

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

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Determining which biological traits influence differences in extinction risk, and how, 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 allow species age to affect extinction risk. This study estimates time-invariant effects in order to characterize background selection so as to provide a base line for determining if the current biodiversity crisis is due to either an intensification of previous processes or a potential shift in the direction of selection along with the occurrence of new selective pressures.

Why extinction risk varies among species remains one of the most fundamental questions in paleobiology (1–5). Here I test for non-randomness of extinction with respect to species-level traits during times of background extinction; which traits have time-invariant effects on species duration; and if extinction is age-independent. I approach these questions together by using a model of species duration whose parameter estimates act as direct tests of these

questions. Cenozoic mammals represent an ideal group and time period because their fossil record is well sampled and well resolved both temporally and spatially, and because individual species ecology and taxonomic position are generally understood (1, 4, 6–10).

The species-level traits studied here are dietary and locomotor categories, bioprovince occupancy, and body mass. These traits are related to different aspects of a species' adaptive zone such as population density, expected range size, potential prey, and dispersal ability (8, 11). It is expected that species with larger geographic ranges have lower extinction rates than species with smaller geographic ranges (12, 13), however traits more directly related to species–environment interactions may play an important role in determining extinction risk.

Body size is a complex trait related to many life history characteristics there are three general hypotheses of how body size may effect extinction risk: 1) positive effect where an increase in body size causes an increase in extinction risk (7, 14), 2) negative effect where an increase in body size causes a decrease in extinction risk because of the expected positive relationship between body size and geographic range, and 3) no effect of body size on extinction risk (9). These three hypotheses are distinguishable by estimating both the effects of mass and the interaction between body size and occupancy on extinction risk.

The only strong expectation of the effect of dietary category on extinction risk is that omnivores will have the lowest extinction risk of all species. This hypothesis is based on both the long standing “survival of the unspecialized” hypothesis (1, 15). It has also been observed that both carnivores and herbivores have greater diversification rates than omnivores, with herbivores diversifying faster than carnivores (16). How this result translates into expectations of differences in extinction risk is currently unknown. In modern taxa, higher trophic levels (e.g. carnivores versus herbivores) have been associated with an increase in extinction risk (14, 17).

Similarly, there are few strong expectations of how locomotor category effects extinction risk. A simple prediction is that arboreal taxa will have the greatest extinction risk of all,

with both scansorial and ground dwelling taxa having lower extinction risks. This hypothesis is based on shift in North American environmental conditions from predominately closed to predominately open environments, with the loss of consistent forest habitat for arboreal taxa (18, 19).

Time-invariant factors are those, have a constant directional effect even if the magnitude varies. Because change in the magnitude of extinction risk is not necessarily the best indicator of a shift from background to mass extinction (20), it is better to look for changes in either the direction of selection, the loss of a selective pressure, or the appearance of novel selective pressures (12).

I use a hierarchical Bayesian survival model of species duration as related to the covariates of interest and in the species' temporal and evolutionary context (i.e. phylogeny). Species duration, in 2 My bins, was modeled as being drawn from either an exponential or Weibull distribution, reparameterized as a hierarchical regression model (21). The exponential is a special case of the Weibull where the shape parameter, α , is 1. The exponential model corresponds to the Law of Constant Extinction which states that extinction is age-independent (2). Origination cohorts were modeled as exchangeable draws from a common distribution. Phylogenetic effect was modeled where species duration was assumed to have evolved via Brownian motion and modeled an individual level effect (22). Extended explanation of the model used here, choice of priors, parameters estimation, and results of multiple posterior predictive checks are provided in the supplementary online text. The results from the Weibull model are detailed here because this model has a better fit to the data (Fig. 1, SFFF-FFF).

Species with greater bioprovince occupancy are found to be associated lower extinction risk than taxa with smaller bioprovince occupancy (Fig. 2) JUST DO SUMMARY STATISTICS; MEAN + SD). This is strongly consistent with prior expectations. Body size has nearly zero association with expected duration, a similar result to previous studies (9) JUST DO SUMMARY

STATISTICS; MEAN + SD). 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 (7). However, these studies were performed at the generic-level which may involve differences in speciation rate associated with body size that are not captured as a part of this model (7, 9).

Some clear patterns emerge from the pairwise differences in effect of each dietary category on expected duration (Fig. 3). Consistent with expectations from the “survival of the unspecialized” hypothesis (1, 15), omnivory appears to be associated with the lowest expected extinction risk. Carnivory is associated a greater expected duration than either herbivory or insectivory, but a greater expected extinction risk than omnivory. Finally, herbivory and insectivory have approximately equal effects on expected duration. Given previous results, these results imply that carnivores have a greater origination rate than omnivores (16). These results also imply 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 categories (16).

For locomotor category, both scansoriality and ground dwelling life habitat are associated with a greater expected duration than arboreal taxa (Fig. 3). Scansorial and ground dwelling taxa also have approximately equal expected effects on extinction risk. This is consistent with the expectation that arboreal taxa will have greater extinction risk due to the loss of associated environment with the shift from open to closed habitat at the Paleogene/Neogene boundary (18).

Of the three sources of variance present in the model, individual species variance accounts for approximately 80% of the observed variance (Fig. 5). Both cohort and phylogenetic effects account for the other 20% of the observed variance. This result mean that extinction risk has both temporal and phylogeny aspects as both contribute greater than 0% of the observed variability in the data (22).

The estimates for the individual cohort effects show a weak pattern of greater extinction risk in older Cenozoic cohorts compared to younger cohorts (Fig. 4). This potential slow-

down in extinction risk is consistent with previous analyses of marine invertebrates (23, 24) and mammals (25, 26). There are two prevailing hypotheses as to the cause of this slow down: 1) extinction risk is constant but varies between clades so over time a clade with a low extinction rate increases in proportion of total diversity and brings down the overall extinction risk and 2) over time taxa increase in mean fitness thus decrease in expected extinction risk (23). The observed decrease in extinction risk with age, along with the variance partitioning results (Fig. 5) are consistent with both of these possible processes playing a role and no single one being more “important” than the other.

Interestingly, the shift from older cohorts with a higher extinction risk to younger cohorts with lower extinction risk is approximately at the Paleogene–Neogene boundary. This transition is marked by the opening up of the landscape, the rise of grazers, and the decline of heavily forested environments. This shift may underlie the association between arboreality and greater expected extinction risk when compared to ground dwelling or scansorial species (Fig. 3). However, because the model used here does not allow for change in time-invariant effects, I cannot identify if there this boundary is associated with shift in the direction or magnitude of the expected effect of arboreality on extinction risk.

The estimate of the Weibull shape parameter, α , is greater than 1 meaning that extinction risk is expected to increase with taxon age (Supplementary table STTT). As the value of α is between 1 and 1.5, extinction risk for a given species only gradually increases with age (Supplementary figure SFFF). There are three possible explanations for this result: 1) older taxa being aged out or out competed by younger taxa (5), 2) this is an artifact of the minimum resolution of the fossil record (27), or 3) upward bias in estimates of α at this sample size, similar to that for scale parameters (21). The analysis, as it stands, is unable to distinguish between these hypotheses.

When these results are compared to current factors contributing to increased extinction risk

in extant mammals, there is a mixture of congruent and incongruent effects. As expected, large range size is always currently associated with lower extinction risk (14, 17, 28, 29). While my analysis found body size to have almost no time-invariant effect on extinction risk (Fig. 2), this is not necessarily the case in extant mammals where increased body size is associated with increased extinction risk (14, 17). However, this pattern is partially clade dependent (28). As stated earlier, higher trophic levels have been found to be associated with greater extinction risk in extant mammals (14, 17). In contrast, I found that omnivory followed by carnivory have a lower expected extinction risk than either insectivores or herbivores (Fig. 3). Finally, phylogeny has been found to be a good predictor of differences in extinction risk in extant mammals as certain clades are at much higher risks than others (29). This effect seems much greater in the Recent than for the whole Cenozoic. 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. If these incongruities are within the standard range of time-variant effects is unknown, though these comparisons across multiple factors do imply that current processes are different than those behind the time-invariant effects found in this study.

There are many intertwined processes encompassed by background extinction. By focusing on estimating how different ecologies and historical factors effect a species' expected extinction risk, it is possible to better understand what processes may have driven the resulting pattern of selection (i.e. diversity). 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 species-level traits such as omnivory and large geographic range size are always associated with lower extinction risk, while other traits such as arboreality are always associated with greater extinction risk. I also found there are non-ignorable effects of cohort and phylogeny on extinction risk. Finally, I found evidence of increasing extinction risk with species age, though this result may be partially due to the

minimum resolution of the fossil record itself (27).

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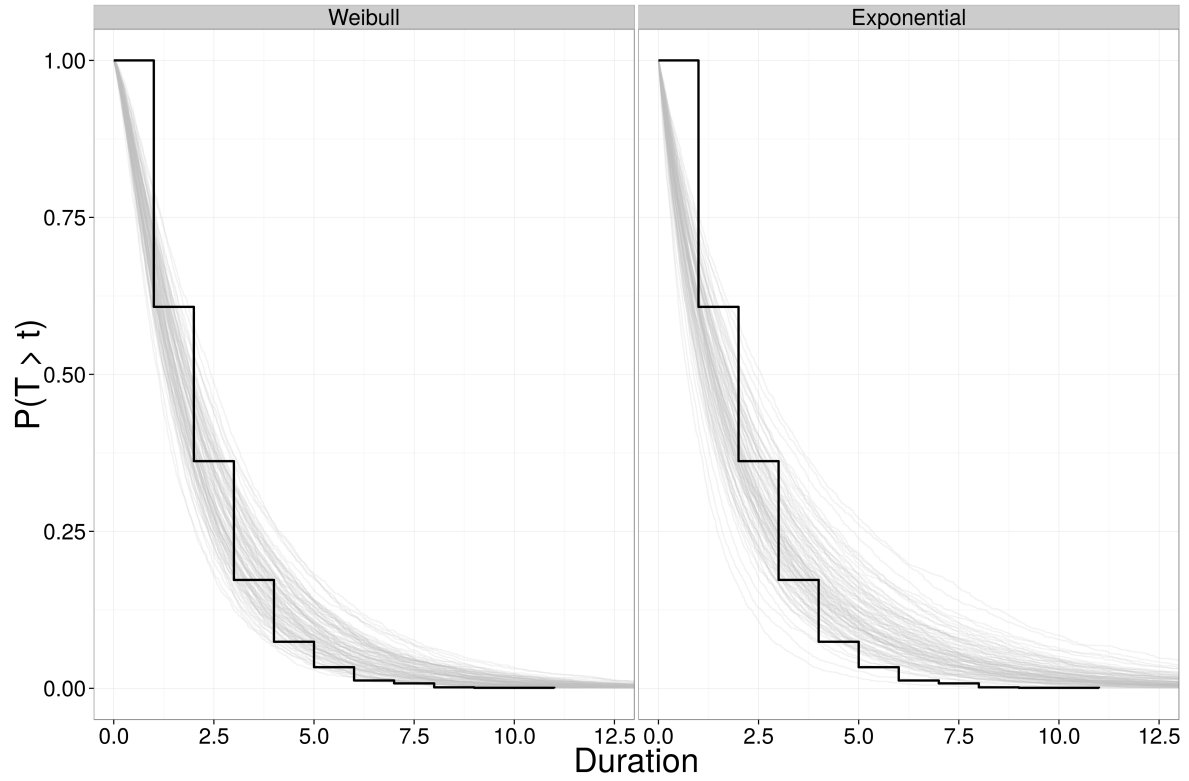


Figure 1: Comparison of K-M estimate of survival function (black) from the observed estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information 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.

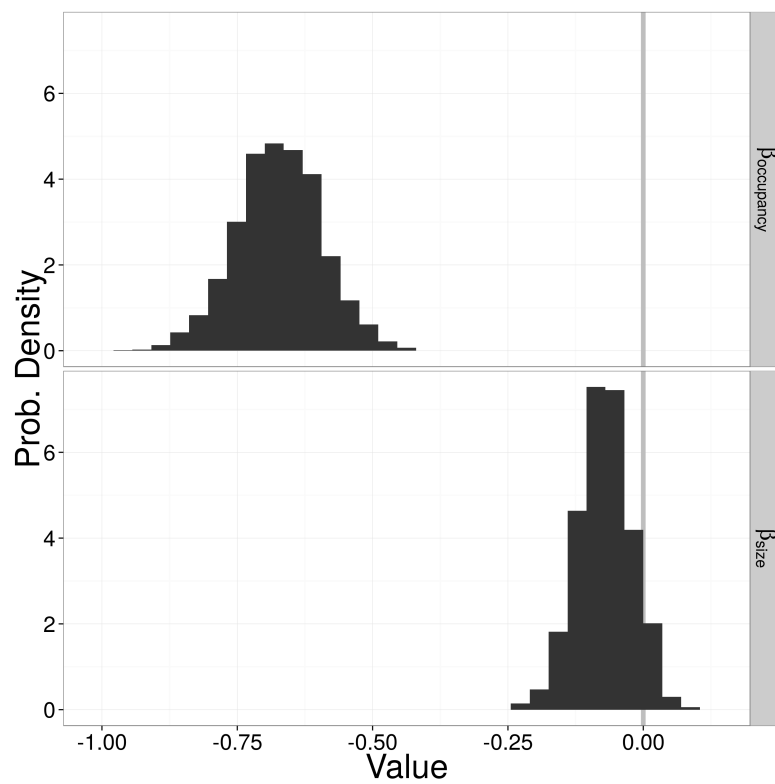


Figure 2: Marginal posterior estimates for regression coefficients for the effect of biogeographic occupancy and body size on species expected duration. Posteriors are approximated from 1000 random samples.

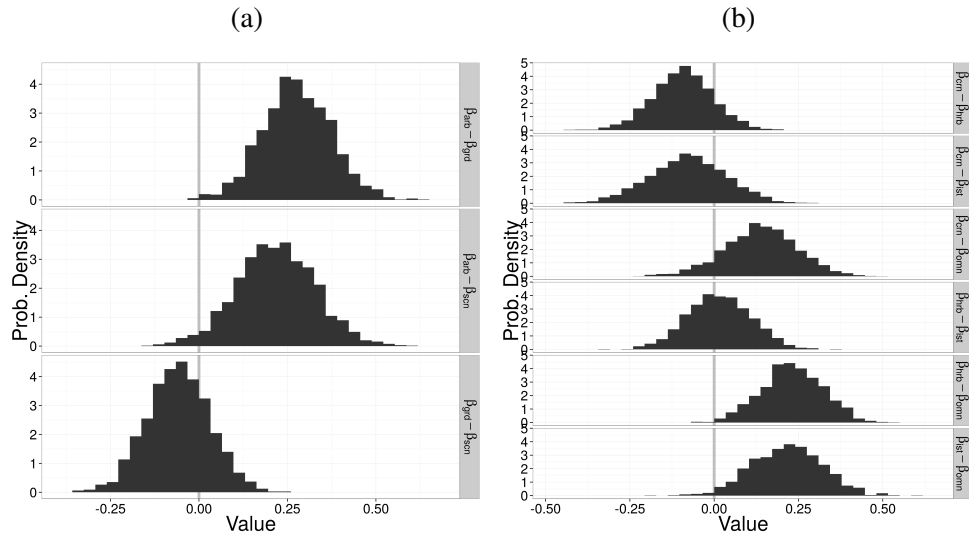


Figure 3: Pairwise differences in effect of the locomotor (**A**) and dietary categories (**B**) on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (**A**), are: arboreal versus ground dwelling, arboreal versus scansorial, and ground dwelling versus scansorial. For dietary category, from top to bottom (**B**): 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.

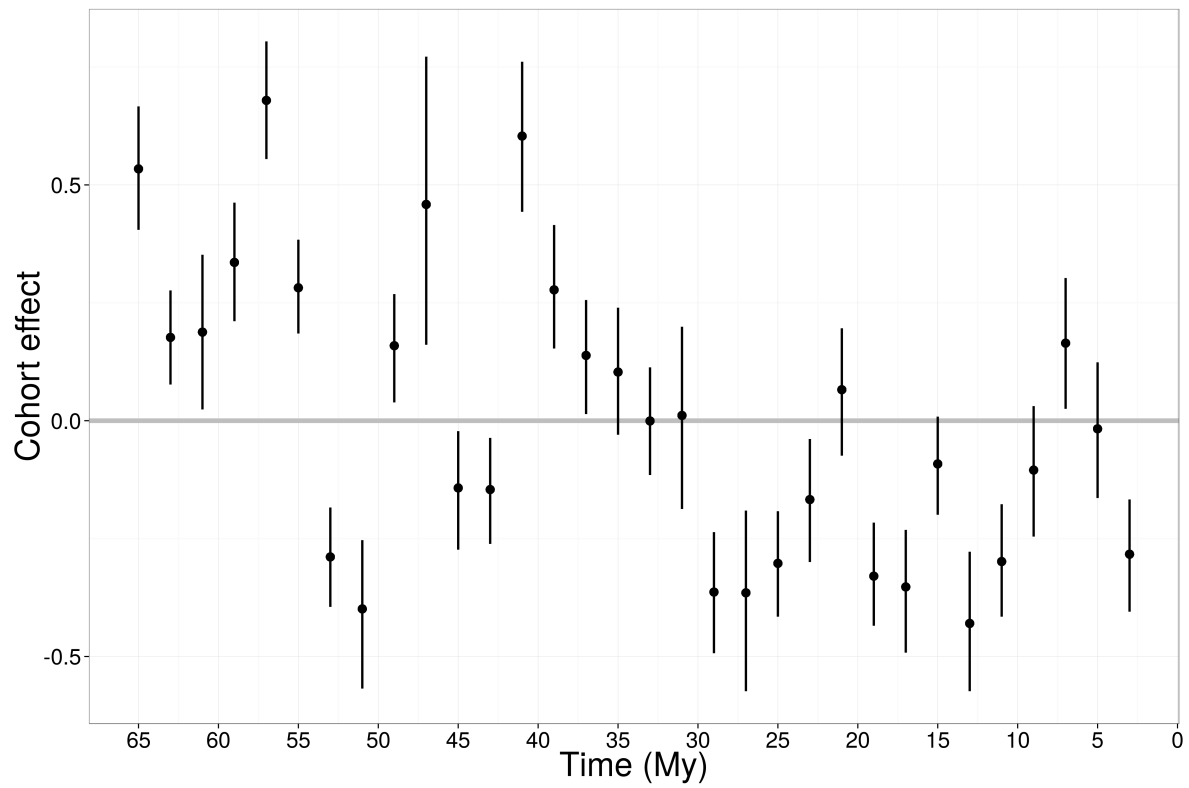


Figure 4: Summaries of posterior estimates of individual cohort effect depicted as medians and 80% credible intervals. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2 My origination cohorts.

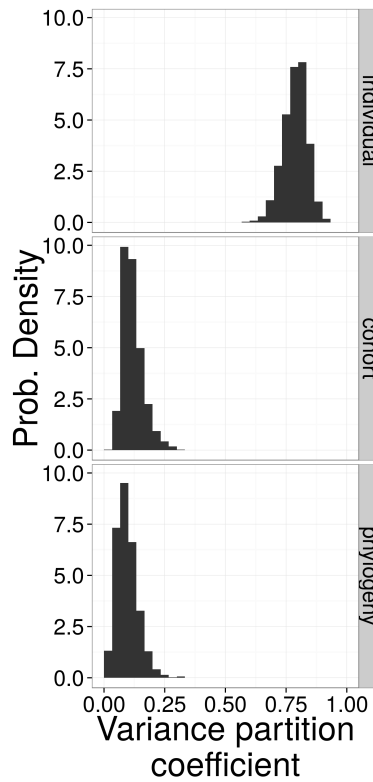


Figure 5: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total observed variance. Each of the estimates is a distribution of 1000 approximating simulations due to the model's non-normally distributed errors.