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ECOLOGICAL CAUSES OF DECELERATING DIVERSIFICATION IN CARNIVORAN MAMMALS

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Clade diversification is a central topic in macroevolutionary studies. Recently, it has been shown that diversification rates appear to decelerate over time in many clades. What causes this deceleration remains unclear, but it has been proposed that competition for limited resources between sympatric, ecologically similar species slows diversification. Employing carnivoran mammals as a model system, we test this hypothesis using a comprehensive time-calibrated phylogeny. We also explore several conceptually related explanations including limited geographic area and limited rates of niche evolution. We find that diversification slowdowns are strong in carnivorans. Surprisingly, these slowdowns are independent of geographic range overlap between related species and are also decoupled from rates of niche evolution, suggesting that slowdowns are unrelated to competition and niche filling. When controlling for the effects of clade diversity, diversification slowdowns appear independent of geographic area. There is a significant effect of clade diversity on diversification slowdowns, but simulations show that this relationship may arise as a statistical artifact (i.e., greater clade diversity increases the ability of the gamma statistic to refute constant diversification). Overall, our results emphasize the need to test hypotheses about the causes of diversification slowdowns with ecological data, rather than assuming ecological processes from phylogenies alone.

KEY WORDS: Area, biogeography, evolution, niche, phylogeny, range, rate .

Diversification is the outcome of speciation and extinction dynamics and is a major factor underlying the differences in species richness across clades and regions (e.g., Ricklefs 1987; Gaston 2000; Ricklefs 2007; Wiens 2011). Given this, understanding what drives diversification is a major challenge in both evolutionary biology and ecology (Ricklefs 2007).

Evidence from many disparate taxa indicates that diversification rates often decline in a clade over time (e.g., McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008; Morlon et al. 2010), but what this pattern actually means and what causes it remains unclear. Many authors have suggested that diversification is a diversity-dependent process, such that its rate decelerates with clade diversity until an equilibrium number of species is reached (e.g., McPeek 2008; Rabosky 2009a; Rabosky and Glor 2010). However, clade richness by itself cannot suppress diversification. For example, if all species in a clade are allopatric and do not biologically interact in any way, then declining diversification rates may have little to do with overall richness or limited resources (Wiens 2011). Thus, it is important to couple phylogenetic information with ecological information to understand why

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and under what conditions diversification rates decelerate. Empirical studies that relate diversification patterns to ecological data are still uncommon (e.g., Kozak and Wiens 2010; Rabosky and Glor 2010; Vamosi and Vamosi 2010; Wiens et al. 2011; Jonsson et al. 2012), and further research is necessary to identify which general ecological factors modulate diversification.

Three ecological factors seem particularly relevant to explaining decelerating diversification rates: limited area of clade distribution, co-occurrence of ecologically similar species, and slow rates of niche evolution. All three are presumably related to competition for limited resources (e.g., Gavrilets and Vose 2005; Gavrilets and Losos 2009). First, smaller geographic areas may lead to greater co-occurrence of species, and also fewer opportunities for allopatric speciation via subdivision of geographic ranges by extrinsic factors (e.g., Rosenzweig 1995; Losos and Schluter 2000). Second, co-occurrence of related species with similar niche requirements may lead to decelerating diversification, possibly due to resource-related limits on the number of ecologically similar species that can coexist (e.g., such that any additional species that arise must be balanced by extinction; McPeek 2008; Phillimore and Price 2008; Rabosky 2009a,b; Vamosi and Vamosi 2010). In such a case, evolution in traits linked to the resource-related niche (Eltonian niche; Soberon 2007) could drive speciation, reduce competition, and allow additional closely related species to co-occur, thus reducing diversification slowdowns (as in classical models of adaptive radiation). However, there may (or may not) be intrinsic limits on Eltonian niche evolution within a clade, which might also lead to diversification slowdowns. Evolution in the Grinnellian niche (Soberon 2007), which determines where species can occur, might also be important. For example, if there is a high rate of climatic niche evolution, clades may be able to spread over a larger geographic area (increasing opportunities for allopatric speciation and decreasing local co-occurrence), and climatic niche divergence may itself drive speciation (e.g., if one species cannot tolerate the conditions where its sister species occurs; Kozak and Wiens 2010). Thus, limited geographic area, species co-occurrence, and limited niche evolution might each act separately or together to cause decelerating diversification within a clade. We address each of these factors in greater detail below.

Several studies have revealed that diversification is strongly influenced by the geographic area available to a clade (Losos and Schluter 2000; Ricklefs 2006; Rabosky 2009b; Rabosky and Glor 2010; Vamosi and Vamosi 2010; but see Kozak and Wiens 2010). Geographic area seems relevant for clade diversification, but it is sometimes unclear how to define the relevant area (e.g., for mainland faunas). Previous studies have simply calculated the area of clade distribution (clade area). However, clade area may be strongly confounded by clade diversity, so that younger clades with few species are likely to have smaller ranges even if all the clades diversified at a constant rate (assuming that range sizes are similar across species and that clade area is expanding over time, among other things). The effect of clade area therefore needs to be examined together with the effect of clade diversity, which has not been done in previous studies. Moreover, it can be argued that clade area is more informative when considering its geographic context (Machac et al. 2011). As clades colonize the available geographic area (e.g., continents), their opportunity for further geographic expansion decreases. As a result, clades may encounter novel environmental conditions less frequently, reducing opportunities for speciation through ecological divergence (e.g., due to differences in climatic conditions). Therefore, diversification declines may reflect the percentage of available area that a clade actually occupies. If this is the case, even clades with large distributions may exhibit diversification slowdowns when they occupy the entire available area (e.g., the whole continent).

As mentioned above, diversification slowdowns may also be related to rates of niche evolution, for both the Grinnellian and Eltonian niche. This hypothesis finds some support in the study of Kozak and Wiens (2010), who found lower diversification rates in plethodontid clades with lower rates of climatic niche evolution. It is also compatible with the concept of key innovations, whereby clades diversify rapidly shortly after acquiring novel ecological traits and invading unoccupied portions of resource-related ecospace (e.g., Rainey and Travisano 1998; Klak et al. 2004; Gavrilets and Vose 2005; Gavrilets and Losos 2009). Thus, we hypothesize that clades with lower rates of niche evolution will show greater diversification slowdowns. Niche evolution may also be connected with the other examined variables, including clade area (e.g., faster rates of climatic niche evolution allow for geographic expansion) or competition (e.g., evolutionary divergence in resource-related traits may reduce competition between sympatric species). In turn, geographic area and competition may themselves limit rates of niche evolution in a clade (e.g., Kozak and Wiens 2010).

Finally, diversification might be constrained by the presence of potential competitors (e.g., Mayr 1947; Gavrilets and Vose 2005; McPeek 2008; Phillimore and Price 2008; Gavrilets and Losos 2009; Rabosky 2009a). Some authors have suggested that co-occurrence of ecologically similar species can stop diversification entirely, so that diversification rate declines to zero when a local environmental carrying capacity is reached (Phillimore and Price 2008; Rabosky 2009a,b; Vamosi and Vamosi 2010). However, even though gradual niche filling and subsequent slowdown in diversification is often observed after a burst of adaptive radiation (review in Gavrilets and Losos 2009), evidence for absolute limits on clade diversity or local richness (i.e., no increase in clade diversity or local richness over time) remains questionable (e.g., Benton 2001; Benton and Emerson 2007; Morlon et al. 2010; Wiens 2011). Instead, competition between co-occurring species may slow diversification without actually stopping it (e.g., Morlon et al. 2010; Wiens et al. 2011). For example, a clade may at first rapidly radiate and diversify into many ecologically divergent species (as in classic adaptive radiation models; Schluter 2000). Once this has occurred, there may be little subsequent divergence and speciation along these same niche axes (slowing diversification), but species might still ecologically diverge and speciate along other niche axes.

Herein, we explore which ecological factors best predict the deceleration of clade diversification. To address this question, we used carnivorans (Carnivora, Mammalia) as a model system. Carnivorans were selected because of the availability of a comprehensive, time-calibrated phylogeny and detailed range maps for all extant species in the group (e.g., Machac et al. 2011; Nyakatura and Bininda-Emonds 2012). Furthermore, carnivorans occupy the top of many terrestrial food chains and have high metabolisms and energy requirements (Donadio and Buskirk 2006), and so may be especially likely to have their diversification patterns influenced by limited ecological resources.

Many previous studies on decelerating diversification focused primarily on patterns within genera (e.g., McPeek 2008; Phillimore and Price 2008; Rabosky and Lovette 2008; Morlon et al. 2010) or orders (Rabosky 2009b). Here, we included all nodes of the carnivoran phylogeny (i.e., all possible monophyletic carnivoran clades), which allowed us to address these questions across a range of phylogenetic scales. For all nodes, we first estimated the deceleration in clade diversification using the widely used gamma statistic (Pybus and Harvey 2000). Then, while controlling for phylogenetic dependence between nodes, we analyzed whether the estimated level of deceleration is best predicted by clade area, proportion of potentially suitable geographic area occupied by the clade, rates of niche evolution, or co-occurrence between related species. Rather than finding a single ecological predictor of decelerating diversification, we compared the relative impacts of the studied factors. This framework allowed us to identify ecological attributes in which strongly decelerating clades differ from the other clades.

Methods

ESTIMATING THE RATE AT WHICH DIVERSIFICATION DECELERATES

To analyze carnivoran diversification, we used a dated supertree that included all extant species of terrestrial carnivorans (i.e., 231 species) from Machac et al. (2011). In addition, we recalibrated divergence times of this phylogeny using an alternative age for the carnivoran crown group relative to that used by Machac et al. (2011), based on additional fossil information (e.g., Tedford et al. 1995; Wesley-Hunt and Flynn 2005; Polly et al. 2006; Tedford et al. 2009). We then examined whether divergence times of the adjusted tree are distributed similarly as in the original tree. Both trees were also compared to the supertree assembled by Nyakatura and Bininda-Emonds (2012). This comparison (see Appendix S1 for details) confirmed that divergence time estimates of all three phylogenies are highly linearly correlated ($r > 0.95$, $P < 10^{-10}$; Fig. S1). Therefore, all phylogenies should yield identical conclusions about diversification, and here we only report results for the original tree of Machac et al. (2011). Marine carnivorans (a single clade of 33 species) were included for calculation of diversification declines but omitted from further analyses, given that many environmental variables would be difficult to compare between marine and terrestrial species.

The rate of decelerating diversification was calculated for each carnivoran clade separately (i.e., for each node of the phylogeny), using the gamma statistic of Pybus and Harvey (2000). Gamma is a standard and widely used statistic in studies of diversification slowdowns (e.g., McPeek 2008; Phillimore and Price 2008). It is based on the distribution of branching times within a clade. If a clade diversifies at a constant rate, gamma should equal zero. Gamma becomes negative when the branching times are concentrated near the root of the clade, which indicates decelerating diversification. The lower the gamma statistic, the more pronounced the slowing is. Because gamma values follow a standard normal distribution (mean = 0, SD = 1), significant slowdowns are indicated when $\gamma < -1.96$. Thus, gamma allowed quantitative comparison of the rate at which diversification decelerated among clades.

There are also other approaches that can be used for evaluating diversification slowdowns, such as lineage-through-time plots (Nee et al. 1992) or likelihood estimation of saturation probability (Morlon et al. 2010). However, we used gamma because it can be calculated for each clade separately and its values are readily interpretable.

ESTIMATING THE EFFECTS OF GEOGRAPHIC AREA ON DIVERSIFICATION

There are several ways to characterize geographic constraints on clade diversification. The simplest approach is to calculate clade area, which is basically the combined extent of the geographic ranges for all species within a clade. Clade area is closely related to clade diversity and species range overlap within a clade. For example, when species have similar range sizes and limited range overlap, clade area is expected to increase with clade diversity. Preliminary analyses revealed a strong correlation between clade area and diversity (phylogenetically corrected generalized linear model [PGLM] correlation: $r = 0.754$, $P < 0.001$) in carnivorans. Therefore, we conducted a path analysis to disentangle the effects of these variables (area, diversity, range overlap) on diversification slowdowns. In addition to clade area, we calculated clade diversity and relative range overlap for each node of the carnivoran tree. To estimate relative range overlap, the range sizes of a clade's constituent species were summed up and divided by the overall clade area. Then, we computed phylogenetically independent contrasts (PIC; using R to implement the equations from Felsenstein 1985) for all of these variables and used path analysis to estimate their partial effects (e.g., effects of clade area when clade diversity is held constant). In addition to the path analysis, we regressed clade area on clade diversity and used residuals from this regression in subsequent PGLM analyses (see below). Using these two independent procedures (PIC and PGLM), we tested whether clade area affects diversification slowdowns above and beyond the effects of clade diversity.

As described above, limited opportunity for geographic range expansion might potentially suppress clade diversification (e.g., due to decreased opportunity for speciation in novel environments or other factors). To test this hypothesis, we first inferred the potential area for each clade based on climatic conditions. Then, we related the potential area to the actual area of clade distribution and used the obtained ratio as a measure of opportunity for geographic expansion. More specifically, the potential area for each carnivoran clade was inferred by means of species distribution modeling (Guisan and Thuiller 2005; Elith et al. 2006). This technique uses climatic conditions within a species' range to infer its potential distribution. Because biotic interactions are not considered, the obtained distribution models can be viewed as geographic projections of the Grinnellian niche (Soberon 2007; Soberon and Nakamura 2009). Herein, we interpret the geographic extent of these models as "potential area of clade distribution," but we acknowledge that environmental tolerances may shift over evolutionary time scales.

To estimate the potential area for a given clade, we first constructed distribution models for each of its constituent species separately by means of the MaxEnt algorithm (Phillips et al. 2006; Elith et al. 2011). This entropy-based method estimates the potential distribution of a species by contrasting environmental conditions at points where the species is present with background referential points. In our case, range maps for individual carnivoran species were taken from the IUCN database (International Union for Conservation of Nature; www.iucnredlist.org). To sample occurrence points from these maps, we used an equidistant 50 km grid (Lawing and Polly 2011; available from http://mypage.iu.edu/~pdpolly/Data.html). For most species (95% out of 231 species), we obtained >10 occurrence points per species. However, for species with smaller geographic range sizes (5% of all species) this number was slightly lower (five to 10 per species). The background referential points needed for MaxEnt were sampled from the area within the species range and its immediate vicinity (i.e., a zone of 4° width surrounding each species' range). Environmental conditions were described by 19 climatic variables from the WorldClim dataset (Hijmans et al. 2005).

Reliability of the obtained distribution models was assessed with a cross-validation procedure (Phillips et al. 2006; Elith et al. 2011). First, the presence data were randomly divided into five training subsets of equal size. Then, only four subsets were used to fit the distribution model while the fifth subset was used for model evaluation. This procedure was conducted iteratively across all subsets and all species. Then, we used the area under the curve (AUC) to assess whether our distribution models efficiently distinguish presence data from the background referential points. The relatively high AUC values ($\mathrm{AUC} = 0.876 \pm 0.077$; mean ± SD) obtained suggested that our models were reliable and could be employed in further analyses (Table S1). Even though the AUC values are extensively used for model evaluation, we note that they have also been criticized (Lobo et al. 2008). In subsequent analyses, we only used the extent of distribution models lying within the continent(s) of the clade's actual occurrence. Distribution models were fitted and evaluated using the R packages *dismo* (Hijmans et al.: <http://dismo.r-forge.r-project.org>), *raster* (Hijmans and Etten: <http://raster.r-forge.r-project.org>), and *sp* (Pebesma et al.: <http://rspatial.r-forge.r-project.org>).

Once the potential distributions for all species in a clade were inferred, they were then overlaid to yield the potential area of the clades. For each clade, the potential area ($\mathrm{AREA}_{\mathrm{pot}}$) was related to the area of its actual distribution ($\mathrm{AREA}_{\mathrm{act}}$):

$$f = \frac{\mathrm{AREA}_{\mathrm{act}}}{\mathrm{AREA}_{\mathrm{pot}}}.$$

The obtained ratio (f) indicates the proportion of the potential area of a clade that is actually occupied. A proportion of $f \approx 0$ indicates that a clade occupies only a tiny fraction of the area on the continent that contains suitable climatic conditions. If the proportion approaches one ($f \approx 1$), then the clade occupies the whole island or continent and is considered to be highly geographically constrained.

ESTIMATING RATES OF NICHE EVOLUTION

Rates of niche evolution indicate how much ecological change has occurred in a clade over time. To calculate rates of niche evolution for carnivorans, we first characterized potentially important axes of their niche in terms of climate (temperature and precipitation within the species ranges) and body size. These attributes are often analyzed in the context of carnivoran diversity and evolution (Freckleton and Jetz 2009; Diniz-Filho et al. 2010). For example, body size may be correlated with many important aspects of carnivoran ecology including dietary preferences, reproductive rates, and population dynamics (e.g., Gittleman 1985; Freckleton and Jetz 2009; Diniz-Filho et al. 2010). Climate may determine the ecological conditions where a species can occur (e.g., Soberon 2007). First, we tested whether these traits are related to carnivoran diversification. Then, we estimated rates of trait evolution across all carnivoran clades. We hypothesize that lower rates of niche evolution will be associated with steeper declines in diversification.

To characterize climatic niches of carnivorans, we first estimated annual mean temperature (Bio1) and annual precipitation (Bio12) for each species. These two variables are standard measures used to describe the climatic niche of species, and most other temperature and precipitation variables should generally correlate with them. Nevertheless, we also used principal component analysis (PCA) to combine all 19 bioclimatic variables at each locality into a series of composite climatic variables (i.e., PCA axes; Table S2). The broken-stick method (MacArthur 1957; Jackson 1993) revealed that only two PCA axes (PC1, PC2) explained more variance than expected under a null model of variance partitioning (Fig. S2), and we therefore selected only these two axes for our further analyses. Mean values of all four climatic variables (Bio1, Bio12, PC1, PC2) were calculated from each species' occurrence points that were sampled across an equidistant 50 km grid (see above). For most species (95% out of 231 species), the climatic means were based on more than 10 occurrence points, whereas for species with smaller ranges (5% of species) the number of points was necessarily lower (five to 10 points).

In addition, data on adult body sizes of individual carnivoran species were compiled from literature summaries (Grzimek 1990; Kingdon 1997). If different body mass values were reported within a species (e.g., across sexes or populations), we used their average. Thus, we obtained five variables characterizing some of the major axes of carnivoran niche space (Bio1, Bio12, PC1, PC2, and body size).

Prior to the analyses of decelerating diversification, we verified whether these traits actually influence carnivoran diversification because traits with no influence on diversification may not be expected to influence diversification slowdowns. To examine whether carnivoran speciation and extinction vary as functions of the examined traits, we used QuaSSE modeling (quantitative trait speciation and extinction) implemented in the R package *diversitree* (FitzJohn 2010). Details of this analysis are described in Appendix S2.

Because we found that climatic niches (but not body size) are significantly associated with carnivoran diversification (see Table S3), we used them in further analyses of evolutionary rates. First, we fitted the Brownian motion (BM) model and the Ornstein–Uhlenbeck (single optimum) model of evolution to our trait data (Butler and King 2004). Then, we used AIC to assess which model fit our trait data better and then used the corresponding estimate of evolutionary rates (sigma) from that model (Butler and King 2004). This procedure was conducted for all nodes of the carnivoran tree, and the estimated evolutionary rates were used to assess whether stronger diversification slowdowns are coupled with lower rates of niche evolution. We note that there are multiple potential sources of error in estimating rates of climatic niche evolution (e.g., climate change, continental drift, and biome contractions and expansions all might introduce noise or bias to rate estimates), and these estimates therefore must be interpreted with caution. Rate estimation and model comparisons were performed using the R packages *ape* (Paradis et al. 2004) and *geiger* (Harmon et al. 2008).

ESTIMATING THE EFFECTS OF SPECIES CO-OCCURRENCE

Verbal theories and mathematical models suggest that co-occurrence of closely related species can also limit diversification, possibly due to niche filling and increasing competition (Mayr 1947; Gavrilets and Vose 2005; McPeek 2008; Phillimore and Price 2008; Gavrilets and Losos 2009). To test this prediction with empirical data, we examined whether diversification slowdowns tend to occur more strongly in sympatric clades (e.g., Wiens et al. 2011). The level of sympatry was expressed in terms of relative range overlap, both within the focal clade (within-clade overlap) and within the focal clade and including all other carnivorans (overlap with all carnivorans). To estimate within-clade overlap, we summed up range sizes of the clade's constituent species and then divided the sum by the clade's geographic area. To calculate overlap with all carnivorans, we summed up the areas of all species ranges of carnivorans lying within the geographic range of the clade (or of those parts of their ranges that lay within the geographic range of the clade) and then divided this sum by the area of the geographic range of the clade. For both measures, relative range overlap equals 1 in purely allopatric clades and increases with the level of sympatry.

In addition, we calculated a simple index of ecological similarity between species by taking the average of pairwise differences in body sizes. This index was calculated (1) for all species within a clade and (2) for all species occurring within the geographic range of a clade. We used these indexes to assess whether the effects of species co-occurrence (relative range overlap within clade and with all carnivorans) change with the ecological similarity of the co-occurring species. As noted above, body size is related to many important aspects of carnivoran ecology, such as diet (e.g., Gittleman 1985; Freckleton and Jetz 2009; Diniz-Filho et al. 2010). Based on previous hypotheses related to competition and niche filling among sympatric species (e.g., Gavrilets and Vose 2005; Phillimore and Price 2008; Gavrilets and Losos 2009; Rabosky 2009a), we predict that clades with steeply decelerating diversification should show higher within-clade range overlap, higher range overlap with all carnivorans, and greater ecological similarity of co-occurring species. Therefore, we would expect a significant PGLM interaction between within-clade overlap and ecological similarity of related species (i.e., slowdowns are stronger if the co-occurring related species are also ecologically

Table 1. Results of the phylogenetically corrected generalized linear model (PGLM) analyses. Decelerating diversification, measured by the gamma statistic, was predicted by a series of ecologically relevant variables. Clade diversity cannot explain decelerating diversification directly, but it is the only significant predictor of the strength of the slowdowns.

	Slope	F	R^2	P
Time and diversity				
Clade diversity	–	65.849	0.291	<0.001
Clade age	–	3.593	0.022	0.059
Geographic area				
Percent of potential area occupied	–	2.418	0.015	0.122
Area of clade distribution[1]	+	1.313	0.008	0.253
Rates of niche evolution				
Bio1 temperature	–	2.741	0.017	0.100
Bio12 precipitation	–	0.036	0.000	0.850
PC1 climate	+	0.417	0.003	0.519
PC2 climate	+	0.662	0.004	0.417
Body size	–	1.553	0.010	0.215
Species co-occurrence				
Range overlap within the clade	+	2.016	0.019	0.159
Range overlap with all carnivorans	–	0.726	0.004	0.395

[1] After accounting for clade diversity.

similar). Significant PGLM interaction should also occur between overlap with all carnivorans and their ecological similarity (i.e., stronger slowdown within a clade results when its geographic range overlaps with many similarly-sized carnivoran species). However, we acknowledge that we are using only a single estimate of body size for each species, and body sizes might shift across a species range depending on which species it co-occurs with in different parts of its range.

COMPARING THE PREDICTORS OF DECELERATING DIVERSIFICATION

To examine the ecological correlates of decelerating diversification, we fitted a set of candidate models in which the gamma statistic (Pybus and Harvey 2000) served as the predicted variable. Our candidate models were divided into four categories with respect to the explanatory variables used: clade age and diversity, geographic area, rates of niche evolution, and relative range overlap (Table 1).

Because carnivoran clades do not represent independent data points, the candidate models were fitted by means of the PGLMs (Freckleton et al. 2002). The PGLM algorithm estimates phylogenetic dependence in the data by searching for the maximum likelihood value of the parameter λ, which varies between 0 and 1 (0 indicates phylogenetic independence, whereas $\lambda = 1$ indicates phylogenetic signal consistent with the BM model). Then, while controlling for the detected phylogenetic dependence, a GLM model is fitted and its phylogenetically corrected parameters are returned (Freckleton et al. 2002). PGLM inference was conducted using statistical code from the R package *caper* (Orme et al.: <http://cran.r-project.org/web/packages/caper>).

To assess the robustness of the results, we reanalyzed the PGLM models using jackknife resampling. In each of 1000 jackknife iterations, we randomly omitted 10% of our data points (i.e., 10% of the analyzed carnivoran clades). The threshold of 10% was chosen arbitrarily, but it should be sufficient to account for potential outliers and extreme values. Subsequently, we recalculated all PGLM models. Consequently, we obtained 95% confidence intervals for all the inferred statistics so that we were able to assess whether our conclusions were sensitive to sampling bias and outliers.

SUPPLEMENTARY SIMULATIONS

Diversification is to some extent stochastic and its rate may oscillate around a long-term average even when the average itself stays constant over time (Ricklefs 2007; Pennell et al. 2012). Clades whose initial diversification exceeds the overall average can rapidly accumulate species and, as a result, may have a higher probability of survival to the present (assuming clades with more species are more likely to survive to the present than species-poor clades). This "sampling bias" toward extant taxa with rapid diversification in their early history may explain many of the observed slowdowns (Phillimore and Price 2008; Pennell et al. 2012). To test whether carnivoran slowdowns might result from this type of sampling bias, we simulated 1000 phylogenies under constant diversification and quantified their apparent slowdowns with the gamma statistic (Pybus and Harvey 2000). Parameters for the simulation procedure were inferred from our carnivoran tree, as described in Nee et al. (1994), with estimated birth = 0.133, death = 0.024, and tree size = 231 species. The estimates of birth and death rates indicate the number of speciation and extinction events, respectively, per lineage per million years. The inferred extinction rate across carnivorans may be an underestimate (given general problems in estimating extinction from phylogenies of extant taxa noted by Purvis 2008; Quental and Marshall 2010), but sampling bias is known to be strongest under low extinction (Pybus and Harvey 2000; Pennell et al. 2012). If estimated carnivoran slowdowns are stronger than estimated slowdowns in phylogenies simulated under relatively weak extinction, it would be strong evidence that carnivoran slowdowns cannot be explained by sampling bias (Pybus and Harvey 2000; Phillimore and Price 2008; Pennell et al. 2012). Then, we would need to search for a different explanation for the observed slowdowns.

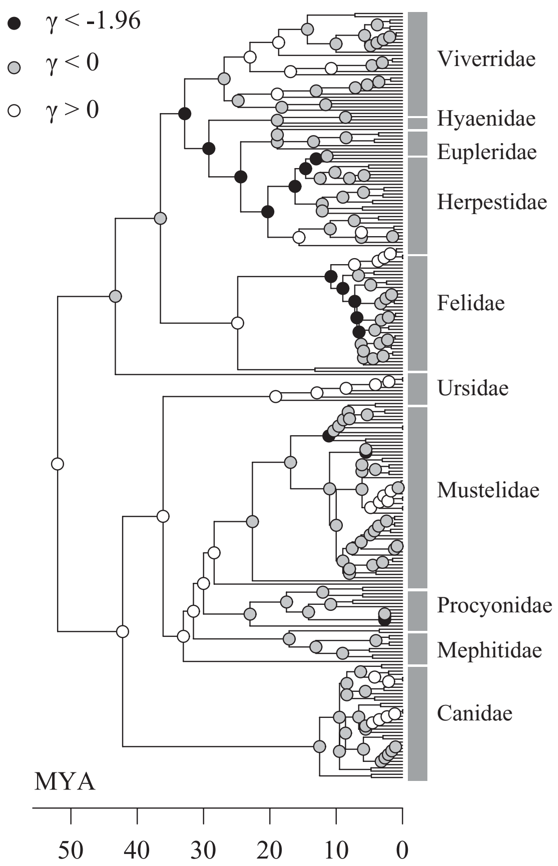

Figure 1. Estimated diversification slowdowns for carnivoran clades based on the gamma statistic. Declining diversification is common in carnivorans and its overall magnitude ($\gamma = -0.935 \pm 0.851$; mean ± SD) is similar to or greater than that observed in many other taxa (as compared to datasets in McPeek 2008; see Results). Diversification did not significantly accelerate in any of the carnivoran clades. Nonsignificant acceleration is indicated by white circles ($\gamma > 0$), whereas gray and black circles indicate nonsignificant ($\gamma < 0$) and significant slowdowns ($\gamma < -1.96$), respectively.

Moreover, since path analysis identified clade diversity as the only significant predictor of decelerating diversification (see Results), we examined its effects further using supplementary simulations. Clade diversity in itself cannot biologically explain diversification slowdowns, but it may represent some important predictor variable which was not directly included in our analyses. It is also theoretically possible that clade diversity and decelerating diversification are only linked statistically; for example, it may be difficult to detect weak slowdowns in species-poor clades. To examine these two scenarios, we conducted three sets of simulations. First, we simulated 1000 phylogenies using parameters estimated from the carnivoran tree (see above) and examined whether correlation between gamma and clade diversity emerges even in the simulated trees. Second, we simulated 1000 phylogenies under randomly generated birth and death rates. If correlation between gamma and clade diversity arises as a statistical artifact, it should hold for any combination of simulation parameters. Third, we simulated phylogenies under decelerating diversification and tested whether the ability of gamma to detect slowdowns in individual clades changes with clade diversity. If constant diversification is easier to refute in large clades, gamma should underestimate slowdowns in species-poor clades, overestimate slowdowns in diverse clades, and correlate negatively with clade diversity. If these predictions are supported, clade diversity might not necessarily be a surrogate for any specific biological variable that actually causes slowdowns. Instead, correlation between gamma and clade diversity might be a statistical artifact. All these simulations were conducted using the R packages *ape* (Paradis et al. 2004) and *geiger* (Harmon et al. 2008) and their detailed description is provided in Appendix S3.

Results

Our analyses indicate that decelerating diversification is common in carnivorans (Fig. 1) and the magnitude of the detected slowdowns are similar to those observed in many other taxa (McPeek 2008). Specifically, values of the gamma statistic were approximately normally distributed across carnivoran clades so that $\gamma = -0.935 \pm 0.851$ (mean ± SD), whereas in the McPeek (2008) dataset, which includes 245 clades of animals and plants, $\gamma = -0.737 \pm 3.102$ (mean ± SD).

The observed carnivoran slowdowns were significantly stronger than those from phylogenies simulated under constant diversification (Wilcoxon signed-rank test: $W = 19{,}577$; $P < 10^{-10}$; Fig. S3). Because we simulated phylogenies under relatively weak extinction, which yields the strongest slowdowns that sampling bias can cause (Pybus and Harvey 2000; Pennell et al. 2012), the even stronger slowdowns observed in carnivorans cannot be explained by sampling bias alone (Appendix S3). If our simulations were conducted under stronger, perhaps more realistic extinction rates, we should have found carnivoran slowdowns to be even more pronounced in comparison to the simulated phylogenies. This is because strong extinction acts against sampling bias and induces spurious patterns of accelerating diversification (an effect known as the “pull of the present”; Nee et al. 1992; Pybus and Harvey 2000; Pennell et al. 2012).

Among the examined variables, clade diversity explained the most variation in diversification slowdowns ($R^2 = 0.291$, $P < 0.001$; see Table 1). None of the other variables showed a significant relationship with slowdowns (Table 1). Path analysis further corroborated the effects of clade diversity and showed that diversity affects both clade area and diversification slowdowns separately (Fig. 2). Supplementary simulations revealed that clade diversity and slowdowns are not linked biologically because they are significantly correlated even in simulated phylogenies

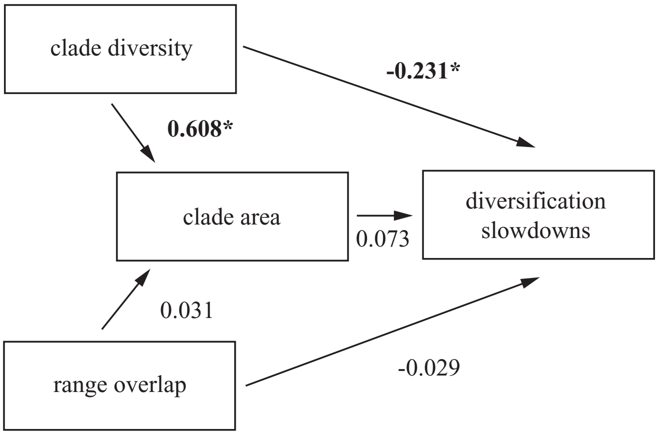

Figure 2. Path analysis of the relationships between clade diversity, clade area, range overlap, and diversification slowdowns. Standardized partial correlation coefficients indicate that the effects of clade area are only miniscule when clade diversity is held constant. Similarly, relative range overlap is largely decoupled from decelerating diversification. The strongest link is between diversification slowdowns and clade diversity, and our simulations show it might be artifactual (see Results). Slowdown strength was measured by the gamma statistic (low gamma indicates strong slowdowns). Significant correlations are indicated by an asterisk (*).

(mean correlation was $r \approx 0.5$, $P < 0.001$; see Figs. 3 and S4). Further simulations suggested the mechanism whereby this occurs: clade diversity increases the ability of gamma to refute constant diversification so that slowdowns are easier to detect in larger clades (Fig. S5).

Interestingly, apart from clade diversity, none of the other examined variables proved significantly related to the strength of diversification slowdowns (Table 1), including clade area (after accounting for clade diversity; $R^2 = 0.008, P = 0.253$), percentage of available area occupied ($R^2 = 0.015, P = 0.122$), rates of climatic niche evolution ($R^2 \approx 0.01, P > 0.1$), and relative range overlap (within-clade and with all carnivorans; $R^2 < 0.02, P > 0.15$). Therefore, contrary to expectations, none of these factors explained the observed variation in slowdown strength. Decelerating diversification was independent of rates of climatic-niche evolution, even though QuaSSE confirmed that the climatic niches themselves were linked to diversification (Table S3).

We also tested for a statistical interaction between relative range overlap (within clades and with all carnivorans) and the index of body-size similarity to examine whether the effects of relative range overlap differ with ecological similarity of the co-occurring species. This interaction, however, was not significant (PGLM interaction between similarity and within-clade overlap: $P = 0.161$; PGLM interaction between similarity and overlap with all carnivorans: $P = 0.771$). The rate of deceleration is therefore independent of whether the co-occurring species are ecologically similar or not, at least in terms of body size.

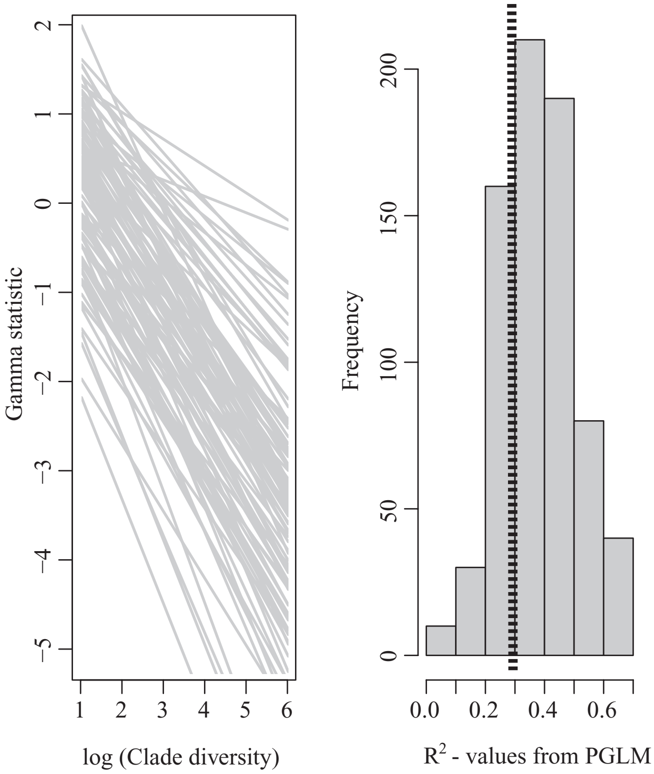

Figure 3. The relationship between clade diversity and slowdowns across 1000 phylogenies simulated under speciation and extinction rates inferred from the carnivoran tree (see Appendix S3). Clade diversity correlates with diversification slowdowns even in simulated phylogenies (left panel). Relationships detected in simulated phylogenies are similar in strength to the empirical relationship in carnivorans ($R^2 = 0.291$; vertical dashed line in the right panel). Therefore, the link between diversity and decelerating diversification may be purely artifactual and so may not require any biological explanation.

Finally, the relative importance of individual explanatory variables (i.e., geographic area, rate of niche evolution, co-occurrence between related species) was not altered by the jackknifing procedure (Table S4). This result confirms that our major conclusions remain unchanged even when some uncertainty is taken into account.

Discussion

Many studies have now documented apparent slowdowns in clade diversification over time in a diversity of taxa (e.g., McPeek 2008; Phillimore and Price 2008), but the meaning of these slowdowns is less than clear. The present study attempts to understand the causes of these slowdowns in the context of clade ecology and biogeography, using carnivorans as a model system. Contrary to expectations, carnivoran slowdowns are decoupled from our measures of geographic range overlap (within each clade and with all carnivorans), rates of niche evolution, clade area (after accounting for clade diversity), opportunity for geographic expansion (based on niche modeling), and ecological similarity of co-occurring species (at least for body size). We also show that even though clade diversity appears to be a strong predictor of decelerating diversification, these strong relationships occur even in simulations in which no biological process links diversity and decelerating diversification. Why diversification appears to decelerate in so many taxa remains uncertain, but our results highlight that slowdowns might not necessarily result from co-occurrence and competition between related species.

It has long been presumed that diversification decelerates as the number of related species increases within a geographically constrained area, with niche filling and competition for resources suppressing diversification (e.g., Mayr 1947). Even though this hypothesis has been assumed by many studies (e.g., Phillimore and Price 2008, Gavrilets and Losos 2009; Rabosky 2009a) and supported by mathematical models (Gavrilets and Vose 2005; McPeek 2008; Rabosky 2009b), empirical evidence for diversification declines due to limiting geographic area and competition for resources is scarce. For example, several empirical studies have documented a relationship between area and diversification (Ricklefs 2006; Rabosky and Glor 2010; Vamosi and Vamosi 2010), but did not explicitly incorporate species co-occurrence. However, it is not possible to address competition without addressing co-occurrence of species.

In carnivorans, we find no support for the idea that diversification slowdowns are associated with increased co-occurrence between related species in smaller geographic areas (Table 1). Most carnivorans are positioned near the top of the trophic pyramid (Donadio and Buskirk 2006), and we would expect them to be strongly limited by competition for dietary resources (Palomares and Caro 1999; Glen and Dickman 2005; Donadio and Buskirk 2006). Although other taxa may support different results, the effects of competition seem even less likely in more ecologically variable clades. It is also possible that the lack of any clear relationship results from some limitations of our methodology. Carnivoran species may avoid competitive exclusion by diverging in other ecological traits not examined here, such as specific dietary preferences or microhabitat (e.g., Davies et al. 2007). Moreover, the employed proxies for the rates of climatic niche evolution (sigma from BM and Ornstein-Uhlenbeck models), potential for geographic spread (percent of potential area occupied), and species co-occurrence (relative range overlap) may have failed to capture the underlying processes accurately enough. However, it appears that if these effects are present, they seem to be very weak (and thus difficult to detect).

Several other issues might also preclude clear-cut conclusions about diversification slowdowns. These include clade delimitation and phylogenetic scaling (Storch and Sizling 2008). As an example of the problem of clade delimitation, some apparent global slowdowns might result if (for a given focal clade) some subclades diversify at a constant rate whereas others approach extinction (Benton and Emerson 2007). Under this scenario, the observed pattern of diversification slowdowns might reflect combining these different subclade patterns rather than slowing diversification due to competition or related ecological factors (Benton and Emerson 2007). Moreover, different forces might operate across different phylogenetic scales. For example, diversification within genera might be constrained by competition between co-occurring species, whereas diversification at higher levels might be modulated by long-term climatic fluctuations or biome area (although if this was the case in carnivorans, we might expect a stronger relationship with co-occurrence, because there are many more within-genus clades than families). Given the potential for conflicting patterns at different scales, a single factor which would explain decelerating diversification completely might be elusive (Benton 2001, 2009; Benton and Emerson 2007). Nevertheless, we find it striking that our results do not show merely weak relationships between decelerating diversification and the expected variables, but no significant relationships at all. These findings highlight that the effects of area, co-occurrence, and competition cannot simply be assumed. Instead, they should be explicitly tested.

Only a few studies to our knowledge have analyzed decelerating diversification in a geographic context. Rabosky and Glor (2010) showed that diversification declines in Caribbean anoles negatively correlated with the area of the four islands of the Greater Antilles. However, the role of area was inferred from only four data points, and the authors did not control for other factors which might explain differential diversification declines among the four islands. Similarly, Vamosi and Vamosi (2010) discussed diversification declines in the context of plant biogeography. These authors found that species richness of plant families (which was used to approximate family diversification) correlates with the area of ecoregions where individual families occur. As the authors acknowledge, this approach cannot resolve whether the effects of area are mediated through increased co-occurrence between related species or through limited opportunity for allopatric speciation. Moreover, even though geographic area may be correlated with diversity, it is not clear whether it is related to diversification slowdowns as well.

Our results suggest that clade area and diversification slowdowns are linked only due to shared correlation with clade diversity. When clade diversity is accounted for, the link between clade area and diversification slowdowns disappears (Table 1, Fig. 2). Moreover, the relationship between clade diversity and diversification slowdowns might be artifactual as well (Figs. 3 and S4).

Our simulations suggest that the ability of the gamma statistic to detect significant slowdowns decreases with clade size, which leads to apparently stronger slowdowns in more diverse clades (Fig. S5, Appendix S3). Carnivoran slowdowns themselves are strong and cannot result from sampling bias (sensu Pennell et al. 2012; Fig. S3), but the actual mechanisms causing these slowdowns remain unclear. Importantly, we still cannot exclude the possibility that the pattern of apparent slowdowns in carnivorans (and other clades) results from another type of statistical artifact rather than from evolutionary or ecological processes.

In summary, we find that decelerating diversification can be unrelated to clade area, rate of niche evolution, and range overlap between related species, contrary to expectations. Therefore, we caution against the common assumption that diversification slowdowns necessarily result from co-occurrence and competition between related species. Why diversification appears to decelerate in so many taxa still remains questionable, but it is clear that this topic needs to be studied in an ecological and biogeographic context rather than using molecular phylogenies alone.

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Supporting Information

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

Appendix S1. Comparison of divergence times for three carnivoran phylogenies.
Appendix S2. Details of the quantitative trait speciation and extinction (QuaSSE) modeling.
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Figure S4. The relationship between clade diversity and slowdowns across 1000 phylogenies simulated under randomly generated speciation and extinction rates.
Figure S5. Ability of gamma to detect slowdowns in clades of varying sizes.