence that the decline in some older clades may be causally related, through increased competition, to the net diversification of younger clades (12, 13).

To reliably tease apart the different mechanisms operating under the neutral and non-neutral models, we may need data on both the diversification rate at the time of dispersal and on the number of descendants each species leaves after dispersal. If diversification rate is increased through increased colonization rate, good dispersers would leave more descendant species than poor dispersers, but they would be unlikely to have a high diversification rate at the time of dispersal in their source area, as discussed above. On the other hand, if non-neutral models prevail, better competitors would both be diversifying faster in their source area and leaving a larger number of

descendant species after successful colonization. The required information to test these predictions has, to the best of our knowledge, not yet been assembled.

With few but increasing exceptions (e.g 13, 14), macro-evolutionary studies to date have been based on phylogenies comprised solely of extant species, where the amount of information often makes it impossible to determine if clades are in diversity decline, or show positive yet density-dependent diversification (15). It has even been suggested that estimation of extinction rates relying solely on extant taxa may not be possible (16, 17). Such problems may be avoided for analyses relying solely on fossil data (18). On the other hand, the exclusion of a phylogenetic tree in such analyses usually only allows for comparison of the diversification rates within pre-defined taxonomic entities like families (see e.g. (13)), unlike tree-based analyses where comparisons can be made between any named or unnamed clades. A combined approach based on phylogenetic trees but also incorporating all suitable fossils may, therefore, be optimal for inferring macro-evolutionary patterns (14, 19, 20).

Here we test the relationship between diversification and transcontinental dispersal rates in mammals by combining the advantages of tree-based and fossil-based methods. We build and analyse a complete species-level phylogeny of all extant and extinct species of mammalian carnivores and related extinct groups (Carnivoramorphia, Hyaenodonta, and Oxyaenidae). Our results provide unequivocal evidence that species with high dispersal capacity both had a higher diversification rate at the time of dispersal and left more descendant species than the species that did not disperse between continents. These results suggest that the underlying process is best explained by a non-neutral, competition-driven model.

## **2 Results**

### **2.1 Diversity accumulation**

We found a nearly continuous increase in diversity across the entire carnivore phylogeny, both globally and within continents, for both phylogenetic and taxonomic diversity (Fig. 1). There were only three main exceptions: 1) Diversity in North America initially peaked at the early Eocene climatic optimum and then decreased in the interval 50 to 45 million years ago (Ma). Given that the majority of species at that time were confined to this continent, a similar decrease was also seen in global

diversity. 2) Diversity in both North America and Eurasia decreased over the last ~10 My. 3) There was a decline in phylogenetic (but not species) diversity in Eurasia between approximately 40 to 35 Ma. Similar results were obtained independently of the length of the time bins being analysed and showed only limited variation across the 100 trees (Fig. 2). These results were based on the assumption of complete sampling. However, the increase in diversity through time could be partially caused by an increase in sampling intensity towards the present. We showed through simulations that this is very unlikely. Our simulations showed very limited effects of incomplete sampling on the observed patterns when using empirically derived sampling intensities (Figure S1).

## 2.2 Higher evolutionary success of dispersers

We estimated the evolutionary success of dispersers using two novel metrics, which we refer to as *pre-dispersal success* and *post-dispersal success* (Fig. 3). *Pre-dispersal success* measures the diversification rate of lineages at the time of their dispersal, whereas *post-dispersal success* measures how many species the dispersing lineages diversify into.

### 2.2.1 Pre-dispersal success

Our analyses of *pre-dispersal success* suggest that the dispersing species belong to clades that, at the time of dispersal, were diversifying faster than non-dispersers (Tables 1, S1-S2). This pattern was observed irrespective of whether comparisons were to all species alive in the time interval, or only to species occurring on the source continents in the time interval (which we refer to as *global* and *continental pre-dispersal success*). We estimated dispersal within time bins rather than in continuous time, but the results were independent of the length of these bins. The best model for *continental pre-dispersal success* showed a difference in success between dispersers and non-dispersers depending on the target continent. In particular, the model showed a substantially smaller difference between dispersers and non-dispersers for species colonizing South America. The best model for *global pre-dispersal success* showed temporal variation, where the difference in success between dispersing and remaining lineages was smaller for older dispersal events. In both cases, however, both models had

lower AIC than the model without any spatial or temporal variation. Thus, the two analyses only disagreed on whether spatial or temporal variation was most important.

Our analyses assumed complete sampling of all extinct species but we tested the consequences of this assumption through simulations. For this, we modelled scenarios of no difference in diversification patterns between dispersers and non-dispersers and assessed if spatial patterns in sampling would create a false signal with such a difference. These simulations showed that the patterns of *pre-dispersal success* were not caused by incomplete sampling (Table S3-S4). The simulations of *global pre-dispersal success* found no significant difference in success between dispersers and non-dispersers and found no support for any spatial or temporal variation in the difference between dispersers and non-dispersers. The simulations of *continental pre-dispersal success* also found no significant difference in success between dispersers and non-dispersers. They did, however, recover weak support based on AIC for models with temporal, but not spatial, variation in the difference between dispersers and non-dispersers. Even then, the estimated effect size for temporal variation was not significantly different from zero. If sampling effort did have an effect on spatial or temporal variation in our results, the effect size must have been minimal.

### 3.2.2 Post-dispersal success

Our results clearly demonstrate that dispersing lineages leave more descendant lineages than lineages that remain within the source continents (Table 2). This applies to both *continental* and *global post-dispersal success* (i.e. comparisons to all other species on the target continent or all species alive at the time of dispersal). This pattern – that dispersers leave more descendant lineages – remained constant irrespective of the length of the analysed time bin and how long after the dispersal the number of descendant species was counted (Tables S5-S6). The model with spatial variation was, however, only supported for *continental* (but not *global*) *post-dispersal success* and similar, although weaker, support for spatial variation was also recovered when we simulated incomplete sampling (Table S7). We, therefore, focus our discussion solely on the strong evidence for higher *post-dispersal success* rather than on any more detailed spatial or temporal patterns regarding the magnitude of this success.

## 3 Discussion

Our results unequivocally show a positive correlation between diversification rate and dispersal in carnivores. The analyses are based on the first species-level phylogeny of carnivores that includes all suitable fossils and all extant species. These results contradict an expected neutral pattern of a trade-off between diversification rate and dispersal, as has been suggested based on analyses of contemporary mammals (6).

### 3.1 Diversity accumulation

The occasional periods of diversity decline detected by our analyses lend biological credence to our results, since a monotonous increase in diversity could point towards a pattern driven by insufficient fossil information. All three declines detected clearly match previous knowledge. The first two declines were likely climatically driven. If carnivores throughout their history have had lower diversity in higher latitudes, similar to what we see today (21), we should expect to see diversity declines during times of global temperature decline, particularly in North America and Eurasia, which have the highest proportions of non-tropical areas. In this regard, the first early decline in North America coincides with a period of Eocene cooling (22) and is temporally similar to a time period recently found to have a low overall mammalian diversity in North America (23). Secondly, the declines in North America and Eurasia during the last 10 My may be explained by the overall climatic cooling during this time period (24).

In contrast, the third decline in phylogenetic diversity in Eurasia may not have been climatically driven. Instead, it probably reflects the so-called ‘Grande Coupure’, where the formerly isolated European fauna was replaced by an immigrant Asian fauna (e.g. 25). The cause of the Grande Coupure is not entirely known (25) but if it represents biotic replacement driven by competition, which is one of the hypotheses (25), it may indicate that such processes are important for carnivores in general.

### 3.2 Neutral or non-neutral models

Our results for *pre-dispersal success* and *post-dispersal success* clearly suggest that dispersal rate and diversification rate are linked in carnivores. As previously noted, the pattern for *post-dispersal success* could be the result of either neutral or non-neutral models or both, but the higher *pre-dispersal success* among good dispersers is only expected under the non-neutral models.

Support for a non-neutral model is further evident in the temporal variation in *pre-dispersal success*. We find an increasing effect for recent dispersals, where the number of free niches would be expected to be lower. This matches the expectations of this model – the non-neutral model would only generate a relationship between *pre-dispersal success* for dispersers and non-dispersers if dispersal to other continents required the displacement of lineages already there. There should be smaller differences if there are free niches open to any coloniser. This non-neutral model, therefore, contrasts with the frequently found priority effects in community ecology where the first coloniser is nearly always more successful (26).

The spatial patterns also support non-neutral models (Table 1). We find elevated *pre-dispersal success* for dispersers to North America and a near-random pattern for dispersers to South America, which matches our expectations. Under non-neutral models, we only expect elevated *pre-dispersal success* for dispersers if these are invading already occupied niches. The South American continent lacked placental carnivores until the mid-Miocene (27), and all invading carnivores would have initially encountered empty ecological niches. The pattern of elevated *pre-dispersal success* in North America is expected because our analyses suggest that carnivores originated in North America. Our results also show that the clade has consistently been highly diverse in that continent (Fig. 1). This North American origin is clear from Oxyaenidae, which is one of the three earliest diverging clades we analyze (28). The origin of the two other clades (Carnivoramorpha and Hyaenodonta) has previously been considered to be Eurasian or African, but even studies suggesting a non-North American origin for these clades have suggested extremely rapid dispersal to, and substantial diversification within, North America (29, 30).

Our results partially contradict earlier work which suggested that dispersal from North America to Eurasia – but not in the opposite direction – was associated with high diversification rate (31). Our results suggest the opposite and we found both higher increases in both *pre-dispersal* and



*post-dispersal success* for dispersers to North America compared to dispersers to the other continents (Tables 1–2). The reason for this difference may partly be a function of the non-phylogenetic approach of Pires et al (31), meaning that the different outcomes of multiple dispersals within the same family could not be distinguished.

As a minor point of uncertainty, we note that we treat the carnivore niche in South America as unoccupied, although it was occupied prior to the arrival of the placental carnivores by the Sparassodonta (Metatheria; sister group to marsupials). It is still unknown if the Sparassodonta went extinct independently of the arrival of placental carnivores, or if they were driven to extinction by competitive replacement (32). Non-placental lineages seem, however, to be inherently inferior competitors to placental carnivores, likely due to effects related to their lack of deciduous teeth (33, 34, 35). It, therefore, seems plausible that if the Sparassodonta were still extant when the carnivores arrived then any member of the group that arrived there may have been able to outcompete them.

### 3.3 Implications

Our results suggest a model of consistent competitive replacement among carnivore clades, although the generality of the observed pattern remains unclear. The methodology we employed was possible because carnivores have a well-understood fossil history, which is why the effects of incomplete sampling were deemed minor (Tables S3–S4, S7; Fig. S1). Furthermore, carnivores are a particularly useful group to study for this purpose because there is strong phylogenetic conservatism in their niche, with few other taxa competing with them. They are thus nearly a monophyletic ecological guild, although there are exceptions to this; some species within the group, such as the giant and red pandas, for instance, are predominantly herbivorous (3). Until the Eocene, carnivores shared the carnivorous niche with other mammalian species of uncertain placement, such as Arctocyoniidae or Cimolestidae (36), but even then, carnivores plausibly comprised the majority of the guild (12). Arguably, the only other large monophyletic mammalian group that behaves like an ecological guild is bats, but they are noteworthy for having a particularly scarce fossil record among mammals (37). It may therefore not be possible at present to directly replicate our analyses using other clades and thereby directly test the generality of the patterns reported here.

Despite the difficulties in applying our methodology to other clades, we find it unlikely that the patterns we report here would be taxon-specific. Taxon specificity could have explained why our results appear to run counter to some studies showing lower diversification rates for species with higher dispersal rates (6, 7). We think, however, that the apparent differences are instead a consequence of the taxonomic scale of the analyses and the inclusion or exclusion of fossil taxa. A lower diversification rate in highly dispersing lineages has been recovered in analyses at the subfamily or family level, whereas our estimates here are conducted at the species level. Direct competition may be strongest between the most closely related species in the case of mammals (38), which is also what would be expected for any traits with phylogenetic conservatism. This would explain the apparent conflict between this and earlier analyses of mammals. Earlier analyses at the subfamily level have suggested a negative relationship between dispersal and diversification rate in mammals (6), whereas in a species-level analysis we here recover a positive relationship between the two.

We are not implying that competition is not frequent between distantly related taxa, as is increasingly being acknowledged (39). However, competition may be expected to be linked to physiological or morphological traits, which are generally more similar for closely related species. There are many examples of convergent evolution within mammals (e.g. 40, 41), but even so, recently diverged species will be more similar than a random pair of species under most evolutionary models. They must, therefore, be expected to rely more on the same resources and the same environmental conditions than random members of a larger clade.

If the pattern we recover is driven by non-neutral biotic interactions, it may only be observable because we included fossil species in our analyses. When species are driven to extinction by other species it may be on too fast a time scale for us to see it clearly based only on extant species in their native ranges. The only clear contemporary evidence for biologically caused extinctions or declines comes from the invasion biology literature (e.g. 42). Competition-driven extinctions could leave signals on the phylogenies of the extant species but, as we noted in the introduction, such declines may be extremely difficult to detect based on phylogenies of extant species only (15, 16, 17). Even in the few situations where declines can be detected, methods solely relying on contemporary species can logically only give a signal if the declining lineages still have at least one extant species.

Some of the clearest cases of clade competition, such as the bone-crushing dogs (Borophaginae) being driven to extinction by related and extant modern dogs (Caninae) (13), are thus impossible to infer without fossils.

In summary, our analysis of a novel species-level phylogeny of all extant and extinct carnivores shows that: 1) lineages that disperse between continents are generally those that diversify more quickly; and 2) lineages that colonise new continents leave more descendant species than lineages already present there. These results are only likely to have emerged because we combined fossil and phylogenetic information, highlighting the need to incorporate both sources of information whenever possible.

## **4 Methods**

### **4.1 Method summary**

We analysed all extant and extinct species of mammalian carnivores and related extinct groups (Carnivoramorphia, Hyaenodonta, and Oxyaenidae). Herein we refer to this entire clade as ‘carnivores’. We revisited the taxonomy of all fossil and extant members of the group and accepted, 1723 species (314 of which are extant). We based our analyses on records in the Paleobiology Database (PBDB; <https://paleobiodb.org/>) and the New and Old Worlds Database of fossil mammals (<http://www.helsinki.fi/science/now/>; NOW), but supplemented these with data from the original literature for 128 species that we consider valid but which, at least when we were collecting data, lacked any records in either of the two databases.

We constructed the phylogeny of all extant and extinct species of carnivores using a tip dating approach under a fossilised birth-death model in MrBayes 3.2 (43). We did this in a two-step procedure combining a backbone tree with a number of smaller phylogenies at lower taxonomic levels. This procedure is similar to that used to construct phylogenies focusing on other large clades (e.g. 44, 45), but it has previously only been used to generate all-taxon phylogenies of all extant species within a clade. This is the first time it has been expanded to include all extant and extinct species within the focal clade. The placement of species without genetic or morphological data was facilitated by a number of constraints based on taxonomy and suggested relationships from taxonomic treatments.

These trees only give species origination time, but the information from these was combined with extinction times generated by the Bayesian program PyRate (46), which estimated likely extinction times based on the temporal distribution of all known records of each species. The resulting phylogeny is attached as appendix 1 giving 1000 trees from the posterior distribution of trees We included pinnipeds to improve the usability of the phylogeny for other researchers, but here we discarded them for all analyses for this paper due to our focus on terrestrial species.

We inferred the ancestral areas of all nodes based on a DEC (dispersal-extinction-cladogenesis) model in BiogeoBEARS (47). We used a DEC rather than the DEC +j model since the underlying mathematical properties of the DEC +j model have been questioned (48). Following the estimation of ancestral areas for all nodes, we inferred dispersal events and times along branches.

We assessed changes in global and continental diversity by plotting species and phylogenetic diversity (49) (i.e. the sum of branch lengths). Following this, we analysed the evolutionary success (estimated as their diversification rate) of dispersers at the time of their dispersal (*pre-dispersal success*) and the number of descendant species they left behind after a set time (*post-dispersal success*).

The analyses related to phylogenetic diversity and diversification rate are only meaningfully interpretable for ultrametric trees. For simplicity, extinction was therefore dealt with in time intervals rather than in continuous time and on trees sliced at various ages, only counting the species (internal or external branches) extant at that point in time. Hence, when using 0.5 My time intervals, two species that went extinct 1.2 and 1.4 Ma were assumed to have survived until 1.0 Ma and would both be included as extant for a tree sliced at 1.0 Ma. To test the effect of this procedure on the results, all analyses were conducted with time intervals of 0.25, 0.5 or 1.0 My duration.

We estimated *pre-dispersal success* based on diversification rate (DR) (45). We sliced the tree at the end of each time interval throughout the Cenozoic and calculated the DR of all lineages alive at that time. For all intercontinental dispersal events occurring in the following time interval, we then identified the lineage at the beginning of the interval that would evolve into the disperser during the interval. This could be either the same species or one of its ancestors, which would be the case for

founder speciation occurring within the time interval. We then calculated the logarithm of the ratio between the diversification rate of the disperser and the median diversification rate for either all lineages alive in the time interval (*global pre-dispersal success*) or the subset of these that was found on the same continent the disperser originated in (*continental pre-dispersal success*). This calculation is outlined in Fig. 3.

We estimated *post-dispersal success* by comparing the tree at the time before dispersal with the tree sliced a number of million years afterwards. For each lineage alive at the first time interval, we identified how many species it had diversified into a few million years later (which was 0 if the lineage had gone extinct in the meantime). We then calculated the ratio between the number of species in the dispersing lineage and the mean for either all other species (*global post-dispersal success*) or all species from the continent dispersed to (*continental post-dispersal success*). In both cases, we square-root-transformed the *post-dispersal success* to improve normality. Separate analyses of *post-dispersal success* were conducted on trees sliced after 3, 5, and 7 My.

Although we have included all known species, an unknown number of extinct species may be missing from the fossil record, which may influence our results, especially since the fraction of missing species is likely to vary in time and space. In order to understand the influence of missing taxa on our results, we, therefore, simulated a number of random phylogenies. We then simulated incomplete sampling on those phylogenies based on spatial and temporal sampling effort estimated in the PyRate analyses described above. Following this, we repeated all analyses described above on both the full and the sampled phylogenies in order to directly measure the effect of incomplete sampling on our results.

A detailed explanation of all steps can be found in the supplementary materials and methods.

## References

- 1) Alfaro, M.E. et al. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106**, 13410–13414 (2009)

- 2) Sepkoski, J. A factor analytic description of the Phanerozoic marine fossil record.  
*Paleobiology* **7**, 36-53 (1981).
- 3) Faurby, S. et al. PHYLACINE 1.2: The phylogenetic atlas of mammal  
macroecology *Ecology* **99**, 2626 (2018)
- 4) Markolf, M. & Kappeler, P. M. Phylogeographic analysis of the true lemurs (genus *Eulemur*)  
underlines the role of river catchments for the evolution of micro-endemism in Madagascar.  
*Front. Zool.* **10**, 70 (2013)
- 5) Heintzman, P.D. et al. A new genus of horse from Pleistocene North America. *eLife* **6**, e29944  
(2017)
- 6) Faurby, S. & Antonelli, A. Evolutionary and ecological success is decoupled in mammals. *J.*  
*Biogeogr.* **45**, 2227–2237 (2018)
- 7) Weeks, B. C. & Claramunt, S. Dispersal has inhibited avian diversification in Australasian  
archipelagos. *Proc. R. Soc. B* **281**, 20141257 (2014)
- 8) Quantal, T. B. & Marshall, C. R. How the Red Queen drives terrestrial mammals to extinction.  
*Science* **341**, 290–292 (2013)
- 9) Žliobaitė, I., Fortelius, M. & Stenseth, N. C. Reconciling taxon senescence with the Red  
Queen’s hypothesis. *Nature* **552**, 92–95 (2017)
- 10) Worthy, T. H. et al. Miocene mammal reveals a Mesozoic ghost lineage on insular New  
Zealand, southwest Pacific. *Proc. Natl Acad. Sci. USA* **103**, 19419–19423 (2006)
- 11) Upham, N., Esselstyn, J. A. & Jetz, W. Ecological causes of uneven diversification and  
richness in the mammal tree of life. *bioRxiv* <https://doi.org/10.1101/504803> (2019)
- 12) Valkenburgh, B. V. Major patterns in the history of carnivorous mammals. *Annu. Rev. Earth*  
*Planet. Sci* **27**, 463–493 (1999)
- 13) Silvestro, D., Antonelli, A., Salamin, N. & Quantal, T. B. The role of clade competition in the  
diversification of North American canids. *Proc. Natl Acad. Sci. USA* **112**, 8684–8689 (2015)
- 14) Cantalapiedra, J. L., Prado, J. L., Hernández Fernández, M. & Alberdi, M. T. Decoupled  
ecomorphological evolution and diversification in Neogene–Quaternary horses. *Science* **355**,  
627–630 (2017)

- 15) Quantal, T. B. & Marshall, C. R. The molecular phylogenetic signature of clades in decline.  
*PLoS One* **6**, e25780 (2011)
- 16) Rabosky, D. L. Extinction rate should not be estimated from molecular phylogenies. *Evolution*  
**64**, 1816–1824 (2010)
- 17) Louca, S. & Pennell, M. W. Phylogenies of extant species are consistent with an infinite array  
of diversification histories. [bioRxiv doi.org/10.1101/719435](https://doi.org/10.1101/719435) (2019)
- 18) Silvestro, D., Schnitzler, J., Liow, L. H., Antonelli, A. & Salamin, N. Bayesian estimation of  
speciation and extinction from incomplete fossil occurrence data. *Syst. Biol.* **63**, 349–367  
(2014)
- 19) Fritz, S.A. et al. Diversity in time and space: wanted dead and alive. *Trends Ecol. Evol.* **28**,  
509–516 (2013)
- 20) Slater, G. J. & Harmon, L. J. Unifying fossils and phylogenies for comparative analyses of  
diversification and trait evolution. *Methods Ecol. Evol.* **4**, 699–702 (2013)
- 21) Sandom, C. et al. Mammal predator and prey species richness are strongly linked at  
macroscales. *Ecology* **94**, 1112–1122 (2013)
- 22) Bohaty, S. M. & Zachos, J. C. Significant Southern Ocean warming event in the late middle  
Eocene. *Geology* **31**, 1017–1020 (2003)
- 23) Brodie, J. F. Environmental limits to mammal diversity vary with latitude and global  
temperature. *Ecol. Lett.* **22**, 480–485 (2019)
- 24) Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms and aberrations  
in global climate 65 Ma to present. *Science* **292**, 686–693 (2001)
- 25) Costa, E., Garces, M., Saez, A., Babrera, L. & López-Blanco, M. The age of the “Grande  
Coupure” mammal turnover: New constraints from the Eocene–Oligocene record of the  
Eastern Ebro Basin (NE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **301**,  
97–107 (2011)
- 26) Fukami, T. Historical contingency in community assembly: Integrating niches, species pools,  
and priority effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23 (2015)

- 27) Webb, S.D. The great American biotic interchange: patterns and processes. *Ann. Missouri Bot. Gard.* **93**, 245–275. (2006)
- 28) Chester, S. G. B., Bloch, J. I., Secord, R. & Boyer, D. M. A new small-bodied species of *Palaeonictis* (Creodonta, Oxyaenidae) from the Paleocene Eocene thermal maximum. *J. Mamm. Evol.* **17**, 227–243 (2010)
- 29) Borths, M. R., Holroy, P. A. & Seiffert, E. R. Hyainailourine and teratodontine cranial material from the late Eocene of Egypt and the application of parsimony and Bayesian methods to the phylogeny and biogeography of Hyaenodonta (Placentalia, Mammalia). *PeerJ* **4**, e2639 (2016)
- 30) Solé, F., Smith, T., De Bast, E., Codrea, V. & Gheerbrant, E. New carnivoraforms from the latest Paleocene of Europe and their bearing on the origin and radiation of Carnivoraformes Carnivoramorpha, Mammalia). *J. Vert. Paleontol.* **36**, e1082480 (2016)
- 31) Pires, M. M., Silvestro, D. & Quental, T. B. Continental faunal exchange and the asymmetrical radiation of carnivores. *Proc. R. Soc. B* **282**, 20151952 (2015)
- 32) Prevosti, F. J., Forasiepi, A. & Zimicz, N. The Evolution of the Cenozoic Terrestrial Mammalian Predator Guild in South America: Competition or Replacement? *J. Mamm. Evol.* **20**, 3–21 (2013)
- 33) Werdelin, L. Jaw geometry and molar morphology in marsupial carnivores: analysis of a constraint and its macroevolutionary consequences. *Paleobiology* **13**, 342– 350 (1987)
- 34) Croft, D.A. Do marsupials make good predators? Insights from predator–prey diversity ratios. *Evol. Ecol. Res.* **8**, 1193–1214 (2006)
- 35) Faurby, S. & Svenning, J. C. The asymmetry in the Great American Biotic Interchange in mammals is consistent with differential susceptibility to mammalian predation. *Glob. Ecol. Biogeogr.* **25**, 1443–1453 (2016)
- 36) Halliday, T. J. D., Upchurch, P. & Goswami, A. Resolving the relationships of Paleocene placental mammals. *Biol. Rev.* **92**, 521 – 550 (2015)
- 37) Barnosky, A. D. et al. Has the Earth’s sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011)



- 38) Cooper, N., Rodríguez, J. & Purvis, A. A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proc. R. Soc. B* **275**, 2031–2037 (2008)
- 39) Wilcox, T. M., Schwartz, M. K. & Lowe, W. H. Evolutionary community ecology: Time to think outside the (taxonomic) box. *Tr. Ecol. Evol.* **33**, 240–250 (2018)
- 40) Chikina, M., Robinson, J. D. & Clark, N. L. Hundreds of genes experienced convergent shifts in selective pressure in marine mammals. *Mol. Biol. Evol.* **33**, 2182–2192 (2016)
- 41) Mazel, F. et al. The geography of ecological niche evolution in mammals. *Curr. Biol.* **27**, 1369–1374 (2017)
- 42) Burbidge, A. A. & Manly, B. F. J. Mammal extinctions on Australian islands: causes and conservation implications. *J. Biogeogr.* **29**, 465–473 (2002)
- 43) Ronquist, F. et al. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **61**, 539–542 (2012)
- 44) Faurby, S., Svenning, J. C. A species-level phylogeny for all extant and Late Quaternary extinct mammals using a novel hierarchical Bayesian approach that accounts for topological uncertainty. *Mol. Phylogenetics Evol.* **84**, 14–26 (2015)
- 45) Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, J. K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012)
- 46) Silvestro, D., Salamin, N. & Schnitzler, J. PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods Ecol. Evol.* **5**, 1126–1131 (2014)
- 47) Matzke, N. J. BioGeography with Bayesian (and Likelihood) evolutionary analysis in R scripts. Retrieved from <https://cran.r-project.org/web/packages/BioGeoBEARS/BioGeoBEARS.pdf> (2013).
- 48) Ree, R. H. & Sanmartin, I. Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *J Biogeogr* **45**, 741–749 (2018)
- 49) Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **284**, 1–10. (1992)

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472 **Supplementary Materials:**

473 Supplementary materials and methods

474 Tables S1-S9.

475 Figures S1-S2.

476 Appendix 1: The produced phylogeny of all carnivores

477 Appendix 2. A description of our treatment of all the individual fossil records

478

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486 added as an appendix. All scripts used for running individual analyses are available from the authors

487 upon request.

488

**Table 1: Pre-dispersal success.**

*Pre-dispersal success* was estimated as the logarithm of the ratio between the diversification rate of the dispersing lineage dispersers and the median of the dispersal rates of the remaining species alive at the time of dispersal (see Fig. 3). Separate analyses were conducted comparing the dispersers with either all species alive (*global pre-dispersal success*) or only the species alive in the source continent (*continental pre-dispersal success*).

The p-values for node age and for global rate are the probability of the estimate in question being greater than 0. For models with different patterns depending on continental source and target, the p-value is based on the probability of being different from the estimated global rate.

This table only lists the results for the simplest model, and models preferred by AIC for either global or *continental pre-dispersal success*. The results from the remaining models are provided in the supplementary material (Tables S1–S2). Values are only given for time intervals of 0.5 million years, but results are similar for the other two intervals (Tables S1–S2).

	<i>Continental pre-dispersal success</i>	<i>Global pre-dispersal success</i>
Simplest model		
Global	0.0835 (0.0194)***	0.1205 (0.0205)***
ΔAIC	5.973	6.178
Temporal variation		
Global	0.1122 (0.0259)***	0.1636 (0.0272)***
Age before present	-0.0018 (0.0012)‘	-0.0027 (0.0013)*
ΔAIC	4.079	0.000
Variation between target continent		
To Africa	0.1160 (0.0373)	0.1468 (0.0372)
To Eurasia	0.0453 (0.0343)	0.1050 (0.0362)
To North America	0.1260 (0.0360)	0.1420 (0.0370)
To South America	0.0017 (0.0503)	0.0423 (0.0528)
ΔAIC	0.000	5.873
‘ 0.10>P>0.05 * 0.05>P>0.01 ** 0.01>P>0.001 *** 0.001>P		

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**Table 2: Post-dispersal success.**

*Post-dispersal success* is estimated as the square root of the ratio between the number of descendants for each dispersing lineage alive 5 million years (My) after dispersal divided by the mean number of descendants for any species alive at the time of dispersal (see Fig. 3). Separate analyses were conducted comparing the dispersers with either all species alive then (*global post-dispersal success*) or only the species alive in the target continent (*continental post-dispersal success*). P-values for node age and for global rate are the probability of the estimate in question being higher than 1 (the null expectation). For models with different patterns depending on continental source and target, the p-value is based on the probability of being different from the estimated global rate.

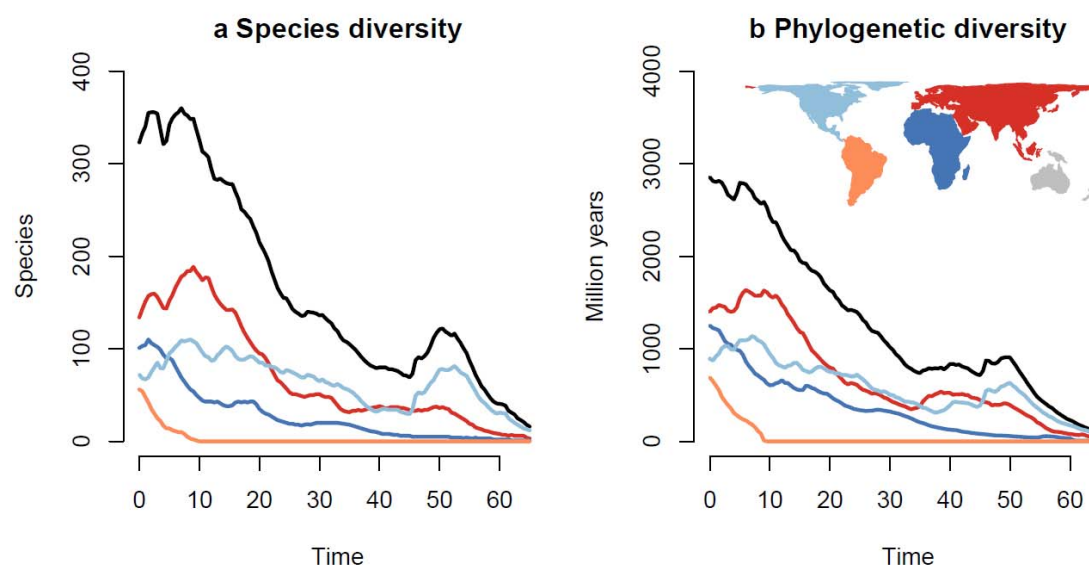
Values are only given for time intervals of 0.5 My and only based on the number of species alive after 5 My, but results are similar for time intervals of 0.25 and 1.00 and after 3 or 7 My (Tables S5–S6). This table only lists the results for the simplest model, and models preferred by AIC for either *global* or *continental post-dispersal success*. The results from the remaining models are provided as supplementary material (Tables S5–S6).

	<i>Continental post-dispersal success</i>	<i>Global post-dispersal success</i>
Simplest model		
Global	1.4433 (0.0730) <sup>***</sup>	1.4606 (0.0730) <sup>***</sup>
ΔAIC	5.792	0.000
Variation between source and target continent		
Africa to Eurasia	1.2666 (0.1727)	1.3557 (0.1777)
Eurasia to Africa	1.3607 (0.1206)	1.3991 (0.1184)
Eurasia to North America	1.6677 (0.1282) <sup>†</sup>	1.5767 (0.1243)
North America to Eurasia	1.4238 (0.1487)	1.4572 (0.1428)
North to South America	1.1263 (0.2925)	1.4005 (0.2835)
ΔAIC	0.000	1.685
<sup>†</sup> 0.10>P>0.05 * 0.05>P>0.01 ** 0.01>P>0.001 *** 0.001>P		

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**Figure 1: Temporal changes in diversity.**

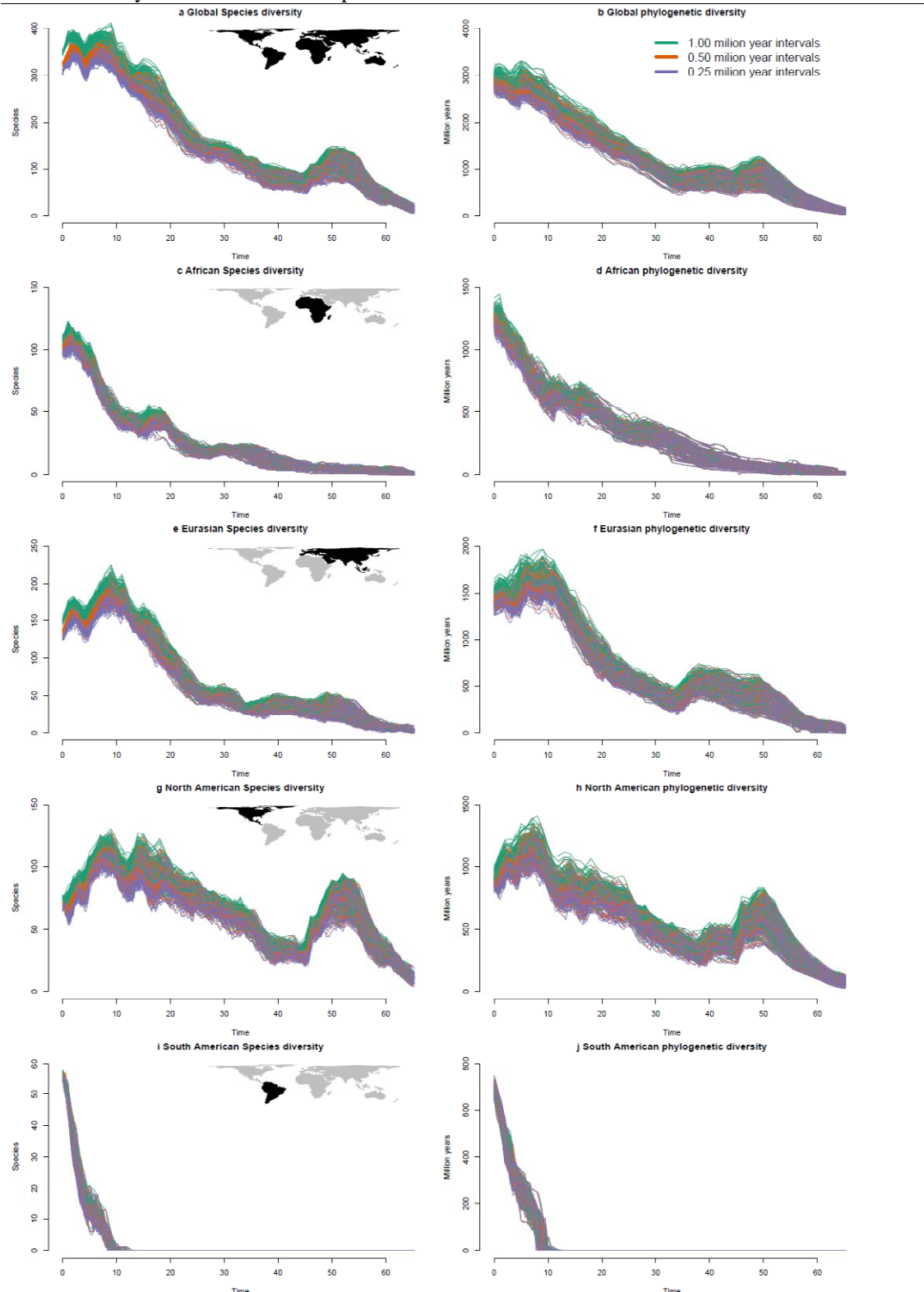
Change in species and phylogenetic diversity through time globally (in black) and separately per continent (different colours). Lines represent median values across 100 trees for 0.5-million-year time intervals. The variation between trees and between lengths of the study interval can be seen in Fig. 2.



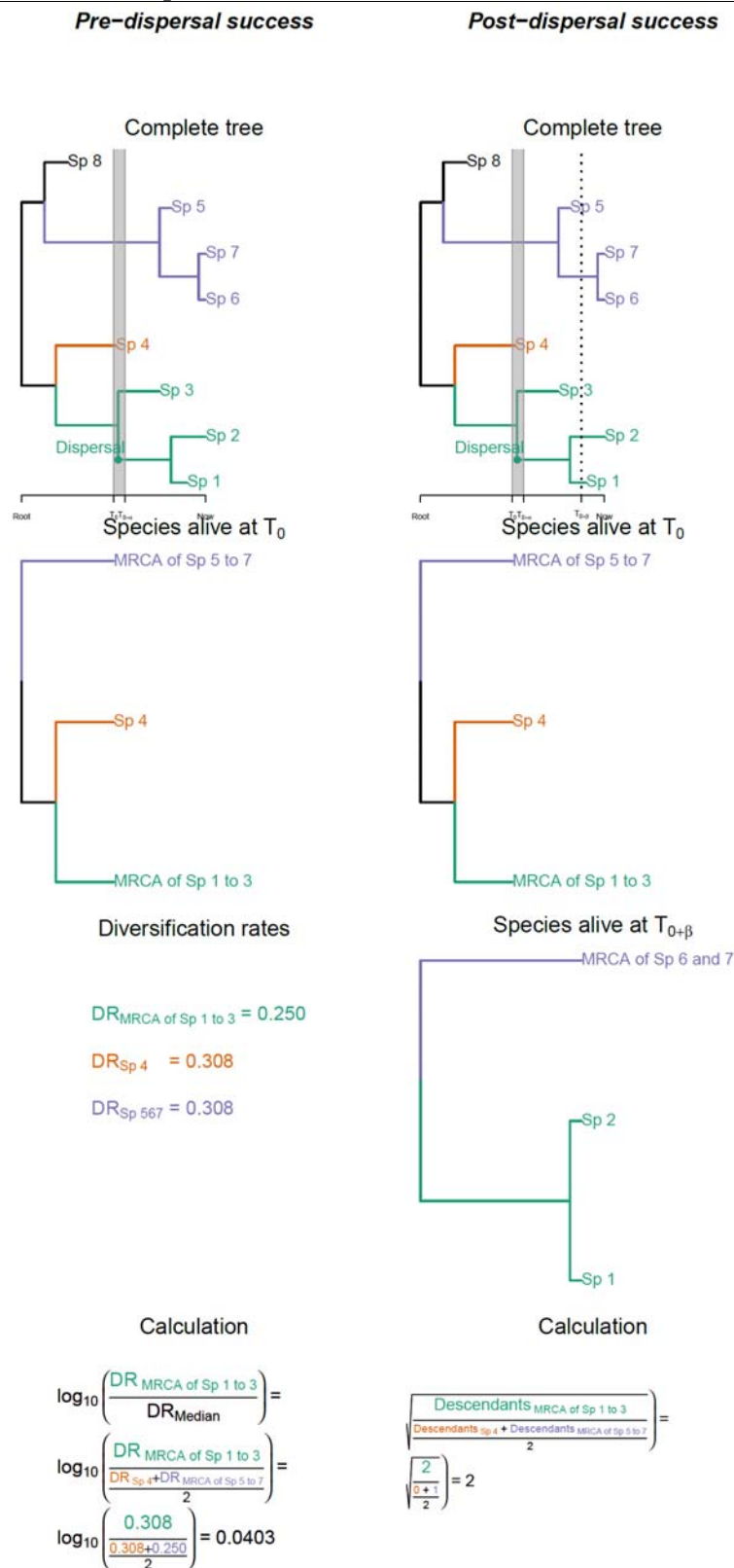
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**Figure 2: Variation in diversification rate among trees.**

Plots of diversity through time for 100 trees drawn from the Bayesian phylogenetic analysis. Results for each tree are drawn as separate lines with results for different sample periods shown in different colours. Due to the strong consistency of results between trees and between lengths of the intervals many lines are drawn on top of each other.



**Figure 3: Estimation of dispersal success.**



In the example above, one dispersal event happened within the interval from  $T_0$  and  $T_{0+\alpha}$ , where  $\alpha$  represents the time interval, which in our case was 0.25, 0.5 or 1.0 million years (My).

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Both *Pre-dispersal success* and *Post-dispersal success* are calculated on the same tree.

The panels on the right illustrate how *Pre-dispersal success* is calculated. In order to improve understanding, we have used the same colours on each panel to show corresponding parts of trees or equations.

The two first panels show the entire tree, and a tree of just the species alive at time  $T_0$ . The third panel shows DR rates estimated as in (44) for the species alive at  $T_0$ . The fourth shows the calculation of *Pre-dispersal success*, which we define as the logarithm to the ratio between the DR of the dispersing lineage and the median of the remaining lineages (see the methods section for details).

The panels on the left illustrate how *Post-dispersal success* is calculated. In order to improve understanding, we have used the same colours on each panel to show corresponding parts of trees or equations.

The first panel shows the entire tree. This is identical to the tree for *Pre-dispersal success* except that a stippled line has been added at time  $T_{0+\beta}$ .  $\beta$  here represents a pre-defined length of time (in our case 3, 5 or 7 My). *Post-dispersal success* compared the trees at  $T_0$  and  $T_{0+\beta}$  and how many descendant species, each species alive at  $T_0$  has diversified into. The next two panels show the trees of the species alive at  $T_0$  and  $T_{0+\beta}$  respectively. The last panel illustrates the calculation of *Post-dispersal success*, which we defined as the square root of the ratio between the number of descendants of the dispersing lineage and the mean number of descendants for any lineage from time  $T_0$  alive at time  $T_{0+\beta}$ . Note that we here only look at the descendants alive at this time point and not all descendants. This, for instance, means that the taxon “*MRCA of Sp 5 to 7*” has only diversified into one species at time  $T_{0+\beta}$  (“*MRCA of Sp 6 and 7*”) because Sp 5 is already extinct by then and the split between Sp 6 and Sp 7 happens at a later stage (see the methods section for details).

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## Supplementary materials

### 5 Supplementary materials and methods

#### 5.1 Phylogeny

##### 5.1.1 Input data

We downloaded all records of carnivores identified at least to genus level from the Paleobiology Database (PBDB; <https://paleobiodb.org/>) on October 10, 2016 and the New and Old Worlds Database of fossil mammals New and Old Worlds Database of fossil mammals (<http://www.helsinki.fi/science/now/>; NOW), on September 30, 2016. We defined the focal clade as Carnivoramorph (Carnivora and Miacoidea) + Creodonta (Hyaenodonta and Oxyaenidae). Hereafter, we refer to this entire clade as ‘carnivores’ and use the term ‘Carnivora’ when referring exclusively to the extant order.

We revisited the taxonomy of all named species to generate a consistent list matching current knowledge of extinct mammals, as well as the taxonomy of species surviving at least until the Late Pleistocene (hereafter ‘extant carnivores’). For the latter, we followed the taxonomy of the Phylacine V 1.2 database (3). Phylacine follows the International Union for Conservation of Nature (IUCN) version 2016-3 for extant species and extinct species with extinction dates post 1500 AD, and an updated version of the database of Faurby and Svenning (44) for species that went extinct between the Late Pleistocene and 1500 AD. The resulting dataset had 7,551 useable records from NOW (6,285 records assigned to a species and 1,266 only to genus, while 94 records from the database were not assignable to any of the genera we accept and were therefore excluded) and 7,984 useable records from PBDB (6,755 records assigned to species and 1,229 only to genus, while 123 were not assignable to any of our genera and therefore excluded).

Our combined dataset consisted of 1,723 species after cleaning, 314 of which are extant. Among the species that went extinct prior to the Late Pleistocene, 631 were included in both NOW and PBDB, 382 only had records in the NOW Database, and 268 only had records in PBDB. An additional 128 species were manually added since they were not included in either of the databases at the time of original download (October 10, 2016, and September 30, 2016 for the PBDB and NOW



databases, respectively; see Table S8). We included a few forms as separate species entities although not formally described as such. Five genera had records only identified at the genus level from North America. For our analyses, we treat these as distinct species, such as “*Parailurus* NorthAmerica”. Although species designation for these has not formally been made, morphological differences have generally been noted (50), which makes species designation plausible. Finally, we treat the records of two small species (*Palaeogale minuta* and *Palaeogale sectoria*) from North America and Eurasia as distinct continental endemics, since both persist on both continents for many million years and it seems biologically implausible for them to maintain population coherence (i.e., gene flow) during that time interval. A full breakdown of records by database can be found in the attached Excel spreadsheet ‘Database summary’.

### 5.1.2 Phylogenetic and dating analyses

The phylogeny of all extant and extinct species of carnivores was constructed using a tip dating approach under a fossilised birth-death model in MrBayes 3.2 (43). The phylogeny was created by combining a backbone phylogeny with 17 smaller phylogenies (for Amphicyonidae, Barbourfelidae, Canidae, Eupleridae, Felidae, Herpestidae, Hyaenodontidae, Hyaenidae, Mustelidae, Nimravidae, Oxyaenidae, *Palaeogale*, Percrocutidae, Pinnipedia, Ursidae, Viverravidae and Viverridae). This procedure requires that all the smaller phylogenies have a known number of species. For two families (Miacidae and Stenoplesictidae) that were not constrained to be monophyletic (see next section), we, therefore, included all species in the backbone phylogeny. Two chains were run for both the backbone and the 17 smaller phylogenies until the average standard deviation of split frequencies was lower than 0.03, but for a minimum of 10 million generations. The analyses were further inspected with Tracer 1.6 (51) to ensure that the Effective Sample Size of the post burn-in for the overall model tree likelihood for the two chains combined was at least 200.

The priors for the analyses were based on earlier tip dating analyses across all mammals from Ronquist et al (52). In particular, we set a uniform prior of the root between 56.3 and 88.0 Ma, representing the span between the oldest fossil in the database and the estimated divergence time between the MRCA of Hyaenodontidae and Carnivora and their combined outgroup, following

Ronquist et al. (52). We further penalised long ‘ghost lineages’ (i.e. lineages existing for very extended time periods without leaving any fossil evidence) in all analyses using the prior “prset fossilizationpr = beta(100,1)” as also suggested by Ronquist et al (52). For all phylogenetic reconstructions, we assumed that all species are included in the analyses. While we have included all known species in the phylogeny, we acknowledge that a fraction of undescribed species must be missing, but this fraction cannot be reliably estimated with any available method.

The backbone phylogeny was constructed based on morphological data for extinct clades and a combination of morphological and genetic data for extant ones. All morphological data were analysed under an MK-model conditioned to only include variable sites and incorporating gamma rate heterogeneity. The morphological data were based on the matrix by Wesley-Hunt and Flynn (53) but supplemented by numerous studies (see Table S9). We added new data for four key taxa representing taxonomic groupings not included in previous analyses (*Percrocuta* sp, *Ginsburgsmilus napakensis*, *Barbourofelis* sp, and *Oxyaena forcipata*) (all four coded by LW). This morphological matrix was supplemented with genetic data from Meredith et al (54). To facilitate the merging of the smaller phylogenies with the backbone phylogeny, we added the oldest known species of each family (in this and all other cases we use the ages as listed in the original data source) to the backbone analysis, with all characters coded as missing data. The 17 smaller phylogenies were for the most part constructed based on one or more morphological data matrices, with genetic data also included for the extant families. Depending on the family, the genetic data were either based almost entirely on a single source although with supplemented searches for missing data of missing species from NCBI, or on NCBI searches for each species (a list of sources can again be found in Table S9).

We made a number of modifications to the nexus files before running MrBayes. We set the best nucleotide substitution model and partition scheme for the genetic data as the optimal one based on AIC as inferred by Partitionfinder 1.1 (55) for both the overall and the smaller phylogenies. We set the age of all fossil taxa and all extant species without genetic data to the age of the oldest known record. Six of the species not included in either NOW or PBDB (*Amphicynodon brachyrostris*, *Amphicynodon cephalogalinus*, *Amphicynodon chardini*, *Amphicynodon crassirostris*, *Phoberogale minor* and *Filholictis filholi*) come from undated deposits. The first five were given uniform priors

between the age of the oldest and youngest species in the genus, whereas the sixth (*Filholictis filholi*) is from a monospecific genus and was given a uniform prior between the youngest and oldest member of the subfamily. For all genera constrained to be monophyletic (see next section), we set the minimum age of the genus to the age of the oldest record in the genus (whether identified to species or not). We did this using a uniform prior on the node age, with a maximum age equal to the rootage of the family. We set the prior on the age of all tips representing fossil species and all extant species lacking genetic data as a uniform prior ranging between the minimum and maximum ages of the oldest known fossil of the species. These are intended to inform the origination time for the species lacking genetic data. For all later analyses, they are treated in the same way as the extant taxa.

We merged the smaller trees with the backbone phylogeny while keeping the dating information for both sets, as described below. For the 17 smaller phylogenies, we set a uniform prior of the rootage between the oldest known fossil in the group and the upper 95% HPD (Highest Posterior Density) for the stem age of the group from the backbone phylogeny. The backbone and the smaller phylogenies were merged so that there was the same correlation between the stem and crown age as between the age of the stem age and the next internal branch in the phylogeny. That is, since Felidae and Barbourufelidae are sister families, the phylogenies were merged so the correlation between the stem and rootage of Felidae is the same as the correlation between the stem age of Felidae and the age of the MRCA (Most Recent Common Ancestor) of Felidae and Barbourufelidae.

For some trees, the resulting family-level clades had crown ages slightly older than the stem ages of the overall tree, and we, therefore, needed to recalibrate the family level trees to avoid negative branch lengths. This was done for all problematic trees (i.e. family level trees with crown ages slightly older than the stem ages from the backbone tree) so that all branch lengths in the new tree were proportional to the branches in the original tree, and the rootage was equal to the stem age of the backbone tree minus 0.01.

### 5.1.3 Constraints

Similar to the assumption of other complete phylogenies, where a number of species lack genetic or morphological data (e.g. 44, 45), we assumed taxonomic clades to be monophyletic unless there is

good evidence against it. This meant that we carefully inspected the paleontological literature regarding each taxonomic unit to judge if they are generally understood to comprise monophyletic entities (all taxonomic constraints are shown in the attached Excel spreadsheet ‘Database summary’).

At the highest level Carnivoramorpha, Hyaenodonta, and Oxyaenidae were each constrained to be monophyletic. Within Carnivoramorpha, Carnivora and Viverravidae, but not Miacidae (which is a paraphyletic assembly; see e.g. 53), were constrained to be monophyletic. Within Carnivora, all taxa were constrained to be either Caniformia or Feliformia. Within Caniformia, we constrained the monophyly of Amphicyonidae, Canidae, Musteloidea, Pinnipedia, and Ursidae and assumed *Lycophocyon hutchisoni* to be outside any of the major lineages. Within Feliformia we constrained the monophyly of Barbourofelidae, Eupleridae, Felidae, Herpestidae, Hyaenidae, Nimravidae, Percrocutidae, Prionodontidae, and Viverridae, but not Stenoplesictidae (which again is generally considered a paraphyletic assemblage; see e.g. 56). This means that we assumed that each genus normally assigned to Stenoplesictidae, as well as *Palaeogale*, was outside any of the major lineages listed above. We further constrained Percrocutidae as sister to Hyaenidae following (57) and Felidae as sister to Barbourofelidae following (58). The morphological dataset started by Wesley-Hunt and Flynn (53) was designed to determine the relatedness between basal taxa and on its own (i.e. without genetic data added) produces improbable relationships between more derived members of extant families within Carnivora. (53). Both Percrocutidae and Barbourofelidae are only known from Miocene fossils, meaning that the morphological matrix may be suboptimal to infer their placement, but unlike the extant families, their relationship cannot be inferred by adding genetic data to the analysis.

At a lower level, we constrained most subfamilies and genera to be monophyletic, but deviated from this in a number of cases for three main reasons: 1) Some of the earliest described genera within families and subfamilies, e.g. *Lutra* for otters, have served as waste-baskets for a number of frequently poorly-defined fossil taxa (59). Many fossil forms within such genera, as well as other poorly known taxa, were therefore allowed to be placed freely within the family or subfamily instead of being constrained to their genera; 2) Other species of uncertain phylogenetic placement belong to distinct genera, but are rarely included in the newer taxonomic treatments and were therefore

not constrained to be within otherwise constrained subfamilies or tribes; and 3) Taxonomy does not always imply genus-level monophyly. For some taxa, there is evidence that named genera are nested within other named genera and we, therefore, allowed such nesting when supported. For example, this is the case for *Neovison* (the American mink and the extinct sea mink), which phylogenetically may be nested within *Mustela* (weasels) (60).

In addition to these taxonomic constraints, we also employed a number of constraints based on stated likely relationships in taxonomical treatments. Finally, we employed a number of biogeographical constraints within lineages or species and often enforced that there would only be a single intercontinental dispersal within a lineage unless there are data to suggest otherwise. A full breakdown of family, subfamily and genus level constraints can be found as part of appendix 2, which contains information on all fossil records and our treatment of them, while a full list of additional constraints and the relevant sources can be found in Table S10.

#### **5.1.4. Extinction times**

The procedure described above only gives the origination times of all lineages, but not the extinction times. To estimate the actual extinction times for all taxa we used the Bayesian program PyRate (45). We did this independently for each continent, which means that we treat a species occurring on multiple continents as two distinct populations that may go extinct independently of each other, rather than as a coherent group of sub-populations with ongoing gene flow.

Firstly, we combined fossil records from NOW and PBDB, keeping as many records as possible while avoiding duplicate records. For each species, we initially accepted all records in either NOW or PBDB (whichever had most records of the species in question). We then examined all records of the other database for the same species, one by one, to assess if they were clearly distinct (in which case they were added) or potential duplicates (in which case they were not). If the latitude and/or longitude rounded to the nearest degree was different from all records already accepted, and/or if the age of the record was non-overlapping with accepted records with the same latitude and longitude, we added the record. If there was only one record already accepted with identical latitude and longitude and overlapping age, we considered the old and new ones to be potential duplicates and

retained the one with the most precise dating. However, we discarded the new record if there was more than one already accepted record with the identical latitude and longitude and overlapping age.

Secondly, we ran PyRate analyses separately for records from South America, North America, Asia, Europe, and Africa, with an additional separate analysis for Pinnipeds (since marine species may have different fossilization potential than terrestrial ones). Sampling intensity (i.e. the product of the number of specimens fossilizing and the fraction of fossils that are identified and placed in the available databases) is a vital component determining how long after the youngest record the true extinction time is likely to have been. Sampling intensity may vary between continents and between marine and terrestrial species. For each continent (and for pinnipeds) we ran 20 separate PyRate analyses, further allowing for variable sampling intensity in each epoch, for example as a consequence of different amounts of exposed rocks of different ages. The analyses of African and South American records (which had fewer records) were run for 10 million generations, whereas all others were run for 20 million generations. Not all analyses converged but we generally used the results from 10 separate chains, where the effective sample size for all key parameters was high (i.e. all parameters related to the overall process but not necessarily the speciation or extinction time of each species, which are treated as individual parameters, had an effective sample size above 200). The exception for this was Europe, where convergence by these criteria was only seen in four chains and only these four were therefore used in the subsequent analyses.

Finally, we combined the estimated extinction dates from the PyRate analyses with the origination times estimated from the phylogenetic analyses. We first sampled random generations across the different PyRate analyses (with the same number of samples for each). Following this, we combined the results from a random PyRate generation with a random tree from the posterior distribution. By doing this, we estimated the extinction time for every species on one continent independently of their extinction time on other continents, which means that we consider them to represent separate distinct populations rather than meta-populations with ongoing gene flow. We treated Eurasia as a continent for all downstream analyses rather than as the distinct continents of Europe and Asia. In doing this we set the Eurasian extinction date as the latest of the inferred European and Asian extinction dates.

## 5.2 Data analyses

### 5.2.1 Dispersal inference

The first analytical step was an estimation of the dispersal dynamics between continents. For this and all further analyses we discarded pinnipeds (which were just included in the datamining elements to maximise the use of our created phylogeny for future evolutionary studies) and thus only analysed terrestrial species. We estimated ancestral geographic range for all nodes with a DEC (dispersal-extinction-cladogenesis) model in BiogeoBEARS (47), using the trees with origination time as described above. We used a DEC rather than the frequently used DEC +j model since the underlying mathematical properties of the DEC +j model have been seriously questioned (48).

We manually specified settings in BiogeoBEARS to match the study system. We did not allow dispersal to South America prior to 10 million years ago (Ma). The oldest carnivore fossils from the continent within our database are two records of the procyonid genus *Amphinasua* dated to 6.8–9 Ma; i.e. the Huayquerian South American Land Mammal Age (SALMA). By doing this we assume that at most one SALMA (the Chasicoan, 9–10 Ma) could lack fossils, even though carnivores actually could be present. We only allowed dispersal between adjoining continents (Africa/Eurasia, Eurasia/North America, and North America/South America). Finally, we allowed the dispersal rate in the Pleistocene (and Holocene) to be potentially higher than the pre-Pleistocene dispersal rate but otherwise kept a single constant dispersal rate. BiogeoBEARS does not generally allow temporal variation in dispersal rates, unless the relative temporal rates are manually specified, but we allowed the dispersal rate in the Pleistocene to be different from the pre-Pleistocene rate by setting the Pleistocene rate as  $d_{\text{Pleistocene}} = d_{\text{Pre-Pleistocene}} * 2^w$ , with  $w$  being a free parameter estimated by BiogeoBEARS.

As a second step, we transformed the probabilistic ancestral states at all nodes of the DEC analysis into binary presence/absences by sampling values based on the estimated probabilities. This was done starting with the most terminal nodes. While sampling ancestral nodes, we only sampled among states that were reasonable considering the states of the descendant nodes. Thus, if the

estimated ancestral state of two daughter nodes was inferred to be Eurasia and North America, the ancestral area of their direct ancestor was restricted to combinations of one or both of these two areas.

Finally, we estimated dispersal times between continents. Whenever mechanistically plausible (e.g. if the ancestor lived in North America and the daughter species lived in Eurasia and North America) dispersal was inferred to be at the time of speciation. When this was not the case, the necessary dispersal events (and potential required extinction events) were placed equidistant from each other on the relevant branches.

We acknowledge that the procedure of assigning areas to nodes and branches can be seen as a violation from the DEC model the data was estimated under, but we consider these violations biologically justifiable. Our estimation procedure means that we can infer jump dispersal whenever it is possible. These do not exist under a standard DEC model, but due to mathematical problems with the extension that explicitly incorporates jump dispersal (DEC+j model), we preferred to use this workaround. If we instead had used stochastic mapping to infer ancestral areas, we would have drastically overestimated the magnitude of dispersal events – especially ones taking place along long branches. This is because the only way to generate the frequent range changes that can be seen for rapidly diversifying clades without having jump dispersal in the model is by having unrealistically high dispersal rates within lineages. To get an idea of the magnitude of this issue, we estimated ancestral areas through stochastic mapping ten times for each of the 100 trees. We found that the smallest overestimation among all these 1,000 replicates was 47% while the median overestimation was 71%. The overestimation of dispersal events based on stochastic mapping would be particularly problematic for our analyses, due to its concentration on longer branches, which would produce biased results in our analyses of the relationship between dispersal rate and diversification.

## 5.2.2 Statistical analyses

We conducted a number of separate analyses on 100 separate trees from the posterior distribution. These analyses dealt with the dispersal dynamics between continents, the build-up of diversity and the macro-evolutionary success of intercontinental dispersers relative to other species. In all cases



described below, we analysed the patterns in standard regression analyses with the results from each of the 100 trees weighted equally.

Some analyses (related to phylogenetic diversity and diversification rate) are only meaningfully interpretable for ultrametric trees. For simplicity, extinction was therefore dealt with in time intervals and on trees sliced at various ages, rather than in continuous time, counting only the species (internal or external branches) extant at that time point. Hence, when using 0.5-million-year time intervals, two species that went extinct 1.2 and 1.4 Ma would both be included as extant for a tree sliced at 1.0 Ma (but extinct in a tree sliced at 0.5 Ma). All analyses were conducted with time intervals of 0.25, 0.5 or 1.0 million years duration in order to test the effect of this procedure on the results.

In the simplest analyses, we calculated species diversity and phylogenetic diversity (49) (i.e. the sum of the branch lengths in the tree) for all species alive in each time interval globally or on each continent. In two other sets of analyses, we tested whether dispersing species were diversifying faster than others were. The first of these sets of analyses, which we call *pre-dispersal success*, investigated if species that disperse belong to lineages that, at their time of dispersal, diversified faster than the other lineages present at that point in time. The second, which we call *post-dispersal success*, investigated if species that disperse leave more descendant species than species that do not disperse.

We estimated *pre-dispersal success* based on the diversification rate (DR) (45). We sliced the tree at the end of each time interval throughout the Cenozoic and calculated the DR of all lineages alive at that time. For all intercontinental dispersal events occurring in the following time interval, we then identified the lineage representing the disperser (this could be either the same species or one of its ancestors). We then calculated the logarithm of the ratio between the diversification rate of the disperser and the median diversification rate for either all lineages alive in the time interval (*global pre-dispersal success*) or the subset of these that was found on the same continent the disperser originated in (*continental pre-dispersal success*). This calculation is outlined in Fig. 3.

We estimated *post-dispersal success* by comparing the tree at the time before dispersal with a tree sliced a number of million years afterwards. For each lineage alive at the first time interval, we identified how many species they had diversified into a few million years later (this would be 0 if

the lineage had gone extinct in the meantime). We then calculated the ratio between the number of species in the dispersing lineage and the mean for either all other species (*global post-dispersal success*) or all species from the continent dispersal is to (*continental post-dispersal success*). In both cases, we square-root transformed the *post-dispersal success* to improve normality. For this measure, we used square-root rather than log transformation and means rather than medians, because zero descendants for both the dispersing and non-dispersing lineages are common. Zero descendants for the dispersing lineages could otherwise require taking the logarithm to zero, while zero descendants for the non-dispersers (if occurring for more than half the species) would otherwise require dividing by zero. Dispersal events were ignored for these analyses if they occurred so recently that the time period a few million years later than that which we compare them to would be in the future. Separate analyses of *post-dispersal success* were conducted on trees sliced after 3, 5, and 7 My (with all dispersal events occurring within the last 3, 5, or 7 My ignored).

### 5.2.3 Simulations

All analyses described in 5.2.2 implicitly assume complete sampling. Although we have included all known species, an unknown number of extinct species may be missing from the fossil record, which can influence our results. This is especially so since the fraction of missing species is expected to vary in time and space. In order to understand the influence of missing taxa on our results, we, therefore, simulated a number of random phylogenies. We then simulated incomplete sampling on those phylogenies, then repeated all analyses described in 5.2.2 on both the full and the sampled phylogenies.

We simulated trees based on a stage-dependent speciation and extinction model. More specifically, we simulated trees based on a seven-class ClaSSE (Cladogenetic State change Speciation and Extinction) model (61) modified into a four-area version of the normally two-area GeoSSE model (62) using Diversitree (63). In this version, each species was given seven potential character states 1: S, 2; SN, 3: N, 4: NE, 5: E, 6: EA, 7: A (where S means South America, N means North America, E means Eurasia and A means Africa). The model included five parameters: sympatric speciation rate ( $\lambda_1$ ) present in all classes; jump dispersal speciation ( $\lambda_2$ ) for single area classes; allopatric speciation

( $\lambda_3$ ) for two area classes; local extinction rate ( $\epsilon$ ); and dispersal rate ( $\delta$ ) only between adjoining regions. The model is outlined in Fig. S2.

We generated plausible trees of the same size as the empirical ones using a rejection sampler to obtain a distribution of trees resembling the empirical ones in shape and geographic ranges. We obtained the ClaSSE parameter values by randomly drawing them from the following uniform distributions:  $\lambda_1 \sim U(0, 0.2)$ ,  $\lambda_2 \sim U(0, 0.05)$ ,  $\lambda_3 \sim U(0, 3)$ ,  $\delta \sim U(0, 0.1)$ , and  $\epsilon \sim U(0, 0.4)$ . We generated phylogenetic trees and geographic ranges at each random draw. The rejection sampler included three summary statistics: 1) the fraction of all taxa that are extant; 2) the total number of dispersals; and 3) the number of extant species occurring on more than one continent. Phylogenetic trees and geographic ranges were only accepted if all summary statistics met the condition:  $x_{sim}/x_{emp} \in [2/3, 1.5]$ , where  $x_{sim}$  is the statistic obtained from the simulation (e.g. the total number of dispersals) and  $x_{emp}$  is the corresponding value obtained from the empirical data. We repeated the simulation until 100 trees were accepted. The branch lengths of these trees were then multiplied by the appropriate factors to have root ages corresponding to those of the 100 empirical trees.

We simulated geographic and spatial variation in preservation rate for each of these random trees based on estimated sample intensity at each epoch as inferred from the PyRate analysis (see 4.1.4). We assumed complete sampling of extant species. Sample intensity for the PyRate analysis was estimated separately for Asia and Europe, due to the large difference in paleontological research conducted in the two continents. For all biogeographical analyses, however, we used a combined Eurasia since the borders between the two are poorly defined and a large fraction of species have ranges spanning both continents. For the simulations (which are intended to mimic the biogeographical analyses), we, therefore, used a combined value for Eurasian sampling. This was estimated as the mean of the European and Asian sampling weighted by the contemporary diversity of carnivores in the two continents. No pre-Miocene South American carnivores exist in the empirical trees and therefore we cannot use empirical values for this continent for the Paleocene, Eocene, and Oligocene. We instead used the mean estimate for Africa and Eurasia (corresponding to substantially lower estimated sampling effort than North America). Estimation of sample intensity in PyRate can be

imprecise for very shallow time intervals such as the Holocene (Daniele Silvestro, pers. comm.). We, therefore, used the Pleistocene value for both the Pleistocene and Holocene.

We carried out one round of random sampling based on the preservation rate defined above for each continent, separately for each branch. We first assessed sampling on all external branches on all continents and accepted presence whenever sampling was simulated to have taken place. After this, we assessed internal branches ranked in order of increasing number of descendants. Whenever an internal branch occurred on, and was sampled in, a continent where none of its occurring descendants were sampled, we considered a random descendant species on the relevant continent as sampled instead. The logic of this treatment can be understood by looking at a small clade of two species, with a long internal branch and an extinction of both species nearly immediately after speciation. In such cases, the probability of sampling both species would be limited but it is more likely that we would sample the lineage before speciation. If we only looked at sampling in external branches, we would thus drastically underestimate the diversity resulting from incomplete sampling.

In order to test the importance of incomplete sampling, we repeated all analyses from 5.2.2 on both the full random trees and the random trees with simulated sampling. After this, we assessed if the effects we observed in the empirical trees matched the differences between the simulated trees with incomplete and complete sampling, in which case extreme care would be needed in the interpretation of the results.

# **Additional references**

- 50) Tedford, R. H. & Gustafson, E. P. First North American record of the extinct panda *Parailurus*. *Nature* **265**, 621–623 (1977)
- 51) Rambaut, A., Drummond, A. J., Xie, D., Baele, G. & Suchard, M. A. Posterior summarization in bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904 (2018)
- 52) Ronquist, F., Lartillot, N. & Phillips, M. J. Closing the gap between rocks and clocks using total–evidence dating. *Philos. Trans. Royal Soc. B* **371**, 20150136 (2016)

- 53) Wesley-Hunt, G., & Flynn J. J. 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 (2005)
- 54) Meredith, R. W. et al. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on  
mammal diversification. *Science* **334**, 521–524 (2011)
- 55) Lanfear, R., Calcott, B., Ho, S. Y. W. & Guindon, S. PartitionFinder: combined selection of  
partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* **29**,  
1695–1701 (2012)
- 56) Werdelin L. & Peigne, S., in *Cenozoic Mammals of Africa*. (eds. Werdelin, L., & Sanders W.  
J.) 603–658 2010. (University of California Press, 2010)
- 57) Figueirido, B., Tseng, Z. J. & Martin-Serra, A. Skull shape evolution in durophagous  
carnivorans. *Evolution* **67**, 1975–1993 (2013)
- 58) Morlo, M., Peigné, S. & Nagel, D. A new species of *Prosansanosmilus*: implications for the  
systematic relationships of the family Barbourfelidae new rank (Carnivora, Mammalia).  
*Zool. J. Linn. Soc.* **140**, 43.61 (2004)
- 59) Willemsen, G. A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta  
Geologica* **101**, 1-115 (1992)
- 60) Koepfli, K. P. et al. Molecular systematics of the Hyaenidae: relationships of a relictual  
lineage resolved by a molecular supermatrix. *Mol. Phylogenet. Evol.* **38**, 603–620 (2006)
- 61) Goldberg, E. E. & Igić, B. Tempo and mode in plant breeding system evolution. *Evolution* **66**,  
3701–3709 (2012)
- 62) Goldberg, E. E., Lancaster, L. T. & Ree, R. H. Phylogenetic inference of reciprocal effects  
between geographic range evolution and diversification. *Syst. Biol.* **60**, 451–465 (2011)
- 63) Fitzjohn, R. G. Diversitree: comparative phylogenetic analyses of diversification in R.  
*Methods Ecol. Evol.* **6**, 1084–1092 (2012)
- 64) Cirot, E. & Bonis, L. Révision du genre *Amphicynodon*, carnivore de l'Oligocène.  
*Palaeontographica Abteilung A* **220**, 103-130 (1992)

- 65) Wang, X. & Tedford, R. H. The Status of genus *Nothocyon* Matthew, 1899 (Carnivora): an Arctoid not a Canid. *J. Vert Paleontol.* **12**, 223–229 (1992)
- 66) Kordikova, E. G., Heizmann, E. P. J. & Mavrin, A. V. Early Miocene Carnivora of Aktau Mountains South Eastern Kazakhstan. *Palaontologische Zeitschrift* **74**, 195–204 (2000)
- 67) Peigné, S. & Heizmann, P. J. The amphicyonidae (mammalia: carnivora) from Ulm-Westtangente MN2, Early Miocene), Baden-Würtemberg, Germany: systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde. Serie B, Geologie und Paläontologie* **343**, 1–131 (2003)
- 68) Ginsburg, L. Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lathan (France). *Geodiversitas* **23**, 381–394 (2001)
- 69) Hunt, R. M. Long-legged pursuit carnivorans (Amphicyonidae, Daphoeninae) from the early Miocene of North America. *Bull. Am. Mus. Nat. Hist.* **318**, 1–95 (2009)
- 70) Raza, S. M., Barry, J. C., Meyer, G. E. & Martin, L. Preliminary report on the geology and vertebrate fauna of the Miocene Manchar Formation, Sind, Pakistan. *J. Vert. Paleontol.* **4**, 584–599 (2010)
- 71) Rybczynski, N., Dawson, M. R. & Tedford, R. H. A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* **458**, 1021–1024 (2009)
- 72) Hartstone-Rose, A. , Kuhn, B. F., Nalla, S., Werdelin, L. & Berger, L. R. A new species of fox from the *Australopithecus sediba* type locality, Malapa, South Africa. *T. Roy. Soc. S. Afr.* **68**, 1–9 (2013)
- 73) Werdelin, L. A new genus and species of Felidae (Mammalia) from Rusinga Island, Kenya, with notes on early Felidae of Africa. *Estudios Geológicos* **67**, 217–222 (2012)
- 74) Peigne, S. *Proailurus*, l'un des plus anciens Felidae (Carnivora) d'Eurasie : systématique et évolution. *Bulletin du Museum National d'Histoire Naturelle Toulouse* **135**, 125–134 (1999)
- 75) Salesa, M. J., Anton, M., Morales, J. & Peigne, S. Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: A new species of Felinae from the Vallesian of Batallones (MN 10, Madrid, Spain). *J. Syst. Palaeontol.* **10**, 87–102 (2012)

- 76) Spassov, N. & Geraads, D. A new felid from the Late Miocene of the Balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). *J. Mamm. Evol.* **22**, 45–56 (2015)
- 77) Solé, F., Falconnet, J. & Yves, L. New proviverrines (Hyaenodontida) from the early Eocene of Europe; phylogeny and ecological evolution of the Proviverrinae. *Zool. J. Linn. Soc.* **171**, 878–917 (2014)
- 78) Zack, S. P. New species of the rare early Eocene creodont *Galecyon* and the radiation of early Hyaenodontidae. *J. Paleontol.* **85**, 315–336 (2011)
- 79) Solé, F. et al. A New Large Hyainailourine from the Bartonian of Europe and Its Bearings on the Evolution and Ecology of Massive Hyaenodonts (Mammalia). *PLoS ONE* **10**, e0141941. (2015)
- 80) Egi, N. et al. Proviverrine hyaenodontids (Creodonta: Mammalia) from the Eocene of Myanmar and a phylogenetic analysis of the proviverrines from the Para-Tethys area. *J. Syst. Palaeontol.* **3**, 337–358 (2005)
- 81) Schmidt-Kittler, N. et al. European reference levels and correlation tables. *Münchner Geowissenschaftliche Abhandlungen A* **10**, 13–31 (1987)
- 82) Lavrov, A. V. New Species of *Paroxyaena* (Hyaenodontidae, Creodonta) from Phosphorites of Quercy, Late Eocene, France. *Paleontol. J.* **41**, 298–311 (2007)
- 83) Werdelin, L. & Solounias, N. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* **30**, 1–104 (1991)
- 84) Werdelin, L. & Lewis, M. E. New species of *Crocota* from the early Pliocene of Kenya, with an overview of early Pliocene hyenas of eastern Africa. *J. Ver. Paleontol.* **28**, 1162–1170 (2008)
- 85) Wang, X. & Qui, Z. Late Miocene Promephitis (Carnivora, Mephitidae) from China. *J. Ver. Paleontol.* **24**, 721–731 (2004)
- 86) Spaulding, M., Flynn, J. J. & Stucky, R. K. A new basal Carnivoramorphan (Mammalia) from the ‘Bridger B’ (Black’s Fork member, Bridger Formation, Bridgerian Nalma, middle Eocene) of Wyoming, USA. *Palaeontology* **53**, 815–832 (2010)

- 87) Smith, T. & Smith, R. A new genus of "miacid" carnivoran from the earliest Eocene of Europe and North America. *Acta Palaeontol. Pol.* **55**, 761–764 (2010)
- 88) Solé, F. New carnivoraforms from the early Eocene of Europe and their bearings on the evolution of the Carnivoraformes. *Palaeontology* **57**, 963–978 (2014)
- 89) Harrison, D. L., Bates, P. J. J., Pearch, M., Michaels, C. & Ward, D. J. New additions to the late middle Eocene mammal fauna of Creechbarrow, Dorset, southern England. *Cainozoic Res.* **9**, 65–85 (2012)
- 90) Heinrich, R. E., Strait, S. G. & Houde, P. Earliest Eocene Miacidae (Mammalia: Carnivora) from Northwestern Wyoming. *J. Paleontol.* **82**, 154–162 (2008)
- 91) Solé, F., Smith, R., Coillot, T., de Bast, E. & Smith, T. Dental and tarsal anatomy of 'Miacis' latouri and a phylogenetic analysis of the earliest carnivoraforms (Mammalia, Carnivoramorpha), *J. Vert. Paleontol.* **34**, 1–21 (2014)
- 92) Raghavan, P., Pickford, M., Patnaik, R. & Gayathri, P. First fossil small-clawed otter, *Amblonyx*, with a note on some specimens of *Lutra*, from the Upper Siwaliks, India. *Estudios Geológicos* **63**, 135–146 (2007)
- 93) Werdelin, L. & Lewis, M. E. *The Carnivora. Koobi Fora Research Project, Vol. 7.* (California Academy of Sciences, 2013)
- 94) Valenciano, A., Abella, J., Göhlich, U. B., Álvarez-Sierra, M. A. & Morales, J. Re-evaluation of the very large *Eomellivora fricki* (Pia, 1939) (Carnivora, Mustelidae, Mellivorinae) from the Late Miocene of Austria. *Palaeontol. Electron.* **20.1.17A**, 1–22 (2017)
- 95) Wolsan, M. & Sotnikova, M. Systematics, evolution, and biogeography of the Pliocene stem meline badger *Ferinestris* (Carnivora: Mustelidae). *Zool. J. Linn. Soc.* **167**, 208–226 (2013)
- 96) Lim, J. D. & Martin, L. D. A new fossil mustelid from the Miocene of South Dakota, USA *Naturwissenschaften* **89**, 270–274 (2002)
- 97) Cherin, M., Iurino, D. A., Willemsen, G. & Carnevale, G. A new otter from the Early Pleistocene of Pantalla (Italy), with remarks on the evolutionary history of Mediterranean Quaternary Lutrinae (Carnivora, Mustelidae). *Quat. Sci. Rev.* **135**, 92–102 (2016)



- 98) Colombero, S., Pavia, M. & Rook, L. *Pannonictis nestii* (Galictinae, Mustelidae), a new  
element in the vertebrate association of the human site of Pirro Nord (Italy, Early Pleistocene).  
*Geodiversitas* **34**, 665–681 (2012)
- 99) Lim, J. D. & Martin, L. D. A new primitive Leptarctine (Mustelidae) from the North  
American Miocene. *Neues Jahrbuch für Geologie und Paläontologie*. **2000**, 632–640 (2000)
- 100) Morales, J. & Pickford, M. Giant bunodont Lutrinae from the Mio-Pliocene of Kenya  
and Uganda. *Estudios Geológicos* **61**, 233–246 (2005)
- 101) Tseng, Z. J., Wang, X. & Stewart, J. D. A new immigrant mustelid (Carnivora,  
Mammalia) from the middle Miocene Temblor Formation of central California. *PaleoBios* **29**,  
13–23 (2009)
- 102) Bonis, L. Précisions sur l'âge géologique et les relations phylétiques de *Mustelictis*  
*olivieri* nov. sp. (Carnivora, Mustelidae), carnassier de l'Oligocène inférieur (MP 22) des  
phosphorites du Quercy (France). *Geobios* **20**, 55–60 (1997)
- 103) Lange, B. Un nouveau Musteline des phosphorites du Quercy *Mustelictis piveteaui*.  
*Comptes rendus de l'Académie des Sciences de Paris, D* **268**, 2870–2872 (1969)
- 104) Barrett, P. Z. Taxonomic and systematic revisions to the North American Nimravidae  
(Mammalia, Carnivora) *PeerJ* **4**, e1658 (2016)
- 105) Peigne, S. New species of *Eofelis* (Carnivora: Nimravidae) from the Phosphorites of  
Quercy, France. *Comptes rendus de l'Académie des Sciences de Paris, D* **330**, 653–658 (2000)
- 106) Averianov, A., Obraztsova, E., Danilov, I., Skutschas, P. & Jin, J. First nimravid skull  
from Asia. *Sci. Rep.* **6**, 25812. (2016)
- 107) Forasiepi, A. M. et al. Carnivorans at the Great American Biotic Interchange: new  
discoveries from the northern neotropics. *Naturwissenschaften* **101**, 965–974 (2014)
- 108) Wolsan, M. & Lange-Badre, B. An arctomorph carnivoran skull from the Phosphorites  
du Quercy and the origin of procyonids. *Acta Palaeontol. Pol.* **41**, 277–298. (1996)
- 109) Hunt, R. M. Evolution of the Aeluroid Carnivora: Diversity of the earliest Aeluroids  
from Eurasia (Quercy, Hsanda-Gol) and the origins of felids. *Am. Mus. Novit.* **3252**, 1–33  
(1998)

- 992 110) Peigné, S. & Bonis, L. The genus *Stenoplesictis* Filhol (Mammalia, Carnivora) from the  
993 Oligocene deposits of the Phosphorites of Quercy, France. *J. Vert. Paleontol.* **19**, 566–575  
994 (1999)
- 995 111) Bonis, L. A new species of *Adelpharctos* (Mammalia, Carnivora, Ursidae) from the late  
996 Oligocene of the “Phosphorites du Quercy” (France). *Estudios Geológicos* **67**, 179–186  
997 (2012)
- 998 112) Abella, J. et al. *Kretzoiarctos* gen. nov., the oldest member of the giant panda clade.  
999 *PLoS ONE* **7**, e48985. (2012)
- 1000 113) Ogino, S., Egi, N., Maung-Thein, Z. M., Htike, T. & Takai, M. New species of  
1001 *Agriotherium* (Mammalia, Carnivora) from the late Miocene to early Pliocene of central  
1002 Myanmar. *J. Asian Earth Sci.* **42**, 408–414 (2011)
- 1003 114) Soibelzon, L. H. & Schubert, B. W. The largest known bear, *Arctotherium angustidens*,  
1004 from the early Pleistocene Pampean region of Argentina: with a discussion of size and diet  
1005 trends in bears. *J. Paleontol.* **85**, 69–75. (2011)
- 1006 115) Bonis, L. Ursidae (Mammalia, Carnivora) from the Late Oligocene of the “Phosphorites  
1007 du Quercy” (France) and a reappraisal of the genus *Cephalogale* Geoffroy, 1862.  
1008 *Geodiversitas* **35**, 787–814. (2013)
- 1009 116) Zhan-Xiang, Q., Tao, D. & Ban-Yue, W. A Late Miocene *Ursavus* skull from Guanghe,  
1010 Gansu, China. *Vertebrata Palasiatica* **52**, 265–302 (2014)
- 1011 117) Meehan, T. J. & Wilson, R. W. New Viverravids from the Torrejonian (Middle  
1012 Paleocene) of Kutz Canyon, New Mexico and the oldest skull of the Order Carnivora. *J.*  
1013 *Paleontol.* **76**, 1091–1101 (2002)
- 1014 118) Beard, K.C. & Dawson, M. R. Early Wasatchian mammals of the red hot local fauna,  
1015 uppermost Tuscaloosa formation, Lauderdale County, Mississippi. *Ann. Carnegie Mus.* **78**,  
1016 193–243 (2009)
- 1017 119) Morales, J. & Pickford, M. A new paradoxurine carnivore from the Late Miocene  
1018 Siwaliks of India and a review of the bunodont viverrids of Africa. *Geobios* **44**, 271–277  
1019 (2011)

- 1020 120) Tomiya, S. A New Basal Caniform (Mammalia: Carnivora) from the Middle Eocene of  
1021 North America and Remarks on the Phylogeny of Early Carnivorans. *PLoS ONE* **6**, e24146  
1022 (2011)
- 1023 121) Spaulding, M. & Flynn, J. J. Phylogeny of the Carnivoramorphs: The impact of  
1024 postcranial characters. *J. Syst. Palaeontol.* **10**, 653–677 (2012)
- 1025 122) Jian, W. & Zhao-Qun, Z. Phylogenetic analysis on Palaeogale (Palaeogalidae,  
1026 Carnivora) based on specimens from Oligocene strata of Saint-Jacques, Nei Mongol.  
1027 *Vertebrata Palasiatica* **10**, 310–334 (2015)
- 1028 123) Peigné, S., Salesa, M. J., Anton, M. & Morales, J. A new Amphicyonine (Carnivora:  
1029 Amphicyonidae) from the Upper Miocene of Batallones-1, Madrid, Spain. *Palaeontology* **51**,  
1030 943–965 (2008)
- 1031 124) Tomiya, S. & Zhijie Tseng, J. Whence the beardogs? Reappraisal of the Middle to Late  
1032 Eocene ‘*Miacis*’ from Texas, USA, and the origin of Amphicyonidae (Mammalia, Carnivora).  
1033 *R. Soc. Open Sci.* **3**, 160518 (2016)
- 1034 125) Robles, J. M. et al. New craniodental remains of the barbourofelid *Albanosmilus*  
1035 *jourdani* (Filhol, 1883) from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula)  
1036 and the phylogeny of the Barbourofelini. *J. Syst. Palaeontol.* **11**, 993–1022 (2013)
- 1037 126) Bardeleben, C., Moore, R. L. & Wayne, R. K. A molecular phylogeny of the Canidae  
1038 based on six nuclear loci. *Mol. Phylogenet. Evol.* **37**, 815–831 (2005)
- 1039 127) Prevosti, F. J. Phylogeny of the large extinct South American Canids (Mammalia,  
1040 Carnivora, Canidae) using a “total evidence” approach. *Cladistics* **26**, 456–481 (2010)
- 1041 128) Slater, G. J. Iterative adaptive radiations of fossil canids show no evidence for  
1042 diversity-dependent trait evolution. *Proc. Natl Acad. Sci. USA* **112**, 4897–4902 (2014)
- 1043 129) Johnson, W. E. et al. The late Miocene radiation of modern Felidae: a genetic  
1044 assessment. *Science* **311**, 73–77 (2006)
- 1045 130) Rothwell, T. Phylogenetic Systematics of North American *Pseudaelurus* (Carnivora:  
1046 Felidae). *Am. Mus. Novit.* **3403**, 1–64 (2003)

- 1047 131) Tseng, Z. T. et al. Himalayan fossils of the oldest known pantherine establish ancient  
1048 origin of big cats. *Proc. R. Soc. B* **281**, 20132686 (2016)
- 1049 132) Werdelin, L. & Flink, T. in *Smilodon: The Iconic Sabertooth* (eds Werdelin, L.,  
1050 McDonald, H. G. & Shaw, C. A.) 14–29 (Johns Hopkins University Press, 2018)
- 1051 133) Koepfli, K. P. et al. Molecular systematics of the Hyaenidae: relationships of a relictual  
1052 lineage resolved by a molecular supermatrix. *Mol. Phylogenet. Evol.* **38**, 603–620 (2006)
- 1053 134) Baskin, J. A. *Bassariscus* and *Probassariscus* (Mammalia, Carnivora, Procyonidae)  
1054 from the early Barstovian (middle Miocene). *J. Ver. Paleontol.* **24**, 709–720. (2004)
- 1055 135) Finarelli, J. A. A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia):  
1056 relationships among basal taxa. *J. Mamm. Evol.* **15**, 231–259 (2008)
- 1057 136) Robles, J. M. et al. New craniodental remains of *Trocharion albanense* Major, 1903  
1058 (Carnivora, Mustelidae), from the Vallès-Penedès Basin (middle to late Miocene, Barcelona,  
1059 Spain). *J. Ver. Paleontol.* **30**, 547–562 (2010)
- 1060 137) Wang, X., Carranza-Castañeda, O. & Aranda-Gómez, J. J. A transitional skunk,  
1061 *Buisnictis metabatos* sp. nov. (Mephitidae, Carnivora), from Baja California Sur and the role  
1062 of southern refugia in skunk evolution. *J. Syst. Palaeontol.* **12**, 291–302 (2014)
- 1063 138) Fulton, T. L. & Strobeck, C. Multiple markers and multiple individuals refine true seal  
1064 phylogeny and bring molecules and morphology back in line. *Proc. R. Soc. B* **277**, 1065–1070  
1065 (2010)
- 1066 139) Berta, A., Kienle, S., Bianucci, G. & Sorbi, S. A Reevaluation of *Pliophoca etrusca*  
1067 (Pinnipedia, Phocidae) from the Pliocene of Italy: Phylogenetic and biogeographic  
1068 implications. *J. Ver. Paleontol.* **35**, e889144 (2015)
- 1069 140) Boessenecker, R. W. & Churchill, M. The oldest known fur seal. *Biol. Lett.* **11**,  
1070 20140835 (2015)
- 1071 141) Cozzuol, M. A. A “northern” seal from the Miocene of Argentina: implications for  
1072 phocid phylogeny and biogeography. *J. Ver. Paleontol.* **21**, 415–421 (2001)

- 1073 142) Kohno, N. Miocene pinniped *Allodesmus* (Mammalia: Carnivora); with special  
1074 reference to the "Mito seal" from Ibaraki Prefecture, Central Japan. *Trans. Proc. Palaeontol.*  
1075 *Soc. Jpn.* **181**, 388–404 (1996)
- 1076 143) Koretsky, I. A. & Rahmat, S. J. A new species of the subfamily Devinophocinae  
1077 (Carnivora, Phocidae) from the central Paratethys. *Rivista Italiana di Paleontologia e*  
1078 *Stratigrafia* **121**, 31–47 (2015)
- 1079 144) Tanaka, Y. & Kohno, N. A new Late Miocene odobenid (Mammalia: Carnivora) from  
1080 Hokkaido, Japan suggests rapid diversification of basal Miocene Odobenids. *PLoS ONE* **10**,  
1081 e0131856 (2015)
- 1082 145) Pages, M. et al. Combined analysis of fourteen nuclear genes refines the Ursidae  
1083 phylogeny. *Mol. Phylogenet. Evol.* **47**, 73–83 (2008)
- 1084 146) Wang, X., McKenna, M. C. & Dashzeveg, D. *Amphicticeps* and *Amphicynodon*  
1085 (Arctoidea, Carnivora) from Hsanda Gol Formation, Central Mongolia and Phylogeny of  
1086 Basal Arctoids with Comments on Zoogeography. *Am. Mu. Novit.* **3483**, 1–57 (2005)
- 1087 147) Morlo, M. & Gunnell, G. F. Small limnocyonines (Hyaenodontidae, Mammalia) from  
1088 the Bridgerian middle Eocene of Wyoming: *Thiocyon*, *Prolimnocyon* and *Imdodon* new genus.  
1089 Contributions from the Museum of Paleontology, University of Michigan **31**, 43–78 (2003)
- 1090 148) Solé, F. New proviverrine genus from the Early Eocene of Europe and the first  
1091 phylogeny of Late Palaeocene-Middle Eocene hyaenodontidans (Mammalia). *J. Syst.*  
1092 *Palaeontol.* **11**, 375–398 (2013)
- 1093 149) Hunt, R. M. Evolution of large carnivores during the Mid-Cenozoic of North America:  
1094 The temnocyonine radiation (Mammalia, Amphicyonidae). *Bull. Am. Mus. Nat. Hist.* **358**, 1–  
1095 153 (2001)
- 1096 150) Hunt, R. M. New amphicyonid carnivorans (Mammalia, Daphoeninae) from the Early  
1097 Miocene of Southeastern Wyoming. *Am. Mus. Novit.* **3385**, 1–41 (2002)
- 1098 151) Hunt, R.M. in *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial*  
1099 *Carnivores, Ungulates, and Ungulatelike Mammals*. (eds. Janis, C. M., Scott, K. M. & Jacobs,  
1100 L. L.) 196–227 (Cambridge University Press, 1998)

- 1101 152) Morales, J., Pickford, M. & Valenciano, A. Systematics of African Amphicyonidae,  
1102 with descriptions of new material from Napak (Uganda) and Grillental (Namibia) *J. Iber.*  
1103 *Geol.* **42**, 131–150 (2016)
- 1104 153) Wang, X. & Tedford, R. H. Fossil dogs (Carnivora, Canidae) from the Sespe and  
1105 Vaqueros formations in Southern California, with comments on relationships of *Phlaocyon*  
1106 *taylori*. *Natural History Museum of Los Angeles County, Science Series* **41**, 225–272 (2008)
- 1107 154) Wang, X. New material of *Osbornodon* from the early Hemingfordian of Nebraska and  
1108 Florida. *Bull. Am. Mus. Nat. Hist.* **279**, 163–176. (2003)
- 1109 155) Nyakatura, K. & Bininda-Emonds, O. R. P. Updating the evolutionary history of  
1110 Carnivora (Mammalia): a new species-level supertree complete with divergence time  
1111 estimates. *BMC Biology* **10**, 12 (2012)
- 1112 156) Bininda-Emonds, O. R. P. et al. The delayed rise of present-day mammals *Nature* **446**,  
1113 507–512 (2007)
- 1114 157) Werdelin, L., Yamaguchi, N., Johnson, W. E. & O'Brien, S. J. in *Biology and*  
1115 *Conservation of Wild Felids* (eds. Macdonald, D. W. & Loveridge, A. J.) 59–82 (Oxford  
1116 University Press, 2010)
- 1117 158) Seymour, K. L. *Panthera onca*. *Mammalian Species*. **340**, 1–9 (1989)
- 1118 159) Barnett, R. et al. Evolution of the extinct sabretooths and the American cheetah-like cat.  
1119 *Cur. Biol.* **15**, R589–90. (2005)
- 1120 160) Werdelin, L. & Lewis, M. E. A revision of the genus *Dinofelis* (Mammalia, Felidae).  
1121 *Zool. J. Linn. Soc.* **132**, 147–258 (2001)
- 1122 161) Patou, M. L. et al. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora)  
1123 with a special emphasis on the Asian *Herpestes*. *Mol. Phylogenet. Evol.* **53**, 69–80 (2009)
- 1124 162) Turner, A., Antón, M. & Werdelin, L. Taxonomy and evolutionary patterns in the fossil  
1125 Hyaenidae of Europe. *Geobios* **41**, 677–687 (2008)
- 1126 163) de Bonis, L. et al. Hyaenidae (Carnivora) from the late Miocene of Toros-Mena. *J. Afr.*  
1127 *Earth Sci.* **58**, 561–579 (2010)

- 1128 164) Morlo, M. & Peigne, S. in. *Carnivoran Evolution: New views on phylogeny, form, and*  
1129 *function* page (eds. Goswami, A. & A. Friscia) 92–140 (Cambridge university press 2010).
- 1130 165) Sotnikova, M. V. A new species of lesser panda *Parailurus* (Mammalia, Carnivora)  
1131 from the Pliocene of Transbaikalia (Russia) and some aspects of ailurine phylogeny.  
1132 *Paleontol. J.* **42**, 90–99. (2008)
- 1133 166) Wang, X. New cranial material of *Simocyon* from China, and its implications for  
1134 phylogenetic relationship to the Red Panda (*Ailurus*). *J. Vert. Paleontol.* **17**, 184-198 (1997)
- 1135 167) Baskin, J. A. in *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial*  
1136 *Carnivores, Ungulates, and Ungulatelike Mammals*. (eds. Janis, C. M., Scott, K. M. & Jacobs,  
1137 L. L.) 152–173 (Cambridge University Press, 1998).
- 1138 168) Nagel, D., Stefen, C. & Morlo, M. The carnivoran community from the Miocene of  
1139 Sandelzhausen (Germany). *Paläontologische Zeitschrift* **83**, 151–174 (2009)
- 1140 169) Prassack, K. A. *Lontra weiri*, sp. nov., a Pliocene river otter (Mammalia, Carnivora,  
1141 Mustelidae, Lutrinae) from the Hagerman Fossil Beds (Hagerman Fossil Beds National  
1142 Monument), Idaho, U.S.A. *J. Vert. Paleontol.* **36**, e1149075 (2016)
- 1143 170) Willemsen, G. F. *Megalenhydris* and its relationship to *Lutra* reconsidered. *Hellenic J.*  
1144 *Geosci.* **41**, 83–87 (2006)
- 1145 171) Cherin, M. & Rook, L. First report of *Lutra simplicidens* (Carnivora, Mustelidae,  
1146 Lutrinae) in the Early Pleistocene of the Upper Valdarno (Italy) and the origin of European  
1147 otters. *Ital. J. Geosci.* **133**, 200-203 (2013)
- 1148 172) Valenciano, A. et al. *Megalictis*, the Bone-Crushing Giant Mustelid (Carnivora,  
1149 Mustelidae, Oligobuninae) from the Early Miocene of North America. *PloS ONE* **11**,  
1150 e0152430 (2016)
- 1151 173) Howell, F. C. & Petter, G. Comparative observations on some middle and upper  
1152 Miocene hyaenids, Genera: *Percrocuta* Kretzoi, *Allohyaena* Kretzoi, *Adcrocuta* Kretzoi  
1153 (Mammalia, Carnivora, Hyaenidae). *Geobios* **18**, 419–491 (1985)

- 1154 174) Paterson, R. S., Rybczynski, N., Kohno, N. & Maddin, H. C. A complete description  
1155 and phylogenetic analysis of *Puijila darwini*, a transitional pinniped. *Canadian Society of*  
1156 *Vertebrate Anatomy conference abstracts* **2016**, 48 (2016)
- 1157 175) Barnes, L. G. A new genus and species of middle Miocene enaliarctine pinniped  
1158 (Mammalia, Carnivora, Otariidae) from the Astoria Formation in coastal Oregon.  
1159 *Contributions in Science* **43**, 1–27 (1992)
- 1160 176) Berta, A. A new species of phocoid pinniped *Pinnarctidion* from the early Miocene of  
1161 Oregon. *J. Vert. Paleontol.* **14**, 405–413 (2010)
- 1162 177) Hunt, R. M. in *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial*  
1163 *Carnivores, Ungulates, and Ungulatelike Mammals*. (eds. Janis, C. M., Scott, K. M. & Jacobs,  
1164 L. L.) 174–195 (Cambridge University Press, 1998)
- 1165 178) Soibelzon, L. H., Tonni, E. P. & Bond, M. The fossil record of South American short-  
1166 faced bears (Ursidae, Tremarctinae). *J. S. Am. Earth Sci.* **20**, 105–113 (2005)
- 1167 179) García, N. & Arsuaga, J. L. *Ursus dolinensis*: a new species of Early Pleistocene ursid  
1168 from Trinchera Dolina, Atapuerca (Spain). *Comptes Rendus de l'Académie des Sciences -*  
1169 *Series IIA - Earth and Planetary Science* **332**, 717–725 (2015)
- 1170 180) Russell, R. D. Effects of climate change on mammalian fauna composition and  
1171 structure during the advent of North American continental glaciation in the Pliocene. Master  
1172 Thesis. The University of Texas at Austin. <http://hdl.handle.net/2152/3226>. (2007).
- 1173 181) Nagel, D. Carnivores from the Middle Miocene deposits of Grund (Lower Austria).  
1174 *Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie,*  
1175 *Geologie und Paläontologie, Anthropologie und Prähistorie* **104**, 297–305 (2002)
- 1176 182) Flunn, J. F. in *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial*  
1177 *Carnivores, Ungulates, and Ungulatelike Mammals*. (eds. Janis, C. M., Scott, K. M. & Jacobs,  
1178 L. L.) 110–123 (Cambridge University Press, 1998)
- 1179 183) Gunnell, G. F. in *Evolution of Tertiary Mammals of North America Volume 1:*  
1180 *Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. (eds. Janis, C. M., Scott, K.  
1181 M. & Jacobs, L. L.) 91–109 (Cambridge University Press, 1998)



1182        184)        Solé, F., Gheerbrant, E. & Godinot, M. New data on the Oxyaenidae from the Early  
 1183                Eocene of Europe; biostratigraphic, paleobiogeographic and paleoecologic implications  
 1184                *Palaeontol. Electron.* **14**, 13A (2011)

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**Table S1: Continental pre-dispersal success.**

The test statistic is the logarithm of the ratio between the diversification rate at the time of dispersal of dispersers and the median of the diversification rates of all species present in the source continent just before the dispersal event (see Fig. 1).

The p-values for the global rate and for the temporal age effect are the probability of being different from 0. For models with different patterns depending on the source and or target continent, the p-value is based on the probability of being different from the estimated global rate.

	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals
Simplest model			
Global	0.0900 (0.0199) <sup>***</sup>	0.0835 (0.0194) <sup>***</sup>	0.0785 (0.0190) <sup>***</sup>
AIC	126.202	120.325	122.352
Temporal variation			
Global	0.1229 (0.0260) <sup>***</sup>	0.1122 (0.0259) <sup>***</sup>	0.1068 (0.0255) <sup>***</sup>
Age	-0.0021 (0.0012) <sup>‘</sup>	-0.0018 (0.0012) <sup>‘</sup>	-0.0018 (0.0012) <sup>‘</sup>
AIC	123.159	118.431	120.740
Variation between source continent			
From Africa	0.0519 (0.0599)	0.0487 (0.0577)	0.0422 (0.0570)
From Eurasia	0.1287 (0.0260)	0.1226 (0.0260)	0.1185 (0.0253)
From North America	0.0386 (0.0331)	0.0303 (0.0330)	0.0240 (0.0329)
From South America	0.1052 (0.1528)	0.1002 (0.1439)	0.0980 (0.1407)
AIC	121.666	115.841	114.379
Variation between target continent			
To Africa	0.1191 (0.0374)	0.1160 (0.0373)	0.1137 (0.0366)
To Eurasia	0.0488 (0.0340)	0.0453 (0.0343)	0.0379 (0.0337)
To North America	0.1351 (0.0356)	0.1260 (0.0360)	0.1214 (0.0346)
To South America	0.0192 (0.0513)	0.0017 (0.0503)	-0.0009 (0.0495)
AIC	121.745	114.352	114.924
Variation between source and target continent			
Africa to Eurasia	0.0519 (0.0600)	0.0487 (0.0577)	0.0422 (0.0570)
Eurasia to Africa	0.1191 (0.0374)	0.1161 (0.0373)	0.1137 (0.0366)
Eurasia to North America	0.1372 (0.0368)	0.1281 (0.0370)	0.1231 (0.0357)
North America to Eurasia	0.0479 (0.0420)	0.0439 (0.0428)	0.0362 (0.0429)
North to South America	0.0192 (0.0513)	0.0018 (0.0503)	-0.0009 (0.0496)
South to North America	0.1051 (0.1529)	0.1002 (0.1439)	0.098 (0.1407)
AIC	124.174	116.893	117.311

<sup>‘</sup> 0.10>P>0.05 \* 0.05>P>0.01 \*\* 0.01>P>0.001 \*\*\* 0.001>P

**Table S2: Global pre-dispersal success.**

The test statistic is the logarithm of the ratio between the diversification rate at the time of dispersal of dispersers and the median of the diversification rates of all species alive globally just before the dispersal event (see Fig. 1).

The p-values for global rate and for the temporal age effect are the probability of being different from 0. For models with different patterns depending on the source and/ or target continent, the p-value is based on the probability of being different from the estimated global rate.

	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals
Simplest model			
Global	0.1295 (0.0212) <sup>***</sup>	0.1205 (0.0205) <sup>***</sup>	0.1142 (0.0206) <sup>***</sup>
AIC	150.586	159.119	159.394
Temporal variation			
Global	0.1757 (0.0271) <sup>***</sup>	0.1636 (0.0272) <sup>***</sup>	0.1562 (0.0271) <sup>***</sup>
Age	-0.0029 (0.0013) <sup>*</sup>	-0.0027 (0.0013) <sup>*</sup>	-0.0026 (0.0013) <sup>*</sup>
AIC	141.937	152.941	147.405
Variation between source continent			
From Africa	0.1101 (0.0651)	0.1010 (0.0612)	0.940 (0.0631)
From Eurasia	0.1516 (0.0266)	0.1455 (0.0267)	0.1414 (0.0266)
From North America	0.1005 (0.0355)	0.0863 (0.0353)	0.0759 (0.0353)
From South America	0.0892 (0.1428)	0.1119 (0.1442)	0.1122 (0.1416)
AIC	153.595	159.794	156.610
Variation between target continent			
To Africa	0.1476 (0.0368)	0.1468 (0.0372)	0.1443 (0.0371)
To Eurasia	0.1131 (0.0373)	0.1050 (0.0362)	0.0959 (0.0369)
To North America	0.1508 (0.0369)	0.1420 (0.0370)	0.1373 (0.0358)
To South America	0.0710 (0.0528)	0.0423 (0.0528)	0.0324 (0.0526)
AIC	154.452	158.814	157.279
Variation between source and target continent			
Africa to Eurasia	0.1100 (0.0651)	0.1009 (0.0612)	0.0941 (0.0631)
Eurasia to Africa	0.1476 (0.0368)	0.1468 (0.0372)	0.1443 (0.0371)
Eurasia to North America	0.1550 (0.0383)	0.1440 (0.0385)	0.1391 (0.0375)
North America to Eurasia	0.1151 (0.0446)	0.1077 (0.0443)	0.0972 (0.0449)
North to South America	0.0710 (0.0528)	0.0443 (0.0529)	0.0324 (0.0527)
South to North America	0.0892 (0.1418)	0.1119 (0.1442)	0.1124 (0.1415)
AIC	156.490	161.911	159.934

<sup>\*</sup> 0.10>P>0.05 <sup>\*</sup> 0.05>P>0.01 <sup>\*\*</sup> 0.01>P>0.001 <sup>\*\*\*</sup> 0.001>P

**Table S3: Continental pre-dispersal success in simulations.**

Values are given for both the full simulated tree and the simulated incomplete sampling. The difference is the median difference between estimates for each tree. In parentheses, we list the number of times where this difference is negative (i.e. how many times the value is larger for incomplete sampling than the full tree).

The test statistic is the logarithm of the ratio between the diversification rate at the time of dispersal of dispersers and the median of the diversification rates of all species in the source continent from just before the dispersal event (see Fig. 1).

For models with different patterns based on the source and/ or target continent, the p-value is based on the probability of being different from the estimated global rate. The p-value for the difference is based on a two-tailed binomial distribution and tests if incomplete sampling is equally likely to lead to larger and smaller values than complete sampling.

	Full tree	Incomplete sampling	Difference
Simplest model			
Global	0.0192 (0.0149)	0.0207 (0.0167)	$-1.75 \times 10^{-3}$ (57/100)
AIC	146.691	126.717	
Temporal variation			
Global	0.0288 (0.0233)	0.0316 (0.0256)	$-1.75 \times 10^{-3}$ (57/100)
Age	-0.0007 (0.0010)	-0.0008 (0.0012)	$1.18 \times 10^{-4}$ (43/100)
AIC	146.503	125.441	
Variation between source continent			
From Africa	NA	NA	NA
From Eurasia	0.0182 (0.0307)	0.0201 (0.0367)	$-6.06 \times 10^{-3}$ (61/100)*
From North America	0.0159 (0.0194)	0.0161 (0.0204)	$-7.62 \times 10^{-5}$ (50/100)
From South America	0.0352 (0.0377)	0.0450 (0.0451)	$-1.15 \times 10^{-2}$ (66/100)**
AIC	148.964	129.271	
Variation between target continent			
To Africa	-0.0019 (0.0560)	-0.0007 (0.0592)	$1.91 \times 10^{-3}$ (47/100)
To Eurasia	0.0323 (0.0283)	0.0339 (0.0282)	$-1.88 \times 10^{-3}$ (54/100)
To North America	0.0293 (0.0257)	0.0376 (0.0310)	$-7.93 \times 10^{-3}$ (61/100)*
To South America	-0.0020 (0.0286)	-0.0035 (0.0291)	$2.30 \times 10^{-3}$ (47/100)
AIC	146.629	127.837	
Variation between source and target continent			
Africa to Eurasia	NA	NA	NA
Eurasia to Africa	-0.0019 (0.0560)	-0.0070 (0.0592)	$1.91 \times 10^{-3}$ (47/100)
Eurasia to North America	0.0238 (0.0362)	0.0313 (0.0437)	$-8.36 \times 10^{-3}$ (60/100)*
North America to Eurasia	0.0323 (0.0283)	0.0338 (0.0282)	$-1.88 \times 10^{-3}$ (54/100)
North to South America	-0.0020 (0.0286)	-0.0035 (0.0291)	$2.30 \times 10^{-3}$ (47/100)
South to North America	0.0352 (0.0377)	0.0450 (0.0451)	$-1.15 \times 10^{-2}$ (66/100)**
AIC	148.457	129.797	

\*  $0.10 > P > 0.05$  \*  $0.05 > P > 0.01$  \*\*  $0.01 > P > 0.001$  \*\*\*  $0.001 > P$

**Table S4: Global pre-dispersal success in simulations.**

Values are given for both the full simulated tree and the simulated incomplete sampling. The difference is the median difference between estimates for each tree. In parentheses, we list the number of times where this difference is negative (i.e. how many times the value is larger for incomplete sampling than the full tree).

The test statistic is the logarithm of the ratio between the diversification rate at the time of dispersal of dispersers and the median diversification rates of all species alive globally just before the dispersal event (see Fig. 1).

For models with different patterns based on the source and/ or target continent, the p-value is based on the probability of being different from the estimated global rate. The p-value for the difference is based on a two-tailed binomial distribution and tests if incomplete sampling is equally likely to lead to larger and smaller values than complete sampling.

	Full tree	Incomplete sampling	Difference
Simplest model			
Global	0.0192 (0.0149)	0.0207 (0.0167)	$-1.75 \times 10^{-3}$ (57/100)
AIC	146.691	126.717	
Temporal variation			
Global	0.0288 (0.0233)	0.0316 (0.0256)	$-1.75 \times 10^{-3}$ (57/100)
Age	-0.0007 (0.0010)	-0.0008 (0.0012)	$1.18 \times 10^{-4}$ (43/100)
AIC	146.503	125.441	
Variation between source continent			
From Africa	NA	NA	NA
From Eurasia	0.0182 (0.0307)	0.0201 (0.0367)	$-6.06 \times 10^{-3}$ (61/100)*
From North America	0.0159 (0.0194)	0.0161 (0.0204)	$-7.62 \times 10^{-5}$ (50/100)
From South America	0.0352 (0.0377)	0.0450 (0.0451)	$-1.15 \times 10^{-2}$ (66/100)**
AIC	148.964	129.271	
Variation between target continent			
To Africa	-0.0019 (0.0560)	-0.0007 (0.0592)	$1.91 \times 10^{-3}$ (47/100)
To Eurasia	0.0323 (0.0283)	0.0339 (0.0282)	$-1.88 \times 10^{-3}$ (54/100)
To North America	0.0293 (0.0257)	0.0376 (0.0310)	$-7.93 \times 10^{-3}$ (61/100)*
To South America	-0.0020 (0.0286)	-0.0035 (0.0291)	$2.30 \times 10^{-3}$ (47/100)
AIC	146.629	127.837	
Variation between source and target continent			
Africa to Eurasia	NA	NA	NA
Eurasia to Africa	-0.0019 (0.0560)	-0.0070 (0.0592)	$1.91 \times 10^{-3}$ (47/100)
Eurasia to North America	0.0238 (0.0362)	0.0313 (0.0437)	$-8.36 \times 10^{-3}$ (60/100)*
North America to Eurasia	0.0323 (0.0283)	0.0338 (0.0282)	$-1.88 \times 10^{-3}$ (54/100)
North to South America	-0.0020 (0.0286)	-0.0035 (0.0291)	$2.30 \times 10^{-3}$ (47/100)
South to North America	0.0352 (0.0377)	0.0450 (0.0451)	$-1.15 \times 10^{-2}$ (66/100)**
AIC	148.457	129.797	
* 0.10>P>0.05 * 0.05>P>0.01 ** 0.01>P>0.001 *** 0.001>P			

**Table S5: Global post-dispersal success.**

The test statistic is the square root of the mean number of species alive after a given number of million years (3, 5 or 7) after dispersal, divided by the mean for all species globally. Significance for the estimate is the probability of being different from 1 (the random expectation), for age it is the probability of being different from 0, and for models with different patterns based on the source and/ or target continent, it is based on the probability of being different from the estimated global rate.

	3 Million years			5 Million years			7 Million years		
	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals
Simplest model									
Global	1.5463 (0.0455)***	1.4808 (0.0495)***	1.4500 (0.0520)***	1.5401 (0.0693)***	1.4606 (0.0730)***	1.4182 (0.0741)***	1.4846 (0.0928)***	1.3909 (0.0939)***	1.3423 (0.0942)***
AIC	558.620	571.858	574.258	646.651	644.155	642.460	700.557	685.244	679.522
Temporal variation									
Global	1.5167 (0.0455)***	1.4427 (0.0732)***	1.4109 (0.0762)***	1.5695 (0.0993)***	1.4782 (0.1049)***	1.4301 (0.1090)***	1.5224 (0.1441)***	1.4120 (0.1489)**	1.3600 (0.1492)*
Age	0.0016 (0.0033)	0.0022 (0.0037)	0.0022 (0.0038)	-0.0012 (0.0046)	-0.0006 (0.0048)	-0.0004 (0.0050)	-0.0017 (0.0056)	-0.0009 (0.0058)	-0.0008 (0.0057)
AIC	557.176	572.007	573.035	647.353	645.788	643.953	701.968	686.662	681.166
Variation between source continent									
From Africa	1.4552 (0.1200)	1.3819 (0.1248)	1.3411 (0.1318)	1.4119 (0.1694)	1.3555 (0.1778)	1.3133 (0.1844)	1.3539 (0.2250)	1.2732 (0.2314)	1.2362 (0.2336)
From Eurasia	1.5800 (0.0577)	1.5106 (0.0624)	1.4763 (0.0648)	1.5725 (0.0837)	1.4938 (0.0877)	1.4487 (0.0890)	1.5377 (0.1155)	1.4492 (0.1192)	1.3973 (0.1210)
From North America	1.5275 (0.0794)	1.4727 (0.0894)	1.4501 (0.0944)	1.5318 (0.1240)	1.4467 (0.1314)	1.4056 (0.1315)	1.4459 (0.1569)	1.3431 (0.1600)	1.2938 (0.1613)
AIC	555.792	569.375	572.882	647.004	645.084	645.226	703.163	687.947	682.634
Variation between target continent									
To Africa	1.5264 (0.0862)	1.4464 (0.0885)	1.4090 (0.0912)	1.4806 (0.1152)	1.3990 (0.1184)	1.3565 (0.1203)	1.4580 (0.1538)	1.3993 (0.1583)	1.3650 (0.1613)
To Eurasia	1.5405 (0.0772)	1.4700 (0.0838)	1.4383 (0.0893)	1.5037 (0.1131)	1.4262 (0.1183)	1.3857 (0.1203)	1.4274 (0.1447)	1.3312 (0.1475)	1.2839 (0.1490)
To North America	1.6248 (0.0810)	1.5622 (0.0851)	1.5306 (0.0885)	1.6591 (0.1234)	1.5781 (0.1241)	1.5358 (0.1255)	1.5990 (0.1588)	1.4831 (0.1614)	1.4171 (0.1631)
To South America	1.3749 (0.1507)	1.3526 (0.1628)	1.3460 (0.1678)	1.5047 (0.2702)	1.4004 (0.2834)	1.3456 (0.2821)	1.3713 (0.3859)	1.2702 (0.3997)	1.2446 (0.4160)
AIC	556.521	570.46	575.529	645.487	644.715	645.327	704.990	690.138	683.700
Variation between source and target continent									
Africa to Eurasia	1.4554 (0.1196)	1.3819 (0.1245)	1.3411 (0.1315)	1.4219 (0.1691)	1.3557 (0.1777)	1.3132 (0.1842)	1.3538 (0.2251)	1.2731 (0.2316)	1.2362 (0.2340)
Eurasia to Africa	1.5264 (0.0862)	1.4464 (0.0885)	1.4091 (0.0912)	1.4806 (0.1152)	1.3991 (0.1184)	1.3565 (0.1203)	1.4579 (0.1540)	1.3993 (0.1583)	1.3649 (0.1614)
Eurasia to North America	1.6284 (0.0814)	1.5675 (0.0857)	1.5368 (0.0893)	1.6573 (0.1233)	1.5767 (0.1243)	1.5312 (0.1257)	1.5989 (0.1590)	1.4827 (0.1616)	1.4167 (0.1634)
North America to Eurasia	1.5829 (0.0945)	1.5122 (0.1043)	1.4842 (0.1108)	1.5392 (0.1355)	1.4572 (0.1428)	1.4178 (0.1431)	1.4570 (0.1707)	1.3539 (0.1735)	1.3011 (0.1732)
North to South America	1.3748 (0.1507)	1.3527 (0.1627)	1.3460 (0.1678)	1.5046 (0.2702)	1.4005 (0.2835)	1.3458 (0.2822)	1.3714 (0.3862)	1.2700 (0.4001)	1.2447 (0.4164)
AIC	552.733	568.98	568.980	645.240	645.840	646.678	706.231	690.988	685.240

\* 0.10>P>0.05 \* 0.05>P>0.01 \*\* 0.01>P>0.001 \*\*\* 0.001>P

**Table S6: Continental post-dispersal success.**

The test statistic is the square root of the mean number of species alive after a given number of million years (3, 5 or 7) after dispersal, divided by the mean for species in the target continent. Significance for the estimate is the probability of being different from 1 (the random expectation), for age it is the probability of being different from 0 and for models with different patterns based on target and/ or source continent it is based on the probability of being different from the estimated global rate.

	3 Million years			5 Million years			7 Million years		
	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals	1.0-million-year intervals	0.5-million-year intervals	0.25-million-year intervals
Simplest model									
Global	1.5321 (0.0463)***	1.4666 (0.0494)***	1.4361 (0.0517)***	1.5197 (0.0699)***	1.4433 (0.0730)***	1.4018 (0.0739)***	1.4622 (0.0952)***	1.3695 (0.0956)***	1.3203 (0.0953)**
AIC	564.200	570.942	572.367	644.765	638.300	642.178	697.054	677.991	671.446
Temporal variation									
Global	1.4876 (0.0679)***	1.4089 (0.0734)***	1.3775 (0.0761)***	1.5430 (0.1023)***	1.4554 (0.1066)***	1.4093 (0.1090)***	1.5087 (0.1477)***	1.4004 (0.1509)**	1.3468 (0.1485)*
Age	0.0025 (0.0033)	0.0031 (0.0037)	0.0032 (0.0039)	-0.0008 (0.0048)	-0.0004 (0.0050)	-0.0002 (0.0051)	-0.0020 (0.0058)	-0.0013 (0.0060)	-0.0012 (0.0059)
AIC	564.603	569.47	568.672	644.363	638.872	642.141	696.491	679.063	671.775
Variation between source continent									
From Africa	1.4041 (0.1199)	1.3302 (0.1234)	1.2907 (0.1303)	1.3310 (0.1674)	1.2666 (0.1741)	1.2263 (0.1800)	1.2344 (0.2187)	1.1587 (0.2241)	1.1230 (0.2282)
From Eurasia	1.6068 (0.0603)	1.5322 (0.0643)	1.4957 (0.0668)	1.6058 (0.0888)	1.5246 (0.0912)	1.4784 (0.0922)	1.5818 (0.1227)	1.4863 (0.1263)	1.4311 (0.1267)
From North America	1.4560 (0.0832)	1.4130 (0.0917)	1.3945 (0.0966)	1.4491 (0.1272)	1.3791 (0.1362)	1.3405 (0.1370)	1.3552 (0.1654)	1.2684 (0.1682)	1.2211 (0.1699)
AIC	556.673	563.667	566.153	643.753	638.831	640.397	693.680	676.812	668.212
Variation between target continent									
To Africa	1.5341 (0.0895)	1.4484 (0.0915)	1.4088 (0.0938)	1.4465 (0.1199)	1.3607 (0.1207)	1.3171 (0.1210)	1.3871 (0.1569)	1.3221 (0.1607)	1.2858 (0.1623)
To Eurasia	1.5136 (0.0785)	1.4472 (0.0850)	1.4160 (0.0911)	1.4491 (0.1161)	1.3761 (0.1232)	1.3360 (0.1248)	1.3552 (0.1516)	1.2667 (0.1541)	1.2212 (0.1569)
To North America	1.6714 (0.0839)*	1.6016 (0.0879)	1.5681 (0.0916)	1.7535 (0.1287)	1.6694 (0.1278)*	1.6222 (0.1303)*	1.7334 (0.1690)	1.6065 (0.1723)	1.5354 (0.1730)
To South America	1.1418 (0.1472)**	1.1366 (0.1643)*	1.1379 (0.1695)*	1.1965 (0.2684)	1.1262 (0.2927)	1.0809 (0.2894)	0.9792 (0.3900)	0.9267 (0.4108)	0.9016 (0.4124)
AIC	550.297	562.453	563.308	635.087	632.828	635.919	690.538	676.756	666.862
Variation between source and target continent									
Africa to Eurasia	1.4042 (0.1183)	1.3303 (0.1222)	1.2907 (0.1292)	1.3311 (0.1658)	1.2666 (0.1727)	1.2263 (0.1787)	1.2345 (0.2171)	1.1588 (0.2232)	1.1231 (0.2276)
Eurasia to Africa	1.5341 (0.0894)	1.4484 (0.0914)	1.4089 (0.0936)	1.4466 (0.1198)	1.3607 (0.1206)	1.3171 (0.1208)	1.3871 (0.1568)	1.3220 (0.1607)	1.2857 (0.1624)
Eurasia to North America	1.6724 (0.0843)	1.6055 (0.0884)	1.5729 (0.0922)	1.7514 (0.1285)*	1.6677 (0.1282)	1.6212 (0.1308)	1.7333 (0.1690)	1.6061 (0.1724)	1.5351 (0.1732)
North America to Eurasia	1.5677 (0.0971)	1.5029 (0.1055)	1.4753 (0.1130)	1.5002 (0.1395)	1.4238 (0.1487)	1.3847 (0.1483)	1.4048 (0.1791)	1.3101 (0.1824)	1.2581 (0.1827)
North to South America	1.1420 (0.1470)**	1.1366 (0.1641)*	1.1379 (0.1692)*	1.1966 (0.2682)	1.1263 (0.2925)	1.0810 (0.2892)	0.9793 (0.3897)	0.9268 (0.4108)	0.9014 (0.4126)
AIC	546.753	557.481	559.768	634.213	632.508	634.331	691.426	678.12	667.401

\* 0.10>P>0.05 \* 0.05>P>0.01 \*\* 0.01>P>0.001 \*\*\* 0.001>P

**Table S7: Post-dispersal success in simulations.**

The test statistic is the square root of the mean number of species alive after 5 million years after dispersal divided by the mean value for all other species globally. Significance for the estimate is the probability of being different from 1 (the random expectation), for age it is the probability of being different from 0 and for models with different patterns based on the source and/ or target continent it is based on the probability of being different from the estimated global rate.

Values are given for both the full simulated tree and the simulated incomplete sampling. The difference is the median difference between estimates for each tree. In parentheses, we list the number of times where this difference is negative (i.e. how many times the value is larger for incomplete sampling than the full tree). The p-value for the difference is based on a two-tailed binomial distribution and tests if incomplete sampling is equally likely to lead to larger and smaller values than complete sampling.

	<i>Global post-dispersal success</i>			<i>Continental post-dispersal success</i>		
	Full tree	Incomplete sampling	Difference	Full tree	Incomplete sampling	Difference
Simplest model						
Global	1.0696 (0.0816)	1.0734 (0.0929)	-6.33 x 10 <sup>-4</sup> (52/100)	1.1226 (0.726)	1.1591 (0.0809)	-3.46 x 10 <sup>-2</sup> (77/100)***
AIC	1252.351	973.833		1251.687	998.474	
Temporal variation						
Global	1.0698 (0.1158)	1.0755 (0.1190)	5.36 x 10 <sup>-3</sup> (47/100)	1.1317 (0.1105)	1.1614 (0.1259)	-2.39 x 10 <sup>-3</sup> (67/100)***
Age	-0.0001 (0.0038)	-0.0003 (0.0045)	5.54 x 10 <sup>-5</sup> (50/100)	-0.0004 (0.0040)	-0.0004 (0.0049)	-4.08 x 10 <sup>-4</sup> (57/100)
AIC	1253.484	974.824		1252.211	998.50	
Variation between source continent						
From Africa	NA	NA	NA	NA	NA	NA
From Eurasia	1.0787 (0.1277)	1.0734 (0.1725)	6.90 x 10 <sup>-3</sup> (41/100)*	1.1020 (0.1321)	1.0951 (0.1701)	1.20 x 10 <sup>-2</sup> (42/100)
From North America	1.0604 (0.0941)	1.0669 (0.1025)	-1.67 x 10 <sup>-3</sup> (51/100)	1.1589 (0.0924)	1.2094 (0.1043)	-4.54 x 10 <sup>-2</sup> (51/100)
From South America	1.0806 (0.1543)	1.1042 (0.1765)	-2.23 x 10 <sup>-2</sup> (59/100)*	1.1048 (0.1597)	1.0258 (0.1791)	-7.86 x 10 <sup>-3</sup> (58/100)
AIC	1254.421	973.611		1252.495	995.151	
Variation between target continent						
To Africa	0.7306 (0.2327)	0.7528 (0.2874)	-9.21 x 10 <sup>-3</sup> (52/100)	0.9970 (0.2512)	1.0127 (0.3101)	1.66 x 10 <sup>-2</sup> (47/100)
To Eurasia	1.0966 (0.1210)	1.0825 (0.1236)	1.84 x 10 <sup>-2</sup> (37/100)*	1.1913 (0.1198)	1.2262 (0.1444)	-3.71 x 10 <sup>-2</sup> (63/100)*
To North America	1.1493 (0.1153)	1.1567 (0.1329)	-3.02 x 10 <sup>-3</sup> (51/100)	1.0794 (0.1236)	1.0766 (0.1397)	4.64 x 10 <sup>-3</sup> (48/100)
To South America	1.0266 (0.1238)	1.0477 (0.1291)	-1.64 x 10 <sup>-2</sup> (62/100)*	1.1297 (0.1273)	1.1822 (0.1247)	-4.25 x 10 <sup>-2</sup> (68/100)***
AIC	1240.512	967.294		1253.755	991.077	
Variation between source and target continent						
Africa to Eurasia	NA	NA	NA	NA	NA	
Eurasia to Africa	0.7305 (0.2326)	0.7528 (0.2875)	-9.21 x 10 <sup>-3</sup> (52/100)	0.9970 (0.2512)	1.0124 (0.3100)	1.66 x 10 <sup>-2</sup> (47/100)
Eurasia to North America	1.2061 (0.1433)	1.2085 (0.1793)	3.91 x 10 <sup>-3</sup> (48/100)	1.1325 (0.1494)	1.1219 (0.1842)	1.42 x 10 <sup>-2</sup> (42/100)
North America to Eurasia	1.0966 (0.1209)	1.0825 (0.1236)	1.84 x 10 <sup>-2</sup> (37/100)*	1.1913 (0.1198)	1.2262 (0.1445)	-3.71 x 10 <sup>-2</sup> (63/100)*
North to South America	1.0267 (0.1238)	1.0477 (0.1291)	-1.64 x 10 <sup>-2</sup> (62/100)*	1.1297 (0.1273)	1.1823 (0.1246)	-4.25 x 10 <sup>-2</sup> (68/100)***
South to North America	1.0806 (0.1537)	1.1042 (0.1759)	-2.23 x 10 <sup>-2</sup> (59/100)*	1.0148 (0.1596)	1.0257 (0.1790)	-7.86 x 10 <sup>-3</sup> (58/100)
AIC	1238.486	967.047		1254.992	991.629	

\* 0.10>P>0.05 \* 0.05>P>0.01 \*\* 0.01>P>0.001 \*\*\* 0.001>P



**Table S8: Additional species not in NOW or PBDB.**

Family	Genus	Species	Reference
Amphicyodontinae	<i>Amphicynodon</i>	<i>brachyrostris</i>	64
Amphicyodontinae	<i>Amphicynodon</i>	<i>cephalocalinus</i>	64
Amphicyodontinae	<i>Amphicynodon</i>	<i>chardini</i>	64
Amphicyodontinae	<i>Amphicynodon</i>	<i>crassirostris</i>	64
Amphicyodontinae	<i>Nothocyon</i>	<i>geismarianus</i>	65
Amphicyonidae	<i>Askazansoria</i>	<i>mavrini</i>	66
Amphicyonidae	<i>Haplocyonoides</i>	<i>suevicus</i>	67
Amphicyonidae	<i>Haplocyonopsis</i>	<i>crassidens</i>	67
Amphicyonidae	<i>Janvierocyon</i>	<i>pontignensis</i>	68
Amphicyonidae	<i>Temnocyon</i>	<i>ferox</i>	69
Amphicyonidae	<i>Vishnucyon</i>	<i>chinjiensis</i>	70
Barbourofelidae	<i>Afrosmilus</i>	<i>turkanae</i>	56
Barbourofelidae	<i>Vampyrictis</i>	<i>vipera</i>	56
Basal Pinnipedia	<i>Puijila</i>	<i>darwini</i>	71
Canidae	<i>Nyctereutes</i>	<i>terblanchei</i>	56
Canidae	<i>Vulpes</i>	<i>skinneri</i>	72
Felidae	<i>Asilifelis</i>	<i>coteae</i>	73
Felidae	<i>Proailurus</i>	<i>bournonnensis</i>	74
Felidae	<i>Proailurus</i>	<i>major</i>	74
Felidae	<i>Styriofelis</i>	<i>vallesiensis</i>	75
Felidae	<i>Yoshi</i>	<i>garevskii</i>	76
Herpestidae	<i>Herpestes</i>	<i>debilis</i>	56
Herpestidae	<i>Herpestides</i>	<i>aequatorialis</i>	56
Herpestidae	<i>Leptoplesictis</i>	<i>mbitensis</i>	56
Herpestidae	<i>Leptoplesictis</i>	<i>rangwai</i>	56
Herpestidae	<i>Suricata</i>	<i>major</i>	56
Hyaenodontidae	<i>Alienetherium</i>	<i>buxwilleri</i>	77
Hyaenodontidae	<i>Allopterodon</i>	<i>bulbosus</i>	77
Hyaenodontidae	<i>Allopterodon</i>	<i>minor</i>	77
Hyaenodontidae	<i>Cynohyaenodon</i>	<i>cailuxy</i>	77
Hyaenodontidae	<i>Cynohyaenodon</i>	<i>lautricensis</i>	77
Hyaenodontidae	<i>Cynohyaenodon</i>	<i>ruetimeyeri</i>	77
Hyaenodontidae	<i>Cynohyaenodon</i>	<i>trux</i>	77
Hyaenodontidae	<i>Eurotherium</i>	<i>matthesi</i>	77
Hyaenodontidae	<i>Galecyon</i>	<i>chronius</i>	78
Hyaenodontidae	<i>Galecyon</i>	<i>peregrinus</i>	78
Hyaenodontidae	<i>Hyaenodon</i>	<i>rossignoli</i>	79
Hyaenodontidae	<i>Kerberos</i>	<i>langebadrae</i>	79
Hyaenodontidae	<i>Masrasector</i>	<i>ligabuei</i>	80
Hyaenodontidae	<i>Matthodon</i>	<i>tritens</i>	77
Hyaenodontidae	<i>Paenoxyaenoides</i>	<i>liguritor</i>	77
Hyaenodontidae	<i>Paracynohyaenodon</i>	<i>schlosseri</i>	77
Hyaenodontidae	<i>Parapterodon</i>	<i>lostangensis</i>	81
Hyaenodontidae	<i>Paroxyaena</i>	<i>galliae</i>	82
Hyaenodontidae	<i>Paroxyaena</i>	<i>pavlovi</i>	82
Hyaenodontidae	<i>Praecodens</i>	<i>acutus</i>	81
Hyaenodontidae	<i>Protoproviverra</i>	<i>palaeonictides</i>	77
Hyaenodontidae	<i>Quercytherium</i>	<i>simplicidens</i>	77
Hyaenodontidae	<i>Quercytherium</i>	<i>tenebrosum</i>	77
Hyaenodontidae	<i>Sivapterodon</i>	<i>lahirii</i>	79

Hyanidae	<i>Chasmaporthetes</i>	<i>exitelus</i>	83
Hyanidae	<i>Crocota</i>	<i>eturo</i>	84
Hyanidae	<i>Hyaenictitherium</i>	<i>pilgrimi</i>	83
Hyanidae	<i>Ictitherium</i>	<i>iberium</i>	83
Hyanidae	<i>Lycyaena</i>	<i>macrostoma</i>	83
Hyanidae	<i>Lycyaenops</i>	<i>rhomboideae</i>	83
Hyanidae	<i>Palinhyena</i>	<i>reperta</i>	83
Hyanidae	<i>Proteles</i>	<i>amplidentus</i>	56
Hyanidae	<i>Protictitherium</i>	<i>punixum</i>	56
Mephetidae	<i>Promephitis</i>	<i>majori</i>	85
Mephetidae	<i>Promephitis</i>	<i>malustenensis</i>	85
Mephetidae	<i>Promephitis</i>	<i>qinensis</i>	85
Miacidae	<i>Dawsonicyon</i>	<i>Isami</i>	86
Miacidae	<i>Gracilocyon</i>	<i>rosei</i>	87
Miacidae	<i>Gracilocyon</i>	<i>rundlei</i>	88
Miacidae	<i>Gracilocyon</i>	<i>solei</i>	87
Miacidae	<i>Paramiacis</i>	<i>teiharti</i>	89
Miacidae	<i>Quercygale</i>	<i>angustidens</i>	88
Miacidae	<i>Quercygale</i>	<i>hastingsiae</i>	88
Miacidae	<i>Quercygale</i>	<i>helvetica</i>	88
Miacidae	<i>Quercygale</i>	<i>smithi</i>	88
Miacidae	<i>Uintacyon</i>	<i>gingerichi</i>	88
Miacidae	<i>Uintacyon</i>	<i>hookeri</i>	88
Miacidae	<i>Vassacyon</i>	<i>boweni</i>	90
Miacidae	<i>Vassacyon</i>	<i>prieuri</i>	30
Miacidae	<i>Vassacyon</i>	<i>taxidiotis</i>	88
Miacidae	<i>Xinyuictis</i>	<i>tenius</i>	90
Miacidae	<i>Zodiacyon</i>	<i>zetesios</i>	91
Mustelidae	<i>Aonyx</i>	<i>indicus</i>	92
Mustelidae	<i>Enhydriodon</i>	<i>afman</i>	93
Mustelidae	<i>Eomellivora</i>	<i>hungarica</i>	94
Mustelidae	<i>Ferinestris</i>	<i>rapax</i>	95
Mustelidae	<i>Leptarctus</i>	<i>bozemanensis</i>	96
Mustelidae	<i>Leptarctus</i>	<i>timmi</i>	96
Mustelidae	<i>Lutraeximia</i>	<i>umbra</i>	97
Mustelidae	<i>Pannonictis</i>	<i>plioaenica</i>	98
Mustelidae	<i>Schultzogale</i>	<i>inexpecta</i>	99
Mustelidae	<i>Sivaonyx</i>	<i>senutae</i>	100
Mustelidae	<i>Sivaonyx</i>	<i>soriae</i>	100
Unassigned Musteloidea	<i>Legionarictis</i>	<i>fortidens</i>	101
Unassigned Musteloidea	<i>Luogale</i>	<i>rusingensis</i>	56
Unassigned Musteloidea	<i>Mustelictis</i>	<i>olivieri</i>	102
Unassigned Musteloidea	<i>Mustelictis</i>	<i>piveteaui</i>	103
Nimravidae	<i>Dinailurictis</i>	<i>bonali</i>	104
Nimravidae	<i>Eofelis</i>	<i>edwardsii</i>	105
Nimravidae	<i>Eofelis</i>	<i>giganteus</i>	105
Nimravidae	<i>Hoplophoneus</i>	<i>villebramarensis</i>	104
Nimravidae	<i>Maofelis</i>	<i>cantonensis</i>	106
Nimravidae	<i>Quercylurus</i>	<i>major</i>	104
Procyonidae	<i>Amphinasua</i>	<i>lutaria</i>	107
Procyonidae	<i>Chapalmalania</i>	<i>ortognatha</i>	107
Procyonidae	<i>Cyonasua</i>	<i>argentina</i>	107

Procyonidae	<i>Pseudobassaris</i>	<i>riggsi</i>	108
Stenoplesictidae	<i>Stenogale</i>	<i>intermedia</i>	109
Stenoplesictidae	<i>Stenoplesictis</i>	<i>crocheti</i>	110
Stenoplesictidae	<i>Stenoplesictis</i>	<i>muhoronii</i>	56
Ursidae	<i>Adelpharctos</i>	<i>ginsburgi</i>	111
Ursidae	<i>Agriarctos</i>	<i>gaali</i>	112
Ursidae	<i>Agriarctos</i>	<i>vighi</i>	112
Ursidae	<i>Agriotherium</i>	<i>myanmarensis</i>	113
Ursidae	<i>Arctotherium</i>	<i>angustidens</i>	114
Ursidae	<i>Arctotherium</i>	<i>vetustum</i>	114
Ursidae	<i>Cephalogale</i>	<i>geoffroyi</i>	115
Ursidae	<i>Cephalogale</i>	<i>gergoviensis</i>	115
Ursidae	<i>Cyonarctos</i>	<i>dessei</i>	115
Ursidae	<i>Filholictis</i>	<i>filholi</i>	115
Ursidae	<i>Kretzoiarctos</i>	<i>beatrice</i>	112
Ursidae	<i>Phoberogale</i>	<i>bonali</i>	115
Ursidae	<i>Phoberogale</i>	<i>minor</i>	115
Ursidae	<i>Ursavus</i>	<i>tedfordi</i>	116
Viverravidae	<i>Bryanictis</i>	<i>paulus</i>	117
Viverravidae	<i>Protictis</i>	<i>minor</i>	117
Viverravidae	<i>Protictis</i>	<i>simpsoni</i>	117
Viverravidae	<i>Viverriscus</i>	<i>omnivorus</i>	118
Viverridae	<i>Civettictis</i>	<i>howelli</i>	56
Viverridae	<i>Kenyalutra</i>	<i>songhorensis</i>	56
Viverridae	<i>Legetetia</i>	<i>Nandii</i>	56
Viverridae	<i>Mioparadoxurus</i>	<i>meini</i>	119

**Table S9: Sources for morphological and genetic data within groups.**

Group	Genetic data	Morphological data
Overall phylogeny	54	30, 53, 91, 120, 121, 122
Carnivora: Amphicyonidae	-	123, 124
Carnivora: Barbourfelidae	-	125
Carnivora: Canidae	126	127, 128
Carnivora: Felidae	129	75, 130, 131, 132
Carnivora: Hyanidae	133	83
Carnivora: Musteloidea	60	95, 134, 135, 136, 137
Carnivora: Nimravidae	-	104
Carnivora: Pinnipedia	138	139, 140, 141, 142, 143, 144
Carnivora: Ursidae (analysed in combination with Amphicyonodontinae)	145	112, 146
Carnivora: Viverridae	-	119
Creodonta: Hyaenodontidae	-	29, 147, 148

**Table S10: Topological constraints.**

Constraint	Source
Carnivora: Amphicyonidae	

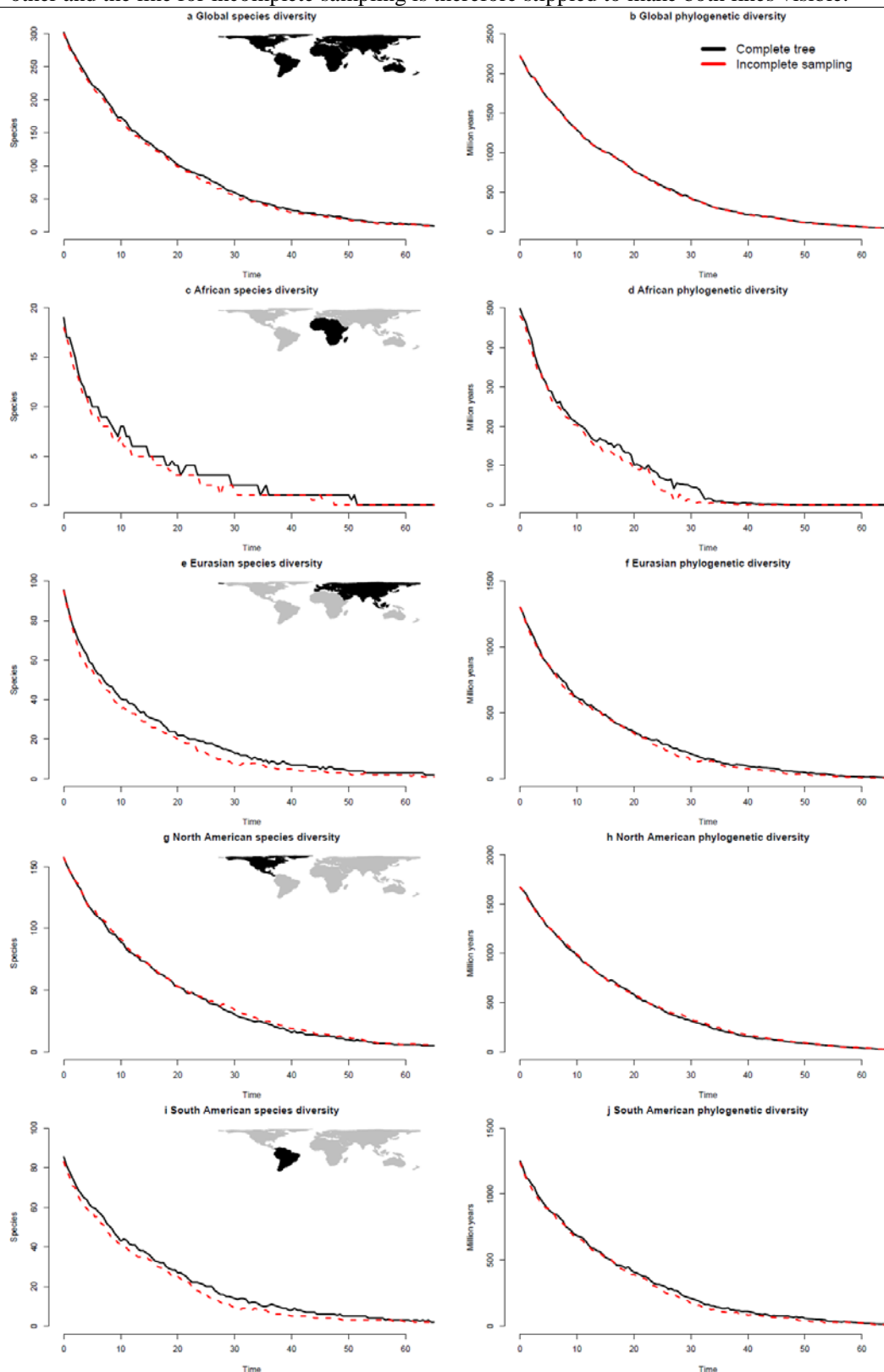
Haplocyoninae paraphyletic	149
Temnocyon paraphyletic	149
<i>Temnocyon altigenis</i> , <i>Temnocyon ferox</i> and <i>Temnocyon subferox</i> monophyletic	149
<i>Daphoenodon</i> and <i>Borocyon</i> sistergenera	150
<i>Adilophontes</i> sister to <i>Daphoenodon</i> and <i>Borocyon</i>	150
<i>Pliocyon</i> nested within American species of <i>Cynelos</i>	151
Asian <i>Amphicyon</i> not enforced to be monophyletic with the rest of the genus	151
<i>Hecubides</i> , <i>Afrocyon</i> and <i>Myacyon</i> combined considered monophyletic	152
North American <i>Amphicyon</i> constrained monophyletic	Biogeography
North American <i>Cynelos</i> (and <i>Pliocyon</i> ) constrained monophyletic	Biogeography
<i>Cynodictis</i> sister to all other members of family	Support in preliminary analysis with outgroup 0.91
<b>Carnivora: Barbourfelidae</b>	
Overall placement as sister to Felidae	58
<b>Carnivora: Canidae</b>	
<i>Phlaocyon taylori</i> sister to <i>Phlaocyon achoros</i> and <i>Phlaocyon multicuspus</i>	153
<i>Osbornodon scitulus</i> sister to <i>Osbornodon iamonsensis</i> , <i>Osbornodon brachypus</i> and <i>Osbornodon fricki</i>	154
<i>Vulpes pallida</i> sister to <i>Vulpes chama</i>	155
<i>Vulpes velox</i> sister to <i>Vulpes macrotis</i>	155
<i>Vulpes corsac</i> , <i>Vulpes bengalensis</i> and <i>Vulpes ferrilata</i> monophyletic	156
The two old American species <i>Vulpes kernensis</i> and <i>Vulpes stenognathus</i> basal to all other <i>Vulpes</i>	Biogeography
<b>Carnivora: Felidae</b>	
<i>Proailurus</i> most basal in family followed by <i>Hyperailurictis</i>	157
<i>Pseudailurus quadridentatus</i> most basal in Machairodontinae	157
Miocene members of extant genera ( <i>Felis christoli</i> , <i>Lynx longignathus</i> , <i>Lynx proterolyncis</i> , and <i>Puma pardoides</i> ) placed freely within the subfamily rather than necessarily within their genus	157
<i>Felis lunensis</i> sister to <i>Felis silvestris</i> and <i>Felis bieti</i> .	157
<i>Diamantofelis ferox</i> sister to <i>Namafelis minor</i>	56
<i>Panthera gombaszoegensis</i> sister to <i>Panthera onca</i> .	158
<i>Miracinonyx</i> potentially nested within <i>Puma</i>	159
<i>Dinofelis aronoki</i> sister to <i>Dinofelis piveteaui</i>	160
<i>Leopardus amnicola</i> sister to <i>Leopardus wiedii</i>	3
<i>Leopardus guttulus</i> sister to <i>Leopardus tigrinus</i>	3
<b>Carnivora: Herpestidae</b>	
Extant Asian <i>Herpestes</i> monophyletic relative to African species of the genus	161
<i>Dologale</i> sister to <i>Helogale</i>	155
<i>Bdeogale jacksoni</i> sister to <i>Bdeogale nigripes</i>	155
<i>Bdeogale crassicauda</i> sister to <i>Bdeogale omnivora</i>	155
African <i>Herpestides</i> monophyletic	Biogeography
<b>Carnivora: Hyanidae</b>	
Relationship between most genera not included in the cladistics analysis based on the taxonomic hypothesis from this source	162
<i>Werdelinus</i> placed within the clade containing <i>Belbus</i> to <i>Crocota</i> since it was a bone crusher based on the species description.	163
African <i>Hyaenictis</i> constrained monophyletic	Biogeography
African <i>Hyaenictitherium</i> constrained monophyletic	Biogeography
<b>Carnivora: Musteloidea: Ailuridae</b>	

Ailurinae ( <i>Ailurus</i> , <i>Magerictis</i> , <i>Pristinailurus</i> and <i>Parailurus</i> ) and Simocyoninae ( <i>Protursus</i> , <i>Protursus</i> and <i>Alopecocyon</i> ) each monophyletic and sisters	164
<i>Parailurus anglicus</i> sister to <i>Parailurus hungaricus</i>	164
<i>Amphictis</i> paraphyletic and basal to Ailurinae and Simocyoninae	164
<i>Amphictis prolongata</i> , <i>Amphictis wintershofensis</i> , and <i>Amphictis cuspidata</i> combined monophyletic	164
<i>Parailurus</i> sister to <i>Ailurus</i>	165
<i>Magerictis</i> sister to <i>Parailurus</i> and <i>Ailurus</i>	165
<i>Simocyon marshi</i> sister to <i>Simocyon primigenius</i>	166
American species of <i>Alopecocyon</i> constrained to be monophyletic	Biogeography
<b>Carnivora: Musteloidea: Mephitidae</b>	
<i>Brachyopsigale dubius</i> sister to <i>Brachyprotoma obtusata</i>	167
<i>Conepatus humboldtii</i> sister to <i>Conepatus semistriatus</i>	155
<i>Spilogale putorius</i> sister to <i>Spilogale angustifrons</i>	155
American species of the family considered monophyletic	Biogeography
<b>Carnivora: Musteloidea: Procyonidae</b>	
<i>Procyon cancrivorus</i> most basal in genus (among extant species)	155
American species of the family considered monophyletic	Biogeography
<b>Carnivora: Musteloidea: Mustelidae (family not enforced monophyletic within superfamily)</b>	
<i>Namibictis senuti</i> sister to <i>Mellalictis mellalensis</i> sisters	56
<i>Hoplictis</i> , <i>Ischyrtis</i> , and <i>Laphictis</i> combined monophyletic since they often are called subgenera	168
<i>Martes occulta</i> , <i>Martes diluviana</i> , <i>Martes paleosinensis</i> , <i>Martes pennanti</i> constrained monophyletic (subgenus <i>Pekania</i> ) but not constrained to be within the genus <i>Martes</i>	<i>Pekania</i> outside <i>Martes</i> in 60
<i>Martes gwatkinsii</i> sister to <i>Martes flavigula</i>	155
<i>Mustela nivalis</i> , <i>M. subpalmata</i> , <i>M. russelliana</i> and <i>M. tonkinensis</i> monophyletic	3
Tribe Aonychini ( <i>Aonyx</i> , <i>Cyonaonyx</i> , and <i>Limnonyx</i> ) monophyletic	59
Tribe Lutrini ( <i>Algarolutra</i> , <i>Lutra</i> (excluding some fossil forms), <i>Lutrogale</i> , <i>Lutravus</i> , <i>Lutraeximia</i> , <i>Mionictis</i> , <i>Paralutra</i> , <i>Pteronura</i> , <i>Sardolutra</i> , <i>Satherium</i> and <i>Siamogale</i> ) monophyletic	59
Enhydriodontini ( <i>Enhydriodon</i> , <i>Paludolutra</i> , <i>Sivaonyx</i> and <i>Vishnuonyx</i> ) monophyletic	100
<i>Satherium</i> sister to <i>Pteronura</i>	169
<i>Algarolutra</i> , <i>Megalenhydriis</i> , <i>Sardolutra</i> and <i>Lutraeximia</i> nested within <i>Lutra</i>	170
<i>Sardolutra</i> sister to <i>Lutra castiglioni</i>	170
<i>Lutra licenti</i> sister to <i>Lontra</i>	97
<i>Lutra simplicidens</i> sister to <i>Lutra fatimazohrae</i>	171
<i>Megalictis frazieri</i> closer related to <i>Megalictis simplicidens</i> than to <i>Megalictis ferox</i>	172
American species of <i>Aonyx</i> constrained to be monophyletic	Biogeography
<b>Carnivora: Nimravidae</b>	
<i>Hoplophoneus mentalis</i> sister to <i>Hoplophoneus primaevus</i>	104
<b>Carnivora: Percrocutidae</b>	
Relationship of most species given by (( <i>Dinocrocota salonicae</i> , <i>Dinocrocota senyureki</i> ), ( <i>Dinocrocota gigantea</i> , <i>Dinocrocota algeriensis</i> )), (( <i>Percrocota abessalomi</i> , <i>Percrocota tobieni</i> ), ( <i>Percrocota miocenica</i> , ( <i>Percrocota tungurensis</i> , <i>Percrocota carnifex</i> )))	173
African <i>Percrocota</i> constrained monophyletic	Biogeography
<b>Carnivora: Pinnepedia</b>	
Assignment of <i>Puijila</i> , <i>Semantor</i> , <i>Potamotherium</i> , and <i>Enaliarctidae</i> as basal to other families	71
Assignment of <i>Kolponomos</i> within the group of basal species mentioned above	174
<i>Pteronarctos</i> and <i>Pacificotaria</i> sistergenera. <i>Enaliarctos</i> sister to both	175
<i>Pinnarctidion</i> basal to <i>Desmatophocidae</i> and <i>Phocidae</i>	176

<b>Carnivora: Ursidae (and Amphicyodontidae)</b>	
Amphicyodontidae paraphyletic and basal to Ursidae	146
( <i>Amphicynodon brachyrostris</i> , ( <i>Amphicynodon crassirostris</i> , <i>Amphicynodon typicus</i> ), ( <i>Amphicynodon velaunus</i> , <i>Amphicynodon leptorhynchus</i> , ( <i>Amphicynodon teilhardi</i> , ( <i>Amphicynodon cephalogalinus</i> , <i>Amphicynodon gracilis</i> ))))). <i>Amphicynodon chardini</i> placed freely in the genus	64
Phoberocyoninae sister to Hemicyoninae	177
<i>Plionarctos</i> sister to <i>Tremarctos</i>	178
<i>Arctodus</i> sister to <i>Arctotherium</i>	178
<i>Arctodus</i> and <i>Arctotherium</i> sister to <i>Plionarctos</i> and <i>Tremarctos</i>	178
<i>Ursus etruscus</i> basal to <i>U. arctos</i> , <i>U. maritimus</i> and <i>U. spelaeus</i>	179
<i>Ursus boeckhi</i> basal to remaining <i>Ursus</i> , <i>Helarctos</i> , and <i>Melursus</i>	180
<b>Carnivora: Viverridae</b>	
<i>Euboictis</i> and <i>Legetetia</i> sistergenera	56
<i>Semigenetta elegans</i> , <i>Semigenetta laugnacensis</i> and <i>Semigenetta sansaniensis</i> considered monophyletic	181
<i>Arctictis</i> , <i>Arctogalidia</i> , <i>Macrogalidia</i> , <i>Mioparadoxurus</i> , <i>Paguma</i> , <i>Paradoxurus</i> constrained to be monophyletic	119
<i>Genetta abyssinica</i> sister to <i>Genetta thierryi</i>	155
<i>Viverra civettina</i> sister to <i>Viverra megaspila</i>	155
<b>Carnivoramorpha: Viverravidae</b>	
<i>Ictidopappus</i> most basal in the family (except for perhaps <i>Pappictidops</i> and <i>Pristinictis</i> )	182
<i>Simpsonictis</i> closer to <i>Viverriscus</i> than any other genus (except for perhaps <i>Pappictidops</i> and <i>Pristinictis</i> )	182
<i>Bryanictis</i> closer to <i>Intyriactis</i> than any other genus (except for perhaps <i>Pappictidops</i> and <i>Pristinictis</i> )	182
<i>Bryanictis</i> , <i>Intyriactis</i> , <i>Protictis</i> and <i>Raphictis</i> monophyletic (although <i>Pappictidops</i> and <i>Pristinictis</i> are allowed to be placed freely in the family)	182
<b>Creodonta: Hyaenodontidae</b>	
North American <i>Arfia</i> constrained monophyletic	Biogeography
European <i>Prototomus</i> constrained monophyletic	Biogeography
<b>Creodonta: Oxyaenidae</b>	
Machaeroidinae basal to other subfamilies.	183
Part of family resolved as ( <i>Dipsalodon churchillorum</i> , ( <i>Dipsalodon matthewi</i> , ( <i>Ambloctonus</i> , ( <i>Palaeonictis peloria</i> , ( <i>Palaeonictis gigantea</i> , ( <i>Palaeonictis occidentalis</i> , <i>Palaeonictis wingi</i> )))))). <i>Sarkastodon</i> and <i>Malfelis</i> free-floating within the subfamily	183, 184
Part of family resolved as ( <i>Dipsalidictis aequidens</i> , ( <i>Dipsalidictis krausei</i> , <i>Dipsalidictis platypus</i> , ( <i>Dipsalidictis transiens</i> , ((( <i>Oxyaena gulo</i> , ( <i>Oxyaena forcipata</i> , <i>Oxyaena intermedia</i> )), <i>Oxyaena woutersi</i> ), (( <i>Patriofelis ferox</i> , <i>Patriofelis ulta</i> ), <i>Protopsalis tigrinus</i> )))))). <i>Sarkastodon</i> and <i>Malfelis</i> free-floating within the subfamily. <i>Oxyaena lupina</i> , <i>Oxyaena pardalis</i> , and <i>Oxyaena simpsoni</i> free-floating within the genus	183, 184

# **Figure S1: Effect of incomplete sampling on diversity estimates.**

The difference in median species and phylogenetic diversity either globally or for individual continents. Due to the limited effect of limited sampling, the two lines are frequently on top of each other and the line for incomplete sampling is therefore stippled to make both lines visible.





# Figure S2: Simulation model.

Schematic drawing of the simulation model, which is a seven classes ClaSSE model transformed into a four-area version of a GeoSSE model. All arrows drawn in full (dispersal rate, extinction rate and allopatric speciation rate) represent cases where the species in question changes class in the ClaSSE model (or completely disappears for extinction from single area classes), whereas stippled lines (sympatric speciation rate and jump dispersal speciation rate) represent cases where the species buds off from another species while the ancestor stays in the region it was before.

