

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, relaxing the Law of Constant Extinction which is the critical assumption underlying the Red Queen Hypothesis. 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 of previous processes or represents the arrival at an environmental “tipping point” or a shift in “macroevolutionary regime” associated with a mass extinction.

Why species go extinct at different rates remains one of the most fundamental questions in paleobiology (1–5). Here I test how non-random extinction is with respect to species-level traits during times of background extinction, if and which traits have time-invariant effects

on species duration, and if extinction is species-age independent? I approach these questions
18 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
20 fossil record is well sampled, well resolved both temporally and spatially, and individual species
ecology and taxonomic position are generally understood (1, 4, 6–10).

22 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
24 zone such as population density, expected range size, potential prey items, and dispersal abil-
ity (8, 11). While it is expected that species with larger geographic ranges have lower extinction
26 rates than species with smaller geographic ranges (12, 13), traits directly related to species–
environment interactions may play an important role in determining extinction risk. This is not
28 only the first time that all of these ecological traits have been included in a single model, this
also represents the first time that extinction selectivity has been analyzed with respect to both
30 species temporal and phylogenetic contexts.

Time-invariant factors are those, that when comparing taxa over a long period of time, there
32 is a consistent effect over the entire period of interest. While the strength of the effect may
vary, the direction does not change. Periods of background extinction represent an opportunity
34 to characterize the selective pattern of a macroevolutionary regime because they are relatively
constant with changes occurring slowly (12, 14).

36 One of the open questions in paleobiology and macroecology is whether the current bio-
diversity crisis qualifies as a mass extinction (15–17). Because change in the magnitude of
38 extinction risk is not necessarily the best indicator of a shift from background to mass extinc-
tion (18), it is better to look for changes in either the direction of selection, the loss of a selective
40 pressure, or the appearance of novel selective pressures. The type and magnitude of these dif-
ferences may indicate the arrival at an environmental tipping point or shift in macroevolutionary

regime (12).

I use a hierarchical Bayesian survival modeling approach to 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). This is the first time such a model has been applied to paleontological data. Species duration was modeled as being drawn from either an exponential or Weibull distribution, with (inverse) scale parameters being reparameterized as hierarchical regression model (19). The exponential model corresponds to the Law of Constant Extinction which states that extinction is age-independent (2). Importantly, the exponential is a special case of the Weibull where the shape parameter, α , is 1. Origination cohorts were modeled as exchangeable and drawn from a common distribution. Phylogenetic effect was modeled where species duration was assumed to have evolved via Brownian motion, which is an individual level multivariate normally distributed effect with covariance matrix equal to species' shared branch lengths multiplied by a constant (20). Extended explanation of the model used here along with the 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).

The effect of dietary category on survival shows a large amount of variation in the pairwise differences of effect on expected duration (Fig. 2). Carnivory appears to be associated with a greater expected duration than herbivory or insectivory, but has an approximately equal effect as omnivory. Omnivory is associated with greater expected duration than either herbivory or insectivory. Finally, herbivory and insectivory have 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 omnivores (21). 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 categories (21).

68 The 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
70 specialized taxa have a lower extinction risk than specialized taxa (1, 22). Because larger effects
are easier to identify, the comparative magnitude of this effect explains both the early origin of
72 this hypothesis (1).

For locomotor category, arboreality is associated with lower expected duration than either
74 scansoriality or a ground dwelling life habit (Fig. 2). Scansoriality and a ground dwelling life
habit have approximately equal effects on expected duration. These results can be interpreted
76 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.

78 Bioprovince occupancy has the largest effect on expected species duration/extinction risk
(Fig. 3). Body size has near zero effect on expected duration, a similar result to previous studies
80 (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
82 were performed at the generic-level which may or may not involve different processes than at
the species-level model (7, 9).

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 effects
86 account for the other 25% of the observed variance. Because VPC_{phylo} is greater than 0, it
is not appropriate to ignore phylogeny when modeling survival (23) as is commonly done in
88 paleontological studies (6, 7, 24–27).

The estimates for the individual cohort effects show a weak pattern of greater extinction
90 risk in older Cenozoic cohorts compared to younger cohorts (Fig. 4). It is interesting to note
that shift from older cohorts with a higher extinction risk to younger cohorts with lower ex-

92 tinction 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 forested en-
94 vironments. This shift may underly the association between arboreality and greater expected
extinction risk when compared to ground dwelling or scansorial species (Fig. 2). However, be-
96 cause 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 certainty.

98 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). The estimate of α is
100 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
102 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
104 with age (Supplementary figure SFFF). 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
106 of the fossil record.

The hypothesis that older taxa are being outcompeted or replaced by younger taxa is also
108 consistent with the some recent results (4, 5). This is also consistent with the observed pattern
of cohort effect estimates (Fig. 4) where Paleogene cohorts may have been replaced or out-
110 competed by younger, Neogene cohorts.

The other possible explanation for the inferred increase in extinction risk with species age
112 is the minimum resolution which might cause an upward bias in estimates of the Weibull shape
parameter α (28), an effect which can be observed by the initial plateau in the Kaplan-Meier
114 estimate of $S(t)$.

I hypothesize that the inferred pattern is most likely a combination of these two explanations
116 working in 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
118 fossil record.

Comparison of the estimated effects of species-level traits analyzed here with previous stud-
120 ies demonstrates a mixture of congruence and incongruence. As expected, large range size is
always currently associated with lower extinction risk (29–32). While I found that body size
122 has no time-invariant effect on extinction risk, large body size is associated with increased ex-
tinction risk in the Recent (29, 31, 32). A higher trophic level (e.g. carnivory versus herbivory)
124 is associated with greater extinction risk (32) which is not congruous with the results found here
that carnivores have lower extinction risk than herbivores. Finally, phylogeny has been found to
126 be a factor underlying current mammal species extinction risk, though this effect seems much
greater in the Recent than for the whole Cenozoic (30). Note that the phylogeny of Recent
128 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
130 of time-variant effects is unknown, though these comparisons across multiple factors do point
to our arrival at a tipping point (16, 17) and potentially a shift in macroevolutionary regime (12).

132 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
134 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.
136 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
138 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
140 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

142 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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186 33. P.D.S would like to thank M. Foote, K. Angielczyk, R. Ree, P.D. Polly for discussion; E.
Sander for draft comments; and J. Alroy and the Fossilworks/Paleobiology Database for data
188 accumulation, entry, and availability. This is Fossilworks/Paleobiology Database publication
number XXX.

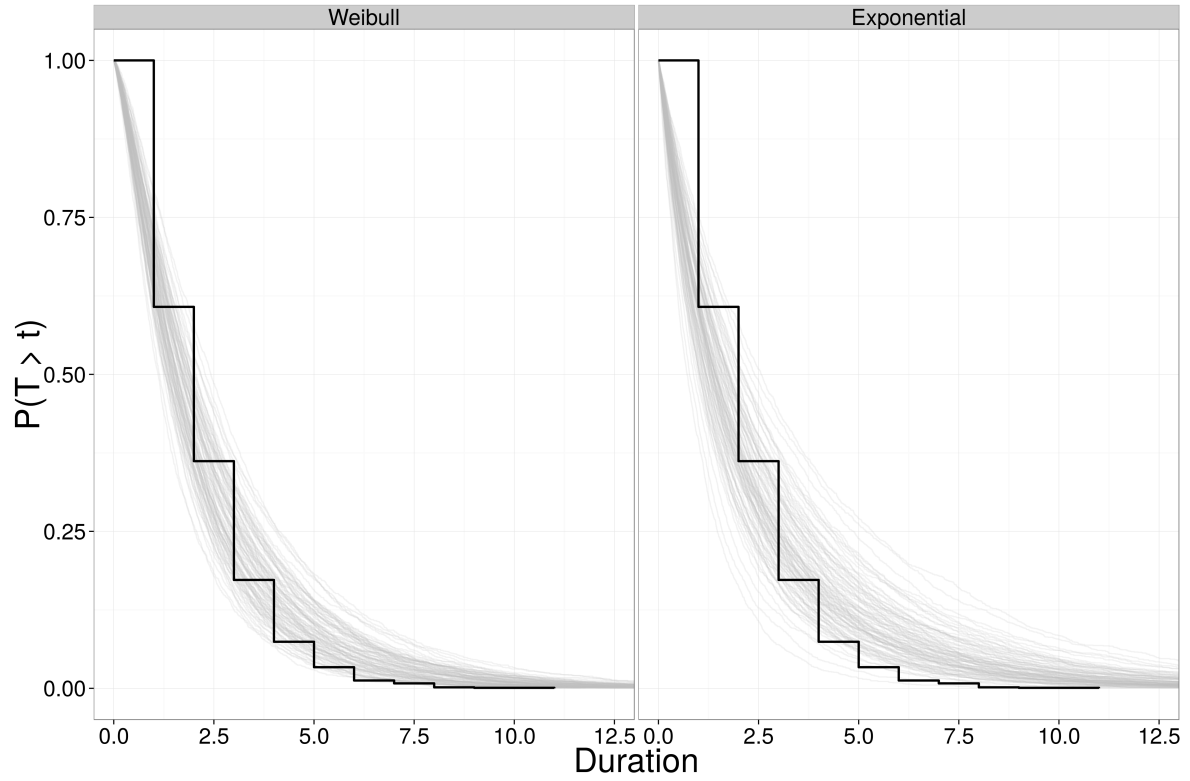


Figure 1: Comparison of K-M estimate of survival function (black) from the observed estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information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

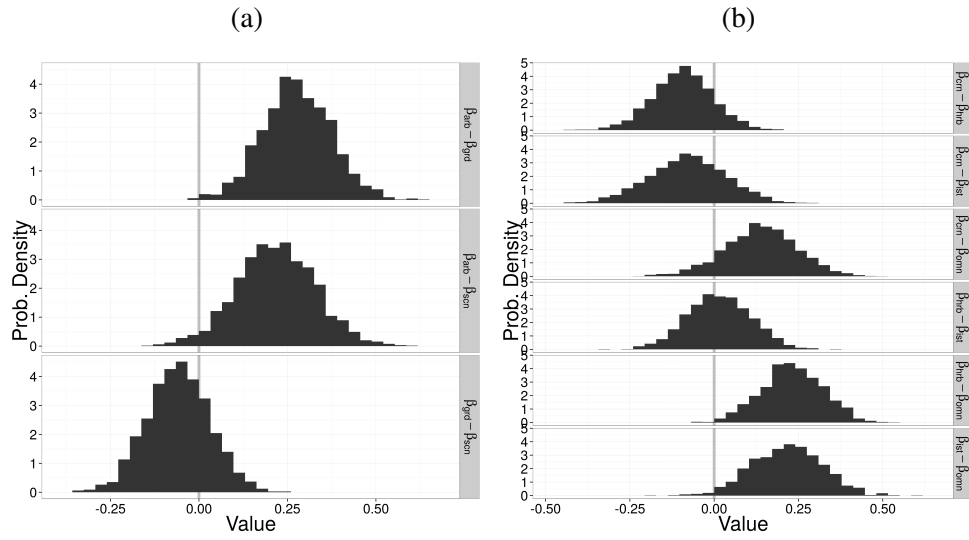


Figure 2: Pairwise differences in effect of the locomotor (**A**) and dietary categories (**B**) on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (**A**), are: arboreal versus ground dwelling, arboreal versus scansorial, and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

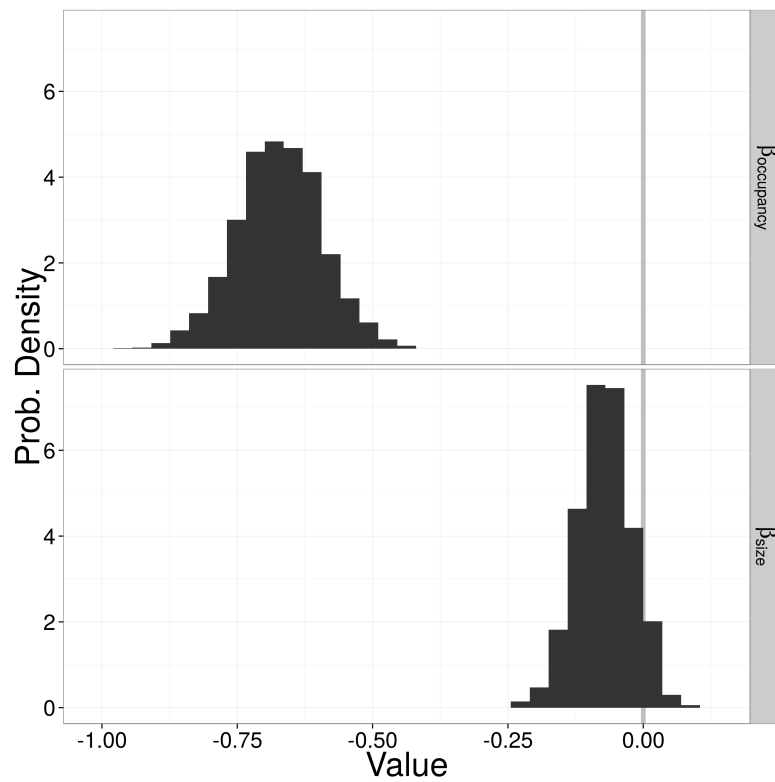


Figure 3: Marginal posterior estimates for regression coefficients for the effect of biogeographic occupancy and body size on species expected duration. Posteriors are approximated from 1000 random samples.

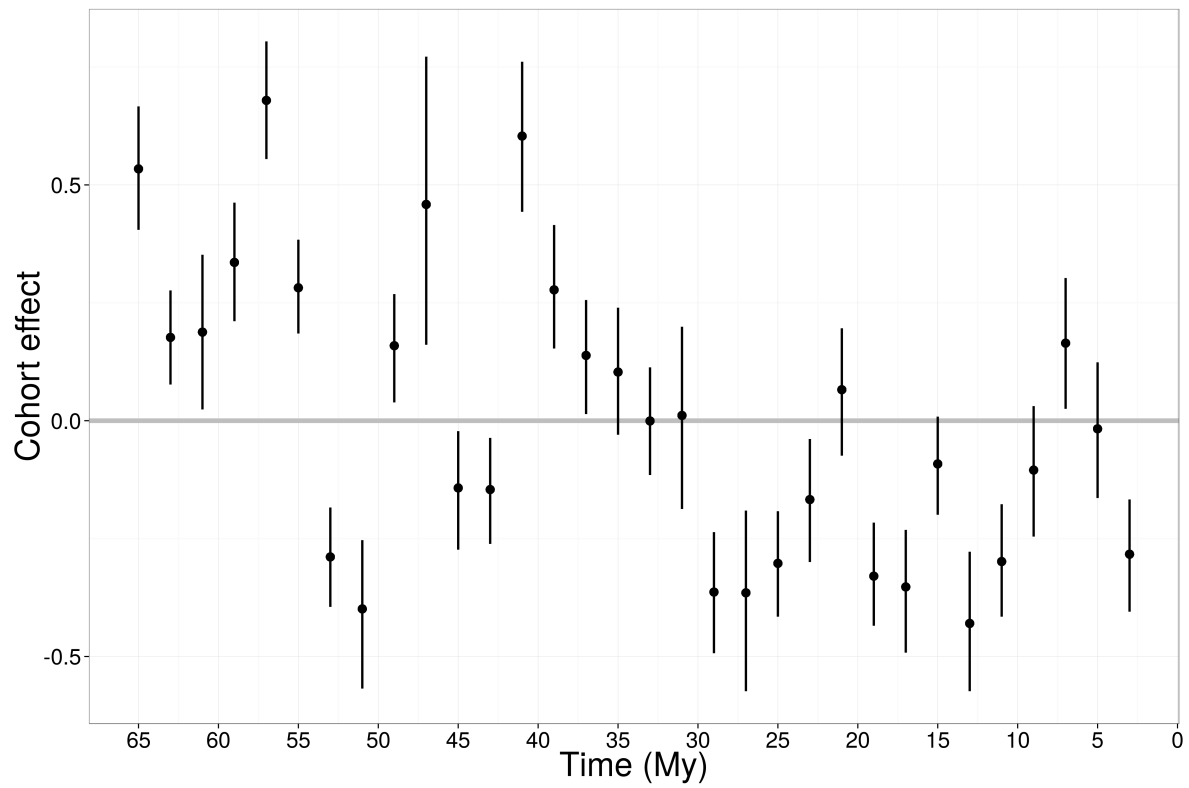


Figure 4: Summaries of posterior estimates of individual cohort effect depicted as medians and 80% credible intervals. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2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

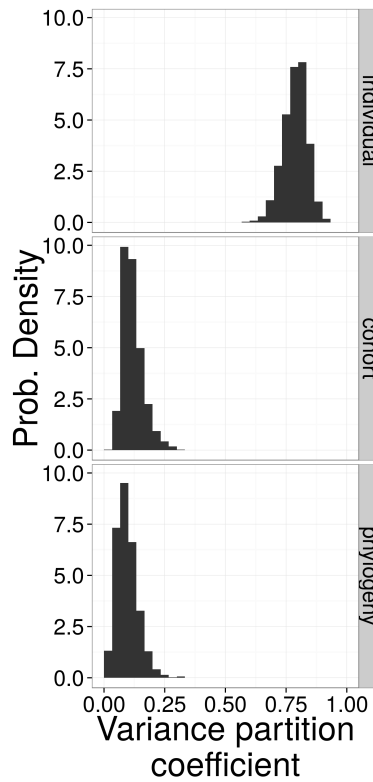


Figure 5: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total observed variance. Each of the estimates is a distribution of 1000 approximating simulations due to the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