

Death and taxa: time invariant differences in species duration

Peter D Smits
Committee on Evolutionary Biology, University of Chicago

January 21, 2015

Abstract

1 Introduction

Why species go extinct at different rates remains one of the most fundamental questions in paleobiology (Jablonski, 2005, Kitchell et al., 1986, Payne and Finnegan, 2007, Quental and Marshall, 2013, Raup, 1991, 1994, Simpson, 1944, Van Valen, 1973, Wagner and Estabrook, 2014). 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. Yet investigations into the factors that affect extinction rate have proved inconclusive and often contradictory results.

I am testing if extinction non-random with respect to ecology during times of background extinction, and if extinction is taxon-age independent among Cenozoic mammals? I use a Bayesian hierarchical survival modeling approach for understanding the effects of organismal and species traits, time of origination, and shared evolutionary history on species duration while allowing for potentially time-dependent extinction. This is a direct extension of the dynamic and cohort survival approaches from paleontology (Baumiller, 1993, Foote, 1988, Raup, 1975, 1978, Sepkoski, 1975, Simpson, 1944, Van Valen, 1973, 1979). 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 (Alroy, 1996, 1998, 2009, Alroy et al., 2000, Blois and Hadly, 2009, Jernvall and Fortelius, 2002, Liow et al., 2008, Marcot, 2014, Quental and Marshall, 2013, Simpson, 1944, Smith et al., 2004a, Tomiya, 2013).

This study focuses on identifying the time invariant effects of organismal and species traits on the expected duration of a species. A time invariant effect is that when comparing taxa over a long time period there is a consistent effect that is generalizable over the entire period of interest. While the strength of that effect may vary over time, the direction does not change. For example, geographic range size has been identified as a generally time-invariant factor throughout the Phanerozoic, where large geographic range is associated with a decreased expected extinction risk (Payne and Finnegan, 2007). In many ways, this is a similar goal as Alroy et al. (2000): they found was no consistent, time invariant evolutionary response to climate change. While it is almost certain that selection pressures vary with time, consistent effects reveal fundamental differences in fitness. Also, a shift in time invariant factors may be an indicator of a change in “macroevolutionary regime” (Jablonski, 1986).

Background extinction, extinction not occurring at a mass extinction event, is considered to involve a mix of different factors which influence the instantaneous extinction risk of any given species (Harnik et al., 2013, Jablonski, 1986, Kitchell et al., 1986, Nürnberg and Aberhan, 2013, Payne and Finnegan, 2007, Wang, 2003). Factors such as geographic range have well known effects on survival (Jablonski, 1987, Payne and Finnegan, 2007) because the effect size is large and thus easy to identify. The relationship between extinction risk and other traits, specifically organismal ones, is less well known because the effect size is most likely much smaller, making inference difficult.

Periods of background extinction provide a great opportunity to study how traits are related to survival because they represent the majority of geologic time, remain relatively predictable, and change slowly (Jablonski, 1986, Raup and Boyajian, 1988). The Law of Constant Extinction (Van Valen, 1973) states that a taxon’s extinction risk within a given adaptive zone is age-independent (memoryless). This law is the foundation for the Red Queen hypothesis as well as most approaches for quantifying extinction. However there is some evidence contrary to this law (Drake, 2014, Finnegan et al., 2008, Raup, 1975, Sepkoski, 1975). By analyzing survival patterns within adaptive zones during periods of background extinction, it should be possible to both estimate the effects of various ecological strategies on survival and determine if extinction is age-independent or dependent.

The organismal and species traits studied here are both dietary and locomotor categories, bioprovince occupancy, and body mass. Each of these traits describe different aspects of a species’ adaptive zone such as energetic cost, population density, expected home range size, set of potential prey items, and dispersal ability (Damuth, 1979, 1981, Jernvall and Fortelius, 2004, Lyons, 2005, Lyons et al., 2010, Smith et al., 2004a, 2008). This is a mixture of well established factors that potentially influence extinction risk (i.e. occupancy and body mass) and less well understood ones (i.e. dietary and locomotor categories). It is expected that species with larger geographic ranges have lower extinction rates than species with smaller geographic ranges (Harnik et al., 2013, Jablonski, 1986,

Jablonski and Roy, 2003, Nürnberg and Aberhan, 2013, Roy et al., 2009), though this pattern may be random with respect to other traits (Raup, 1991). 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.

Dietary category roughly describes the trophic relations of a species, a central component of its biotic environment. The categories used here are coarse groupings of similar ecologies: carnivore, herbivore, omnivore, and insectivore. The first three of these represent commonly used groupings of mammals in paleobiological and macroevolutionary studies (Jernvall and Fortelius, 2004, Price et al., 2012), while the fourth is a biologically important grouping. Price et al. (2012) found that mammalian herbivores and carnivores have a greater diversification rates than omnivores which may indicate that these traits are better for survival. An increase in diversification can be due to either an increase in speciation relative to extinction or a decrease in extinction relative to speciation. Which scenario occurred, however, is currently impossible to determine from a phylogeny of only extant organisms (Rabosky, 2010). By analyzing the fossil record of extinct organisms, the results of Price et al. (2012) can be decomposed into the relative contributions of speciation and extinction.

Locomotor categories describe the motility of a species, plausibility of occurrence in a particular habitat, and dispersal ability. Dispersal ability is important for determining both the extent of a species’ geographic range and ability to track changing environments (Birand et al., 2012, Gaston, 2009, Jablonski and Hunt, 2006) which then affects both extinction risk and community similarity. Here, mammals are categorized as either arboreal, ground dwelling, or scansorial. With the transition from primarily closed to open environments during the Cenozoic (Blois and Hadly, 2009, Janis, 1993, Strömberg, 2005, Strömberg et al., 2013), it is expected that arboreal species during the Paleogene will have a greater expected duration than Neogene species while the opposite will be true for ground dwelling species. In comparison, the durations of scansorial species are expected to remain relatively similar between the two time periods because it represents a mixed environmental preference that may be viable in either closed or open environments.

Body size, here defined as mass, has an associated energetic cost in order to maintain homeostasis which in turn necessitates a supply of prey items. Many life history traits are associated with body size such as reproductive rate, metabolic rate, and home range size Brown and Maurer (1987), Damuth (1979), Peters (1983), Smith et al. (2004a). Body size may affect extinction risk because as body size increases, home range size increases (Damuth, 1979). If individual home range size scales up to reflect a species geographic range, this would mean that extinction risk would decrease. Alternatively, it could be argued that as body size increases, reproductive rate decreases (Johnson, 2002), populations get smaller (White et al., 2007), and generations get longer (Martin and Palumbi,

1993), all of which increase extinction risk. A negative relationship between mammal body size and duration of genera has been observed (Davidson et al., 2012, Liow et al., 2008) though this is inconsistent between continents (Liow et al., 2008, Tomiya, 2013).

I analyze the effect of each of these species traits along with shared origination cohort and shared evolutionary history (i.e. phylogeny) in the context of a Bayesian survival model. Survival analysis is concerned with the time till an event (Klein and Moeschberger, 2003), in this case the time from origination to extinction. The parametric model used here is parameterized in a hierarchical, or mixed effects, context so that known structure in the data can be modeled along with the traits of interest. In that way, the importance and contribution to variance of species traits can be compared with these hierarchical effects.

The purpose of this study is to estimate the time-invariant effects of organismal- and species-level traits upon expected duration while also estimating the effect of taxon age upon extinction risk. The Bayesian model used here allows for comparison of the marginal posterior estimates of each of the parameters acts as tests of the multiple trait effect hypotheses. All of these traits are analyzed with respect to the individual species origination cohort and phylogenetic position. From there the relative contribution species, cohort, and phylogeny to the unexplained variance can be estimated. Finally, the effect of time on extinction risk is explicitly modeled allowing for inference about the applicability of the Law of Constant Extinction (Van Valen, 1973).

2 Methods

2.1 Species information

Fossil occurrence information was downloaded from the Paleobiology Database (PBDB; <http://paleodb.org/>). Occurrence, taxonomic, stratigraphic, and biological information was downloaded for all North American mammals. 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 done using the assignments in initial the PBDB which were then reassigned into coarser categories (Table 1). This was done to improve interpretability, increase sample size per category, and make results comparable to previous studies (Jernvall and Fortelius, 2004, Price et al., 2012).

Fossil occurrences were assigned to 2 My bins ranging through the entire Cenozoic. Taxon duration was measured as the number of bins from the first bin of occurrence to the last bin of occurrence, inclusive. This bin size was chosen because it approximately reflects the resolution of the North American Cenozoic

mammal fossil record (Alroy, 2009, Alroy et al., 2000, Marcot, 2014). The youngest cohort, 0-2 My, was excluded from this analysis.

Species body size estimates were sourced from a large selection of primary literature and data base compilations, principally the PBDB, PanTHERIA (Jones et al., 2009), the Neogene Old World Mammal database (Now; <http://www.helsinki.fi/science/now/>), and other large scale data collection efforts (Brook and Bowman, 2004, Freudenthal and Martín-suárez, 2013, McKenna, 2011, Raia et al., 2012, Smith et al., 2004b). In many cases, species body mass was estimated from anatomical dimensions such as tooth size. These estimates were made using a variety of published regression equations. See Appendix: Data for a complete list of individual sources and equations.

2.1.1 Bioprovince occupancy

For each 2 My time bin, a bipartite biogeographic network was created between species occurrences and spatial units, defined as 2x2 latitude–longitude grid cells from an azimuthal equal-area map projection. In these bipartite networks, taxa can only be linked to localities and *vice versa*. Taxa are not linked to each other, nor are localities linked. Emergent bioprovinces within the biogeographic occurrence network were identified using the map equation (Rosvall and Bergstrom, 2008, Rosvall et al., 2009). A bioprovince is a set of species–locality connections that are more interconnected within the group than without. This was done for each bin’s biogeographic network using the **igraph** package for R (Csardi and Nepusz, 2006, R Core Team, 2014). The relative number of bioprovinces occupied per time bin was then determined for each species. This approach to understanding biogeographic patterns of species occurrence was first used by Sidor et al. (2013) and Vilhena et al. (2013).

2.1.2 Informal phylogeny

Because there exists no phylogenetic hypothesis of all Cenozoic fossils mammals from North America, it was necessary to construct a semi-formal supertree. This was done by combining taxonomic information for all the observed species and a few published phylogenies.

The taxonomic information from the PBDB served as the basis for additional revision. The taxonomy of many species was updated using the Encyclopedia of Life (<http://eol.org/>), which collects and collates taxonomic information in a single database. This was done programatically using the **taxize** package for R (Scott Chamberlain and Eduard Szocs, 2013). This was additionally correct using various published phylogenies and taxonomies of fossil mammals (Janis et al., 1998, 2008, Raia et al., 2012), producing a tree that was a series of nested polytomies.

Polytomies were resolved in order of species first appearance. The resulting tree was then time scaled using the `paleotree` package via the “minimum branch length” approach with a minimum length of 0.1 My (Bapst, 2012). The minimum length is necessary to avoid zero-length branches which cause the phylogenetic covariance matrix not be positive definite, which is important for computation (see below). While other time scaling approaches are possible (Bapst, 2013, Hedman, 2010) this method was chosen for it’s simplicity and not requiring additional information about diversification rates which are of interest in this study.

2.2 Survival model

The statistical model described here was the final model at the end of a continuous model development framework where the sampling and prior distributions were iteratively modified to best reflect theory, knowledge of the data, the inclusion of important covariates, and to fit the data. This follows the approach described in Gelman and Hill (2007) and Gelman et al. (2013). A survival model was fit in a Bayesian context where species duration were assumed to be drawn from a Weibull distribution (Eq. 1) with shape α and scale σ parameters.

$$\begin{aligned} p(y_i|\alpha, \sigma) &= \text{Weibull}(y_i|\alpha, \sigma) \\ &= \frac{\alpha}{\sigma} \left(\frac{y_i}{\sigma}\right)^{\alpha-1} \exp\left(-\left(\frac{y_i}{\sigma}\right)^\alpha\right) \end{aligned} \quad (1)$$

α was assumed constant, which is standard practice in survival analysis (Klein and Moeschberger, 2003). α was given a weakly informative half-Cauchy prior. σ was reparameterized as an exponentiated regression model (Eq. 2). Note that the inclusion of α in the denominator of the exponentiated term is a standard parameterization for survival models using a Weibull distribution (Klein and Moeschberger, 2003).

$$\sigma = \exp\left(\frac{-(h_i + \eta_{j[i]} + \sum \beta^T \mathbf{X}_i)}{\alpha}\right) \quad (2)$$

K species-level covariates were included as a $n \times K$ matrix, \mathbf{X} . Two of the covariates of interest are the logit of mean relative occupancy and the logarithm of body size (g). The discrete covariate index variables of dietary and locomotor category were transformed into $n \times (k - 1)$ matrices where each column is an indicator variable (0/1) for that species’s category, k being the number of categories of the index variable (3 and 4, respectively). Only $k - 1$ indicator variables are necessary as the intercept takes on the remaining value. Finally, a vector of 1-s were included in the matrix \mathbf{X} whose corresponding β coefficient is the intercept, making K equal eight.

β is a vector of regression coefficients, where each element was given a unique, weakly informative Normally distributed prior. These priors were chosen because it is expected that the effect size of each variable on duration will be small, as is generally the case with binary covariates.

Regression coefficients are not directly comparable without first standardizing the input variables to have equal standard deviations. This is accomplished by subtracting the mean of the covariate from all values and then dividing by the standard deviation, resulting in a variable with mean of zero and a standard deviation of one. This linear transform greatly improves the interpretability of the coefficients as expected change in mean duration given a difference of one standard deviation in the covariate (Schielzeth, 2010). However, because the expected standard deviation for a binary variable is 0.5, in order to make comparisons between the binary and continuous variables, the continuous inputs must instead be divided by twice their standard deviation (Gelman, 2008). The above model was fit with both unstandardized and standardized continuous inputs for illustrative purposes.

2.2.1 Hierarchical effects

The two hierarchical effects of interest in this study are origination cohort and shared evolutionary history, or phylogeny. Hierarchical modeling can be considered an intermediate between complete and no pooling of groups (Gelman and Hill, 2007), where complete pooling is when the differences between groups are ignored and no pooling is where different groups are analyzed separately. By allowing for partial pooling, we are modeling the appropriate compromise between these two extremes, allowing for better and potentially more informative overall inference. This is done by having all of the groups share the same Normal prior with mean 0 and a scale parameter estimated from the data, which then acts as an indicator of the amount of pooling. A scale of 0 and ∞ indicate complete and no pooling, respectively. The choice of mean 0 allows for the individual groups estimates to be interpreted as deviations from the mean. Hierarchical modeling is analogous to mixed-effects modeling (Gelman and Hill, 2007).

Origination cohort is defined as the group of species which originated during the same 2 My temporal bin. Because the most recent temporal bin, 0-2 Mya was excluded, there are 32 different cohorts. The effect of origination cohort j was modeled with each group being a sample from a common cohort effect, η , which was considered Normally distributed with mean 0, and standard deviation σ_c . The value of σ_c was then estimated from the data itself, corresponding to the amount of pooling in the individual estimates of η_j . This approach is a conceptual unification between dynamic and cohort survival analysis in paleontology (Baumiller, 1993, Foote, 1988, Raup, 1975, 1978, Van Valen, 1979), with σ_c acting as a compromise between these two end members.

$$\begin{aligned}\eta_j &\sim \mathcal{N}(0, \sigma_c) \\ \sigma_c &\sim \text{halfCauchy}(0, 2.5)\end{aligned}$$

The choice of the half-Cauchy prior on σ_c follows Gelman (2006)

The impact of shared evolutionary history, or phylogeny, was modeling as an individual effect where each observation, i , is distributed as a multivariate normal, h , where the covariance matrix was assumed known up to a constant, σ_p^2 (Housworth et al., 2004, Lynch, 1991). This is written

$$\begin{aligned}h &\sim \text{Multi}\mathcal{N}(0, \mathbf{\Sigma}) \\ \mathbf{\Sigma} &= \sigma_p^2 \mathbf{V}_{phy} \\ \sigma_p &\sim \text{halfCauchy}(0, 2.5),\end{aligned}$$

with \mathbf{V}_{phy} being the phylogenetic covariance matrix defined as an $n \times n$ matrix where the diagonal elements are the distance from root to tip, in branch length, for each observation and the off-diagonal elements are the amount of shared history, measured in branch length, between observations i and j . σ_p was given a weakly informative half-Cauchy hyperprior.

2.2.2 Censored observations

An important part of survival analysis is the inclusion of “censored” observations (Ibrahim et al., 2001, Klein and Moeschberger, 2003) or observations where the failure time has not been observed. The most common censored observation is right censored, where the point of extinction had not yet been observed in the period of study. In this case, this means taxa that are still extant. Left censored observations, on the other hand, correspond to observations that went extinct any time between 0 and some known point. In this study, taxa occurring in only a single time bin were left censored. Because of the minimum resolution of the record, we cannot observe if these taxa went extinct in less than that single bin or not.

To model censored data, the survival function, $S(t)$ must first be defined (Klein and Moeschberger, 2003). $S(t)$ for a Weibull model is

$$S(t|\alpha, \sigma) = \exp\left(-\left(\frac{t}{\sigma}\right)^\alpha\right), \quad (3)$$

where σ is defined as above (Eq. 2). $S(t)$ is the probability that an observation will survive longer than a given time, t . The likelihood of uncensored observations is evaluated as as normal using Equation 1 while right censored observations are

evaluated at $S(t)$ and left censored observations are evaluated at $1 - S(t)$. Note, $1 - S(t)$ is equivalent to the cumulative density function and $S(t)$ is equivalent to the complementary cumulative density function (Gelman et al., 2013).

Fully, the likelihood for both uncensored and both right and left censored observations is written

$$L \propto \prod_{i \in C} \text{Weibull}(y_i | \alpha, \sigma) \prod_{j \in R} S(y_j | \alpha, \sigma) \prod_{k \in L} (1 - S(y_k | \alpha, \sigma)),$$

where C is the set of uncensored observations, R is the set of right censored observations, and L is the set of left censored observations.

A summary of the entire model, save for calculations for censored observations, along with the exact priors for every estimated parameter is presented in Figure 1.

2.2.3 Estimation

Parameter posteriors were approximated using a Markov-chain Monte Carlo (MCMC) routine implemented in the Stan programming language (Stan Development Team, 2014). Stan implements a Hamiltonian Monte Carlo using a No-U-Turn sampler (Hoffman and Gelman, 2011). Posterior approximation was done using four parallel MCMC chains. Chain convergence was evaluated using the scale reduction factor, \hat{R} . Values of \hat{R} close to 1, or less than or equal to 1.1, indicate approximate convergence. Convergence means that the chains are approximately stationary and the samples are well mixed (Gelman et al., 2013).

In order to speed up the MCMC routine, a custom multivariate normal sampler was used for estimating the unknown constant term in the covariance matrix. This is necessary because inverting and solving the complete covariance matrix on every iteration is a memory intense procedure. The custom sampler limits the necessary number of operations and matrix inversions per iteration.

Four different MCMC chains were run for 20000 steps and were thinned to every twentieth sample split evenly between warm-up and sampling.

2.3 Posterior predictive checks

The most basic assessment of model fit is that simulated data generated using the fitted model should be similar to the observed. This is the idea behind posterior predictive checks. Using the predictors from each of the observed durations, and randomly drawn parameter estimates from their marginal posteriors, a simulated data set y^{rep} was generated. This process repeated 1000 times and the distribution of y^{rep} was compared with the observed y (Gelman et al., 2013). This was done both graphically and numerically.

An example posterior predictive check used in this study is a graphical comparison of the Kaplan-Meier (K-M) survival curve estimated from the observed data with the survival curves from 1000 simulations. K-M survival curves are non-parametric estimates of the function $S(t)$ or the probability of a species going extinct given that it has lived to time t (Klein and Moeschberger, 2003). Other posterior predictive checks included comparison of the mean and quantiles of the observed durations to the distributions of the same quantities from the simulations, and inspection of the deviance residuals, defined below.

In standard linear regression, the residuals are defined as $r = y - y_{est}$. For hierarchical models, this definition is inadequate. For survival analysis, the equivalent values are deviance residuals. To define how deviance residuals are calculated, we first define the cumulative hazard function (Klein and Moeschberger, 2003). Given $S(t)$ (Eq. 3), we define the cumulative hazard function as

$$\Lambda(t) = -\log(S(t)).$$

Next, we define martingale residuals, m , which are defined in relation to the inclusion vector I

$$m_i = I_i - \Lambda(t_i).$$

I is as a vector of length n , where $I_i = 1$ means the observation is completely observed and $I_i = 0$ means the observation is censored.

Martingale residuals have a mean of 0 and ranges between 1 and $-\infty$ and can be viewed as the difference between the observed number of deaths between 0 and t_i and the expected number of deaths based on the model. However, martingale residuals are difficult to interpret, can be asymmetrically distributed, and are not equivalent to standard residuals.

The solution to this is to use the deviance residuals, D . This is defined as a function of martingale residuals and takes the form

$$D_i = \text{sign}(m_i) \sqrt{-2[m_i + I_i \log(I_i - m_i)]}.$$

2.4 Variance partitioning

There are three different variance components in this model (Fig. 1): sample σ_y^2 , cohort σ_c^2 , and phylogenetic σ_p^2 . The sample variance, σ_y^2 , is similar to the residual variance from a normal linear regression. Partitioning the variance between these sources allows the relative amount of unexplained variance of the sample to be compared. However, the model used here (Eq. 1) does not include an estimate of overall variance, as the errors are not normally distributed. The partitioning of the variance between these three components was instead approximated via a simulation approach modified from Goldstein et al. (2002).

The procedure is as follows:

1. Simulate w (50,000) values of η ; $\eta \sim \mathcal{N}(0, \sigma_c)$.
2. For a given value of $\beta^T \mathbf{X}$, calculate σ^{c*} (Eq. 2) for all w simulations, holding h constant at 0.
3. Calculate v_c , the Weibull variance (Eq. 4) of each element of σ^{c*} with α drawn from the posterior estimate.
4. Draw a random value from the diagonal of \mathbf{V}_{phy} , p_r
5. Simulate w values of h ; $h \sim \mathcal{N}\left(0, \sqrt{\sigma_p^2 \times p_r}\right)$
6. For a given value of $\beta^T \mathbf{X}$, calculate σ^{p*} (Eq. 2) for all w simulations, holding η constant at 0.
7. Calculate v_p , the Weibull variance (Eq. 4) of each element of σ^{p*} with α drawn from the posterior estimate.
8. $\sigma_{y*}^2 = \frac{1}{2} \left(\left(\frac{1}{w} \sum_i^w v_{pi} \right) + \left(\frac{1}{w} \sum_j^w v_{cj} \right) \right)$
9. $\sigma_{c*}^2 = var(v_c)$ and $\sigma_{p*}^2 = var(v_p)$

The simulated values of h were drawn from a univariate normal distribution because each simulated value is in isolation, so there are no concern of phylogenetic autocorrelation. The chosen value for $\beta^T \mathbf{X}$ was a draw from the posterior estimate of the intercept. Because input variables were standardized prior to model fitting, the intercept corresponds to the estimated effect on survival of the sample mean.

Weibull variance is calculated as

$$var(x) = \sigma^2 \left(\Gamma \left(1 + \frac{2}{\alpha} \right) - \left(\Gamma \left(1 + \frac{1}{\alpha} \right) \right)^2 \right), \quad (4)$$

where Γ is the gamma function.

The variance partitioning coefficients are then calculated $VPC_{phylo} = \frac{\sigma_{p*}^2}{\sigma_{y*}^2 + \sigma_{c*}^2 + \sigma_{p*}^2}$ and similar for the other variance components.

I used ratios of the variances and variance partitioning coefficients (VPC) to measure the amount of partial pooling. The former, when compared to the sample size of the hierarchical effect such as the number of cohorts, is an estimate of the relative amount of pooling, while the latter is a measure of the relative importance of the different variance components (Gelman and Hill, 2007). Phylogenetic heritability, h_p^2 (Housworth et al., 2004), is effectively identical to the VPC of the phylogenetic effect. Additionally, because phylogenetic effect was estimated using a principally taxonomy based tree the estimates derived here can be considered minimum estimates of the tree effect.

Table 1: Species trait assignments in this study are a coarser version of the information available in the PBDB. Information was coarsened to improve per category sample size and uniformity and followed this table.

This study		PBDB categories
Diet	Carnivore	Carnivore
	Herbivore	Browser, folivore, granivore, grazer, herbivore.
	Insectivore	Insectivore.
	Omnivore	Frugivore, omnivore.
Locomotor	Arboreal	Arboreal.
	Ground dwelling	Fossorial, ground dwelling, semifossorial, saltatorial.
	Scansorial	Scansorial.

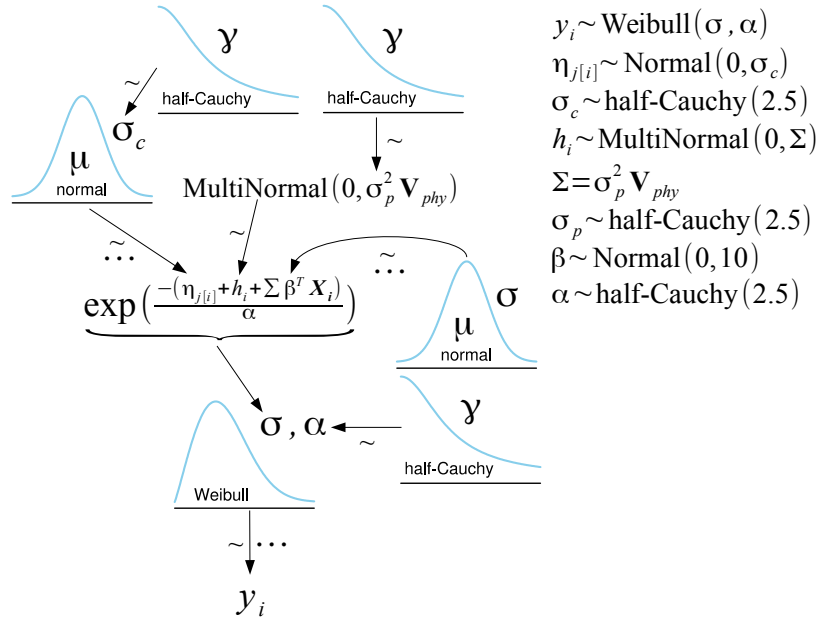


Figure 1: Graphical depiction of full survival model, save censoring, used here. Exact values for the hyperparameters are presented to the right. The observed duration of the i th observation is indicated towards the bottom left as y_i , which is assumed to follow a Weibull distribution.

3 Results

With all marginal posterior estimates having converged ($\hat{R} < 1.1$) it is possible to examine the quality of fit of the model (Table 2). If the model is an adequate descriptor of the observed data, then relatively confident inference can be made (Gelman et al., 2013).

Visual examination of the deviance residuals from twelve different sets of posterior predictive values indicate little systematic problems (Fig. 2). The only concern is that the residuals are slightly skewed, with some predictions having longer durations than the observed. However, this bias appears very small. This can also be observed when comparing the K-M estimate of the empirical survival function to 100 estimated survival functions from posterior simulations (Fig. 3).

Posterior predictive comparisons of the observed 25th, 50th, 75th quantiles, and mean durations to the results from simulation indicate adequate model fit (Fig. 4). Between all of these different posterior predictive checks, the inferred model appears adequate at capturing the observed variation.

Given that the model appears adequate, it is possible to interpret the parameter estimates with some degree of confidence. The estimates for diet and locomotor categories were inferred as contrasts between the intercept and one of the $k - 1$ other states (Table 2). In order to interpret these estimates, I compared the differences between each of the different states to get an estimate of whether either of two traits was associated with a greater mean duration or not. This was done for all pairwise comparisons for diet and locomotor category separately (Fig. 5).

Dietary category has a large amount of variation in the pairwise differences of the effect on expected duration (Fig. 5a). 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.

For locomotor category, arboreality appears to be associated with a lower expected duration than either scansoriality or a ground dwelling life habit (Fig. 5b). Scansoriality and a ground dwelling life habit have approximately equal expected durations.

The effects of both body size and bioprovince occupancy on expected duration are best interpreted from estimates from the model fit standardized data (Fig. 6). Of all the traits of interest, bioprovince occupancy has the largest effect size with larger occupancy associated with a longer expected duration. Body size has a very small, near zero effect on expected duration, similar to the lack of relationship between body size and generic duration (Tomiya, 2013).

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. 7). 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 55 and 50 My that have a much lower extinction risk than other cohorts of similar age.

Because the estimate of the Weibull shape parameter, α , is greater than 1 this means that extinction risk is expected to increase with taxon age (Table 2). The estimate of α is also rather tightly constrained with 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 $h(t)$, calculated for a Weibull distribution as

$$h(t) = \frac{\alpha}{\sigma} \left(\frac{t}{\sigma} \right)^{\alpha-1}. \quad (5)$$

$h(t)$ 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 will gradually increase with age (Fig. 8).

Of the three sources of variance present in the model, variation in individual species accounts for at least 70% of unexplained variance (Fig. 9). Both cohort and phylogenetic effects account for approximately 30% of the unexplained variance. Both of these factors are related to some aspect of the relationship between taxa, either temporal and through shared evolutionary history. While both of these effects accounts for approximately 15% of unexplained variance individually, the total combined effect of these factors indicates that neither can be ignored.

For example, Housworth et al. (2004) state that when the value of phylogenetic heritability is greater than 0, phylogenetic effect cannot be ignored. As VPC_{phylo} is equivalent to phylogenetic heritability and is greater than 0, the effect of shared evolutionary history on duration is non-ignorable.

The low amount of variance of phylogenetic effect estimated from the model (Table 2) may explain previously found lack of “phylogenetic signal” in generic duration (Tomiya, 2013).

Table 2: Summaries of 1000 samples drawn from the marginal posteriors for the principle parameters of interest. Because of variable standardization, the intercept can be interpreted as the estimate for the mean observed species. As such, the other values are expected effects of trait values 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 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

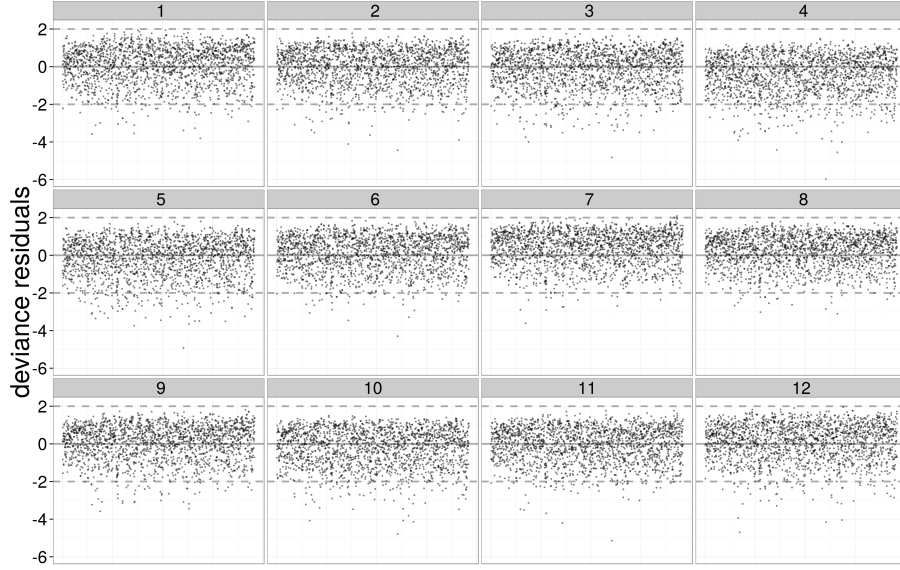


Figure 2: Deviance residuals from the fitted survival model. Each graph depicts the residuals from single draws from the posteriors distributions of all estimated parameters. Positive values indicate an under estimate of the observed duration, while negative values indicate an over estimate of the observed duration. Twelve difference examples are provided here to indicate the lack of individual observation based biases.

4 Discussion

The number and structure of the parameters from the fitted model allows many different hypotheses to be addressed and inferences to be made. First, I interpret the results in terms of hypotheses of trait effects on survival. Second, I address implications for future paleobiological modeling. Third and finally, I discuss additional model improvements and complexities that can be used to further address other hypotheses.

As expected, bioprovince occupancy has the single largest effect of expected species duration. The other factors all appear to have small effect sizes which is also consistent with expectations.

I found that carnivores are expected to have a greater average duration than herbivores and insectivores, while omnivores have approximately equal or greater expected durations than carnivores. Omnivorous taxa are also associated with a greater expected duration than both herbivores and insectivores. These results

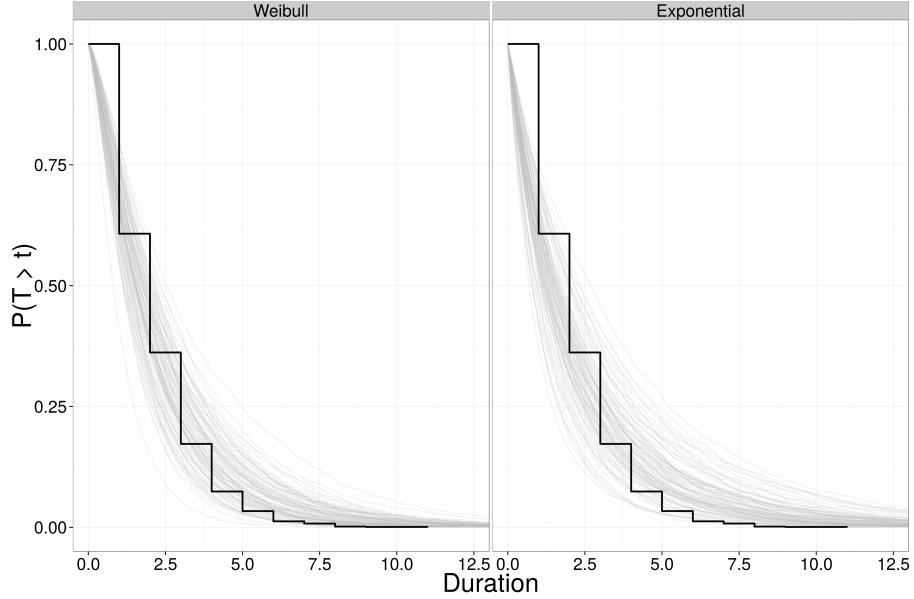


Figure 3: Comparison between K-M estimate of survival function (black) from the observed versus K-M estimates from 100 simulated data sets using the fitted model (dark grey). Simulated data sets were generated by drawing parameter values randomly from their estimated posteriors and using the observed covariate information to estimate durations for all the observed species. On the left are the results from the full survival model (Fig. 1), while on the right are the results from a simplified model where duration follows an exponential distribution and there is no phylogenetic effect.

sit nicely beside those of Price et al. (2012).

Given that carnivores and omnivores have approximately equal expected durations, and that Price et al. (2012) found that carnivores have a greater diversification rate than omnivores, this implies that carnivores have a greater origination rate than omnivores. In comparison, given the results of this study and Price et al. (2012), this also implies that herbivores which have the lowest expected duration must have a very high origination rate in order to have the greatest diversification rate of these three categories.

The comparisons between the effects of locomotor category on expected species duration are consistent with the hypotheses that arboreality has the lowest effect on expected duration when compared with scansoriality and ground dwelling taxa. Importantly, scansoriality appears to not influence any difference in duration 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 may

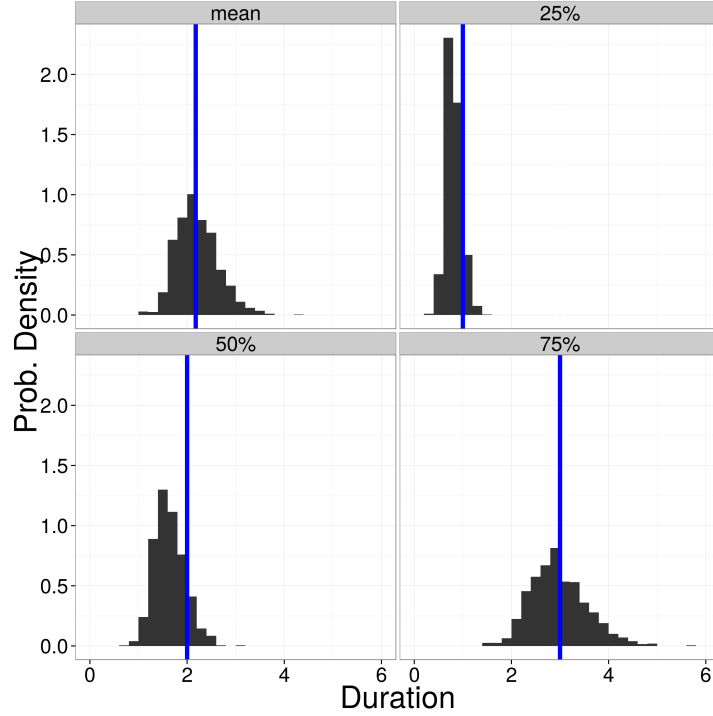


Figure 4: The results of additional posterior predictive checks for four summaries of the observed durations, as labeled. Blue vertical indicate the observed value. None of the observed are significantly different from the posterior predictive distributions.

prevent species persistence.

The very weak if non-existent effect of body size on expected duration, which can be considered not “significant”, is consistent with Tomiya (2013). The direction/sign of the effect, however, is not consistent with the prediction of decrease of duration associated with increase in body size (Liow et al., 2008). Importantly, however, the other studies were performed at the generic-level which may or may not involve different processes that are not included in this species-level model (Liow et al., 2008, Tomiya, 2013).

While explicit phylogenetic relations between taxa are frequently not included in paleobiological studies of diversity (Alroy, 2009, Alroy et al., 2000, Foote and Miller, 2013, Hunt, 2007, Jablonski and Hunt, 2006, Jernvall and Fortelius, 2002, 2004, Liow et al., 2008, Marcot, 2014, Payne and Finnegan, 2007), there have been more recent studies which analyze fossil diversification in an explicitly phylogenetic context (Harnik et al., 2014, Simpson et al., 2011, Slater et al., 2012, Slater, 2013, Tomiya, 2013). The partitioning of the different sources of

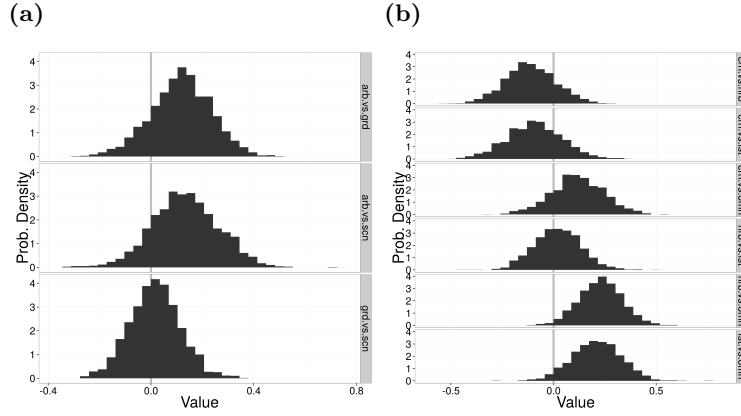


Figure 5: Pairwise differences in effect of the locomotor (a) and dietary categories (b) on expected duration from 1000 samples from the posterior distribution. Comparisons of locomotor categories, from top to bottom (a), are: arboreal versus ground dwelling, arboreal versus scansorial, and ground dwelling 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.

variance involved in this model shows that phylogeny or shared evolutionary history accounts for approximately 10-15% of the unexplained variance. Because VPC of phylogeny is greater than 0, it is not appropriate to ignore phylogeny when modeling survival in paleontological studies (Housworth et al., 2004). An addition 10-15% of unexplained variance was due to shared origination cohort. Between these two sources of variance, it is clear that a shared evolutionary history and temporal occurrence are non-ignorable in paleontological studies or survival.

Comparison of time-invariant effects from the Cenozoic, the “signature” of a regime, to the predictions of selection for current biodiversity crisis. This presupposes that the current biodiversity crisis may involve fundamentally different selection pressures than experienced over the Cenozoic.

Interaction between species level effects.

Varying intercept, varying slope model. We have an intercept, diet, loco, body, occ in a $k \times k$ shared multivariate prior situation. This is really complicated and makes interpretation and inference much more difficult. Each species has an origination cohort.

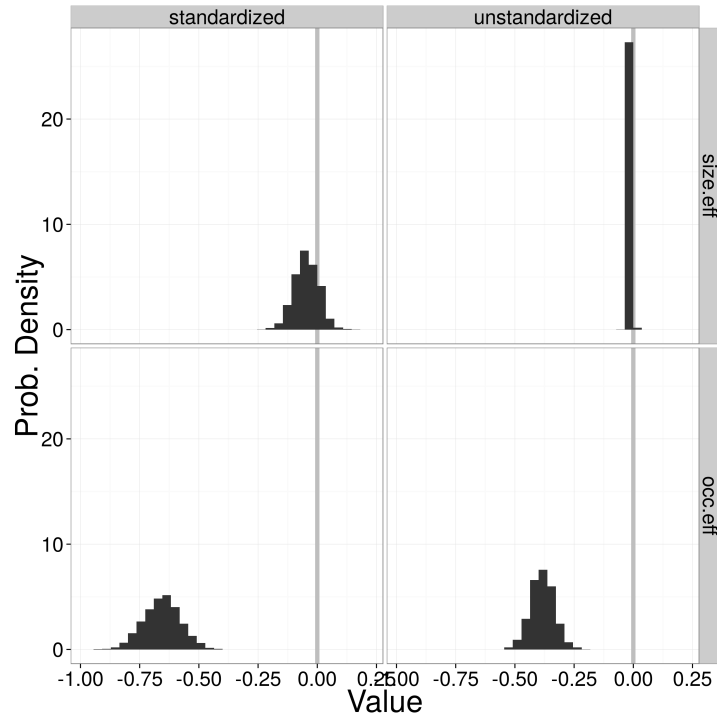


Figure 6

This allows for each cohort to effectively have it's own model while also estimating the shared time-invariant model. The goal of this would be very different that this study.

Better phylogeny. For such a well sampled group, it is surprising that a phylogeny across the whole Cenozoic. Of even just the Eocene.

References

- J. Alroy. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127:285–311, 1996.
- J. Alroy. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, 280:731–734, 1998. doi: 10.1126/science.280.5364.731.
- J. Alroy. Speciation and extinction in the fossil record of North American mammals. In R. K. Butlin, J. R. Bridle, and D. Schluter, editors, *Speciation and patterns of diversity*, pages 302–323. Cambridge University Press, Cambridge, 2009.

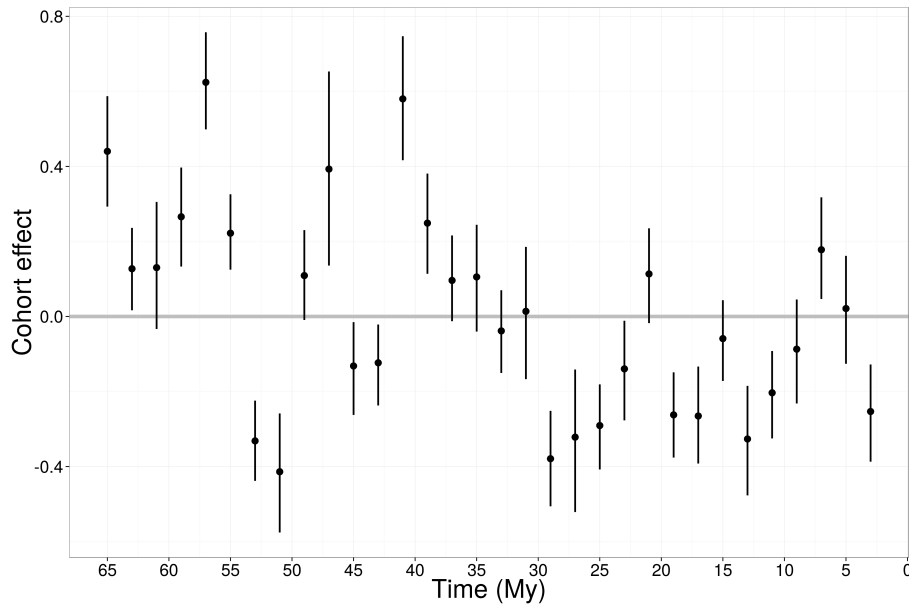


Figure 7: Summaries of estimated individual cohort effect posteriors. Depicted are medians and 80% credible intervals of the estimated posterior distributions. High values correspond to shorter species durations while lower values correspond to greater species durations compared to the mean duration. Lines are placed at the middle of the 2 My origination cohorts.

- J. Alroy, P. L. Koch, and J. C. Zachos. Global climate change and North American mammalian evolution. *Paleobiology*, 26(1981):259–288, 2000.
- D. W. Bapst. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, 3:803–807, 2012. doi: 10.1111/j.2041-210X.2012.00223.x. URL <http://doi.wiley.com/10.1111/j.2041-210X.2012.00223.xpapers2://publication/doi/10.1111/j.2041-210X.2012.00223.x>.
- D. W. Bapst. A stochastic rate-calibrated method for time-scaling phylogenies of fossil taxa. *Methods in Ecology and Evolution*, 4(8):724–733, Aug. 2013. ISSN 2041210X. doi: 10.1111/2041-210X.12081. URL <http://doi.wiley.com/10.1111/2041-210X.12081>.
- T. K. Baumiller. Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. *Paleobiology*, 19(3):304–321, 1993.
- A. Birand, A. Vose, and S. Gavrillets. Patterns of species ranges, speciation, and extinction. *The American naturalist*, 179(1):1–21, Jan. 2012. ISSN 1537-5323. doi: 10.1086/663202. URL <http://www.ncbi.nlm.nih.gov/pubmed/22173457>.

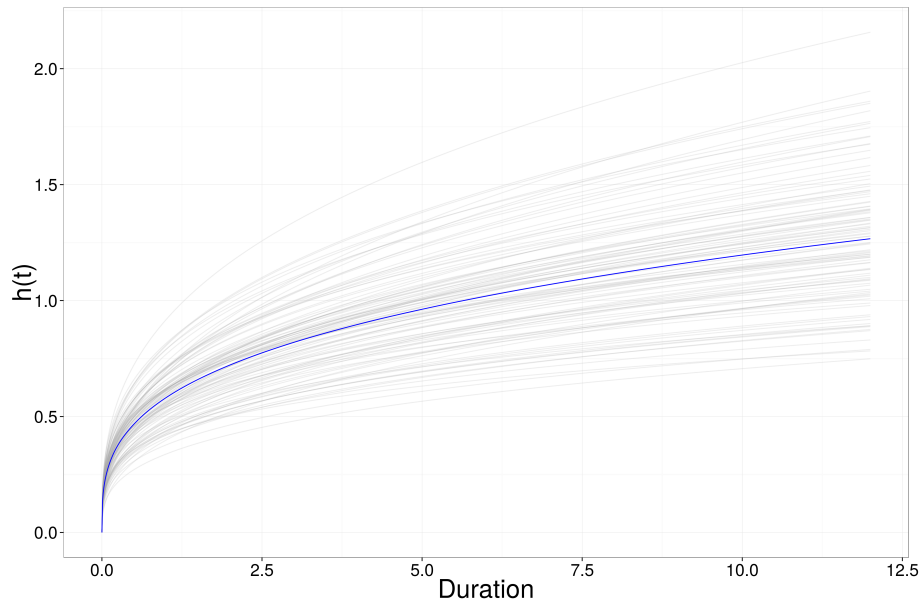


Figure 8: 100 estimates of the hazard function ($h(t)$) for the observed species mean (grey), along with the median estimated hazard function. $h(t)$ is an estimate of the rate at which a species of age t is expected to go extinct. Hazard functions were estimated from random draws from the estimated posterior distributions and evaluated with all covariate information set to 0, which corresponds to the expected duration of the mean species.

- J. L. Blois and E. A. Hadly. Mammalian Response to Cenozoic Climatic Change. *Annual Review of Earth and Planetary Sciences*, 37(1):181–208, May 2009. ISSN 0084-6597. doi: 10.1146/annurev.earth.031208.100055.
- B. W. Brook and D. M. J. S. Bowman. The uncertain blitzkrieg of Pleistocene megafauna. *Journal of Biogeography*, 31(4):517–523, Apr. 2004. ISSN 03050270. doi: 10.1046/j.1365-2699.2003.01028.x. URL <http://doi.wiley.com/10.1046/j.1365-2699.2003.01028.x>.
- J. H. Brown and B. A. Maurer. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *The American Naturalist*, 130(1):1–17, 1987.
- G. Csardi and T. Nepusz. The igraph software package for complex network research. *InterJournal*, Complex Systems:1695, 2006. URL <http://igraph.org>.
- J. Damuth. Home range, home range overlap, and species energy use among herbivorous mammals. *Biological Journal of the Linnean Society*, 15:185–193, 1979.

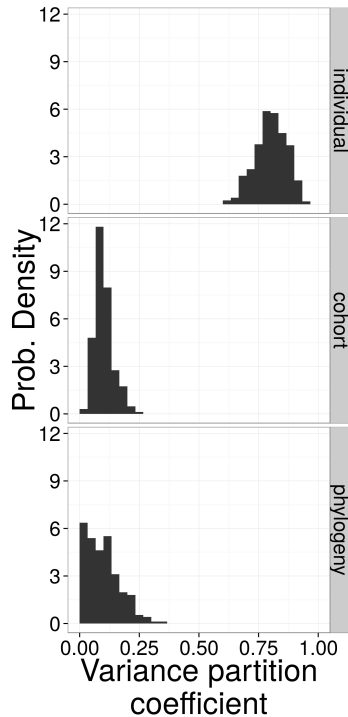


Figure 9: Estimates of the variance partitioning coefficients for the three different sources of variance: species, cohort, and phylogeny. Higher values correspond to greater contribution to total unexplained variance. Each of the estimates is a distribution of 1000 approximating simulations due to the model’s non-normality.

- J. Damuth. Population density and body size in mammals. *Nature*, 290:699–700, 1981. URL <http://www.jstor.org/stable/10.2307/2461771><http://www.nature.com/nature/journal/v290/n5808/abs/290699a0.html>.
- A. D. Davidson, A. G. Boyer, H. Kim, S. Pompa-Mansilla, M. J. Hamilton, D. P. Costa, G. Ceballos, and J. H. Brown. Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences*, 109(9):3395–400, Feb. 2012. ISSN 1091-6490. doi: 10.1073/pnas.1121469109. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3295301&tool=pmcentrez&rendertype=abstract>.
- J. M. Drake. Tail probabilities of extinction time in a large number of experimental populations. *Ecology*, page 140206083444001, Feb. 2014. ISSN 0012-9658. doi: 10.1890/13-1107.1. URL <http://www.esajournals.org/doi/abs/10.1890/13-1107.1>.
- S. Finnegan, J. L. Payne, and S. C. Wang. The Red Queen revisited: reevaluating the age selectivity of Phanerozoic marine genus extinctions. *Paleobiology*,

- 34(3):318–341, Sept. 2008. ISSN 0094-8373. doi: 10.1666/07008.1. URL <http://www.bioone.org/doi/abs/10.1666/07008.1>.
- M. Foote. Survivorship analysis of Cambrian and Ordovician Trilobites. *Paleobiology*, 14(3):258–271, 1988.
- M. Foote and A. I. Miller. Determinants of early survival in marine animal genera. *Paleobiology*, 39(2):171–192, Mar. 2013. ISSN 0094-8373. doi: 10.1666/12028. URL <http://www.bioone.org/doi/abs/10.1666/12028>.
- M. Freudenthal and E. Martín-suárez. Estimating body mass of fossil rodents. *Scripta Geologica*, 145:1–130, 2013.
- K. J. Gaston. Geographic range limits: achieving synthesis. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1395–406, Apr. 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1480. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677218&tool=pmcentrez&rendertype=abstract>.
- A. Gelman. Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, 1(3):515–533, 2006.
- A. Gelman. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, pages 2865–2873, 2008. doi: 10.1002/sim.
- A. Gelman and J. Hill. *Data Analysis using Regression and Multi-level/Hierarchical Models*. Cambridge University Press, New York, NY, 2007.
- A. Gelman, J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. *Bayesian data analysis*. Chapman and Hall, Boca Raton, FL, 3 edition, 2013.
- H. Goldstein, W. Browne, and J. Rasbash. Partitioning variation in multilevel models. *Understanding Statistics*, 1(4):1–12, 2002. URL http://www.tandfonline.com/doi/abs/10.1207/S15328031US0104_02.
- P. G. Harnik, C. Simpson, and J. L. Payne. Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B: Biological Sciences*, 282(1801), Oct. 2013. ISSN 0962-8452. doi: 10.1098/rspb.2012.1902. URL <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2012.1902>.
- P. G. Harnik, P. C. Fitzgerald, J. L. Payne, and S. J. Carlson. Phylogenetic signal in extinction selectivity in Devonian terebratulide brachiopods. *Paleobiology*, 40(4):675–692, June 2014. ISSN 0094-8373. doi: 10.1666/14006. URL <http://www.bioone.org/doi/abs/10.1666/14006>.
- M. M. Hedman. Constraints on clade ages from fossil outgroups. *Paleobiology*, 36(1):16–31, 2010.
- M. D. Hoffman and A. Gelman. The no-U-turn sampler: Adaptively setting path lengths in Hamiltonian Monte Carlo. *arXiv*, 1111(4246), 2011. URL <http://arxiv.org/abs/1111.4246>.

- E. A. Housworth, P. Martins, and M. Lynch. The Phylogenetic Mixed Model. *The American Naturalist*, 163(1):84–96, 2004.
- G. Hunt. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. In *Proceedings of the National Academy of . . .*, 2007. URL <http://www.pnas.org/content/104/47/18404.shortpapers2://publication/uuid/DE43904B-DCEC-49C7-A107-93353C9A7ABE>.
- J. G. Ibrahim, M.-H. Chen, and D. Sinha. *Bayesian Survival Analysis*. Springer, New York, 2001.
- D. Jablonski. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.
- D. Jablonski. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. *Science*, 238(4825):360–363, Oct. 1987. ISSN 0036-8075. doi: 10.1126/science.238.4825.360. URL <http://www.ncbi.nlm.nih.gov/pubmed/17837117>.
- D. Jablonski. Mass extinctions and macroevolution. *Paleobiology*, 31(sp5):192–210, 2005. URL <papers2://publication/uuid/F296080D-6609-4C57-9514-C74E5E726340>.
- D. Jablonski and G. Hunt. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *The American naturalist*, 168(4):556–64, Oct. 2006. ISSN 1537-5323. doi: 10.1086/507994. URL <http://www.ncbi.nlm.nih.gov/pubmed/17004227>.
- D. Jablonski and K. Roy. Geographical range and speciation in fossil and living molluscs. *Proceedings. Biological sciences / The Royal Society*, 270(1513):401–6, Feb. 2003. ISSN 0962-8452. doi: 10.1098/rspb.2002.2243. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691247&tool=pmcentrez&rendertype=abstract>.
- C. M. Janis. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, 24:467–500, 1993.
- C. M. Janis, K. M. Scott, and L. L. Jacobs. *Evolution of Tertiary mammals of North America. Vol. 1. Terrestrial carnivores, ungulates, and ungulatelike mammals*. Cambridge University Press, Cambridge, 1998.
- C. M. Janis, G. F. Gunnell, and M. D. Uhen. *Evolution of Tertiary mammals of North America. Vol. 2. Small mammals, xenarthrans, and marine mammals*. Cambridge University Press, Cambridge, 2008.
- J. Jernvall and M. Fortelius. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature*, 417(6888):538–40, May 2002. ISSN 0028-0836. doi: 10.1038/417538a.
- J. Jernvall and M. Fortelius. Maintenance of trophic structure in fossil mammal

- communities: site occupancy and taxon resilience. *American Naturalist*, 164 (5):614–624, Nov. 2004. ISSN 1537-5323. doi: 10.1086/424967.
- C. N. Johnson. Determinants of loss of mammal species during the Late Quaternary ‘megafauna’ extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society B: Biological Sciences*, 269:2221–2227, 2002. doi: 10.1098/rspb.2002.2130.
- K. E. Jones, J. Bielby, M. Cardillo, S. A. Fritz, J. O’Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, G. M. Mace, and A. Purvis. PanTHERIA : a species-level database of life history , ecology , and geography of extant and recently extinct mammals. *Ecology*, 90(9):2648, 2009.
- J. A. Kitchell, D. L. Clark, and A. M. Gombos. Biological selectivity of extinction: a link between background and mass extinction. *Palaeos*, 1(5):504–511, 1986.
- J. P. Klein and M. L. Moeschberger. *Survival Analysis: Techniques for Censored and Truncated Data*. Springer, New York, 2nd edition, 2003.
- L. H. Liow, M. Fortelius, E. Bingham, K. Lintulaakso, H. Man- nila, L. Flynn, and N. C. Stenseth. Higher origination and extinction rates in larger mammals. *Proceedings of the National Academy of Sciences*, 105(16):6097, 2008. URL papers2://publication/uuid/5A93DDA3-204F-4D9C-AFAC-A15722A18C61.
- M. Lynch. Methods for the analysis of comparative data in evolutionary biology. *Evolution*, 45(5):1065–1080, 1991.
- S. K. Lyons. A quantitative model for assessing community dynamics of pleistocene mammals. *The American naturalist*, 165(6):E168–85, June 2005. ISSN 1537-5323. doi: 10.1086/429699. URL <http://www.ncbi.nlm.nih.gov/pubmed/15937741>.
- S. K. Lyons, P. J. Wagner, and K. Dzikiewicz. Ecological correlates of range shifts of Late Pleistocene mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365 (1558):3681–93, Nov. 2010. ISSN 1471-2970. doi: 10.1098/rstb.2010.0263. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2981999&tool=pmcentrez&rendertype=abstract>.
- J. D. Marcot. The fossil record and macroevolutionary history of North American ungulate mammals: standardizing variation in intensity and geography of sampling. *Paleobiology*, 40(2):237–254, Feb. 2014. ISSN 0094-8373. doi: 10.1666/13052. URL <http://www.bioone.org/doi/abs/10.1666/13052>.
- A. P. Martin and S. R. Palumbi. Body size, metabolic rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences*, 90(9):4087–91, May 1993. ISSN 0027-

8424. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=46451&tool=pmcentrez&rendertype=abstract>.
- R. T. McKenna. *Potential for Speciation in Mammals Following Vast , Late Miocene Volcanic Interruptions in the Pacific Northwest*. Masters, Portland State University, 2011.
- S. Nürnberg and M. Aberhan. Habitat breadth and geographic range predict diversity dynamics in marine Mesozoic bivalves. *Paleobiology*, 39(3):360–372, Apr. 2013. ISSN 0094-8373. doi: 10.1666/12047. URL <http://www.bioone.org/doi/abs/10.1666/12047>.
- J. L. Payne and S. Finnegan. The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 104(25):10506–11, June 2007. ISSN 0027-8424. doi: 10.1073/pnas.0701257104. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1890565&tool=pmcentrez&rendertype=abstract>.
- R. H. Peters. *The ecological implications of body size*. Cambridge University Press, Cambridge, 1983.
- S. A. Price, S. S. B. Hopkins, K. K. Smith, and V. L. Roth. Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 109(18):7008–12, May 2012. ISSN 1091-6490. doi: 10.1073/pnas.1117133109. URL <http://www.ncbi.nlm.nih.gov/pubmed/22509033>.
- T. B. Quental and C. R. Marshall. How the Red Queen Drives Terrestrial Mammals to Extinction. *Science*, 341(6143):290–292, Sept. 2013. ISSN 0022-1376. doi: 10.1086/627905. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/627905>.
- R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2014. URL <http://www.R-project.org/>.
- D. L. Rabosky. Extinction rates should not be estimated from molecular phylogenies. *Evolution*, 64(6):1816–24, June 2010. ISSN 1558-5646. doi: 10.1111/j.1558-5646.2009.00926.x. URL <http://www.ncbi.nlm.nih.gov/pubmed/20030708>.
- P. Raia, F. Carotenuto, F. Passaro, D. Fulgione, and M. Fortelius. Ecological specialization in fossil mammals explains Cope’s rule. *The American naturalist*, 179(3):328–37, Mar. 2012. ISSN 1537-5323. doi: 10.1086/664081. URL <http://www.ncbi.nlm.nih.gov/pubmed/22322221>.
- D. M. Raup. Taxonomic survivorship curves and Van Valen’s Law. *Paleobiology*, 1(1):82–96, Jan. 1975. ISSN 0036-8075. doi: 10.1126/science.49.1254.50. URL <http://www.ncbi.nlm.nih.gov/pubmed/17777225>.

- D. M. Raup. Cohort Analysis of generic survivorship. *Paleobiology*, 4(1):1–15, 1978.
- D. M. Raup. *Extinction: Bad Genes or Bad Luck?* Norton, New York, 1991.
- D. M. Raup. The role of extinction in evolution. *Proceedings of the National Academy of Sciences*, 91(July):6758–6763, 1994.
- D. M. Raup and G. E. Boyajian. Patterns of generic extinction in the fossil record. *Paleobiology*, 14(2):109–125, 1988.
- M. Rosvall and C. T. Bergstrom. Maps of random walks on complex networks reveal community structure. *Proceedings of the National Academy of Sciences*, 105(4):1118–23, Jan. 2008. ISSN 1091-6490. doi: 10.1073/pnas.0706851105. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2234100&tool=pmcentrez&rendertype=abstract>.
- M. Rosvall, D. Axelsson, and C. Bergstrom. The map equation. *The European Physical Journal Special Topics*, 178(14):13–24, 2009. URL <http://www.springerlink.com/index/H8193132U6432363.pdf>.
- K. Roy, G. Hunt, D. Jablonski, A. Z. Krug, and J. W. Valentine. A macroevolutionary perspective on species range limits. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1485–93, Apr. 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1232. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677224&tool=pmcentrez&rendertype=abstract>.
- H. Schielzeth. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2):103–113, Feb. 2010. ISSN 2041210X. doi: 10.1111/j.2041-210X.2010.00012.x. URL <http://doi.wiley.com/10.1111/j.2041-210X.2010.00012.x>.
- Scott Chamberlain and Eduard Szocs. taxize - taxonomic search and retrieval in r. *F1000Research*, 2013. URL <http://f1000research.com/articles/2-191/v2>.
- J. J. Sepkoski. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology*, 1(4):343–355, 1975.
- C. A. Sidor, D. A. Vilhena, K. D. Angielczyk, A. K. Huttenlocker, S. J. Nesbitt, B. R. Peacock, J. S. Steyer, R. M. H. Smith, and L. A. Tsuji. Provincialization of terrestrial faunas following the end-Permian mass extinction. *Proceedings of the National Academy of Sciences*, 110(20):8129–33, May 2013. ISSN 1091-6490. doi: 10.1073/pnas.1302323110.
- C. Simpson, W. Kiessling, H. Mewis, R. C. Baron-Szabo, and J. Müller. Evolutionary diversification of reef corals: a comparison of the molecular and fossil records. *Evolution; international journal of organic evolution*, 65(11):3274–84, Nov. 2011. ISSN 1558-5646. doi: 10.1111/j.1558-5646.2011.01365.x. URL <http://www.ncbi.nlm.nih.gov/pubmed/22023591>.

- G. G. Simpson. *Tempo and Mode in Evolution*. Columbia University Press, New York, 1944.
- G. Slater, L. Harmon, and M. Alfaro. Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution*, 2012. doi: 10.5061/dryad.q96d7. URL <http://onlinelibrary.wiley.com/doi/10.1111/j.1558-5646.2012.01723.x/full>.
- G. J. Slater. Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary. *Methods in Ecology and Evolution*, 4(8):734–744, Aug. 2013. ISSN 2041-210X. doi: 10.1111/2041-210X.12084. URL <http://doi.wiley.com/10.1111/2041-210X.12084>.
- F. A. Smith, J. Brown, J. Haskell, and S. Lyons. Similarity of mammalian body size across the taxonomic hierarchy and across space and *The American Naturalist*, 2004a. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/382898papers2://publication/uuid/D5606802-FD91-49EB-BE2F-E2D314A5E71D>.
- F. A. Smith, J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, E. A. Hadly, K. E. Jones, D. M. Kaufman, P. A. Marquet, B. A. Maurer, K. J. Niklas, W. P. Porter, B. Tiffney, and M. R. Willig. Similarity of Mammalian Body Size across the Taxonomic Hierarchy and across Space and Time. *The American Naturalist*, 163(5): 672–691, 2004b.
- F. A. Smith, S. K. Lyons, S. Morgan Ernest, and J. H. Brown. Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, 32(2):115–138, Apr. 2008. ISSN 0309-1333. doi: 10.1177/0309133308094425. URL <http://ppg.sagepub.com/cgi/doi/10.1177/0309133308094425>.
- Stan Development Team. Stan: A c++ library for probability and sampling, version 2.5.0, 2014. URL <http://mc-stan.org/>.
- C. A. E. Strömberg. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 102(34):11980–4, Aug. 2005. ISSN 0027-8424. doi: 10.1073/pnas.0505700102. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1189350&tool=pmcentrez&rendertype=abstract>.
- C. A. E. Strömberg, R. E. Dunn, R. H. Madden, M. J. Kohn, and A. A. Carlini. Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature communications*, 4:1478, Jan. 2013. ISSN 2041-1723. doi: 10.1038/ncomms2508. URL <http://www.ncbi.nlm.nih.gov/pubmed/23403579>.
- S. Tomiya. Body Size and Extinction Risk in Terrestrial Mammals Above the Species Level. *The American Naturalist*, pages E000–E000, Sept. 2013. ISSN

00030147. doi: 10.1086/673489. URL <http://www.jstor.org/stable/info/10.1086/673489>.
- L. Van Valen. A new evolutionary law. *Evolutionary Theory*, 1:1–30, 1973. URL <http://ci.nii.ac.jp/naid/10011264287/>.
- L. Van Valen. Taxonomic survivorship curves. *Evolutionary Theory*, 4:129–142, 1979.
- D. A. Vilhena, E. B. Harris, C. T. Bergstrom, M. E. Maliska, P. D. Ward, C. A. Sidor, C. A. E. Strömberg, and G. P. Wilson. Bivalve network reveals latitudinal selectivity gradient at the end-Cretaceous mass extinction. *Scientific reports*, 3:1790, May 2013. ISSN 2045-2322. doi: 10.1038/srep01790.
- P. J. Wagner and G. F. Estabrook. Trait-based diversification shifts reflect differential extinction among fossil taxa. *Proceedings of the National Academy of Sciences of the United States of America*, pages 1–6, Oct. 2014. ISSN 1091-6490. doi: 10.1073/pnas.1406304111. URL <http://www.ncbi.nlm.nih.gov/pubmed/25331898>.
- S. C. Wang. On the continuity of background and mass extinction. *Paleobiology*, 29(4):455–467, Dec. 2003. ISSN 0094-8373. doi: 10.1666/0094-8373(2003)029<0455:OTCOBA>2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1666/0094-8373%282003%29029%3C0455%3AOTCOBA%3E2.0.CO%3B2>.
- E. P. White, S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. Relationships between body size and abundance in ecology. *TRENDS in Ecology and Evolution*, 22(6):323–30, June 2007. ISSN 0169-5347. doi: 10.1016/j.tree.2007.03.007. URL <http://www.ncbi.nlm.nih.gov/pubmed/17399851>.