

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

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Determining which biological traits influence differences in 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 allow species age to affect extinction risk. This study estimates time-invariant effects in order to characterize background selection, providing a baseline 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. I find a that the current biodiversity crisis is partially incongruous with previous patterns, implying that the current biodiversity crisis is not just an intensification of the past but is instead potentially a mass extinction.

Why extinction risk varies among species remains one of the most fundamental questions in paleobiology and conservation biology (1–5). Here I test for associations between extinction

risk and multiple species-level traits during times of background extinction; which traits have
18 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
20 tests of these questions. Cenozoic mammals are an ideal focus for this study because their fossil
record is well sampled and well resolved both temporally and spatially, and because individual
22 species ecology and taxonomic position are generally understood (1, 4, 6–10).

The species-level traits studied here are bioprovince occupancy, body mass, and both dietary
24 and locomotor categories. 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
26 is expected that species with larger geographic ranges have lower extinction rates than species
with smaller geographic ranges (12, 13), but traits more directly related to species–environment
28 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
30 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
32 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
34 risk (9).

The strongest expectation of the effect of dietary category on extinction risk is that omni-
36 vores 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
38 both carnivores and herbivores have greater diversification rates than omnivores, with herbi-
vores diversifying faster than carnivores (16). How this result translates into expectations of
40 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, most

likely because of human extermination of top predators (14, 17).

Similarly, there are few simple expectations of how locomotor category effects extinction risk. During the Cenozoic there was a shift at the Paleogene/Neogene boundary from predominately closed to predominately open environments (18, 19). Based on this observation, 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.

Time-invariant factors are those that 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 predicted by the covariates of interest and 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 parameterized as a hierarchical regression (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). This is strongly consistent with prior

expectations. Body size has nearly zero association with expected duration, a similar result to
68 previous studies (9). The direction/sign of the modal estimate of effect is not consistent with
the prediction of increased extinction risk associated with increased body size (7). However,
70 these studies were performed at the generic-level and were unable to determine how body size
may effect species level extinction, as the effect of either extinction or speciation cannot be
72 distinguished (7, 9).

Some clear patterns emerge from the pairwise differences in effect of each dietary category
74 on expected duration (Fig. 3). Consistent with expectations from the “survival of the unspecial-
ized” hypothesis (1, 15), omnivory appears to be associated with the lowest expected extinction
76 risk. Carnivory is associated a greater expected duration than either herbivory or insectivory,
but a greater expected extinction risk then omnivory. Finally, herbivory and insectivory have
78 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
80 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).

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

Of the three sources of variance present in the model, individual species variance accounts
88 for approximately 80% of the observed, unmodeled variance (Fig. 5). Both cohort and phy-
logenetic effects account for the other 20% of the observed variance. This result mean that
90 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 within 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; or 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. For example, given the association with arboreality (a heritable trait) and increased extinction risk, the decrease in expected extinction risk over time might relate to the preferential loss of arboreal taxa over the Cenozoic.

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 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 this boundary is associated with shift in the direction or magnitude of the expected effect of arboreality on extinction risk.

When these results are compared to 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, 27, 28). 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 (27). As stated

earlier, higher trophic levels have been found to be associated with greater extinction risk in
118 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
120 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 (28). This effect seems much greater in the Recent
122 than for the whole Cenozoic, implying that current extinction risk is more phylogenetically
concentrated than previous mammal extinctions.

124 If these incongruities are within the standard range of time-variant effects is unknown,
though these comparisons do imply that current processes are different than those identified
126 by this study. These incongruities also imply that the fossil record may not provide a guide
for conservation biology. However, this is not a model of what makes taxa vulnerable during
128 mass extinctions which, if mass extinctions are qualitatively different than background extinc-
tion (12), may account for the incongruities.

130 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
132 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
134 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
136 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
138 found evidence of increasing extinction risk with species age, the cause of which is unknown.

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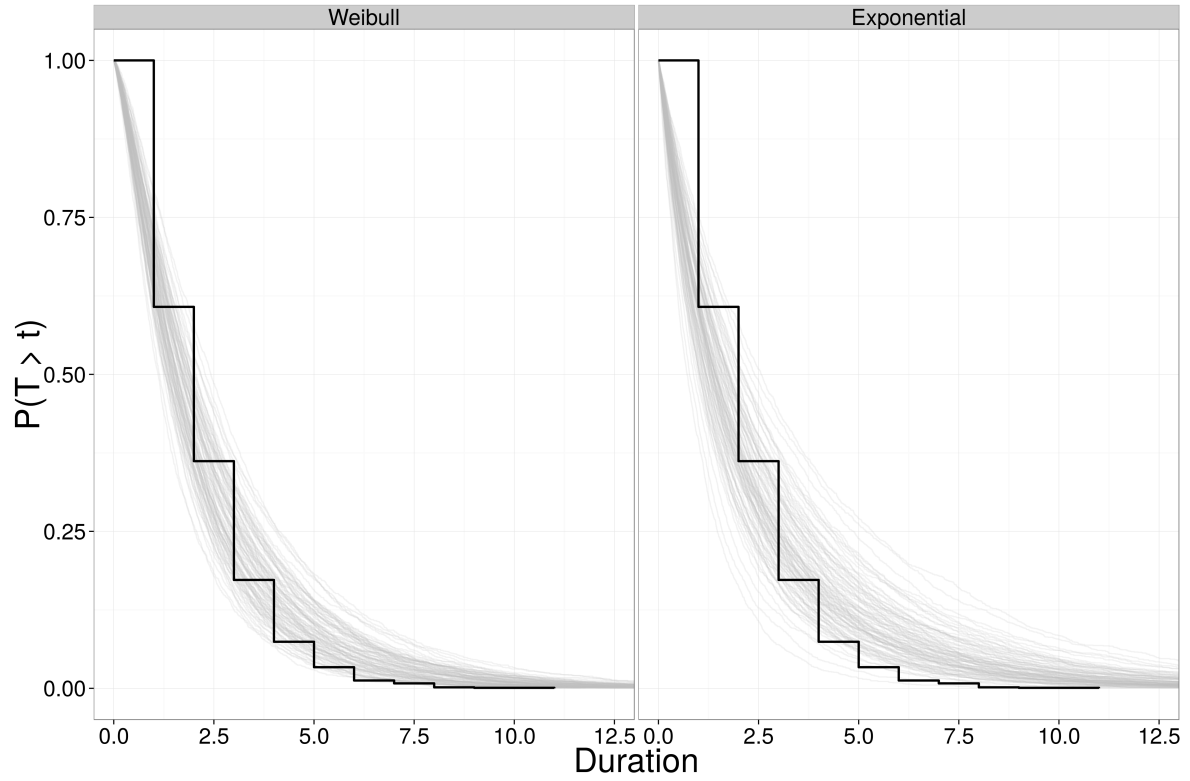


Figure 1: Comparison of K-M estimate of survival function (black) from the observed estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information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

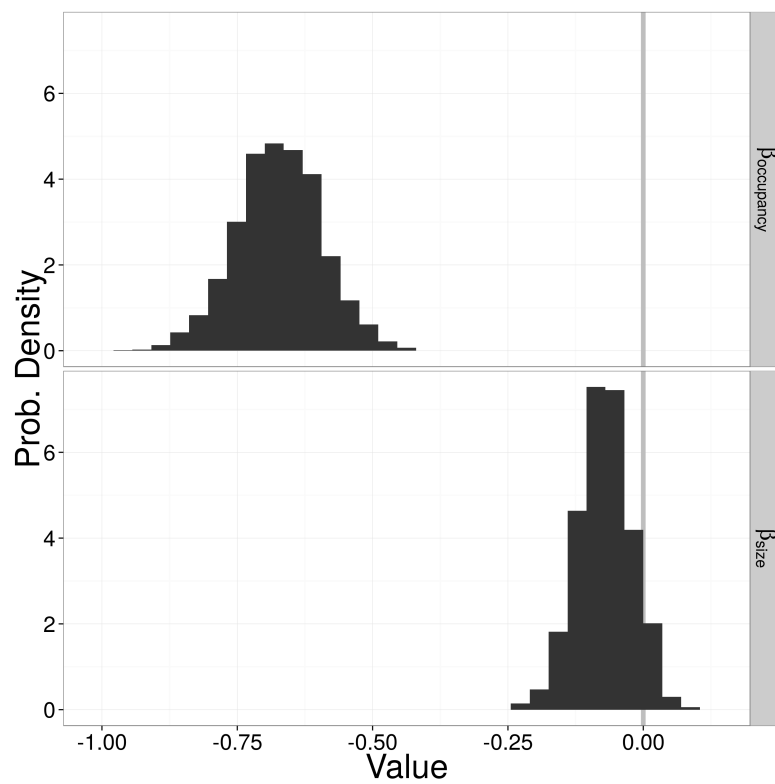


Figure 2: Marginal posterior estimates for regression coefficients for the effect of biogeographic occupancy and body size on species expected duration. Posteriors are approximated from 1000 random samples.

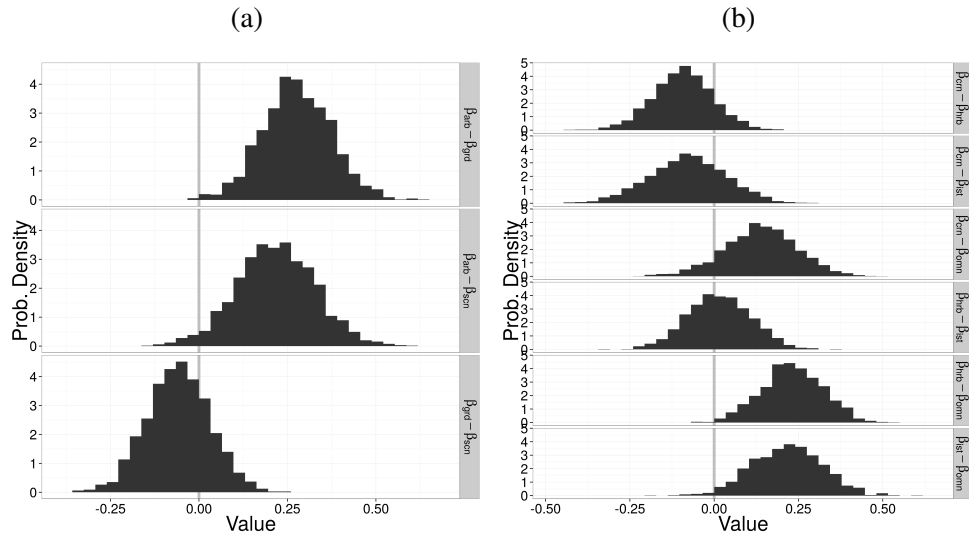


Figure 3: Pairwise differences in effect of the locomotor (**A**) and dietary categories (**B**) on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (**A**), are: arboreal versus ground dwelling, arboreal versus scansorial, and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

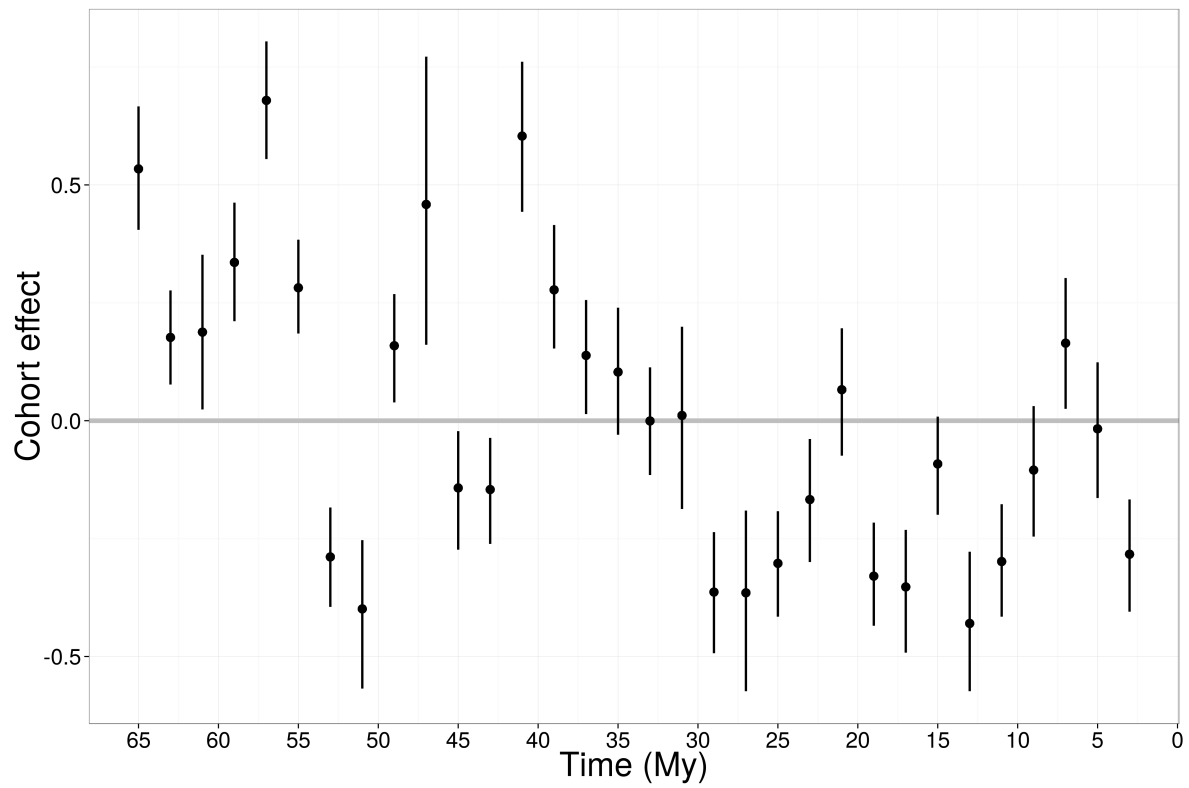


Figure 4: Summaries of posterior estimates of individual cohort effect depicted as medians and 80% credible intervals. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2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

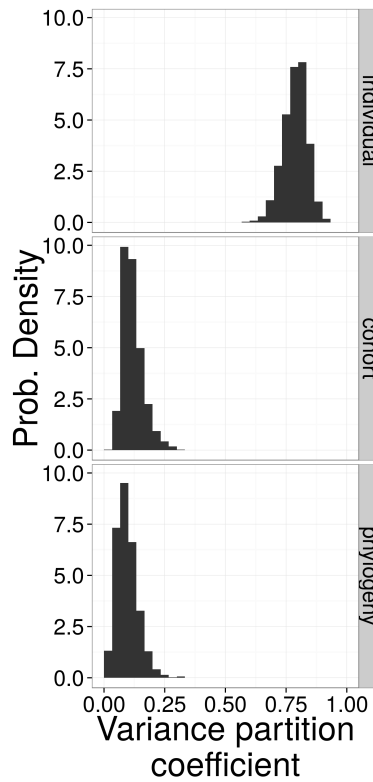


Figure 5: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total observed variance. Each of the estimates is a distribution of 1000 approximating simulations due to the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