

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

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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 allow for species age to effect 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 species-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
18 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).

20 The species-level traits studied here are dietary and locomotor categories, bioprovince occu-
pancy, and body mass. Each of these traits are related to different aspects of a species' adaptive
22 zone such as population density, expected range size, potential prey items, and dispersal abil-
ity (8, 11). It is expected that species with larger geographic ranges have lower extinction rates
24 than species with smaller geographic ranges (12, 13), however traits directly related to species–
environment interactions may play an important role in determining extinction risk. Body size
26 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
28 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
30 size and geographic range, and 3) no effect of body size on extinction risk (9). These three hy-
potheses are distinguishable by estimating both the effects of mass and the interaction between
32 body size and occupancy on extinction risk.

The only strong expectation of the effect of dietary category on extinction risk is that omni-
34 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 both
36 carnivores and herbivores have greater diversification rates than omnivores, with herbivores di-
versifying faster than carnivores (16). How this result translates into expectations of differences
38 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, 18). Sim-
40 ilarly, 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 (19, 20).

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 (21), 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 species duration in relation to the covariates of interest and in the context of their shared origination cohort and evolutionary history (i.e. phylogeny). Species duration was modeled as being drawn from either an exponential or Weibull distribution, reparameterized as a hierarchical regression model (22). 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 (23). 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).

Bioprovince occupancy has a large, negative effect on expected extinction risk, with more widespread species having a lower extinction risk than restricted species (Fig. 3). This is strongly consistent with prior expectations. Body size has near zero effect on expected duration, a similar result to previous studies (9). 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
68 in speciation rate associated with body size that are not captured as a part of this model (7, 9).

The effect of dietary category on survival shows a large amount of variation in the pairwise
70 differences of effect on expected duration (Fig. 2). Consistent with expectations from the
“survival of the unspecialized” hypothesis (1, 15), omnivory appears to be associated with the
72 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
74 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
76 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
78 (16).

For locomotor category, both scansoriality and ground dwelling life habitat are associated
80 with a greater expected duration than arboreal taxa (Fig. 2). Scansorial and ground dwelling
taxa also have approximately equal expected effects on extinction risk. This is consistent with
82 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 (19).

84 Of the three sources of variance present in the model, individual species variance accounts
for approximately 75% of the observed variance (Fig. 5). Both cohort and phylogenetic ef-
86 fects account for the other 25% 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
88 variability in the data (23).

The estimates for the individual cohort effects show a weak pattern of greater extinction risk
90 in older Cenozoic cohorts compared to younger cohorts (Fig. 4). This potential slowdown in
extinction risk is consistent with previous analyses of marine invertebrates (24, 25) and mam-

92 mals (26, 27). There are two prevailing hypotheses as to the cause of this slow down: 1) clades
have constant extinction risk over time but a clade with a lower extinction rates than others
94 increases in proportion of total diversity and brings down the overall extinction risk CITATION
and 2) over time taxa increase in mean fitness thus decrease in expected extinction risk (24).
96 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
98 being more “important” than the other.

Interestingly, the shift from older cohorts with a higher extinction risk to younger cohorts
100 with lower extinction risk is approximately at the Paleogene–Neogene boundary. This transition
is marked by the opening up of the landscape and the rise of grazers and the decline heavily
102 forested environments. This shift may underlie the association between arboreality and greater
expected extinction risk when compared to ground dwelling or scansorial species (Fig. 2).
104 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
106 the expected effect of arboreality on extinction risk.

The estimate of the Weibull shape parameter, α , is greater than 1 meaning that extinction
108 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
110 (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
112 resolution of the fossil record (28), or 3) upward bias in estimates of α at this sample size,
similar to that for scale parameters (22). The analysis, as it stands, is unable to distinguish
114 between these hypotheses.

Comparison of the estimated effects of species-level traits analyzed here with previous stud-
116 ies demonstrates a mixture of congruence and incongruence. As expected, large range size is

always currently associated with lower extinction risk (14, 17, 18, 29). 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 (14, 17, 18). A higher trophic level (e.g. carnivory versus herbivory)
is associated with greater extinction risk (18) 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 (29). 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 point
to our arrival at a tipping point (30, 31) and potentially a shift in macroevolutionary regime (12).

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). 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 (28).

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184 Database publication number XXX.

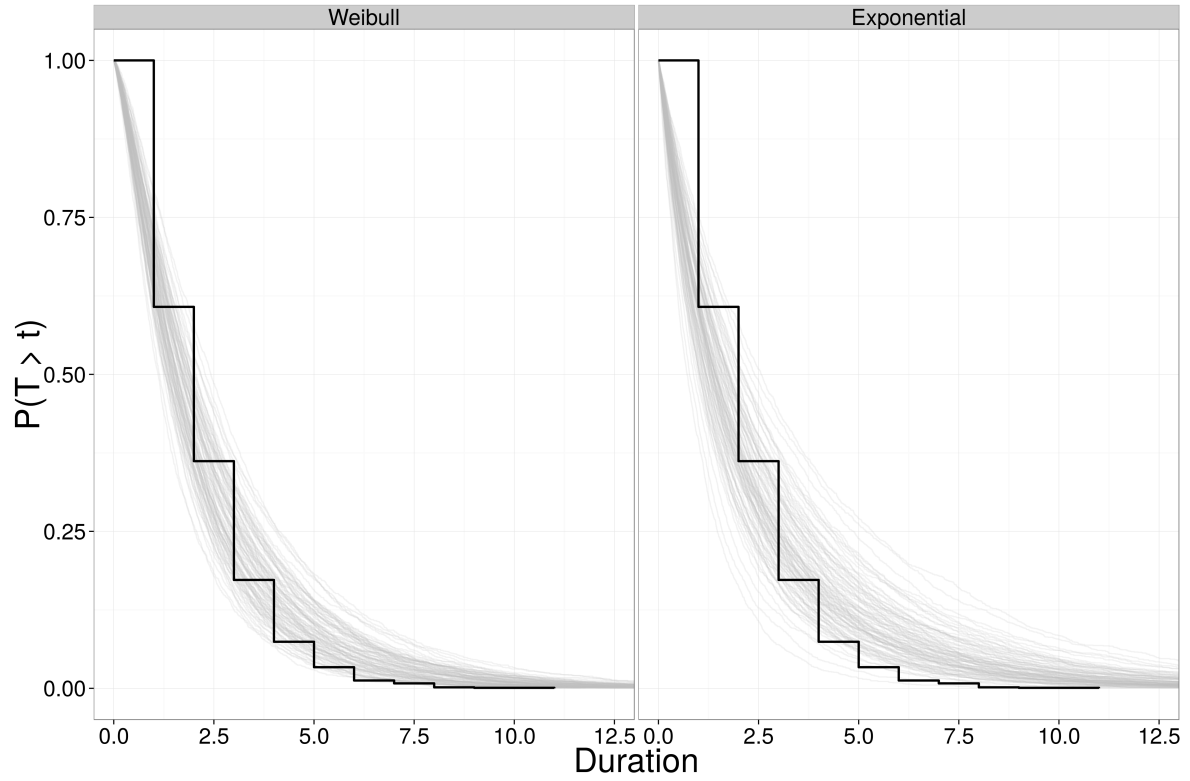


Figure 1: Comparison of K-M estimate of survival function (black) from the observed estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information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

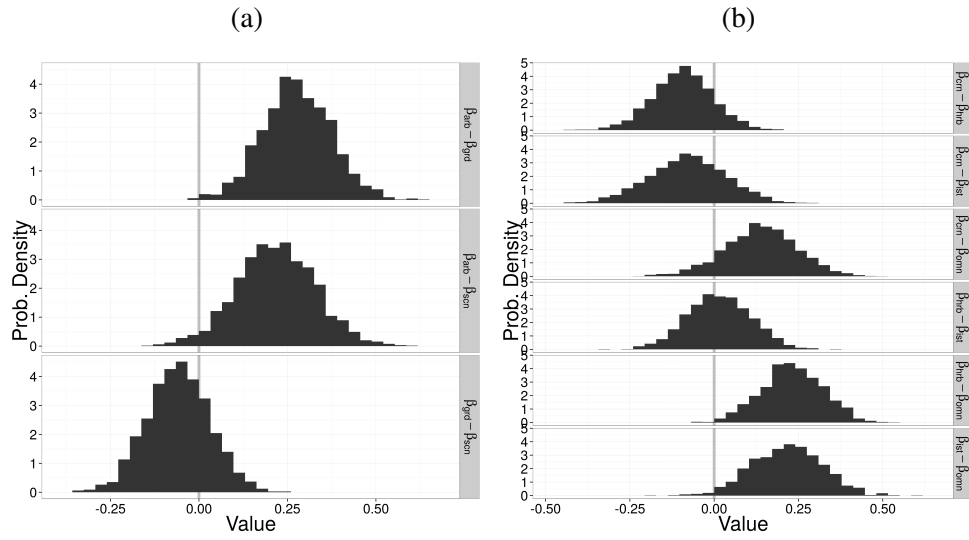


Figure 2: Pairwise differences in effect of the locomotor (**A**) and dietary categories (**B**) on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (**A**), are: arboreal versus ground dwelling, arboreal versus scansorial, and 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.

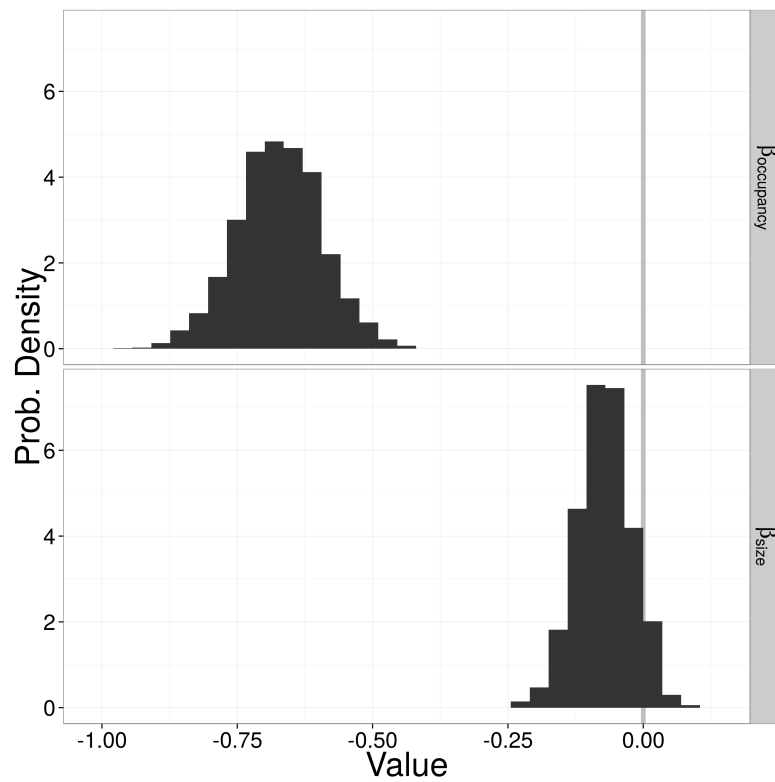


Figure 3: Marginal posterior estimates for regression coefficients for the effect of biogeographic occupancy and body size on species expected duration. Posteriors are approximated from 1000 random samples.

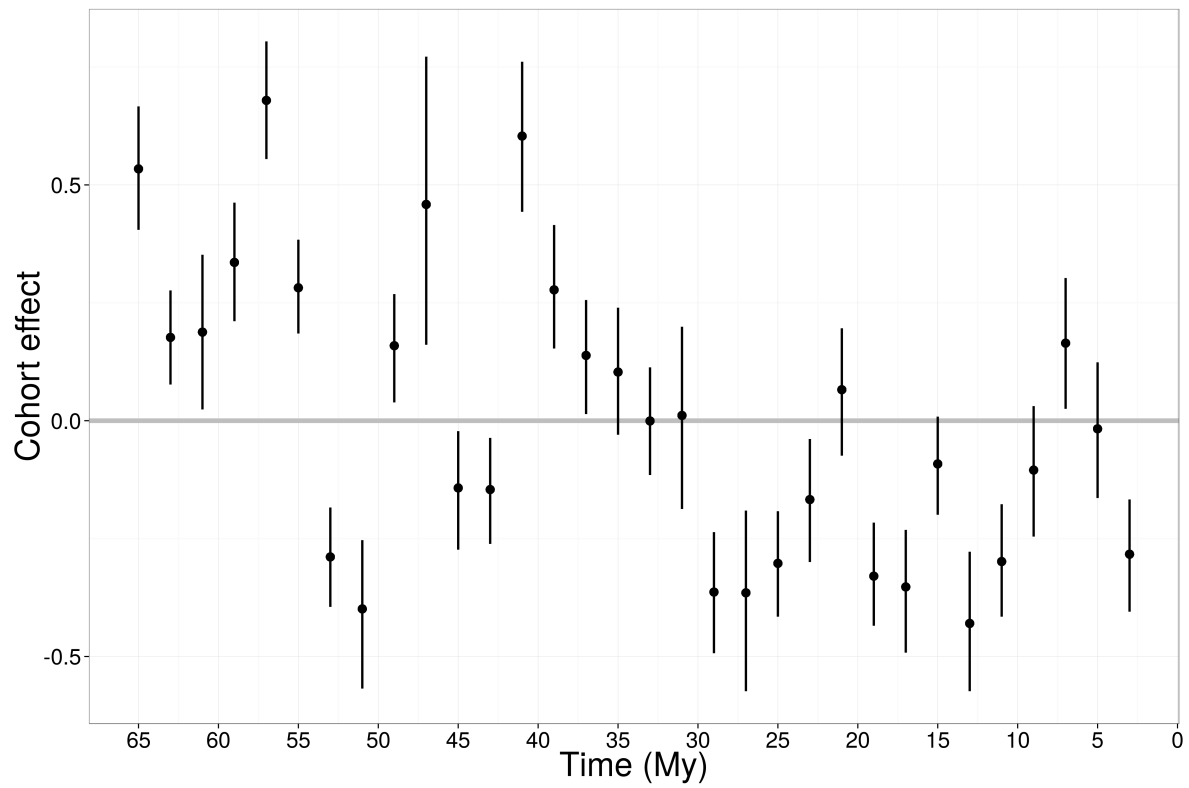


Figure 4: Summaries of posterior estimates of individual cohort effect depicted as medians and 80% credible intervals. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2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

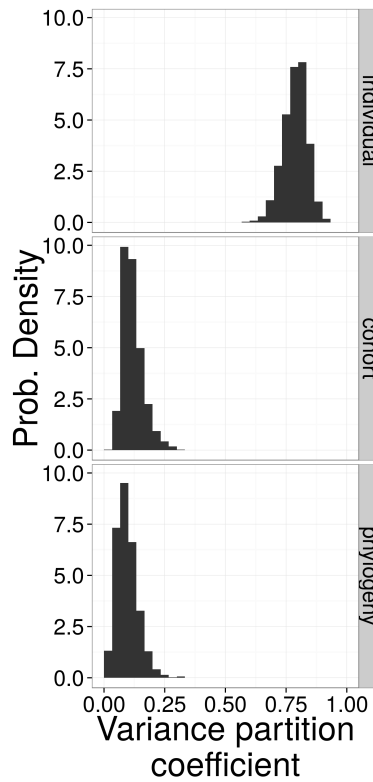


Figure 5: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total observed variance. Each of the estimates is a distribution of 1000 approximating simulations due to the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