

Interactions within and between clades shaped the diversification of terrestrial carnivores

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A longstanding debate in evolutionary biology and paleontology is whether ecological interactions such as competition impose diversity dependence on speciation and extinction rates. Here, we analyze the fossil record of terrestrial mammalian carnivores in North America and Eurasia using a Bayesian framework to assess whether their diversity dynamics were affected by diversity dependence within and between families (12 in Eurasia, 10 in North America). We found eight instances of within-clade diversity dependence suppressing speciation rates and detected between-clade effects increasing extinction rates in six instances. Diversity dependence often involved lineages that migrated between continents and we found that speciation was more responsive to diversity changes within the clade, whereas extinction responded to diversity of taxa in other clades. The analysis of the fossil record of Carnivora suggests that interactions within and between clades are associated with different speciation and extinction regimes, opening room for a broader theory of diversity dependence.

KEY WORDS: Carnivora, competition, diversification, fossils, mammals.

Biological diversity is highly dynamic, with species and entire lineages rising and falling over time. The dynamics of diversification are determined by the balance between speciation and extinction rates, which may vary in response to catastrophic events (Alvarez et al. 1980; Renne et al. 1995), changing environments (Alroy et al. 2000; Fortelius et al. 2006; Ezard et al. 2011), and biotic interactions (Jablonski and Sepkoski 1996; Liow et al. 2015; Silvestro et al. 2015). Although major macroevolutionary phenomena such as mass extinctions seem to be largely driven by abiotic factors (Benton 2009), ecological interactions most certainly played a significant role in shaping the diversification of several lineages (Voje et al. 2015).

A longstanding debate in paleontology and evolutionary biology concerns whether diversity is limited at global and regional scales. Although some examples support the notion that diversity is not limited (Harmon and Harrison 2015), others suggest that diversification slows down over time, presumably owing

to diversity dependence mechanisms within the clade of interest (Rabosky 2013; Rabosky and Hulbert 2015; Ezard and Purvis 2016), hereafter termed self-diversity dependence. The effects of diversity on diversification dynamics would act via speciation, when the emergence of new taxa is hindered by the lack of ecological opportunities in saturated habitats (Simpson 1953; Schluter 2000) or via extinction, resulting from competitive displacement by ecologically similar taxa (Van Valen 1985).

Although self-diversity dependence has been a prevailing subject in paleobiology (Foote and Miller 2006), a slowdown in diversification may not necessarily respond to the diversity of the lineage itself, but could in theory occur in response to the rising diversity of distantly related clades whose taxa share similar ecologies (Stanley 1973; Sepkoski 1996; Van Valkenburgh 1999; Jablonski 2008). Recent work has shown that using the fossil record and the adequate methodological framework we may be able to uncover how the diversification of different lineages

interfered with each other's (Liow et al. 2015; Silvestro et al. 2015). Studying if and how diversity dependence within and between clades affected diversification dynamics can help us bridge ecology and macroevolution, one of the greatest challenges in evolutionary biology (Jablonski 2008).

A number of replacement instances, in which a clade rises at the same time or after another ecologically similar clade falls, have been discussed as possible outcomes of ecological interactions between taxa from different clades (Van Valen and Sloan 1966; Krause 1986; Benton 1987; Miller and Sepkoski 1988; Sepkoski 1996). The fossil record of mammalian carnivores (order Carnivora) is particularly rich in such supposed replacement episodes (Werdelin and Turner 1996; Van Valkenburgh 1999). Although the diversification dynamics of Carnivora as a whole is characterized by roughly constant diversification rates (Liow and Finarelli 2014), the dynamics within continents was more variable (Pires et al. 2015; Finarelli and Liow 2016). Finarelli and Liow (2016) showed that even though the diversification of carnivores in Eurasia and North America fluctuated around zero, fluctuations were not synchronous. Such differences between continents may result from differences in the timing and magnitude of environmental changes (Pires et al. 2015; Finarelli and Liow 2016). The fact that diversification rates rove around zero in both continents suggests that diversity dependence could have contributed to shape diversification dynamics at the level of Carnivora as whole and potentially within its lineages. For example, the diversification of Canidae seems to have been affected by diversity-dependent effects from within the clade but also from other clades such as Felidae (Silvestro et al. 2015). Rise-and-fall diversification patterns, where functionally similar clades potentially displaced or replaced a declining clade have also been identified for other Eurasian and North American carnivores (Van Valkenburgh 1999). Moreover, the analysis of individual clades reveals that certain lineages that have migrated between North America and Eurasia underwent evolutionary radiations, where diversification rates were initially high and dropped thereafter (Pires et al. 2015). It is therefore likely that diversity-dependent effects played an important role in the diversification of clades within Carnivora, and such effects may have been structured very differently in each continent.

Diversity dependence within clades has been investigated mainly by testing whether diversification slowed down over time (Sepkoski 1978; Phillimore and Price 2008), whereas instances of diversity dependence between clades proposed in the past were based on the incidence of double wedge patterns in diversity trajectories (Sepkoski 1996; Van Valkenburgh 1999). Here we go a step forward into formally testing diversity dependence by using a novel hierarchical Bayesian approach (Silvestro et al. 2015, 2016) where the relationship between diversity and diversification of multiple clades is explicitly examined. We test to what

extent self-diversity dependence and between-clade interference acting via speciation and extinction shaped diversification dynamics in mammalian carnivores in the Northern hemisphere. Considering our recent results on the diversification of Carnivora (Pires et al. 2015) we expected to find self-diversity dependence to be more common in Eurasia than in North America. We also tested the hypothesis that some of the carnivoran clade replacements proposed previously (Van Valkenburgh 1999) were in fact driven by diversity-dependent effects and whether these effects acted primarily through speciation or extinction dynamics. Finally, we examined how diversity dependence patterns resulting from the analysis of Carnivora as a whole relate to the patterns obtained from the analysis of lower level clades representing more ecologically cohesive evolutionary lineages. We found evidence that self-diversity dependence affects primarily speciation, that between-clade interference preferentially shaped extinction dynamics, and that the contribution of diversity dependence within and between clades to diversification dynamics is dependent upon regional settings and how lineages are organized into clades.

Materials and Methods

DATASET

We used a dataset of Carnivora fossils from North America and Eurasia compiled from PBDB (Paleobiology Database; paleobiodb.org) and NOW databases (New and Old Worlds database of fossil mammals www.helsinki.fi/science/now/). This dataset has been thoroughly checked for synonyms, misspellings, and duplicates and is available online (Pires et al. 2015). The dataset includes more than 7000 occurrences and about 980 species from all Carnivora families present in each continent (data summarized in Table S1). Stem taxa that are not placed in the analyzed families in the most recent taxonomic analyses, but are thought to be within the crown group of Carnivora, such as early Musteloidea and Arctoidea (Flynn et al. 2005; Wesley-Hunt and Flynn 2005) were only included in the analyses of the diversification of Carnivora as a whole. In the analyses at the family level, we also included the family Hyaenodontidae (Creodonta), because these are mammalian carnivores that overlapped temporally and ecologically with carnivorans. We excluded pinnipeds from the analyses because the group includes only marine taxa and was thus subjected to a very different ecological and geographical context when compared to terrestrial clades. Detailed analyses on the diversity-dependent effects between clades only include families with diversity greater than five species in each continent (see Table S1).

ESTIMATING DIVERSITY DEPENDENCE EFFECTS

We used the Bayesian framework PyRate to estimate diversification rates from fossil occurrences (Silvestro et al. 2014a,b).

PyRate assumes the observed fossil occurrences to result from the interplay between the preservation process and a birth–death process with rates of speciation (λ) and extinction (μ) measured as events per lineage per Myr (Million years; Silvestro et al. 2014a, b). PyRate allows jointly estimating from a set of fossil occurrences the rates of speciation (λ) and extinction (μ) and their change over time, as well as the times of speciation (s) and extinction (e) for each taxon, and the rates of preservation (q). We have previously used this method to investigate the dynamics of speciation and extinction rates of each family of Carnivora within North America and Eurasia (Pires et al. 2015). Here, we first use PyRate to assess diversification rates for Carnivora as a whole in each continent. Next, we infer (1) the effects of diversity dependence in the diversification of Carnivora as a whole and (2) within- and between-clade diversity dependence for each of the families within Carnivora.

To estimate diversity dependence effects within and between families from fossil data, we used the Multiple Clade Diversity Dependence (MCDD) model (Silvestro et al. 2015, 2016), which jointly estimates the effects of diversity changes in a single or multiple clades on the speciation and extinction rates of each clade. Under the MCDD model, the rates $\lambda_i(t)$ and $\mu_i(t)$ of a clade i at any time t are modeled as linear functions of the diversity $\delta_j(t)$ of any given clade j :

$$\lambda_i = \max \left\{ 0, \lambda_i - \sum_{j=1}^C \lambda_i [\delta_j(t) g_{i,j}^\lambda] \right\},$$

$$\mu_i = \max \left\{ 0, \mu_i + \sum_{j=1}^C \mu_i [\delta_j(t) g_{i,j}^\mu] \right\},$$

where λ_i and μ_i are baseline rates of speciation and extinction, that is, the rates when diversification is not affected by diversity, and the parameters g_{ij}^λ and g_{ij}^μ represent the effect of diversity of clade j on the rates of clade i . Because the reciprocal effects (g_{ij} and g_{ji}) are modeled as independent parameters, the model is directional, that is, effects can be asymmetric. When $i = j$, the interaction term g_{ij} represents diversity dependence effects within the clade (self-diversity dependence).

We used the latest implementation of the MCDD model, which uses a Horseshoe prior (Carvalho et al. 2010) on the interaction parameters g (Silvestro et al. 2016). The interaction parameters are assigned a normal prior distribution with mean = 0 and variance controlled by two hyperparameters, the local (ϵ) and global (τ) shrinkage parameters, which are themselves estimated from the data and assigned half-Cauchy prior distributions, $C^+(0, 1)$ (Silvestro et al. 2016), heavy-tailed distributions with mode at zero. The Horseshoe prior distribution has an infinitely tall spike at zero causing the shrinkage of negligible interaction effects—which can be considered as noise—and heavy tails that allow

potentially strong positive or negative values for the interaction effects when identified as signal. The global shrinkage parameter τ captures the overall signal of diversity dependence when considering the effects of multiple clades, whereas ϵ_{ij} represents the shrinkage of the specific signals relative to each pair of clades. A shrinkage weight can be calculated from the estimated local and global shrinkage parameters as $\omega_{ij} = 1 - [1/(1 + \tau^2 \epsilon_{ij}^2)]$ (Carvalho et al. 2010). Greater shrinkage weights (close to 1) indicate evidence for diversity dependence effects, whereas weights close to 0 indicate noise.

This implementation has been shown to be less prone to false positives, albeit more prone to false negatives (Silvestro et al. 2016) than the previous one (Silvestro et al. 2015). Therefore, we use here a conservative method and explore only the strongest signals of interference between clades, which are highly unlikely to represent noise. We infer the significance of the signal of diversity dependence based on the estimates of the shrinkage weights. We consider interaction terms (g_s), and thus diversity dependence, to have moderate support when $0.5 < \omega_{ij} < 0.6$, and strong support whenever $\omega_{ij} > 0.6$ (Silvestro et al. 2016). We explored diversity dependence in Eurasia and in North America by running independent MCDD analyses including the carnivore families occurring in each continent (Table S1).

We also tested whether temporal variation in speciation and extinction rates of each analyzed clade can be explained by climate change. We used estimates of relative global temperature through time as a proxy for climatic variations (Alroy et al. 2000; Zachos et al. 2008). We then analyzed the data using a birth–death model in which speciation and extinction rates change through time as an exponential function of a continuous covariate (Silvestro et al. 2015). The model includes four parameters: the baseline speciation and extinction rates (λ_0 and μ_0) and the parameters g_{iT}^λ and g_{iT}^μ , which quantify the effect of temperature on speciation and extinction rates. Thus, $g < 0$ can be interpreted as a negative correlation and $g > 0$ a positive correlation between temperature and rates.

The parameters in PyRate and in the MCDD model are jointly estimated using MCMC algorithms specific to each model (Silvestro et al. 2014b, 2016). We ran 2×10^7 iterations, discarded 10% as burn-in and sampled every 10^4 iteration to obtain the posterior estimates. We monitored chain mixing and effective sample sizes using Tracer version 1.6 (Rambaut et al. 2014). To accommodate uncertainties associated with the temporal resolution of fossil occurrences, we built 100 randomized datasets by assigning, to each occurrence, ages randomly drawn within the occurrence range (Silvestro et al. 2014b). We then analyzed each of the 100 replicates and combined the results to incorporate dating uncertainties. All analyses described above were run using PyRate, an open source package written in Python and R (<https://github.com/dsilvestro/PyRate>).

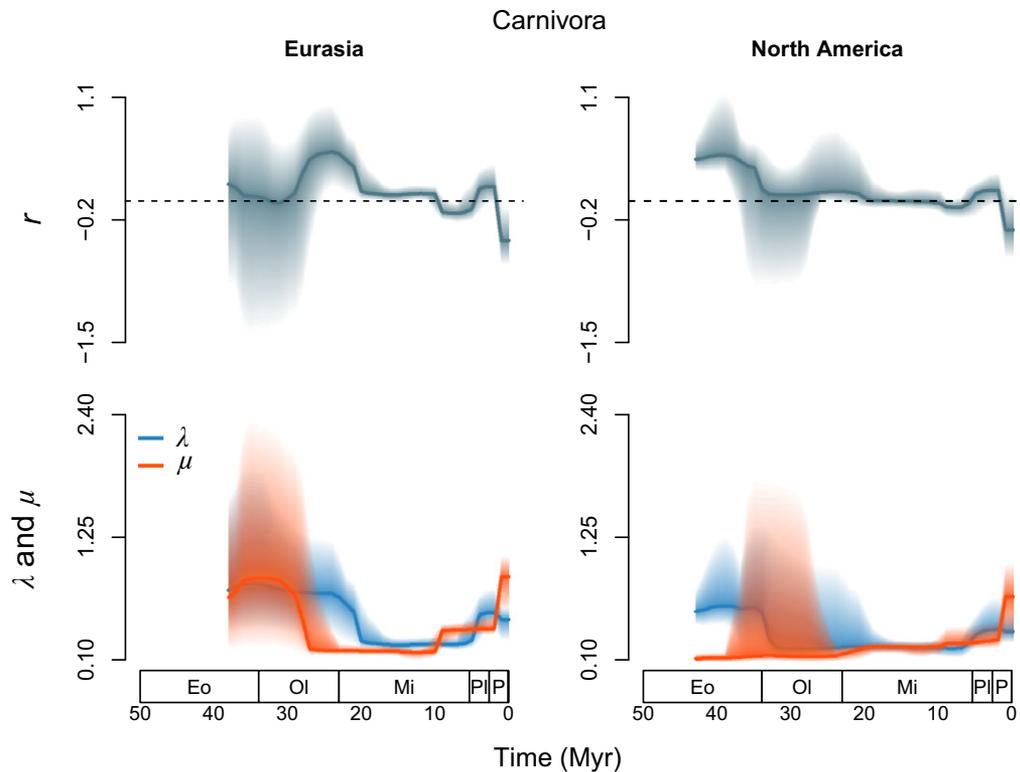


Figure 1. Net diversification ($r = \lambda - \mu$), speciation (λ), and extinction (μ) rates of Carnivora in Eurasia and North America through time. Posterior estimates of the rates are summarized as mean values (lines) and 95% HPDs (Highest posterior density; shaded areas).

Results

We first analyzed the diversification dynamics for Carnivora in North America and Eurasia. In Eurasia, we found an increase in net diversification close to the Oligocene-Miocene Boundary (~ 24 Myr) driven by a decrease in the extinction rate while the speciation rate was high. The speciation rate decreased shortly after, leading to a period of constant diversification during the Miocene until extinction increased and diversification decelerated in the latest Miocene. During the Pliocene, speciation rose and diversification showed another peak but was soon followed by increasing rates of extinction (Fig. 1). In North America diversification was high in mid Eocene (~ 40 Myr) driven by high speciation rates, which dropped in the Oligocene (Fig. 1). A slight increase in extinction rates in the Miocene reduced diversification rates, but speciation rose again in the Pliocene leading to a smaller peak in diversification followed by another drop driven by increased extinction.

We then tested whether there is evidence for diversity dependence driving the dynamics in each continent. In Eurasia, speciation significantly decreased with increasing diversity ($g^\lambda < 0$; Fig. 2). The drop in speciation rate close to the Oligocene-Miocene (Fig. 1) boundary followed the diversity accumulation concentrated around this period (Fig. S1). Extinction rates did not show evidence of diversity dependence ($g^\mu \approx 0$). In North

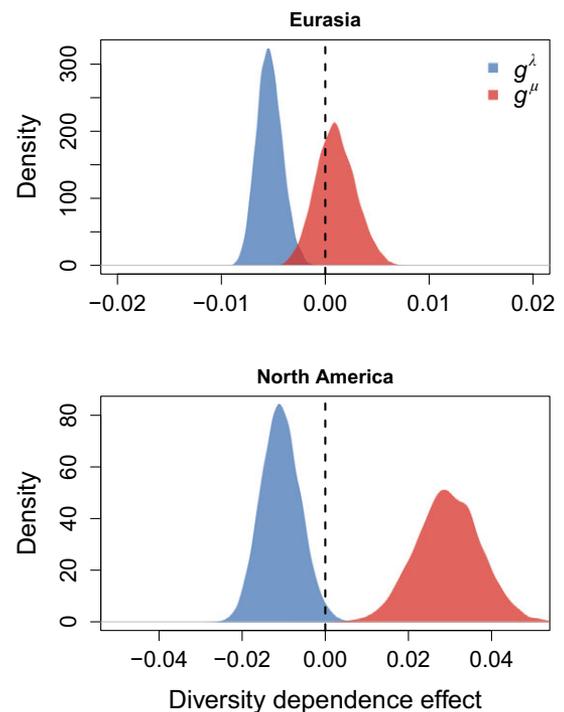


Figure 2. Posterior estimates of diversity dependence in speciation (g^λ) and extinction rates (g^μ) of Carnivora in Eurasia and North America. g^λ and g^μ represent the effect of diversity on the rates of speciation and extinction.

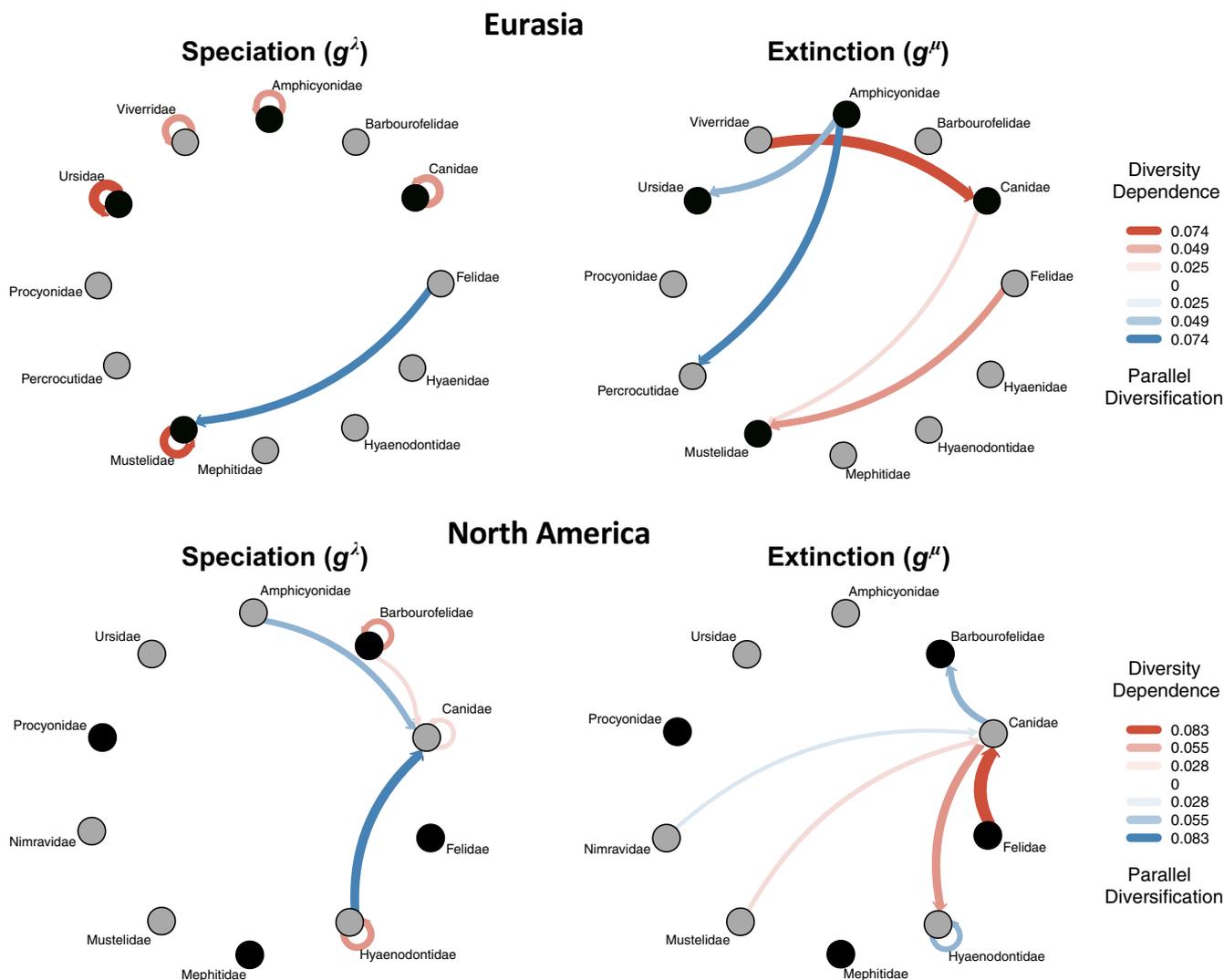


Figure 3. Diversity-dependent effects within and between clades on speciation and extinction rates of carnivorans and Hyenaodontidae (Creodonta) in Eurasia and North America. Black filled circles depict clades that were identified as possible immigrants in each continent (Pires et al. 2015). Only significant ($\omega > 0.5$) interaction terms are depicted. Color intensity and thickness of arrows are proportional to the magnitude of interaction effects. Estimated values for interaction effects (g) and shrinkage weights (ω) are presented in Tables S2–S5.

America diversity dependence significantly affects extinction ($g^{\mu} > 0$; Fig. 2), which increased steadily starting in the Miocene (Fig. 1) following the diversity peak in the clade as a whole during this period (Fig. S1). We also found moderate support for diversity dependence in speciation rates of North American Carnivora ($g^{\lambda} \leq 0$; Fig. 2).

A finer grained analysis, where Carnivora in each continent are divided into families and analyzed under the MCDD model shows two main patterns. First, self-diversity dependence is mostly found to negatively affect the rates of speciation, whereas between-clade diversity effects affected extinction more frequently (Fig. 3). Second, self-diversity dependence seems to have been more prevalent in the diversification of mammalian carnivores in Eurasia, whereas in North America between-clade

effects seem to have been more important in shaping diversification dynamics (Fig. 3).

In Eurasia, the speciation rates of Amphicyonidae, Ursidae, Mustelidae, Viverridae, and Canidae decreased as a function of their own increasing diversity (Fig. 3; Table S2). This pattern is apparent in individual plots showing that speciation dropped drastically as diversity in these groups increased (Figs. S2–S6). We also detected possible effects of the increase in diversity of Viverridae increasing extinction in Canidae (Fig. S7, Table S3), whereas the increase in diversity of Felidae and Canidae was associated with increasing extinction rate in Mustelidae (Figs. 3 and S8–S9 and Table S3). In North America, we detect self-diversity dependence in the speciation of Barbourfelidae, Hyenaodontidae, and Canidae (Figs. 3 and S10–S12; Table S4). The extinction rate of

hyaenodontid creodonts also appears to have been affected by the diversity of Canidae (Figs. 3 and S13; Table S5). The strongest signal of diversity affecting diversification was the increase in the extinction rate of canids associated with the increase in diversity of felids (Figs. 3 and S14 and Table S5).

The prevalence of diversity-dependent speciation rates in Eurasia and diversity-dependent extinction rates in North America, when we look at individual clades, agrees with the pattern detected when analyzing Carnivora as a whole (Fig. 2). We also found multiple instances of parallel diversification, where diversity increases in one lineage are statistically associated with either increasing speciation or decreasing extinction in others, or where diversity decrease is associated with either decreasing speciation or increasing extinction (Fig. 3).

Our tests on the relationship between global temperature and diversification rates suggest no relationship between speciation and temperature variation (Figs. S15 and S16). However, the models support a negative relationship between extinction and changes in global temperature for most clades in both continents, that is, extinction rates tended to increase as temperature decreased (Figs. S15 and S16).

Discussion

We found evidence suggesting that the diversification dynamics of Carnivora as a whole were constrained by diversity in both continents. In Eurasia, the speciation rate tended to decrease with increasing diversity, whereas in North America the main effect was an increase in extinction rate with rising diversity. The self-diversity dependence expressed at the order level can be further teased apart into diversity-dependent effects within and between families. The speciation rates of Eurasian lineages of Amphicyonidae, Mustelidae, Canidae, Ursidae, and Viverridae slowed down as their diversity increased. The first four lineages in fact underwent evolutionary radiations in Eurasia (Pires et al. 2015). These radiations produced the large-bodied forms of ursids and amphicyonids, such as the hemicyonine bears and amphicyonines (Hunt 2002; Figueirido et al. 2011), and a great taxonomic and functional diversity of mustelids (Koepfli et al. 2008). Likewise, the late invasion and radiation of canids in the Old World resulted in many of the recent groups, including foxes and wolves (Wang et al. 2004). All these radiations followed episodes of major climatic and vegetation change, such as the Oligocene cooling and the Messinian salinity crisis (Janis 1993; Koepfli et al. 2008), and generally coincided with an apparent scarcity of ecological analogues of carnivorans (Van Valkenburgh 1991; Pires et al. 2015). Collectively these results imply that the diversity of carnivoran clades in Eurasia was spurred by ecological opportunity created by changes in the biotic and abiotic environment, but as diversity in each clade increased such

opportunities dwindled, limiting diversification by constraining speciation.

For North American lineages, the strongest relationship between diversity and diversification rates are within Hyaenodontidae, Barbouriidae, and Canidae. In these three clades, speciation slowed down as diversity increased. Canidae diversified early in North America and radiated in a broad diversity of ecologies (Van Valkenburgh 1991). The early radiation of canids may have prevented the radiation of other groups that established later in the continent (Pires et al. 2015), which might explain why self-diversity dependence was not as important, or easily detected, for as many lineages in North America as in Eurasia.

Beyond self-diversity dependence, we also detected instances of between-clade diversity effects. Van Valkenburgh (1999) examined a number of possible replacement cases between carnivores while accounting for functional similarity. Our results suggest that in North America only the replacement of hyaenodontids by canids, and the decline of canids when felids arose involved diversity-dependent effects affecting the extinction regime of the declining clade. The evolution of body size and hypercarnivory has been suggested as an important element in the diversification of Canidae, negatively affecting species longevity (Van Valkenburgh 2004; Wang et al. 2004). Such evolutionary trends might have affected the interactions with species in other lineages (Van Valkenburgh 1991). The canid subfamily Hesperocyoninae evolved hypercarnivory and taxa increased in size at the time Hyaenodontidae and Nimravidae were declining. Similarly, the evolution of hypercarnivorous large-sized borophagine canids occurred as amphicyonids and Hemicyoninae bears declined (Van Valkenburgh 2004; Wang et al. 2004). The increase in ecological similarity might have caused the active displacement of Hyaenodontidae. However, we found no evidence that the diversity of Canidae affected the diversification of Ursidae or Amphicyonidae, which supports the hypothesis that the second rise of hypercarnivorous canids was related to opportunistic (passive) replacement (Van Valkenburgh 1999). The effects of Felidae on Canidae in North America also occurred at the time when borophagine canids attained large-sized hypercarnivorous forms (Van Valkenburgh 2004; Silvestro et al. 2015). Whether hypercarnivory affected this outcome is amenable to further investigation.

Although Felidae seems to have strongly interfered with the diversification of Canidae in North America, we did not detect an effect of Felidae on Eurasian canids. The effects of felids on North American canids affected preferentially the subfamily Borophaginae, whereas the subfamily Caninae kept diversifying (Silvestro et al. 2015). Only Caninae invaded and established in Eurasia suggesting that this was the only Canidae subfamily able to overcome ecological barriers imposed by incumbent Eurasian carnivores such as felids. Our analyses considering Eurasian lineages only point to possible effects of Canidae and Felidae on Mustelidae;

and Viverridae affecting the diversification of Canidae. Judging by the ecology of extant viverrids and canids and the late arrival of Canidae in Eurasia, an effect of Viverridae on the extinction rate of Eurasian Canidae seems unexpected and could result from opposite responses to an external factor such as vegetation changes.

The strongest effects between clades in North America involved the immigration of Felidae, and all the between-clade effects detected in Eurasia involve immigrant lineages (although the continent of origin of Mustelidae is disputable; Pires et al. 2015). These results are consistent with the hypothesis that competitive asymmetries can be more pronounced between taxa that evolved in different biogeographical regions (Germain et al. 2016). Moreover, self-diversity dependence on speciation in Eurasia is associated preferentially with the clades that migrated from North America, which presumably found plenty ecological opportunity to diversify (Pires et al. 2015). A possible interpretation of these results is that migrations may disrupt the in situ dynamics by generating evolutionary radiations or impacting the diversification of resident clades due to the introduction of new ecologies.

A slowdown in diversification is not necessarily a consequence of diversity dependence (Moen and Morlon 2014). We explicitly searched for signals of diversity dependence here, but it is possible that diversification dynamics were affected by multiple factors. Environmental changes driven by changes in climate may affect diversification dynamics in different ways (Alroy et al. 2000; Fortelius et al. 2006), including generating signals of constrained diversification. For most clades we found no association between temperature variation and speciation, but a negative relationship between temperature and extinction. The lack of association between temperature and speciation suggests that the signatures of self-diversity dependence on speciation are unlikely to result from responses to climatic changes. Moreover, the instances of interference through extinctions we detected are unlikely to have been driven by responses to climate, because most clades seem to respond in the same way to temperature, while clade interference occurs when diversification changes in opposite directions for different clades (e.g., one clade expands at the expense of the decline of the other). We acknowledge, however, that other unaccounted for factors could have contributed to the diversification of Carnivora clades.

Besides the negative diversity-dependent effects, we found several indications of parallel diversification, where speciation rate in one clade is positively correlated or extinction is negatively correlated with diversity in other clades. We interpret such instances as similar evolutionary responses in different clades to the same underlying driver. Because we found that climate had similar effects on extinction in virtually all clades, the instances of parallel diversification via extinction could have been mediated by climate change. In fact, most clades show concomitant increase in extinction close to the Miocene/Pliocene boundary

(Pires et al. 2015), a period of intensified climatic changes at the scale of continents (Fortelius et al. 2006; Finarelli and Liow 2016). Alternatively, some of the parallel diversification results we detect here could result from evolutionary processes that promote diversification, such as evolutionary escalation (Vermeij 2013).

Diversity dependence is often associated with the effects of ecological interactions such as competition (Rabosky 2013). However, scaling up the effects of ecological interactions to macroevolutionary scales is not trivial (Benton 1987; Sepkoski 1996). Interactions such as competition and predation occur at local scales affecting the densities of populations in ecological time, but if the consequences of interactions are consistent over time and across a species range, interactions may generate emergent responses at the species level and leave signatures in diversification dynamics (Jablonski and Sepkoski 1996; Sepkoski 1996). With the currently available data, it is virtually impossible to verify with local-scale resolution whether the taxa examined overlapped spatially for a significant portion of time due to the inevitable incompleteness of the fossil record. However, fossil occurrences of many taxa were found at the same locality or geographically very close to each other, suggesting that the assumption that many of these taxa co-occurred is reasonable (see Figs. S17–S22).

In addition to the insights on mammalian evolution, our findings may have broader implications for the understanding of diversity-dependent diversification dynamics. We found self-diversity effects to mostly affect speciation, whereas between-clade diversity effects occurred mainly through extinction. Our results on self-diversity dependence in speciation agree with previous analyses considering diversity dynamics within clades, which indicate stronger constraints to diversification on speciation regimes than on extinction regimes (Alroy 1996; Foote 2000; Ezard et al. 2011). The pervasiveness of between-clade diversity-dependent effects remains an open question, but our results suggest that while interactions among closely related species may inhibit speciation, interactions among distantly related taxa have larger effects on extinction. Interestingly, as we scale from the order to the family level, and from the family to the subfamily level (at least for Canidae where this has been done; see Silvestro et al. 2015), self-diversity dependence breaks into within and between clade diversity dependence. These results suggest that diversification may be affected by ecological limits at different levels and the detection of within versus between lineage effects is scale-dependent.

A long-standing tenet in the study of competition is that closely related species should compete more intensely (Darwin 1859) because ecological similarity is generally related to phylogenetic distance. However, some clades bear high diversity of ecological niches. For instance, extant felids include some large-bodied taxa such as lions and tigers and many small-sized forms such as the small spotted cats (*Leopardus* spp.), which are

ecologically more akin to weasels or foxes (Goswami and Friscia 2010). Thus, the possibility that between clade diversity effects could be as relevant as self-diversity dependence is conceivable once we account for the diversity of ecologies within clades and the ecological overlap between taxa in different clades. Recent results on plant competition experiments suggest that competition effects related to fitness differences might be even stronger among distantly related species (Godoy et al. 2014). Hence, as discussed by Marshall and Quental (2016), it is the ecological species pool, not the phylogenetic species pool that should be relevant for competitive interactions and therefore affect diversity-dependent dynamics.

The debate on diversity dependence has revolved around whether there are ecological limits to diversity (Rabosky and Hulbert 2015) or whether diversity is unbounded (Harmon and Harrison 2015). Here, we specifically test for diversity dependence instead of analyzing patterns predicted by equilibrium or nonequilibrium processes. In fact, processes in both classes may simultaneously govern the dynamics of clade diversification (Ezard and Purvis 2016; Marshall and Quental 2016). Any phenomena that alter how organisms interact with the environment might result in changes in potential forces limiting diversity. This includes changes in the abiotic but also the biotic context due to the emergence and diversification of co-occurring clades. The combination of within- and between-clade effects on diversification may help reconcile the equilibrium and nonequilibrium views of diversity, opening room for a broader theory of diversity dependence.

AUTHOR CONTRIBUTIONS

MMP, DS, and TBQ designed the research; MMP and DS analyzed the data; and MMP, DS, and TBQ wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Number of species and occurrences in each clade within each continent.

Table S2. Estimated effect of diversity of clade j (rows) on the speciation (g_{ij}^{λ}) of clade i (columns) in Eurasia.

Table S3. Estimated effect of diversity of clade j (rows) on the extinction rate (g_{ij}^{μ}) of clade i (columns) in Eurasia.

Table S4. Estimated effect of diversity of clade j (rows) on the speciation rate (g_{ij}^{λ}) of clade i (columns) in North America.

Table S5. Estimated effect of diversity of clade j (rows) on the extinction rate (g_{ij}^{μ}) of clade i (columns) in North America.

Figure S1. Diversity trajectory of Carnivora in Eurasia and North America.

Figure S2. Changes in speciation rate of Amphicyonidae in Eurasia in response to changes in its own diversity when removing possible effects of other clades.

Figure S3. Changes in speciation rate of Ursidae in Eurasia in response to changes in its own diversity when removing possible effects of other clades.

Figure S4. Changes in speciation rate of Mustelidae in Eurasia in response to changes in its own diversity when removing possible effects of other clades.

Figure S5. Changes in speciation rate of Viverridae in Eurasia in response to changes in its own diversity when removing possible effects of other clades.

Figure S6. Changes in speciation rate of Canidae in Eurasia in response to changes in its own diversity when removing possible effects of other clades.

Figure S7. Changes in extinction rate of Canidae in Eurasia in response to changes in the diversity of Viverridae when removing possible effects of other clades.

Figure S8. Changes in speciation and extinction rate of Mustelidae in Eurasia in response to changes in the diversity of Felidae when removing possible effects of other clades.

Figure S9. Changes in extinction rate of Mustelidae in Eurasia in response to changes in the diversity of Canidae when removing possible effects of other clades.

Figure S10. Changes in speciation rate of Barboourofelidae in North America in response to changes in its own diversity when removing possible effects of other clades.

Figure S11. Changes in speciation and extinction rate of Hyaenodontidae (Creodonta) in North America in response to changes in its own diversity when removing possible effects of other clades.

Figure S12. Changes in speciation rate of Canidae in North America in response to changes in its own diversity when removing possible effects of other clades.

Figure S13. Changes in extinction rate of Hyaenodontidae (Creodonta) in North America in response to changes in the diversity of Canidae when removing possible effects of other clades.

Figure S14. Changes in extinction rate of Canidae in North America in response to changes in the diversity of Felidae when removing possible effects of other clades.

Figure S15. Posterior estimates of parameters representing the association between global temperature and speciation (g^{λ} ; blue) and extinction rates (g^{μ} ; red).

Figure S16. Posterior estimates of parameters representing the association between global temperature and speciation (g^{λ} ; blue) and extinction rates (g^{μ} ; red).

Figure S17. Occurrences of all taxa of each clade with self-diversity dependence in Eurasia.

Figure S18. Occurrences of all taxa of each clade with self-diversity dependence in North America.

Figure S19. Occurrences of all taxa of Canidae (714 occurrences of 59 taxa) and Viverridae (occurrences of 28 taxa), which show possible between-clade diversity dependence in Eurasia.

Figure S20. Occurrences of all taxa of Mustelidae (814, occurrences of 176 taxa) and Felidae (839, occurrences of 81 taxa), which show possible between-clade diversity dependence in Eurasia.

Figure S21. Occurrences of all taxa of Canidae (1342 occurrences of 119 taxa) and Hyaenodontidae (465 occurrences of 42 taxa), which show possible between-clade diversity dependence in North America.

Figure S22. Occurrences of all taxa of Canidae (1342 occurrences of 119 taxa) and Felidae (284 occurrences of 36 taxa), which show possible between-clade diversity dependence in North America.