

Title: The interplay between extinction intensity and selectivity:
2 correlation in trait effects on taxonomic survival

Running title: Variation in trait effects on taxonomic survival

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Abstract

While the effect of geographic range on extinction risk is well documented, how other traits may increase or decrease extinction risk is less well known. I analyze patterns of Paleozoic brachiopod genus durations and their relationship to geographic range, affinity for epicontinental seas versus open ocean environments, and body size. Additionally, I allow for environmental affinity to have a nonlinear effect on duration. Using a hierarchical Bayesian approach, I also model the interaction between the effects of biological traits and a taxon's time of origination. My analysis framework eschews the traditional distinction between background and mass extinction, instead the entire time period is analyzed where these are part of the same continuum. I find evidence that as baseline extinction risk increases, the effect of geographic range increases but the effect of environmental preference tends to decrease. Additionally, I find strong evidence for correlation between the effects of geographic range and the non-linear aspect of environmental preference which may help explain this pattern. For parts of the Paleozoic I find support for a "survival of the generalists" scenario, though there are times where this relationship is absent or even reversed. These results support the hypothesis that as extinction intensity increases, overall extinction selectivity decreases.

1 Introduction

How do biological traits affect extinction risk? Biological traits are defined here as descriptors of a taxon's adaptive zone, which is the set of all biotic–biotic and biotic–abiotic interactions that a taxon can experience (Simpson, 1944). In effect, these are descriptors of a taxon's broad-sense ecology. Jablonski (1986) observed that during a mass extinction event, the effects of biological traits on

taxonomic survival decreased in size. However, this pattern was not the case for
40 the effect of geographic range on survival (Jablonski, 1986).

Jablonski (1986) phrased his conclusions in terms of background versus mass
42 extinction, but this scenario is readily transferable to a continuous variation
framework as there is no obvious distinction in terms of extinction rate between
44 these two states (Wang, 2003). Additionally, the Jablonski (1986) scenario has
strong model structure requirements in order to test its proposed
46 macroevolutionary mechanism; not only do the taxon trait effects need to be
modeled, but the correlation between trait effects need to be modeled as well.

48 There are two end-member macroevolutionary mechanisms which may underlie
the pattern observed by Jablonski (1986): the effect of geographic range on
50 predictive survival remains constant and those of other biological traits decrease,
or the effect of geographic range in predicting survival increases and those of
52 other biological traits stay constant. Reality, of course, may fall somewhere
along this continuum.

54 Conceptually, taxon survival can be considered an aspect of “taxon fitness”
along with expected lineage specific branching/origination rate (Cooper, 1984,
56 Palmer and Feldman, 2012). A taxon with a beneficial trait should persist for
longer, on average, than a taxon without that beneficial trait. Here I model
58 brachiopod taxon durations because trait based differences in extinction risk
should manifest as differences in taxon durations. Brachiopods are an ideal
60 group for this study as they are well known for having an exceptionally
complete fossil record (Foote, 2000). I focus on the brachiopod record from most
62 of the Paleozoic, from the start of the Ordovician (approximately 485 Mya)
through the end Permian (approximately 252 Mya) as this represents the time
64 of greatest global brachiopod diversity (Alroy, 2010).

The analysis of taxon durations, or time from origination to extinction, falls
66 under the purview of survival analysis, a field of applied statistics commonly
used in health care (Klein and Moeschberger, 2003) but has a long history in
68 paleontology (Simpson, 1944, 1953, Van Valen, 1973, 1979). I adopt a
hierarchical Bayesian survival modeling approach, which represents both a
70 conceptual and statistical unification of the paleontological dynamic and cohort
survival analytic approaches (Baumiller, 1993, Foote, 1988, Raup, 1975, 1978,
72 Simpson, 2006, Van Valen, 1973, 1979). By using a Bayesian framework I am
able to quantify the uncertainty inherent in the estimates of the effects of
74 biological traits on survival, especially in cases where the covariates of interest
(i.e. biological traits) are themselves known with error.

76 **1.1 Factors affecting brachiopod survival**

Geographic range is widely considered the most important taxon trait for
78 estimating differences in extinction risk at nearly all times, with large
geographic range associated with low extinction risk (Jablonski, 1986, 1987,
80 Jablonski and Roy, 2003, Payne and Finnegan, 2007), though Foote and Miller
(2013) find that this generalization does not hold in the Mesozoic. For the
82 Paleozoic, however, I expect this to hold true for the entire period analyzed.

Epicontinental seas are a shallow-marine environment where the ocean has
84 spread over the surface of a continental shelf with a depth typically less than
100m. In contrast, open-ocean coastline environments have much greater
86 variance in depth, do not cover the continental shelf, and can persist during
periods of low sea level. Because of this, it is strongly expected that taxa which
88 favor epicontinental seas would be at great risk during periods of low sea levels,
such as during glacial periods, when epicontinental seas are drained. During the

90 Paleozoic (approximately 541–252 My), epicontinental seas were widely spread
91 globally but declined over the Mesozoic (approximately 252–66 My) and have
92 nearly disappeared during the Cenozoic (approximately 66–0 My) as open-ocean
93 coastlines became the dominant shallow-marine setting (Johnson, 1974, Miller
94 and Foote, 2009, Peters, 2008).

Miller and Foote (2009) demonstrated that during several mass extinctions taxa
96 associated with open-ocean environments tend to have a greater extinction risk
97 than those taxa associated with epicontinental seas. During periods of
98 background extinction, however, they found no consistent difference between
99 taxa favoring either environment. These two environment types represent the
100 primary environmental dichotomy observed in ancient marine systems (Miller
101 and Foote, 2009, Peters, 2008, Sheehan, 2001).

102 Given these findings, I predict that as extinction risk increases, the extinction
103 risk associated with favoring open-ocean environments should generally increase.
104 Additionally, there is a possible nonlinear relationship between environmental
105 preference and taxon duration. A long standing hypothesis is that generalists or
106 unspecialized taxa will have greater survival than specialists (Baumiller, 1993,
107 Liow, 2004, 2007, Nürnberg and Aberhan, 2013, 2015, Simpson, 1944). In this
108 analysis I allowed for environmental preference to have a parabolic effect on
109 taxon duration

110 Body size, measured as shell length, was also considered as a potential trait that
111 influences extinction risk (Payne et al., 2014). Body size is a proxy for metabolic
112 activity and other correlated life history traits (Payne et al., 2014). There is no
113 strong hypothesis of how body size effects extinction risk in brachiopods, such
114 that a positive, negative, or zero effect are all plausible.

2 Materials and Methods

116 2.1 Fossil occurrence information

The dataset analyzed here was sourced from the Paleobiology Database
118 (<http://www.paleodb.org>) which was then filtered based on taxonomic,
temporal, stratigraphic, and other occurrence information that was necessary
120 for this analysis. These filtering criteria are very similar to those from Foote and
Miller (2013) with an additional constraint of being present in the body size
122 data set from Payne et al. (2014). Epicontinental versus open-ocean assignments
for each fossil occurrence are partially based on those from Miller and Foote
124 (2009), with additional occurrences assigned similarly (Miller and Foote,
personal communication).

126 Fossil occurrences were analyzed at the genus level which is common for
paleobiological, macroevolutionary, or macroecological studies of marine
128 invertebrates (Alroy, 2010, Foote and Miller, 2013, Harnik et al., 2013, Kiessling
and Aberhan, 2007, Miller and Foote, 2009, Nürnberg and Aberhan, 2013, 2015,
130 Payne and Finnegan, 2007, Simpson and Harnik, 2009, Vilhena et al., 2013).
Although species diversity dynamics tend to be of much greater interest than
132 those of higher taxa, the nature of the fossil record makes accurate and precise
taxonomic assignments at the species level for all occurrences extremely difficult
134 if not impossible. Additionally, there is evidence of real differences in biological
patterns at the genus level versus the species level (Jablonski, 1987). As such,
136 the choice to analyze genera as opposed to species was in order to assure a
minimum level of confidence and accuracy in the data analyzed here.

138 Genus duration was calculated as the number of geologic stages from first
appearance to last appearance, inclusive. Durations were based on geologic

¹⁴⁰ stages as opposed to millions of years because of the inherently discrete nature
of the fossil record; dates are not assigned to fossils themselves but instead
¹⁴² fossils are known from a geological interval which represents some temporal
range. Stages act as effectively irreducible globally consistent temporal intervals
¹⁴⁴ in which taxa occur. Of note, however, is that stages are of variable length
which may cause origination cohorts to have artificially larger or smaller
¹⁴⁶ membership. The hierarchical Bayesian framework used here may help control
for this potentiality as cohorts with smaller samples or effects will be drawn
¹⁴⁸ towards to over all mean instead of standing on their own (Gelman et al., 2013).

Genera with a last occurrence in or after the Changhsingian stage were right
¹⁵⁰ censored at the Changhsingian. Genera with a duration of only one stage were
left censored (Appendix A). The covariates used to model genus duration were
¹⁵² geographic range size (r), environmental preference (v, v^2), and body size (m).

Geographic range was calculated using an occupancy approach. First, all
¹⁵⁴ occurrences were projected onto an equal-area cylindrical map projection. Each
occurrence was then assigned to one of the cells from a 70×34 regular raster
¹⁵⁶ grid placed on the map. Each grid cell represents approximately 250,000 km².
The map projection and regular lattice were made using shape files from
¹⁵⁸ <http://www.naturalearthdata.com/> and the **raster** package for R (Hijmans,
2015).

¹⁶⁰ For each stage, the total number of occupied grid cells, or cells in which a fossil
occurs, was calculated. Then, for each genus, the number of grid cells occupied
¹⁶² by that genus was calculated. Dividing the genus occupancy by the total
occupancy gives the relative occupancy of that genus. Mean relative genus
¹⁶⁴ occupancy was then calculated as the mean of the per stage relative occupancies
of that genus.

¹⁶⁶ Body size data was sourced directly from Payne et al. (2014). Because those
measurements are presented without error, a measurement error model similar
¹⁶⁸ to the one for environmental affinity could not be implemented (Appendix A).

Prior to analysis, geographic range and body size were transformed and
¹⁷⁰ standardized in order to improve interpretability of the results. Geographic
range, which can only vary between 0 and 1, was logit transformed. Body size,
¹⁷² which is defined for all positive real values, was natural log transformed. These
covariates were then standardized by mean centering and dividing by two times
¹⁷⁴ their standard deviation following Gelman and Hill (2007).

2.2 Analytical approach

¹⁷⁶ Hierarchical modelling is a statistical approach that explicitly takes into account
the structure of the observed data in order to model both the within and
¹⁷⁸ between group variance (Gelman et al., 2013, Gelman and Hill, 2007). The units
of study (e.g. genera) each belong to a single grouping (e.g. origination cohort).
¹⁸⁰ These groups are considered separate draws from a shared probability
distribution (e.g. all cohorts, observed and unobserved). The group-level
¹⁸² parameters are then estimated simultaneously with the other parameters of
interest (e.g. covariate effects) (Gelman et al., 2013). The subsequent estimates
¹⁸⁴ are partially pooled together, where parameters from groups with large samples
or effects remain large while those of groups with small samples or effects are
¹⁸⁶ pulled towards the overall group mean.

This partial pooling is one of the greatest advantages of hierarchical modeling.
¹⁸⁸ By letting the groups “support” each other, parameter estimates better reflect
our statistical uncertainty. Additionally, this partial pooling helps control for
¹⁹⁰ multiple comparisons and possibly spurious results as effects with little support

are drawn towards the overall origination cohort mean (Gelman et al., 2013,
192 Gelman and Hill, 2007).

All covariate effects (regression coefficients), as well as the intercept term
194 (baseline extinction risk), were allowed to vary by group (origination cohort).
The covariance/correlation between covariate effects was also modeled. This
196 hierarchical structure allows inference for how covariates effects may change
with respect to each other while simultaneously estimating the effects
198 themselves, propagating our uncertainty through all estimates.

Additionally, instead of relying on point estimates of environmental affinity, I
200 treat environmental affinity as a continuous measure of the difference between
the taxon's environmental occurrence pattern and the background occurrence
202 pattern (Appendix A). Background occurrence pattern for a single genus is
defined as the distribution of environmental occurrences for all other genera
204 present during the duration of the genus of interest.

2.3 Survival model

206 Genus durations were assumed to follow either an exponential or Weibull
distribution, both of which make different assumptions about how a taxon's
208 duration may effect its instantaneous extinction risk (Klein and Moeschberger,
2003). The exponential distribution assumes that extinction risk is independent
210 of duration. In contrast, the Weibull distribution allows for age dependent
extinction via the shape parameter α , though only as a monotonic function of
212 duration. Importantly, the Weibull distribution is equivalent to the exponential
distribution when $\alpha = 1$.

214 The following variables are here defined: y_i is the duration of genus i in geologic
stages, X is the matrix of covariates including a constant term, B_j is the vector

216 of regression coefficients for origination cohort j , Σ is the covariance matrix of
 218 the regression coefficients, τ is the vector of scales (standard deviations) of the
 between-cohort variation in regression coefficient estimates, Ω is the correlation
 220 matrix of the regression coefficients, and α_j is the shape parameter for cohort j
 with a is the overall mean shape parameter and π is the variance between
 estimates of α_j .

222 The exponential model is defined

$$y_i \sim \text{Exponential}(\lambda)$$

$$\lambda_i = \exp(\mathbf{X}_i B_{j[i]})$$

$$B \sim \text{MVN}(\vec{\mu}, \Sigma)$$

$$\Sigma = \text{Diag}(\vec{\tau}) \Omega \text{Diag}(\vec{\tau})$$

$$\mu_k \sim \begin{cases} \mathcal{N}(0, \psi_k \nu) & \text{if } k \neq r, \text{ or} \\ \mathcal{N}(-1, 1) & \text{if } k = r \end{cases} \quad (1)$$

$$\tau_k \sim C^+(1)$$

$$\psi_k \sim C^+(1) \text{ if } k \neq r$$

$$\nu \sim C^+(1)$$

$$\Omega \sim \text{LKJ}(2).$$

Similarly, the Weibull model is defined

$$\begin{aligned}
y_i &\sim \text{Weibull}(\alpha_{j[i]}, \sigma) \\
\sigma_i &= \exp \left(\frac{-(\mathbf{X}_i B_{j[i]})}{\alpha_{j[i]}} \right) \\
B &\sim \text{MVN}(\vec{\mu}, \Sigma) \\
\Sigma &= \text{Diag}(\vec{\tau}) \Omega \text{Diag}(\vec{\tau}) \\
\log(\alpha) &\sim \mathcal{N}(a, \pi) \\
\mu_k &\sim \begin{cases} \mathcal{N}(0, \psi_k \nu) & \text{if } k \neq r, \text{ or} \\ \mathcal{N}(-1, 1) & \text{if } k = r \end{cases} \\
\tau_k &\sim C^+(1) \\
a &\sim N(0, 1) \\
\pi &\sim C^+(1) \\
\psi_k &\sim C^+(1) \text{ if } k \neq r \\
\nu &\sim C^+(1) \\
\Omega &\sim \text{LKJ}(2).
\end{aligned} \tag{2}$$

²²⁴ The principal difference between the exponential and Weibull models is the inclusion of the shape parameter α . Note that σ is approximately equivalent to ²²⁶ $1/\lambda$.

For an explanation of how these two models were developed, parameter ²²⁸ explanations, and choice of priors, please see Appendix B. Note that these models as written (Eq. 1, 2) do not include how the uncertainty in ²³⁰ environmental affinity is included nor how censored observations are included. For an explanation of both of these aspects, see Appendices A and C.

²³² **2.4 Parameter estimation**

The joint posterior was approximated using a Markov chain Monte Carlo routine that is a variant of Hamiltonian Monte Carlo called the No-U-Turn Sampler (Hoffman and Gelman, 2014) as implemented in the probabilistic programming language Stan (Stan Development Team, 2014). The posterior distribution was approximated from four parallel chains run for 10,000 draws each, split half warm-up and half sampling and thinned to every 10th sample for a total of 5000 posterior samples. Chain convergence was assessed via the scale reduction factor \hat{R} where values close to 1 ($\hat{R} < 1.1$) indicate approximate convergence, meaning that the chains are approximately stationary and the samples are well mixed (Gelman et al., 2013).

2.5 Model evaluation

Models were evaluated using both posterior predictive checks and an estimate of out-of-sample predictive accuracy. The motivation behind posterior predictive checks as tools for determining model adequacy is that replicated data sets using the fitted model should be similar to the original data (Gelman et al., 2013). Systematic differences between the simulations and observations indicate weaknesses of the model fit. An example of a technique that is very similar would be inspecting the residuals from a linear regression.

The strategy behind posterior predictive checks is to draw simulated values from the joint posterior predictive distribution, $p(y^{rep}|y)$, and then compare those draws to the empirically observed values (Gelman et al., 2013). To accomplish this, for each replicate, a single value is drawn from the marginal posterior distributions of each regression coefficient from the final model as well as estimates of α_j for the Weibull model (Eq. 1, 2). Then, given the covariate

information \mathbf{X} , a new set of n genus durations are generated giving a single
258 replicated data set y^{rep} . This is repeated 1000 times in order to provide a distribution of possible values that could have been observed given the model.

260 In order to compare the fitted model to the observed data, various graphical comparisons or test quantities need to be defined. The principal comparison
262 used here is a comparison between non-parameteric approximation of the survival function $S(t)$ as estimated from both the observed data and each of the
264 replicated data sets. The purpose of this comparison is to determine if the model approximates the same survival/extinction pattern as the original data.

266 The exponential and Weibull models were compared for out-of-sample predictive accuracy using the widely-applicable information criterion (WAIC) (Watanabe,
268 2010), a more fully Bayesian alternative to AIC or DIC (Gelman et al., 2013). Out-of-sample predictive accuracy is a measure of the expected fit of the model
270 to new data. However, because the Weibull distribution reduces to the exponential distribution when $\alpha = 1$, my interest is not in choosing between
272 these models. Instead, comparisons of WAIC values are useful for better understanding the effect of model complexity on out-of-sample predictive
274 accuracy. The calculation of WAIC used here corresponds to the “WAIC 2” formulation recommended by Gelman et al. (2013). For an explanation of how
276 WAIC is calculated, see Appendix D. Lower values of WAIC indicate greater expected out-of-sample predictive accuracy than higher values.

278 3 Results

As stated above, posterior approximations for both the exponential and Weibull
280 models achieved approximate stationarity after 10,000 steps, as all parameter estimates have an $\hat{R} < 1.1$.

²⁸² Comparisons of the survival functions estimated from 1000 posterior predictive
²⁸³ data sets to the estimated survival function of the observed genera demonstrates
²⁸⁴ that Weibull models approximately capture the observed pattern of extinction
²⁸⁵ (Fig. 1). This is partially expected given that the unit of analysis is genus
²⁸⁶ duration instead of species duration, which can alter the shape of $S(t)$ (Foote,
²⁸⁷ 2001, Raup, 1975, 1978, 1985). Additionally, the Weibull model is expected to
²⁸⁸ have better out-of-sample predictive accuracy than the exponential model
²⁸⁹ (WAIC 4534 versus 4604). Because the difference in WAIC between these two
²⁹⁰ models is large, only those results from the Weibull model will be discussed.

Estimates of the overall mean covariate effects μ can be considered
²⁹² time-invariant generalizations for brachiopod survival during the Paleozoic
²⁹³ (Table 1). Consistent with prior expectations, geographic range size has a
²⁹⁴ negative effect on extinction risk: genera with large ranges are expected to have
greater durations than genera with small ranges.

²⁹⁶ I infer that body size has no distinguishable effect on brachiopod taxonomic
²⁹⁷ survival. While the mean estimate of the effect of body size on extinction risk is
²⁹⁸ negative, this estimate is within 2 standard deviations of 0 (mean $\mu_m = -0.07$,
standard deviation 0.08; Table 1).

³⁰⁰ Interpretation of the effect of environmental preference v on duration is slightly
³⁰¹ more involved. Because a quadratic term is the equivalent of an interaction
³⁰² term, both μ_v and μ_{v^2} have to be interpreted together because it is illogical to
³⁰³ change values of v without also changing values v^2 . To determine the nature of
the effect of v on duration I calculated the multiplicative effect of environmental
preference on extinction risk.

³⁰⁶ Given mean estimated extinction risk $\tilde{\sigma}$, we can define the extinction risk

multiplier of an observation with environmental preference v_i as

$$f(v_i) = \exp\left(\frac{-(\mu_v v_i + \mu_{v^2} v^2)}{\exp(a)}\right). \quad (3)$$

This function $f(v_i)$ has a y-intercept of $\exp(0)$ or 1 because it does not have a non-zero intercept term. Equation 3 can be either concave up or down. A concave down $f(v_i)$ may indicate that genera of intermediate environmental preference have greater durations than either extreme, and *vice versa* for concave up function.

The expected effect of environmental preference as a multiplier of expected extinction risk can then be visualized (Fig. 2). This figure depicts 1000 posterior predictive estimates of Eq. 3 across all possible values of v . The number indicates the posterior probability that the function is concave down, with generalists having lower extinction risk/greater duration than either type of specialist. Note that the inflection point of Figure 2 is approximately $x = 0$, something that is expected given the estimate of μ_v (Table 1). Given the amount of variation (Fig. 2), the interpretation is that while evidence for “survival of the unspecialized” is weak it is still more probable than not (posterior probability 74%).

Coefficients with greater values of τ have greater between-cohort variation (Table 1). The covariate effects with the greatest between origination cohort variation are β_r , β_v , and β_{v^2} . Estimates of β_m have negligible between cohort variation, as there is less between cohort variation than the between cohort variation in baseline extinction risk β_0 .

The correlations between the intercept term β_0 and the effects of the taxon traits are of particular interest for evaluating the Jablonski (1986) scenario (Fig. 3A first row or column). The correlation terms of Ω (Fig. 3A) describe the

relationship between the coefficients and how their estimates may vary together
332 across cohorts. Keep in mind that when β_0 is low, extinction risk is low; and
conversely, when β_0 is high, then extinction risk is high.

334 Marginal posterior probabilities of the correlations between the level of baseline
extinction risk β_0 and the effects of the taxon traits indicate that the correlation
336 between expected extinction risk and both geographic range β_r and β_{v^2} are of
particular note (Fig. 3B).

338 There is an approximately 85% probability that β_0 and β_r are negatively
correlated (Fig. 3B), meaning that as extinction risk increases, the
340 effect/importance of geographic range on genus duration may increase. There is
a 93% probability that β_0 and β_{v^2} are negatively correlated (Fig. 3B), meaning
342 that as extinction risk decreases, the peakedness of $f(v_i)$ may increase and the
relationship tends towards concave down. Additionally, there is a 94%
344 probability that values of β_r and β_{v^2} are positively correlated (Mean correlation
0.45, standard deviation 0.26).

346 While the overall group level estimates are of particular importance when
defining time-invariant differences in extinction risk, it is also important and
348 useful to analyze the individual level parameter estimates in order to better
understand how parameters actually vary across cohorts.

350 In comparison to the overall mean extinction risk μ_0 , cohort level estimates β_0
show some amount of variation through time as expected by estimates of τ_0
352 (Fig. 4). A similar, if slightly greater, amount of variation is also observable in
cohort estimates of the effect of geographic range β_r (Fig. 4). Again, smaller
354 values of β_0 correspond to lower expected extinction risk. Similarly, smaller
values of β_r correspond to greater decrease in extinction risk with increasing
356 geographic range

How the effect of environmental affinity varies between cohorts can be observed
358 by using the cohort specific coefficients estimates. Following the same procedure
used earlier (Eq. 3), but substituting cohort specific estimates of β_v and β_{v^2} for
360 μ_v and μ_{v^2} , the cohort specific effect of environmental preference as a multiplier
of mean extinction risk can be calculated. This was done only for the Weibull
362 model, though the observed pattern should be similar for the exponential model.

As expected based on the estimates of τ_v and τ_{v^2} , there is greater variation in
364 the peakedness of $f(v_i)$ than there is variation between convave up and down
functions (Fig. 5). Twelve of the 33 cohorts have less than 50% posterior
366 probability that generalists are potentially expected to be shorter lived than
specialists, though two of those cases have approximately a 50% probability of
368 being either concave up or down. This is congruent with the 0.74 posterior
probability that μ_{v^2} is positive/ $f(v_i)$ is concave down.

370 Additionally, for some cohorts there is a quite striking pattern where the effect
of environmental preference v has a nearly-linear relationship (Fig. 5). These are
372 scenarios where one of the end member preferences is expected to have a greater
duration than either intermediate or the opposite end member preference.

374 Whatever curvature is present in these nearly-linear cases is due to the
definition of $f(v)$ as it is not defined for non-negative values of σ (Eq. 3). For all
376 stages between the Givetian through the Viséan, inclusive, intermediate
preferences are expected to be of intermediate extinction risk when compared
378 with epicontinental specialists (lowest risk) or open-ocean specialists (highest
risk). This time period represents most of the Devonian through the early
380 Carboniferous.

Interestingly, the estimates of α_j have low between cohort variation with most
382 cohorts having approximately the same estimate as the overall estimate of α
(Fig. 4). Also, for the majority of the time analyzed there is evidence for

³⁸⁴ accelerating extinction with taxon age. If this is due to biological causes
(Rosindell et al., 2015, Wagner and Estabrook, 2014) or an artifact of
³⁸⁶ preservation/the minimum observable duration of a genus (Sepkoski, 1975) is
unknown. While it is expected that a non-exponential model will better fit
³⁸⁸ genus-level data, this would be reflected as decelerating extinction risk with
taxon age as opposed to accelerating (Foote, 2001, Raup, 1975, 1978, 1985).
³⁹⁰ This uncertainty remains an open issue for future analysis.

4 Discussion

³⁹² My results demonstrate that both the effects of geographic range and the
peakedness/concavity of environmental preference are both negatively
³⁹⁴ correlated with baseline extinction risk, meaning that as baseline extinction risk
increases the effect size of geographic range increases but the curvature of the
³⁹⁶ effect of environmental preference decreases (Fig. 3B).

However, the interaction between geographic range and origination cohort,
³⁹⁸ although weak, indicates that neither of the two proposed end-member
macroevolutionary mechanisms is strictly right. The evidence for a correlation
⁴⁰⁰ between changes in the effect of geographic range and the curvature of the effect
of environmental preference may help explain this result. I hypothesize that
⁴⁰² because taxa with large geographic ranges encompass more possible
environments, when extinction intensity is high there is little coherent difference
⁴⁰⁴ in the environmental preference among the surviving taxa. The intensity
decreases the selectivity such that the effect of environmental preference is
⁴⁰⁶ effectively washed out by the strength of the effect of geographic range; this is
consistent with similar hypotheses presented in Raup (1991).

⁴⁰⁸ For the approximately 233 My period analyzed there is an approximate 74%

posterior probability that brachiopod genera with intermediate environmental
410 preferences are expected to have a lower extinction risk than either end
members. However, the over all curvature of $f(v_i)$ is not very peaked meaning
412 that when averaged over the entire Phanerozoic this relationship may not lead
to large differences in extinction risk (Fig. 2). Note that the duration of the
414 period analyzed is approximately four times then length of the Cenozoic (e.g.
time since the extinction of the non-avian dinosaurs). This result gives very
416 weak support for the universality of the hypothesis that environmental
generalists have greater survival than environmental specialists (Liow, 2004,
418 Nürnberg and Aberhan, 2013, 2015, Simpson, 1944).

The posterior variance in the estimate of overall $f(v_i)$ reflects the large between
420 cohort variance in cohort specific estimates of $f(v_i)$ (Fig. 5). Given that there is
only a 74% posterior probability that the expected overall estimate of $f(v_i)$ is
422 concave down, it is not surprising that there are some stages where the
estimated relationship is in fact the reverse of the prior expectation.
424 Additionally, some of those same stages where $f(v_i)$ does not resemble the prior
expectation of a concave down nonlinear relation are instead is highly skewed
426 and effectively linear (Fig. 5). These results demonstrate that, while the
group-level estimate may only weakly support one hypothesis, the cohort-level
428 estimates may exhibit very different characteristics.These results are also
consistent with aspects of Miller and Foote (2009) who found that the effect of
430 environmental preference on extinction risk was quite variable and without
obvious patterning during times of background extinction.

432 There are two mass extinction events that are captured within the time frame
considered here: the Ordovician-Silurian and the Frasnian-Famennian. The
434 cohorts bracketing these events are worth considering in more detail.

The proposed mechanism for the end Ordovician mass extinction is a decrease

436 in sea level and the draining of epicontinental seas due to protracted glaciation
(Johnson, 1974, Sheehan, 2001). My results are broadly consistent with this
438 scenario with both epicontinental and open-ocean specialists having a much
lower expected duration than intermediate taxa (Fig. 5). All of the stages
440 between the Darriwillian and the Llandovery, except the Hirnantian, have a
high probability (90+) that $f(v)$ is concave down. The pattern for the
442 Darriwillian, which proceeds the supposed start of Ordovician glacial activity,
demonstrates that taxa tend to favor open-ocean environments are expected to
444 have a greater duration than either intermediate or epicontinental specialists, in
decreasing order.

446 For nearly the entire Devonian estimates of $f(v)$ indicate that one of the
environmental end members is favored over the other end member of
448 intermediate preference (Fig. 5). For almost the entirety the Givetian through
the end of the Devonian and into the Viséan, I find that epicontinental favoring
450 taxa are expected to have a greater duration than either intermediate or
open-ocean specialists. Additionally, for nearly the entire Devonian and through
452 to the Visean, the cohort-specific estimates of $f(v)$ are concave-up. This result,
however, seems to reflect the intensity of the seemingly nearly-linear difference
454 in expected duration across the range of v as opposed to an inversion of the
weakly expected curvilinear pattern.

456 The use of genera as the unit of the study and how to exactly interpret the
effects of the biological traits is a remaining concern. For example, if any of the
458 traits analyzed here are associated with increases in speciation rates, this might
increase the duration of genera through self-renewal (Raup, 1991, 1994), which
460 would be an example of the difference in biological pattern between species and
genera (Jablonski, 1987, 2007, 2008). This could lead to a trait appearing to
462 decrease generic level extinction risk by increasing species level origination rate

instead of decreasing species level extinction risk. However, given the nature of
464 the fossil record and maintaining a minimum level of data consistency/quality,
there is no simple solution to decreasing this uncertainty in the interpretations
466 of how the biological traits studied at the genus-level may translate to the
species-level.

468 The model used here could be improved through either increasing the number of
analyzed taxon traits, expanding the hierarchical structure of the model to
470 include other major taxonomic groups of interest, and the inclusion of explicit
phylogenetic relationships between the taxa in the model as an additional
472 hierarchical effect. An example taxon trait that may be of particular interest is
the affixing strategy or method of interaction with the substrate of the taxon,
474 which has been found to be related to brachiopod survival where, for
cosmopolitan taxa, taxa that are attached to the substrate are expected to have
476 a greater duration than those that are not (Alexander, 1977).

It is theoretically possible to expand this model to allow for comparisons within
478 and between major taxonomic groups. This approach would better constrain the
brachiopod estimates while also allowing for estimation of similarities and
480 differences in cross-taxonomic patterns. The major issue surrounding this
particular expansion involves finding an similarly well sampled taxonomic group
482 that is present during the Paleozoic. Example groups include Crinoidea,
Ostracoda, and other members of the “Paleozoic fauna” (Sepkoski Jr., 1981).

484 Taxon traits like environmental preference or geographic range (Hunt et al.,
2005, Jablonski, 1987) are most likely heritable, at least phylogenetically
486 (Housworth et al., 2004, Lynch, 1991). Without phylogenetic context, this
analysis assumes that differences in extinction risk between taxa are
488 independent of the shared evolutionary history of those taxa (Felsenstein, 1985).
In contrast, the origination cohorts only capture shared temporal context. For

example, if taxon duration is phylogenetically heritable, then closely related taxa may have more similar durations as well as more similar biological traits.

Without taking into account phylogenetic similarity the effects of these biological traits would be inflated solely due to inheritance. The inclusion of phylogenetic context as an additional individual-level hierarchical effect independent of origination cohort would allow for determining how much of the observed variability is due to shared evolutionary history versus shared temporal context versus actual differences associated with biological traits (Smits, 2015).

In summary, patterns of Paleozoic brachiopod survival were analyzed using a fully Bayesian hierarchical survival modelling approach while also eschewing the traditional separation between background and mass extinction. I find that as baseline extinction risk increases, the form of the selectivity of extinction changes such that during periods of low extinction risk the effect environmental preference is expected to change from nonlinear to potentially linear or even absent while the effect of geographic range increases. In particular, the correlation between the effect of geographic range and the curvature of the effect of environmental preference on taxon survival supports the hypothesis that during periods of high extinction intensity of the effect of geographic range effectively washes out the effects of other biological traits (Jablonski, 1987, Raup, 1991). Finally, I find weak support for “survival of the unspecialized” (Liow, 2004, 2007, Nürnberg and Aberhan, 2013, 2015, Simpson, 1944) as a general characterization of the effect of environmental preference on extinction risk (Fig. 2), most origination cohorts conforming to this hypothesis (Fig. 5).

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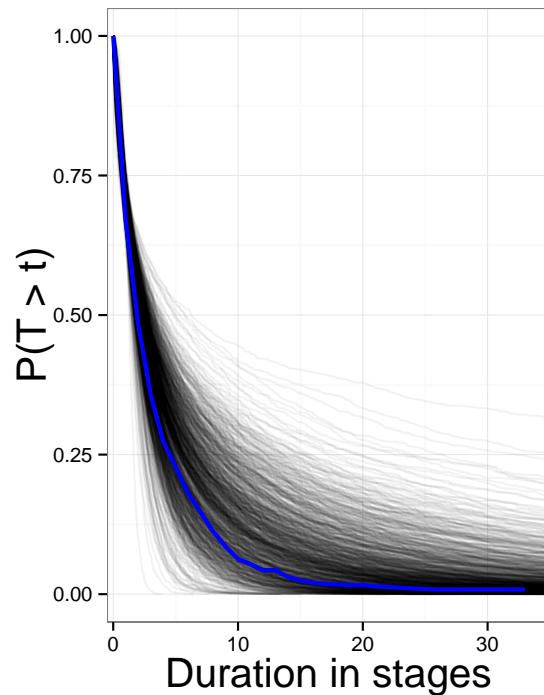


Figure 1: Comparison of the empirical estimate of $S(t)$ (blue) versus estimates from 1000 posterior predictive data sets (black). $S(t)$ corresponds to $P(T > t)$ as it is the probability that a given genus observed at age t will continue to live. This is equivalent to the probability that t is less than the genus' ultimate duration T .

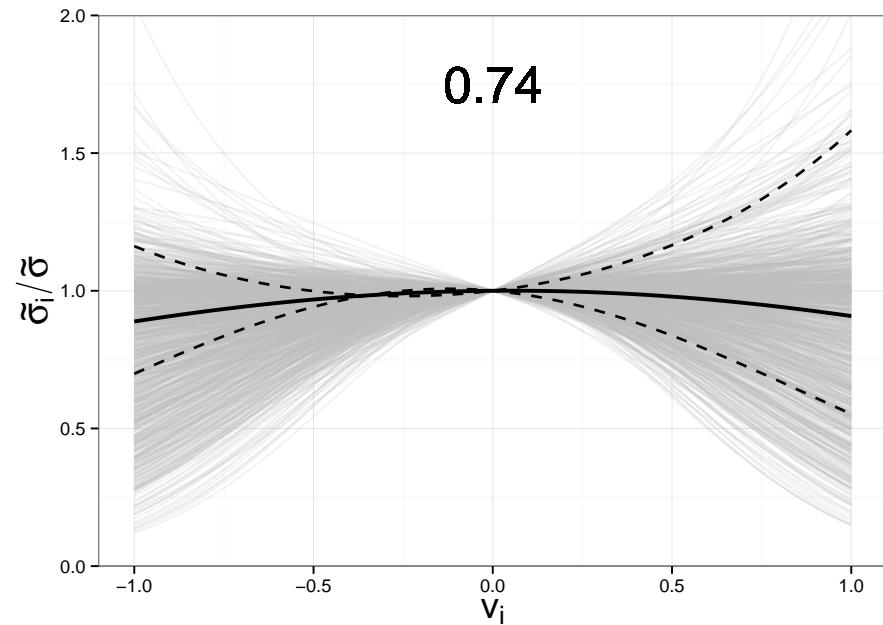


Figure 2: The overall expected relationship $f(v_i)$ between environmental affinity v_i and a multiplier of extinction risk (Eq. 3). Each grey line corresponds to a single draw from the posterior predictive distribution, the solid black line corresponds to the median of the posterior predictive distribution, and the dashed black lines correspond to the median relationship plus or minus one standard deviation. The overall shape of $f(v_i)$ is concave down with an optimum of close 0, which corresponds to affinity approximately equal to the expectation based on background environmental occurrence rates.

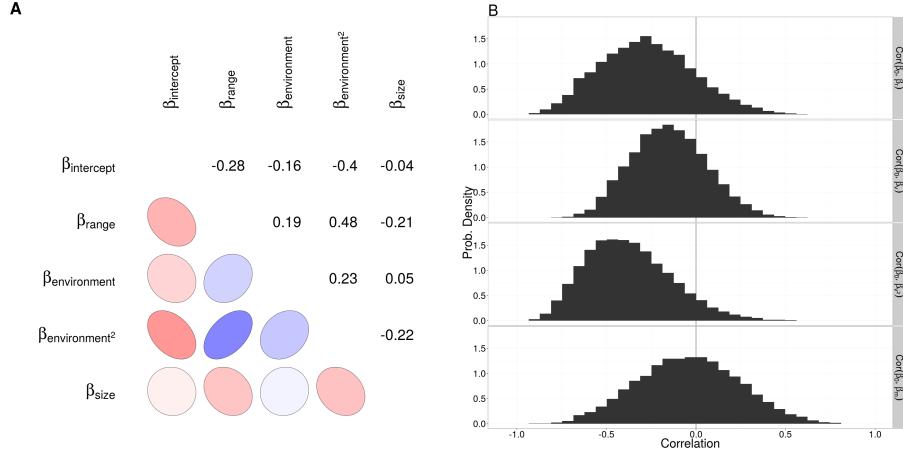


Figure 3: **A:** Graphical representation of the correlation matrix Ω between cohort-level covariate effects. These correlations are between the estimates of the cohort-level effects of covariates, along with intercept/baseline extinction risk. The median estimates of the correlations are presented numerically (upper-triangle) and as idealized ellipses representing that much correlation (lower-triangle). **B:** Marginal posterior distributions of the correlations between intercept terms/baseline extinction risk and the effects of each of the covariates.

parameter	mean	standard deviation	10%	90%
μ_i	-1.52	0.16	-1.73	-1.32
μ_r	-1.39	0.13	-1.55	-1.23
μ_v	-0.04	0.16	-0.24	0.11
μ_{v2}	0.30	0.45	-0.07	0.97
μ_m	-0.07	0.08	-0.19	0.01
τ_i	0.77	0.14	0.61	0.95
τ_r	0.40	0.13	0.24	0.56
τ_v	1.05	0.23	0.79	1.35
τ_{v^2}	1.87	0.64	1.10	2.68
τ_m	0.24	0.13	0.07	0.40

Table 1: Group-level estimates of the intercept terms the effects of biological traits on brachiopod generic survival from equation 2. μ values are the location parameters of the effects, while τ values are the scale terms describing the variation between cohorts. The mean, standard deviation, 10th and 90th quantiles are presented for each estimate. The subscripts correspond to the following: i intercept, r geographic range, v environmental affinity, v^2 environmental affinity squared, m body size.

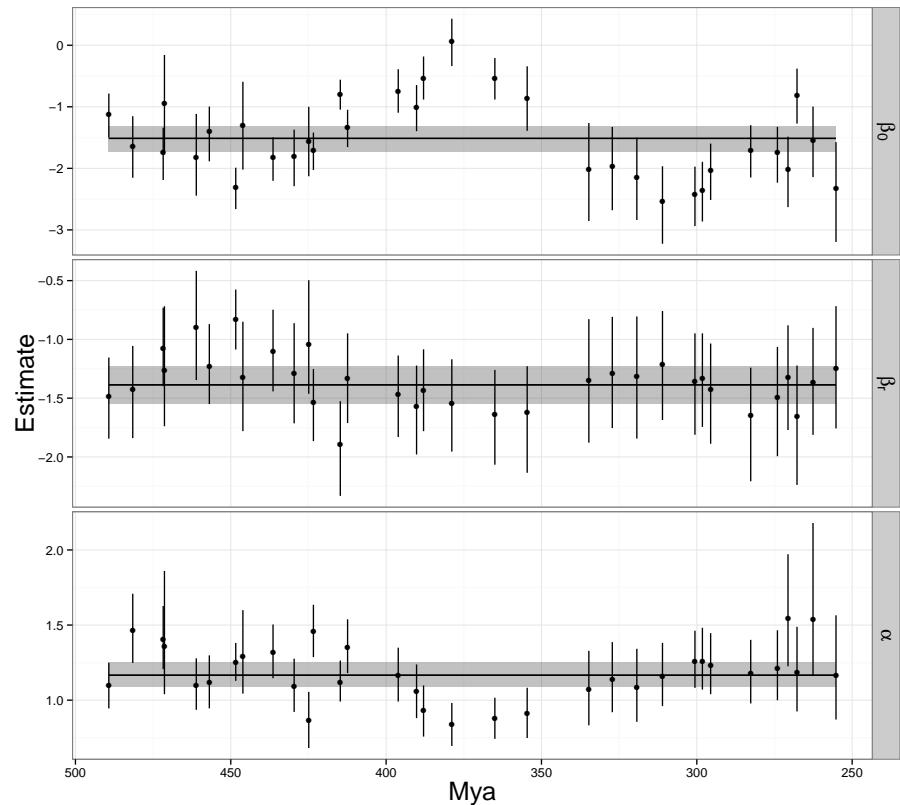


Figure 4: Comparison of cohort-specific estimates of β_0 (first row), cohort-specific estimates of the effect of geographic range on extinction risk β_r (second row), and cohort-specific estimates of the Weibull shape parameter α where values greater than 1 correspond to accelerating extinction with age, and those below 1 to decelerating extinction with age. Points correspond to the median of the cohort-specific estimate, along with 80% credible intervals. The horizontal line is the median estimate of the overall baseline extinction risk along with 80% credible intervals.

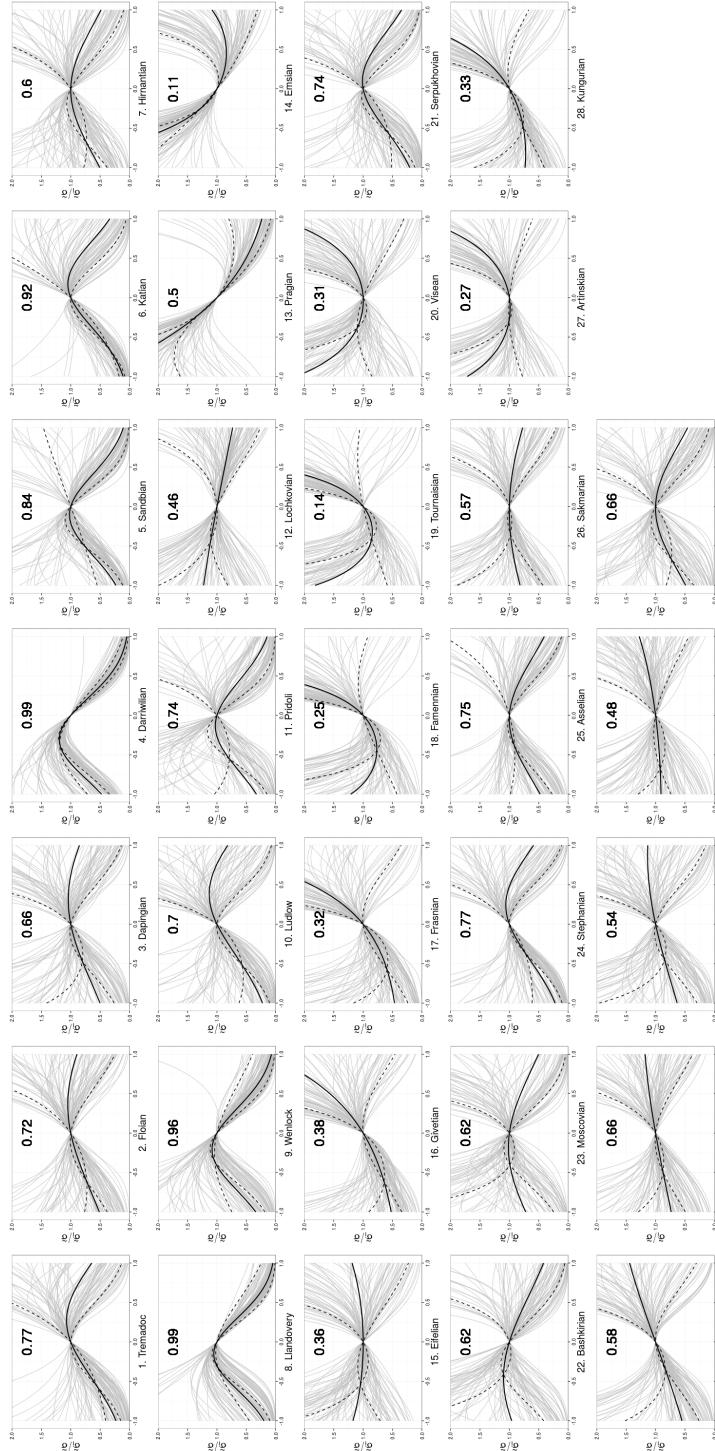


Figure 5: Comparison of the cohort-specific estimates of $f(v_i)$ (Eq. 3) for the 33 analyzed origination cohorts. The stage of origination is labeled on the x-axis of each panel. The oldest stage is in the upper left, while the youngest is in the lower left. The number in each panel corresponds to the posterior probability that $f(v_i)$ is concave down. Those that are highlighted in red have less than 51% posterior predictive probability that $f(v_i)$ is concave down. Each grey line corresponds to a single draw from the posterior predictive distribution, the solid black line corresponds to the median of the posterior predictive distribution, and the dashed black lines correspond to the median relationship plus or minus one standard deviation. Note that all estimates must pass through $y = 1$ when $x = 0$ (Eq. 3).