

Death and taxa: time-invariant differences in mammal species duration

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Why species go extinct at different rates remains one of the most fundamental questions in paleobiology ¹⁻⁵. Determining which and how biological traits influence extinction risk is vital for understanding the differential diversification of life during the Phanerozoic and for making predictions about species' vulnerability to anthropogenic impacts. Here I present a hierarchical Bayesian survival model of North American Cenozoic mammal species durations as predicted by species-level ecological factors, time of origination, and phylogenetic relationships. I also explicitly model the effect of species age on extinction risk, relaxing the Law of Constant Extinction which is the critical assumption underlying the Red Queen Hypothesis ². This study focuses on time-invariant effects in an effort to characterize aspects of the selective patterns of background extinction in an effort to determine if the current biodiversity crisis is congruent with an intensification of previous processes or represents the arrival at an environmental “tipping point” ^{7,8} or a shift in

“macroevolutionary regime”⁶ associated with a mass extinction.

Here I test how non-random extinction is with respect to organismal- and species-level traits during times of background extinction, if and which traits have time-invariant effects on species duration, and if extinction is taxon-age independent among Cenozoic mammals? These questions are dealt with using a single model of species duration and survival whose parameter estimates directly test these questions. Cenozoic mammals represent an ideal group and time period because their fossil record is well sampled, well resolved both temporally and spatially, and the ecology and taxonomy of individual species are generally understood^{1,4,9–13}.

Time-invariant factors are those, that when comparing taxa over a long period of time, there is a consistent effect that is generalizable over the entire period of interest. While the strength of the effect may vary over time, the direction does not change. These consistent effects reveal fundamental differences between selective regimes. Periods of background extinction represent an opportunity to characterize the selective pattern of a given macroevolutionary regime given that they are relatively constant with changes occurring slowly^{6,14}.

The organismal- and species-level traits studied here are dietary and locomotor categories, bioprovince occupancy, and body mass. Each of these traits are related to different aspects of a species' adaptive zone such as homeostatic energetic cost, population density, expected home range size, set of potential prey items, and dispersal ability ^{11,15}. It is expected that species with larger geographic ranges have lower extinction rates than species with smaller geographic ranges ^{6,16}. However, organismal traits directly related to species–environment interactions may play an important role in determining extinction risk. By modeling extinction via traits related to environmental preference, the relative importance of species- and organismal-level properties can be elucidated. These traits are analyzed in the context of both shared species origination cohort and phylogenetic position. From there the relative contribution of the three sources of variance (i.e. species, cohort, and phylogeny) to the total unexplained variance can be estimated.

The parameter estimates of the model demonstrate that dietary category has a large amount of variation in the pairwise differences of effects on expected duration (Fig.). Carnivory appears to be associated with a greater expected duration than herbivory or insectivory, while approximately equal to or less than the expected duration of an omnivore. Omnivory is associated with greater expected

duration than either herbivory or insectivory. Finally, herbivory and insectivory are associated with approximately equal effects on expected duration. Given that carnivores and omnivores have approximately equal extinction risk, and it has been found previously that carnivores have a greater diversification rate than omnivores, this implies that carnivores have a greater origination rate than omnivores¹⁷. This comparison implies that herbivores, which have the greatest extinction risk, must also have a very high origination rate in order to have the greatest diversification rate of these three categories¹⁷.

For locomotor category, arboreality appears to be associated with a lower expected duration than either scansoriality or a ground dwelling life habit (Fig.). Scansoriality and a ground dwelling life habit have approximately equal expected durations. These results consistent with the hypotheses that arboreality is associated with a greater expected extinction risk than either with scansoriality and ground dwelling taxa. Importantly, scansoriality appears to not influence any difference in extinction risk when compared with ground dwelling taxa. This can be interpreted that arboreal taxa, which require a specific kind of environment, may be more prone to extinction because the lack of permanency of those environments preventing species persistence.

The large difference in time-invariant extinction risk between omnivores and both herbivores and insectivores is most likely related to the concept of “survival of the unspecialized” where less specialized taxa have a lower expected extinction risk than specialized taxa ^{1,18}. Because larger effects are easier to identify, the magnitude of this effect also explains both the early identification and origin of this hypothesis ¹. The lack of effect of body size on extinction risk is consistent with some previous results ¹². The direction/sign of the modal estimate of effect is not consistent with the prediction of increase in extinction risk associated with increase in body size ¹⁰. However, the other studies were performed at the generic-level which may or may not involve different processes than at the species-level model ^{10,12}.

As expected, bioprovince occupancy has the largest effect on expected species duration/extinction risk 5). Body size has near zero effect on expected duration, similar to the lack of relationship between body size and generic duration ¹².

Of the three sources of variance present in the model, individual species variance accounts for approximately 70% of the observed variance (Fig. 8). Both cohort and phylogenetic effects account for the other 30% of the observed variance. While both of these effects are the source of approximately 15% of observed

variance individually, the total combined effect factors indicates that neither can be ignored. As VPC_{phylo} , which is equivalent to phylogenetic heritability, is greater than 0 it is not appropriate to ignore phylogeny when modeling survival¹⁹ as is commonly done in paleontological studies^{9,10,20–23}.

The estimates for the individual cohort effects show a weak pattern of increased extinction risk in older Cenozoic cohorts and decreased extinction risk in younger cohorts (Fig. 6). However, this pattern is not very strong as there is a large amount of variation, particularly for older cohorts. For example, note the two cohorts between 50 and 55 My that have a much lower extinction risk than other cohorts of similar age. However, it is interesting to note that the apparent shift from older cohorts with a higher extinction risk to younger cohorts with lower extinction risk is approximately 30 Mya or the Paleogene–Neogene boundary. This transition is marked by the opening up of the landscape and the rise of grazers and the decline heavily forested environments. This shift may underly the inferred increased extinction risk associated with arboreal species compared to ground dwelling or scansorial species (Fig.). However, because the model used here does not allow for change in time-invariant effects, I cannot identify this transition as a tipping point or shift in selective regime with any certainty^{7,8}.

The estimate of the Weibull shape parameter, α , is greater than 1 meaning that extinction risk is expected to increase with taxon age (Table 1). The estimate of α is also rather tightly constrained, having a small posterior standard deviation. α is related to the strength of time on extinction risk and is a key parameter in the hazard function $h(t)$ which can be interpreted as the rate, or approximate probability, of an individual of age t going extinct. As the value of α is between 1 and 1.5, extinction risk for a given species only gradually increases with age (Fig. 7). This result has two possible explanations: (1) older taxa being aged out or out competed by younger taxa, or (2) as an artifact of the minimum resolution of the fossil record.

The hypothesis that older taxa are being outcompeted or replaced by younger taxa is also consistent with the some recent results ^{4,5}, both of which require that older taxa have a greater extinction risk than younger taxa. This is also consistent with the cohort effect (Fig. 6) where Paleogene cohorts may have been replaced or out-competed by younger, Neogene cohorts.

The other possible explanation for the inferred increase in extinction risk with species age is the minimum resolution which might cause an upward bias in estimates of the Weibull shape parameter α ²⁴, an effect which can be observed

by the initial plateau in the K-M estimate of $S(t)$ for the observed (Fig. 2). This plateau is a hallmark of the original paleontological survival analyses² which was identified as partially a product of minimum resolution of the fossil records of the different studied groups.

Given this known biasing factor and previous results^{4,5}, I hypothesize that the inferred pattern is most likely a combination of these two explanations working on concert. In order to determine the relative importance of these two explanations, more work is required into approaches for directly modeling the minimum resolution of the fossil record.

One of the open questions in paleobiology and macroecology is whether the current biodiversity crisis qualified as a mass extinction^{7,8,25}. Because change in the magnitude of extinction risk is not necessarily the best indicator of a shift from background to mass extinction²⁶, it is more fruitful to look for changes in the direction of selection, loss of a selective pressure, or the appearance of novel selective pressures. Comparison of the estimated effects of organismal- and species-level traits analyzed here with previous studies demonstrates a mixture of congruence and incongruence.

As expected, large range size is always associated with lower extinction risk in the Recent ²⁷⁻³⁰. While I found that body size has no time-invariant effect on extinction risk, large body size is associated with increased extinction risk in the Recent, though this is variable across environments and clades ^{27,29,30}. A higher trophic level (e.g. carnivory versus herbivory) is associated with greater extinction risk in Primates and Carnivora ³⁰ which is not congruous with the results found here that carnivores have lower extinction risk than herbivores. Finally, phylogeny has been found to be a factor underlying current mammal species extinction risk, though this effect seems much greater in the Recent than for the whole Cenozoic ²⁸. Note that the phylogeny of Recent mammals is much better than the primarily taxonomy based phylogeny used here, which may partially account for the difference in effect.

How many of these incongruities are within the standard range of time-variant effects is unknown, though these comparisons across multiple factors do point to our arrival at a tipping point ^{7,8} and potentially a shift in macroevolutionary regime ⁶.

There are a few data quality concerns in this study which are also inherent to almost any paleontological study. Almost all of the body mass estimates

were obtained using published regression equations that estimate mass from some other body part (e.g. tooth). These estimates are known with error, which was not included in the model. If the standard deviation of the residuals from each of these regression equations was known, it would be possible to directly model this as measurement error³¹ though this greatly adds to model complexity and decreases some amount of interpretability. Incidentally, this has never been done in any paleontological studies. Also phylogeny used here is only a coarse, baseline estimate of the actual species relationships. Because of this, the analysis of phylogenetic effect on survival represents a minimum estimate. As it stands though, these results point to the importance of including shared evolutionary history in diversification models.

There are many processes encompassed by background extinction and identifying the exact cause of any one species' reason for extinction is extremely difficult. By focusing on estimating the effects of different ecologies and historical factors on average extinction risk, it is possible to better understand what processes may have driven the resulting pattern of selection (i.e. diversity). Here, I focused on time-invariant factors and their relation to biological selectivity of extinction, possible reasons for the observed time-invariant effects, and the effects

of taxon-age on extinction risk. I found that some organismal- and species-level traits such as omnivory and large geographic range size have time-invariant effects on mammal species extinction risk. I also found that there are small but non-ignorable effects of cohort and phylogeny. Finally, I found putative evidence of increasing extinction risk with species age, though this result may be partially due to the minimum resolution of the fossil record itself ²⁴.

Methods

Data and covariate information. Fossil occurrence information was downloaded from the Paleobiology Database (PBDB). This data set was filtered so that only occurrences identified to the species-level, excluding all “sp.”-s. All aquatic and volant taxa were also excluded. Additionally, all occurrences without latitude and longitude information were excluded.

Species dietary and locomotor category assignments were based on assignments in initial the PBDB which were then reassigned into coarser categories.

All individual fossil occurrences were assigned to 2 My bins ranging through the entire Cenozoic. Species duration was measured as the number of bins from the first occurrence to the last occurrence, inclusive. This bin size was chosen

because it approximately reflects the temporal resolution of the North American Cenozoic mammal fossil record ^{9,13}. The youngest origination cohort, 0-2 My, was excluded from analysis.

Species body size estimates were sourced from a large selection of primary literature and data base compilations, principally the PBDB, the Neogene Old World Mammal database, and other large scale data collection efforts ^{32–36}.

For each 2 My bin, a bipartite biogeographic network was created between species occurrences and spatial units, defined from a 70 x 34 regular lattice overlay on a global equal-area cylinder map projection where each cell is approximately 25 km². Emergent bioprovinces within the biogeographic occurrence network were identified using the map equation ^{37,38}. A bioprovince is a set of species–locality connections that are more interconnected within the group than without.

There is no single, formal phylogenetic hypothesis of all Cenozoic fossils mammals from North America, it was necessary to construct a supertree as a minimum estimate of phylogenetic relations so for this study I developed a supertree combining multiple, large species-level phylogenies with a large, taxonomy-based phylogeny ^{34,39–41}. This was done using matrix representation parsimony where the resulting phylogeny represents a minimum estimate of the actual relationships.

Polytomies were resolved in the order of species first appearance and then time-scaled using the “minimum branch length” approach where all branches were a minimum of 0.1 My.

Survival model. Species duration was modeled as being drawn from either an exponential with one inverse-scale parameter λ or a Weibull distribution with shape parameter α and scale parameter σ . When $\alpha = 1$ the Weibull and exponential are equivalent. Both distributions were parameterized as regression models using a log link function. For the exponential distribution this is $\lambda = \exp(\beta^T \mathbf{X})$ where $\beta^T \mathbf{X}$ represents the set of covariates and associated regression coefficients. For the Weibull distribution reparameterization is a bit different where $\sigma = \exp(\frac{-(\beta^T \mathbf{X})}{\alpha})$ where α is constant for all observations.

These regression model included eight species-level coefficients for the covariates (dietary and locomotor categories, body size, mean bioprovince occupancy) along with an intercept term. Both continuous covariates were standardized by subtracting the mean value and dividing by 2 times the standard deviation so that the inferred values were comparable with the coefficients from the binary variables⁴². Each of these regression coefficients was given a weakly informative normally distributed prior.

Two hierarchical terms, one for the effect of shared origination cohort and one for individual phylogenetic effect, were included in this model. The effect of shared origination cohort was assumed to be normally distributed with mean 0 and an unknown standard deviation to be estimated from the data. This standard deviation term was given a weakly informative half-Cauchy prior ³¹. Individual phylogenetic effect was modeled assuming that, if phylogenetically heritable, duration evolved via Brownian motion. This assumption allows for individual phylogenetic effect to be modeled as being multivariate normally distributed with mean vector of all 0s and covariance matrix (Σ) defined as the matrix of shared branch lengths multiplied by an estimated constant ^{19,43}.

An important part of survival analysis is the inclusion of censored observations where the failure time (i.e. extinction) has not been observed. A right censored is where the point of extinction had not yet been observed in the period of study, such as taxa that are still extant. Left censored observations correspond to observations that went extinct any time before some known point. In order to account for the minimum resolution of the fossil record encountered here, taxa that occurred in only a single time bin were left censored.

Parameters were estimated using the Markov Chain Monte Carlo routine

implemented in the Stan probabilistic programming language ⁴⁴ where 4 chains were run in parallel for 20000 samples, thinned to every 20th sample, and divided evenly between warm-up and sampling.

Model adequacy was assessed through multiple posterior predictive checks to determine if the model accurately reflected the observed species durations ³¹. An example posterior predictive check used here is the comparison of an observed summary statistic (e.g. mean) to the distribution of that same statistic as estimated from 1000 simulated data sets.

To characterize the contribution to total observed variance of the different data levels (i.e. individual species, cohort, phylogenetic position), variance partitioning coefficients were calculated using a variation of a randomization approach used for models with non-normally distributed errors ⁴⁵.

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Acknowledgements P.D.S would like to thank M. Foote, K. Angielczyk, R. Ree, P.D. Polly for discussion. J. Alroy and the Fossilworks/Paleobiology Database for data accumulation, entry, and availability. This is Fossilworks/Paleobiology Database publication number XXX.

Competing Interests The author declares that they have no competing financial interests.

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Table 1: Marginal posterior estimates for the parameters of interest based on 1000 posterior samples. The intercept can be interpreted as the estimate for the mean observed species. The other values are the effect of a trait on the expected species duration as expressed as deviation from the mean. The categorical variables are binary index variables where an observation is of that category or not. \hat{R} values of less than 1.1 indicate approximate chain convergence for the posterior samples.

| | mean | sd | 2.5% | 25% | 50% | 75% | 97.5% | \hat{R} |
|------------------|-------|------|-------|-------|-------|-------|-------|-----------|
| alpha | 1.31 | 0.03 | 1.25 | 1.29 | 1.31 | 1.34 | 1.38 | 1.01 |
| intercept | -0.82 | 0.18 | -1.17 | -0.94 | -0.82 | -0.70 | -0.48 | 1.00 |
| ground dwelling | -0.12 | 0.12 | -0.34 | -0.20 | -0.12 | -0.04 | 0.12 | 1.00 |
| scansorial | -0.13 | 0.13 | -0.38 | -0.22 | -0.13 | -0.05 | 0.12 | 1.00 |
| herbivore | 0.11 | 0.12 | -0.13 | 0.03 | 0.12 | 0.19 | 0.35 | 1.00 |
| insectivore | 0.09 | 0.13 | -0.17 | 0.00 | 0.09 | 0.19 | 0.36 | 1.00 |
| omnivore | -0.12 | 0.13 | -0.37 | -0.20 | -0.12 | -0.04 | 0.14 | 1.00 |
| logit(occupancy) | -0.66 | 0.08 | -0.81 | -0.71 | -0.65 | -0.60 | -0.50 | 1.00 |
| log(size) | -0.05 | 0.05 | -0.15 | -0.08 | -0.05 | -0.01 | 0.05 | 1.00 |
| sd cohort | 0.33 | 0.07 | 0.22 | 0.29 | 0.33 | 0.37 | 0.48 | 1.00 |
| sd phylogeny | 0.21 | 0.10 | 0.07 | 0.14 | 0.19 | 0.26 | 0.46 | 1.05 |

Figure 1: Deviance residuals from the fitted survival model. Each graph depicts the residuals from single draws from the posteriors distributions of all estimated parameters. Positive values indicate an under estimate of the observed duration, while negative values indicate an over estimate of the observed duration. Twelve difference examples are provided here to indicate the lack of individual observation based biases.

Figure 2: Comparison between K-M estimate of survival function (black) from the observed versus K-M estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information to estimate durations for all the observed species. On the left are the results from the full survival model, while on the right are the results from a simplified model where duration follows an exponential distribution and there is no phylogenetic effect.

Figure 3: The results of additional posterior predictive checks for four summaries of the observed durations, as labeled. Blue vertical indicate the observed value. None of the observed are significantly different from the posterior predictive distributions.

Figure 4: Pairwise differences in effect of the locomotor () and dietary categories () on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (), are: arboreal versus ground dwelling, arboreal versus scansorial, and ground dwelling versus scansorial. For dietary category, from top to bottom (): carnivore versus herbivore, carnivore versus insectivore, carnivore versus omnivore, herbivore versus insectivore, herbivore versus omnivore, and insectivore versus omnivore. Values to the left indicate that the first category is expected to have a greater duration than the second, while values to the right indicate that the first category is expected to have a shorter duration.

Figure 5:

Figure 6: Summaries of posterior estimates of individual cohort effect depicted as medians and 80% credible intervals. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2 My origination cohorts.

Figure 7: 100 estimates of the hazard function ($h(t)$) for the observed species mean (grey), along with the median estimated hazard function. $h(t)$ is an estimate of the rate at which a species of age t is expected to go extinct. Hazard functions were estimated from random draws from the estimated posterior distributions and evaluated with all covariate information set to 0, which corresponds to the expected duration of the mean species.

Figure 8: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total observed variance. Each of the estimates is a distribution of 1000 approximating simulations due to the model's non-normally distributed errors.