

**Title:** How macroecology affects macroevolution: the interplay  
2 between extinction intensity and trait-dependent extinction in  
brachiopods.

4 **Running title:** Trait-dependent extinction in brachiopods

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## Abstract

As extinction intensity increases, how do the effects of traits on  
 14 taxonomic survival change? Does the extinction rate associated with  
 certain traits increase while that of others decreases? Using a hierarchical  
 16 Bayesian approach, I develop a model of how the effects of biological  
 traits on extinction risk can vary with respect to extinction intensity,  
 18 origination cohort (i.e. time of origination), and in relation to each other.  
 The emergent traits I analyze in relation to their patterns of  
 20 Paleozoic brachiopod genus durations are geographic range, affinity for  
 epicontinental seas versus open ocean environments, and body size.  
 22 Additionally, I estimate the effects of environmental generalization versus  
 specialization on taxonomic survival by allowing environmental preference  
 24 to have a nonlinear effect on duration. My analytical framework eschews  
 the traditional distinction between background and mass extinction, and  
 26 instead considers extinction intensity as a continuum. I find that the  
 cohort-specific effects of geographic range and environmental preference  
 28 are negatively correlated with baseline extinction intensity. Additionally, I  
 find support for greater survival of environmental generalists versus  
 specialists in all origination cohorts. These results support the conclusion  
 30 that for Paleozoic brachiopods, as extinction intensity increases overall  
 extinction selectivity increases.  
 32

## 1 Introduction

34 Extinction is one half of the diversification process (Raup, 1994, Stanley, 1975,  
 1979), second only to speciation or origination in shaping changes to diversity; it  
 36 can also be the ultimate manifestation of selection as a taxon with a beneficial  
 trait should persist for longer on average than a taxon without that beneficial  
 38 trait (Jablonski, 2008, Rabosky and McCune, 2010, Raup, 1994, Stanley, 1975).

Species duration is a measure of species fitness CITATION, and trait-associated  
40 differences in fitness is the hallmark of (species) selection CITATION.

Jablonski (1986) observed that for bivalves at the end Cretaceous mass  
42 extinction event, previous trait-associated differences in survival no longer  
mattered except for the case of geographic range. Based on this evidence,  
44 Jablonski (1986) proposed the idea of "macroevolutionary modes" and that  
mass extinction and background extinction are fundamentally different  
46 processes. However, based on estimates of extinction rates over time, there is no  
evidence of there being two or more "types" of extinction (Wang, 2003). Instead,  
48 extinction rates for marine invertebrates form a unimodal distribution where  
estimates of extinction rate/intensity show continuous variation.

50 The apparent disconnect between the theory of macroevolutionary modes and  
the observation of continuous variation in extinction rates implies the possibility  
52 of a relationship between the strength of selection (extinction **intensity**) and  
the association between of traits and differences in fitness (extinction  
54 **selectivity**) CITATION PAYNE. As extinction intensity increases, what  
happens to extinction selectivity? How do trait-associated differences in fitness  
56 change as average extinction rate changes over time?

Here I model brachiopod taxon durations as a function of multiple functional  
58 taxon traits because trait-dependent differences in extinction risk should be  
associated with differences in taxon duration CITATION. Brachiopods are an  
60 ideal group for this study as they have an exceptionally complete fossil record  
(Foote, 2000b, Foote and Raup, 1996). I focus on the brachiopod record from  
62 the post-Cambrian Paleozoic, from the start of the Ordovician (approximately  
485 My) through the end Permian (approximately 252 My) as this represents  
64 the time of greatest global brachiopod diversity (Alroy, 2010) which results in a  
large sample size.

66 The analysis of taxon durations, or time from origination to extinction, falls  
under the purview of survival analysis, a field of applied statistics commonly  
68 used in health care and engineering (Klein and Moeschberger, 2003) but has a  
long history in paleontology (Crampton et al., 2016, Simpson, 1944, 1953, Smits,  
70 2015, Van Valen, 1973, 1979). I adopt a hierarchical Bayesian modeling  
approach (Gelman et al., 2013, Gelman and Hill, 2007) in order to unify the  
72 previously distinct dynamic and cohort paleontological survival approaches  
(Baumiller, 1993, Crampton et al., 2016, Ezard et al., 2012, Foote, 1988, Raup,  
74 1975, 1978, Simpson, 2006, Van Valen, 1973, 1979).

To analyze a potential association between extinction intensity and extinction  
76 selectivity, average extinction rate and the trait-based differences in extinction  
rate need to be estimated. In particular, how these values vary over time needs  
78 to be estimated; this is a data intensive and parameter rich requirement. In  
general, there are two approaches to this problem, which I will call phylogenetic  
80 comparative (PCM) or paleobiological. PCM approaches uses branch length  
information from a time-scaled phylogeny in order to estimate the speciation  
82 and extinction rates from a birth-death model that best fits the phylogeny's  
topology (Fitzjohn, 2010, Goldberg et al., 2011, 2005, Maddison et al., 2007,  
84 Rabosky et al., 2013, Stadler, 2013, Stadler and Bokma, 2013, ?) MORE  
CITATION. In contrast, the paleobiological approach to estimating extinction  
86 rates, as well as trait-dependent differences in those rates, is a type of  
time-series analysis where the occurrence and sampling histories of fossil taxa  
88 are used to estimated the underlying rates of a birth-death process (with  
incomplete observation) that fits the observed data.

90 While the capabilities of the PCM approach have increased dramatically from  
their first inception, being capable of estimating time-varying rates as well as  
92 possible trait-dependent or clade-dependent differences in those rates

CITATION, there are known analytical limitations that hamper analysis of  
94 extinction rates and more specifically trait-dependent differences in extinction  
in non-ultrametric trees (i.e. those with fossil tips), estimates which are critical  
96 to answering the question of how extinction intensity relates to extinction  
selectivity. Additionally, many fossil invertebrate groups do not have an inferred  
98 phylogeny that covers a significant portion of history of a clade CITATION; this  
is the case for post-Cambrian Paleozoic brachiopods. What phylogenies do exist  
100 for this group exist at relatively small taxonomic and temporal scales  
CITATION, and are unsuited for questions which require large datasets in order  
102 to fit parameter rich models. This reality means that a paleobiological approach  
to this question is more appropriate than a PCM one.

104 Previous work that has dealt with extinction intensity versus selectivity  
approached this problem by independently estimating the extinction intensity  
106 and selectivity at different time points or for different origination cohorts and  
then comparing those estimates CITATION. I find this approach problematic  
108 for a few reasons. First, by treating each time point or cohort as independent  
the estimates from each model are not relative to each other and they do not  
110 represent the greatest compromise across all available data CITATIONS.  
Second, by treating each time point or cohort as independent any and all  
112 post-hoc analyses are at risk of false positive results because of multiple  
comparisons CITATIONS. Third, post-hoc analysis of correlations between  
114 maximum likelihood estimates is much less satisfying or coherent than including  
those correlations as estimates of the initial model, something that is not  
116 possible when each time point or cohort is considered independent CITATION.

The hierarchical Bayesian approach used here involves developing a single model  
118 to estimate all of time points or cohorts simultaneously while also estimating  
the group averages for all parameter CITATION. By averaging across groups,

<sup>120</sup> the analytical advantages of specific prior choices can induce the partial pooling  
<sup>121</sup> and regularization of parameter estimates which smooths over groups with small  
<sup>122</sup> sample sizes or weakly estimated effects. Additionally, individual estimates are  
<sup>123</sup> much more comparable, not only between time points or cohorts, but also  
<sup>124</sup> relative to the groups average CITATION. This approach is conceptually and  
<sup>125</sup> analytically similar to mixed-effects modeling but the Bayesian framework  
<sup>126</sup> allows the use of strongly regularizing priors in order to better constrain  
parameter estimates.

## <sup>128</sup> 1.1 Factors affecting brachiopod survival

Conceptually, taxon survival can be considered an aspect of “taxon fitness”  
<sup>130</sup> (Cooper, 1984, Palmer and Feldman, 2012). Traits associated with taxon  
survival are thus examples of species (or higher-level) selection, as differences in  
<sup>132</sup> survival are analogous to differences in fitness. The traits analyzed here are all  
examples of emergent and aggregate traits (Jablonski, 2008, Rabosky and  
<sup>134</sup> McCune, 2010); specifically I analyze genus-level traits. Emergent traits are  
those which are not measurable from individuals of the lower level (e.g.  
<sup>136</sup> organisms within species) such as geographic range, or even fossil sampling rate.  
Aggregate traits, like body size or environmental preference, are the average of a  
<sup>138</sup> shared trait across all members of a lower level.

Geographic range is widely considered the most important biological trait for  
<sup>140</sup> estimating differences in extinction risk at nearly all times, with large  
geographic range associated with low extinction risk (Finnegan et al., 2012,  
<sup>142</sup> Harnik et al., 2012, Jablonski, 1986, 1987, 2008, Jablonski and Roy, 2003, Payne  
and Finnegan, 2007). This stands to reason even if extinction is completely at  
<sup>144</sup> random; a taxon with an unrestricted range is less likely to go extinct at

random than a taxon with a restricted range.

<sup>146</sup> Epicontinental seas are a shallow-marine environment where the ocean has spread over the continental interior or craton with a depth typically less than  
<sup>148</sup> 100m. In contrast, open-ocean coastline environments have much greater variance in depth, do not cover the continental craton, and can persist during  
<sup>150</sup> periods of low sea level (Miller and Foote, 2009). Because of this, a simple hypothesis that taxa which favor epicontinental seas would be at great risk  
<sup>152</sup> during periods of low sea levels, such as during glacial periods, when epicontinental seas are drained. During the Paleozoic (approximately 541–252  
<sup>154</sup> My), epicontinental seas were widely spread globally but declined over the Mesozoic (approximately 252–66 My) and have nearly disappeared during the  
<sup>156</sup> Cenozoic (approximately 66–0 My) as open-ocean coastlines became the dominant shallow-marine setting (Johnson, 1974, Miller and Foote, 2009, Peters,  
<sup>158</sup> 2008, Sheehan, 2001). Taxa in epicontinental environments could also have a greater extinction susceptibility than taxa in open-ocean environments due to  
<sup>160</sup> anoxic events due to enhanced water stratification or poor water circulation (Peters, 2007).

<sup>162</sup> Miller and Foote (2009) demonstrated that during several mass extinctions taxa associated with open-ocean environments tend to have a greater extinction risk  
<sup>164</sup> than those taxa associated with epicontinental seas. During periods of background extinction, however, they found no consistent difference between  
<sup>166</sup> taxa favoring either environment. Miller and Foote (2009) hypothesize that open-ocean taxa may have a greater extinction rate because these environments  
<sup>168</sup> would be more strongly affected by waterborne hazards such as fallout from impacts or volcanic events which would propagate more quickly than in  
<sup>170</sup> epicontinental environments with sluggish circulation. These two environment types represent the primary identifiable environmental dichotomy observed in

<sup>172</sup> ancient marine systems (Miller and Foote, 2009, Sheehan, 2001). Given these  
<sup>174</sup> findings, I would hypothesize that as extinction risk increases, the extinction  
risk associated with open-ocean environments should generally increase.

<sup>176</sup> Because environmental preference is defined here as the continuum between  
occurring exclusively in open-ocean environments versus epicontinental  
<sup>178</sup> environments, intermediate values are considered “generalists” in the sense that  
they favor neither end member. A long-standing hypothesis is that generalists or  
<sup>180</sup> unspecialized taxa will have greater survival than specialists (Baumiller, 1993,  
Liow, 2004, 2007, Nürnberg and Aberhan, 2013, 2015, Simpson, 1944, Smits,  
<sup>182</sup> 2015). Because of this, the effect of environmental preference was modeled as a  
quadratic function where a concave down relationship between preference and  
expected duration indicates that generalists are favored over specialists  
<sup>184</sup> end-members.

<sup>186</sup> Body size, measured as shell length, is also considered as a trait that may  
potentially influence extinction risk (Harnik, 2011, Payne et al., 2014). Body  
size is a proxy for metabolic activity and other correlated life history traits  
<sup>188</sup> (Payne et al., 2014). Harnik et al. (2014) analyzed the effect of body size  
selectivity in Devonian brachiopods in both a phylogenetic and  
<sup>190</sup> non-phylogenetic context; finding that body size was not found to be associated  
with differences in taxonomic duration. It has also been found that, at least in  
<sup>192</sup> the case of some bivalve subclades, body size can be as important a factor as  
geographic range size in determining extinction risk (Harnik, 2011). Given these  
<sup>194</sup> results, I expect that if body size has any effect on brachiopod taxonomic  
survival it is very small.

<sup>196</sup> It is well known that, given the incompleteness of the fossil record, the observed  
duration of a taxon is an underestimate of that taxon’s true duration (Alroy,  
<sup>198</sup> 2014, Foote and Raup, 1996, Liow and Nichols, 2010, Solow and Smith, 1997,

Wagner and Marcot, 2013, Wang and Marshall, 2004). Because of this, the  
200 concern is that a taxon's observed duration may reflect its relative chance of  
being sampled and not any of the effects of the covariates of interest. In this  
202 case, for sampling to be a confounding factor there must be consistent  
relationship between the quality of sampling of a taxon and its apparent  
204 duration (e.g. greater sampling, longer duration). If there is no relationship  
between sampling and duration then interpretation can be made clearly; while  
206 observed durations are obviously truncated true durations, a lack of a  
relationship would indicate that the amount and form of this truncation is not a  
208 major determinant of the taxon's apparent duration. By including sampling as a  
covariate in the model, this effect can be quantified and can be taken into  
210 account when interpreting the estimates of the effects of the other covariates.

## 2 Materials and Methods

### 212 2.1 Fossil occurrence information

The brachiopod dataset analyzed here was sourced from the Paleobiology  
214 Database (<http://www.paleodb.org>) which was then filtered based on  
taxonomic (Rhyconelliformea: Rhynchonellata, Chileata, Obolellida,  
216 Kutorginida, Strophomenida, Spiriferida), temporal (post-Cambrian Paleozoic),  
stratigraphic, and other occurrence information used in this analysis. Analyzed  
218 occurrences were restricted to those with paleolatitude and paleolongitude  
coordinates, assignment to either epicontinental or open-ocean environment,  
220 and belonging to a genus present in the body size dataset (Payne et al., 2014).  
Epicontinental versus open-ocean assignments for each fossil occurrence are  
222 partially based on those from Miller and Foote (2009), with additional

occurrences assigned similarly (Miller and Foote, personal communication).

<sup>224</sup> These filtering criteria are very similar to those from Foote and Miller (2013)  
with an additional constraint of being present in the body size data set from  
<sup>226</sup> Payne et al. (2014). In total, there 1130 were genera included in the dataset.

Fossil occurrences were analyzed at the genus level which is common for  
<sup>228</sup> paleobiological, macroevolutionary and macroecological studies of marine  
invertebrates (Alroy, 2010, Foote and Miller, 2013, Harnik et al., 2012, Kiessling  
<sup>230</sup> and Aberhan, 2007, Miller and Foote, 2009, Nürnberg and Aberhan, 2013, 2015,  
Payne and Finnegan, 2007, Simpson and Harnik, 2009, Vilhena et al., 2013).

<sup>232</sup> While species diversity dynamics are frequently of much greater interest than  
those of higher taxa (though see Foote 2014, Hoehn et al. 2015), the nature of  
<sup>234</sup> the fossil record makes accurate, precise, and consistent taxonomic assignments  
at the species level difficult for all occurrences. As such, the choice to analyze  
<sup>236</sup> genera as opposed to species was in order to assure a minimum level of  
confidence and accuracy in the data analyzed here.

<sup>238</sup> Genus duration was calculated as the number of geologic stages from first  
appearance to last appearance, inclusive. Durations were based on geologic  
<sup>240</sup> stages as opposed to millions of years because of the inherently discrete nature  
of the fossil record; dates are not assigned to individual fossils themselves but  
<sup>242</sup> instead fossils are assigned to a geological interval which represents some  
temporal range. In this analysis, stages are effectively irreducible temporal  
<sup>244</sup> intervals in which taxa may occur. Genera with a last occurrence in or after  
Changhsingian stage (e.g. the final stage of the study interval) were right  
<sup>246</sup> censored at the Changhsingian; genera with a duration of only one stage were  
left censored (Klein and Moeschberger, 2003). How the likelihood of censored  
<sup>248</sup> observations is calculated is detailed in section 2.2.

The covariates of duration included in this analysis are geographic range size

<sup>250</sup> ( $r$ ), environmental preference ( $v, v^2$ ), the statistical interactions between  
geographic range size and environmental preference ( $r \times v, r \times v^2$ ), body size  
<sup>252</sup> ( $m$ ), and sampling ( $s$ ). The interaction terms are important to include because  
of the known multidirectional relationship between geographic range,  
<sup>254</sup> environmental preference, and duration CITATION.

<sup>256</sup> Geographic range was calculated as relative occupancy corrected for incomplete  
sampling. First, the paleolatitude-paleolongitude coordinates for all occurrences  
were projected onto an equal-area cylindrical map projection. Each occurrence  
<sup>258</sup> was then assigned to one of the cells from a  $70 \times 34$  regular raster grid placed  
on the map. Each grid cell represents approximately 250,000 km<sup>2</sup>. The map  
<sup>260</sup> projection and regular lattice were made using shape files from  
<http://www.naturalearthdata.com/> and the **raster** package for R (Hijmans,  
<sup>262</sup> 2015). For each stage, the total number of occupied grid cells was calculated.  
Then, for each temporal bin, the relative occurrence probability of the observed  
<sup>264</sup> taxa was calculated using the JADE method developed by Chao et al. (2015).  
This method accounts for the fact that taxa with an occupancy of 0 cannot be  
<sup>266</sup> observed which means that occupancy follows a truncated Binomial distribution.  
This correction is critical when comparing occupancies from different times with  
<sup>268</sup> different geographic sampling. Finally, for each genus, the mean relative  
occurrence probability was calculated as the average of that genus' occurrence  
<sup>270</sup> probabilities for all stages it was sampled to yield relative occupancy, my proxy  
for geographic range.

<sup>272</sup> Environmental preference was defined as probability of observing the ratio of  
epicontinental occurrences to total occurrences ( $\theta_i = e_i/E_i$ ) or greater given the  
<sup>274</sup> background occurrence probability  $\theta'_i$  as estimated from all other taxa occurring  
at the same time ( $e'_i/E'_i$ ). This measure of environmental preference is

<sup>276</sup> expressed.

$$\begin{aligned} p(\theta'_i | e'_i, E'_i) &\propto \text{Beta}(e'_i, E'_i - e'_i) \text{Beta}(1, 1) \\ &= \text{Beta}(e'_i + 1, E'_i - e'_i + 1), \end{aligned} \tag{1}$$

<sup>278</sup> where  $v$  is the percent of the distribution defined in equation 1 less than or equal to  $\theta_i$ . The Beta distribution is used here because it is a continuous distribution bounded at 0 and 1, which is idea for modeling percentages.

<sup>280</sup> Body size, measured as shell length, was sourced directly from Payne et al. (2014). These measurements were made from brachiopod taxa figured in the <sup>282</sup> *Treatise on Invertebrate Paleontology* (Williams et al., 2007).

<sup>284</sup> The sampling probability for individual taxa was calculated using the standard gap statistic (Foote, 2000a, Foote and Raup, 1996). The gap statistic is calculated as the number of stages in which the taxon was sampled minus two <sup>286</sup> divided by the duration of the taxon minus two. Subtracting two from both the numerator and denominator is because the first and last appearance stages are <sup>288</sup> by definition sampled. Because taxa that were right censored only include a first appearance, one was subtracted from the numerator and denominator instead of <sup>290</sup> two.

<sup>292</sup> The minimum duration for which a gap statistic can be calculated is three stages, so I chose the impute the gap statistic for all observations with a <sup>294</sup> duration less than 3. Imputation is the “filling in” of missing observations based on the observed values (Gelman and Hill, 2007, Rubin, 1996). This is fairly <sup>296</sup> straight forward in a Bayesian framework because both covariates and parameters are considered random variables, meaning that the missing values of <sup>298</sup> sampling can be modeled as coming from some probability distribution. The model for imputing sampling probability is described in section 2.3.

Prior to analysis, geographic range was logit transformed and body size was

<sup>300</sup> natural-log transformed; both of these transformations make these variables  
<sup>301</sup> defined for the entire real line. Sampling probability was transformed as  
<sup>302</sup>  $(s(n - 1) + 0.5)/n$  where  $n$  is the sample size as recommended by Smithson and  
<sup>303</sup> Verkuilen (2006); this serves to slightly shrink the range of the data so that  
<sup>304</sup> there are no values of 0 or 1. All covariates except for sampling were  
<sup>305</sup> standardized by subtracting the mean from all values and dividing by twice its  
<sup>306</sup> standard deviation, which follows Gelman and Hill (2007). This standardization  
<sup>307</sup> means that the associated regression coefficients are comparable as the expected  
<sup>308</sup> change per 1-unit change in the rescaled covariates. Finally,  $D$  is defined as the  
total number of covariates, excluding sampling, plus one for the intercept term.

## <sup>310</sup> 2.2 Details of model

Hierarchical modelling is a statistical approach which explicitly takes into  
<sup>311</sup> account the structure of the observed data in order to model both the within  
and between group variance (Gelman et al., 2013, Gelman and Hill, 2007). The  
<sup>312</sup> units of study (e.g. genera) each belong to a single group (e.g. origination  
cohort). Each group is considered a draw from a shared probability distribution  
<sup>313</sup> (e.g. prior) of all cohorts, observed and unobserved. The group-level parameters,  
or the hyperparameters of this shared prior, are themselves given (hyper)prior  
<sup>314</sup> distributions and are also estimated like the other parameters of interest (e.g.  
covariate effects) (Gelman et al., 2013). The subsequent estimates are partially  
<sup>315</sup> pooled together, where parameters from groups with large samples or effects  
remain large while those of groups with small samples or effects are pulled  
<sup>316</sup> towards the overall group mean. All covariate effects (regression coefficients), as  
well as the intercept term (baseline extinction risk), were allowed to vary by  
<sup>317</sup> group (origination cohort). The covariance between covariate effects was also  
modeled.

326 Genus durations were assumed to follow a Weibull distribution which allows for  
 age-dependent extinction (Klein and Moeschberger, 2003):  $y \sim \text{Weibull}(\alpha, \sigma)$ .  
 328 The Weibull distribution has two parameters: scale  $\sigma$ , and shape  $\alpha$ . When  
 $\alpha = 1$ ,  $\sigma$  is equal to the expected duration of any taxon.  $\alpha$  is a measure of the  
 330 effect of age on extinction risk where values greater than 1 indicate that  
 extinction risk increases with age, and values less than 1 indicate that  
 332 extinction risk decreases with age. Note that the Weibull distribution is  
 equivalent to the exponential distribution when  $\alpha = 1$ .  
 334 In the case of the right- and left-censored observations mentioned above, the  
 probability of those observations has a different calculation (Klein and  
 336 Moeschberger, 2003). For right-censored observations, the likelihood is  
 calculated  $p(y|\theta) = 1 - F(y) = S(y)$  where  $F(y)$  is the cumulative distribution  
 338 function. In contrast, the likelihood of a left-censored observation is calculated  
 $p(y|\theta) = F(y)$ .  
 340 The scale parameter  $\sigma$  was modeled as a regression following Kleinbaum and  
 Klein (2005) with both varying intercept and varying slopes and the effect of  
 342 sampling; this is expressed

$$\sigma_i = \exp\left(\frac{-\mathbf{X}_i B_{j[i]} + \delta s_i}{\alpha}\right) \quad (2)$$

where  $i$  indexes across all observations where  $i = 1, \dots, n$  where  $n$  is the total  
 344 number of observations,  $j[i]$  is the cohort membership of the  $i$ th observation  
 where  $j = 1, \dots, J$  where  $J$  is the total number of cohorts,  $X$  is a  $N \times D$  matrix  
 346 of covariates along with a column of 1's for the intercept term,  $B$  is a  $J \times D$   
 matrix of cohort-specific regression coefficients, and  $\delta$  is the regression  
 348 coefficient for the effect of sampling  $s$ .  $\delta$  does not vary by cohort.

Each of the rows of matrix  $B$  are modeled as realizations from a multivariate

<sup>350</sup> normal distribution with length  $D$  location vector  $\mu$  and  $J \times J$  covariance matrix  $\Sigma$ :  $B_j \sim \text{MVN}(\mu, \Sigma)$ . The covariance matrix was then decomposed into a length  $J$  vector of scales  $\tau$  and a  $J \times J$  correlation matrix  $\Omega$ , defined  $\Sigma = \text{diag}(\tau)\Omega\text{diag}(\tau)$  where “diag” indicates a diagonal matrix.

<sup>354</sup> The elements of  $\mu$  were given independent normally distributed priors. The effects of geographic range size and the breadth of environmental preference <sup>356</sup> were given informative priors reflecting the previous findings while the others were given weakly informative favoring no effect. The correlation matrix  $\Omega$  was <sup>358</sup> given an LKJ distributed prior (Lewandowski et al., 2009) that slightly favors an identity matrix as recommended by ?. These priors are defined

$$\begin{aligned}\mu^0 &\sim \mathcal{N}(0, 5) \\ \mu^r &\sim \mathcal{N}(-1, 1) \\ \mu^v &\sim \mathcal{N}(0, 1) \\ \mu^{v^2} &\sim \mathcal{N}(1, 1) \\ \mu^{r \times v} &\sim \mathcal{N}(0, 1) \\ \mu^{r \times v^2} &\sim \mathcal{N}(1, 1) \\ \mu^m &\sim \mathcal{N}(0, 1) \\ \tau &\sim \text{C}^+(1) \\ \Omega &\sim \text{LKJ}(2).\end{aligned}\tag{3}$$

<sup>360</sup> The log of the shape parameter  $\alpha$  was given a weakly informative prior  $\log(\alpha) \sim \mathcal{N}(0, 1)$  centered at  $\alpha = 1$ , which corresponds to the Law of Constant <sup>362</sup> Extinction (Van Valen, 1973).

## 2.3 Imputation of sampling probability

364 The vector sampling  $s$  has two parts: the observed part  $s^o$ , and the unobserved  
part  $s^u$ . Of the 1130 total observations, 539 have a duration of 3 or more and  
366 have an observed gap statistic. The gap statistic for the remaining 591  
observations was imputed. As stated above, the unobserved part is the imputed,  
368 or filled in, based on the observed part  $s^o$ . Because sampling varies between 0  
and 1, I chose to model it as a Beta regression with matrix  $W$  being a  
370  $N \times (D - 3)$  matrix of covariates (i.e. geographic range size, environmental  
preference, body size; no interactions) as predictors of sampling; this assumes  
372 that the sampling value for all taxa come from the same distribution.  
Importantly, I make no assumptions of causal structure.

374 Predicting sampling probability using the other covariate that are then included  
in the model of duration is acceptable and appropriate in the case of imputation  
376 where the sample goal is accurate prediction (Gelman and Hill, 2007, Rubin,  
1996). Not including these covariates can lead to biased estimates of the  
378 imputed variable; if the covariates themselves are related, not including them  
will bias this correlation towards zero which then leads to improper imputation  
380 and inference (Rubin, 1996).

The Beta regression is defined

$$s^o \sim \text{Beta}(\phi = \text{logit}^{-1}(X^o\gamma), \lambda), \quad (4)$$

382 where  $\gamma$  is a length  $D$  vector of regression coefficients, and  $X$  defined as above.

The Beta distribution used in the regression is reparameterized in terms of a  
384 mean parameter

$$\phi = \frac{\alpha}{\alpha + \beta} \quad (5)$$

and total count parameter

$$\lambda = \alpha + \beta \quad (6)$$

<sup>386</sup> where  $\alpha$  and  $\beta$  are the characteristic parameters of the Beta distribution  
(Gelman et al., 2013).

<sup>388</sup> The next step is to then estimate  $s^u|s^o, X^o, X^u, \gamma$ , the posterior distribution of  
which are folded back into  $s$  and used as a covariate of duration (Eq. 2). All the  
<sup>390</sup> elements of  $\gamma$ , and both  $\delta$  (Eq. 2) and  $\lambda$  (Eq. 4) were given weakly informative  
priors where

$$\begin{aligned} \gamma &\sim \mathcal{N}(0, 1) \\ \delta &\sim \mathcal{N}(0, 1) \\ \lambda &\sim \text{Pareto}(0.1, 1.5). \end{aligned} \quad (7)$$

## <sup>392</sup> 2.4 Posterior inference and posterior predictive checks

The joint posterior was approximated using a Markov-chain Monte Carlo  
<sup>394</sup> routine that is a variant of Hamiltonian Monte Carlo called the No-U-Turn  
Sampler (Hoffman and Gelman, 2014) as implemented in the probabilistic  
<sup>396</sup> programming language Stan (Stan Development Team, 2014). The posterior  
distribution was approximated from four parallel chains run for 10,000 steps  
<sup>398</sup> each, split half warm-up and half sampling and thinned to every 10th sample for  
a total of 4000 posterior samples. Chain convergence was assessed via the scale  
<sup>400</sup> reduction factor  $\hat{R}$  where values close to 1 ( $\hat{R} < 1.1$ ) indicate approximate  
convergence. Convergence means that the chains are approximately stationary  
<sup>402</sup> and the samples are well mixed (Gelman et al., 2013).

Model adequacy was evaluated using a couple of posterior predictive checks.  
<sup>404</sup> Posterior predictive checks are a means for understanding model fit or adequacy  
where the basic idea is that replicated data sets simulated from the fitted model

406 should be similar to the original data and systematic differences between the  
407 simulations and observations indicate weaknesses of the model fit (Gelman  
408 et al., 2013). For both approaches used here, each posterior predictive datasets  
409 were generated from a unique draw from the posterior distribution of each  
410 parameter. The two posterior predictive checks used in this analysis are a  
411 comparison of a non-parametric estimate of the survival function  $S(t)$  from the  
412 empirical dataset to the non-parametric estimates of  $S(t)$  from the 100 posterior  
413 predictive datasets, and comparison of the observed genus durations to the  
414 average posterior predictive estimate of  $\log(\sigma)$  (Eq. 2). The former is to see if  
415 simulated data has a similar survival pattern to the observed, while the latter is  
416 to see if the model systematically over- or under- estimates taxon survival.

### 3 Results

418 Comparison of the posterior predictive estimates of  $S(t)$  to the empirical  
419 estimate reveal few obvious biases except for the case of values from the far  
420 right tail of observed durations (Fig. 1). This result is reinforced by the  
421 additional posterior predictive comparison where most estimates are not  
422 systematically biased except for a consistent under-estimate of  $\log(\sigma)$  for older  
423 taxa (Fig. 2). The results of both posterior predictive checks indicate that, for  
424 the majority of observations, model fit is generally not biased.

The cohort-level estimate of the effect of geographic range size indicates that as  
426 a taxon's geographic range increases, that taxon's duration is expected to  
427 increase (Table 1). Given the estimates of  $\mu^r$  and  $\tau^r$ , there is a less than 3.7%  
428 ( $\pm 0.04\%$  SD) probability that this relationships would be reversed  
 $(\text{Pr}N(\mu^r, \tau^r) > 0)$ ). The between-cohort variance  $\tau^r$  is the lowest of all the  
430 regression coefficients (Table 1).

Body size is estimated to have no effect on taxon duration, with the estimate  
432 being nearly 0 (Table 1). The variance between the cohort-specific estimates of  
the effect of body size  $\tau^m$  is estimated to be greater than the variance of  
434 between-cohort estimates of the effect of geographic range size  $\tau^r$ .

The group-level estimate of the effect of environmental preference is estimated  
436 from both  $\mu^v$  and  $\mu^{v^2}$ .

The estimate of  $\mu^v$  indicates that epicontinental favoring taxa are expected to  
438 have a greater duration than open-ocean favoring taxa (Table 1). Additionally,  
given the estimate of between-cohort variance  $\tau^v$ , there is approximately 18%  
440 ( $\pm 7\%$  SD) probability that, for any given cohort, taxa favoring open-ocean  
environments would have a greater expected duration than taxa favoring  
442 epicontinental environments ( $\Pr(\mathcal{N}(\mu^v, \tau^v) > 0)$ ).

The estimate of  $\mu^{v^2}$  indicates that the overall relationship between  
444 environmental preference and  $\log(\sigma)$  is concave down (Fig. ??), with only a 2.7%  
 $(\pm 3\%$  SD) probability that any given cohort is convex up ( $\Pr(\mathcal{N}(\mu^{v^2}, \tau^{v^2}) < 0)$ ).

446 The cohort-specific estimates of all the regression coefficients demonstrate a lot  
of between cohort variance, with no obvious trends. As indicated in Table 1 and  
448 detectable visually (Fig. 6), the between-cohort estimates for  $\beta^0$ ,  $\beta^r$ , and  $\beta^m$  all  
have much lower variance than the between-cohort estimates of both  $\beta^v$  and  
450  $\beta^{v^2}$ .

While most cohort-specific estimates are very similar to the overall cohort-level  
452 estimate, there are a few notable excursions away from the overall mean (Fig.  
6). There are simultaneous excursions in both  $\beta^0$  and  $\beta^v$  for cohorts originating  
454 in the Givetian (387-382 My) and Frasnian (382-372 My) stages; both of which  
directly precede the late Devonian mass extinction event at the  
456 Frasnian/Famennian boundary. These cohorts are marked by both a high

extinction intensity and an increase in expected duration for taxa favoring  
458 epicontinental environments over open-ocean ones; this is consistent with the  
results of Miller and Foote (2009).

460 Cohorts originating from the Silurian through the Early Devonian have a  
slightly lower extinction intensity than the overall mean; these cohorts are those  
462 originating in the Llandovery (443-443 My) through the Emsian (407-393 My).  
This is also a time period is also when there is the lowest overall probability  
464 that epicontinental favoring taxa are expected to have greater duration than  
open-ocean favoring taxa. Both the Silurian and Devonian periods are notable  
466 for having been periods with a mostly “hothouse” climate, with no polar icecaps  
and a high sea-level (Edwards and Fanning, 1985, Joachimski et al., 2009,  
468 Munnecke et al., 2010).

The cohort-specific relationships between environmental preference and  $\log(\sigma)$   
470 were calculated from the estimates of  $\beta^0$ ,  $\beta^v$ , and  $\beta^{v^2}$  (Fig. ??) and reflect how  
these three parameters act in concert and not just individually (Fig. 6). Beyond  
472 results already discussed above in the context of the parameters individually, it  
is notable that the cohort originating in the Kungurian (279-272 My) is least  
474 like the overall expected relationship and has the most sharply curved  
appearance due to a high estimate  $\beta^{v^2}$  (Fig. 6). This cohort has the biggest  
476 difference in extinction risk between environmental generalists and specialists.

The cohorts originating during the Emsian (407-393 My) and Frasnian (382 -  
478 372 My) are tied for second in sharpness of curvature. The least sharply curved  
cohorts include those originating during Tremadocian (484-477 My), Hirnantian  
480 (445-443 My), Llandovery (443-433 My), and Ludlow (427-423 My). Except for  
the Tremadocian cohort, most of these cohorts originate during the Silurian  
482 through the Early Devonian range identified earlier as having lower expected  
extinction intensity than what is expected from the group-level estimate.

- 484 The correlations of the cohort-specific estimates of the regression coefficients are  
 estimated as the off-diagonal elements of the correlation matrix  $\Omega$ . Only two of  
 486 the elements of  $\Omega$  are distinguishable from 0: the correlation of  $\beta^0$  (extinction  
 intensity) with both  $\beta^r$  and  $\beta^v$  (Fig. 10).
- 488 There is an approximate 90% probability that the cohort-specific estimates of  
 baseline extinction intensity  $\beta^0$  and the effect of geographic range  $\beta^r$  are  
 490 negatively correlated; this means that for cohorts experiencing a lower  
 extinction intensity ( $\beta^0$  decreases), the magnitude of the effect of geographic  
 492 range is expected to decrease as well, and *vice versa*; this is in contrast to the  
 observation made by Jablonski (1986) with regards to late Cretaceous bivalves.
- 494 Similarly, there is an approximate 97.4% probability that the cohort-specific  
 estimates of  $\beta^0$  and  $\beta^v$  are negatively correlated; this means that as extinction  
 496 intensity increases it is expected that epicontinental taxa become more favored  
 over open-ocean environments (i.e. as  $\beta^0$  increases,  $\beta^v$  decreases).
- 498 There is only an approximate 30% probability that  $\beta^r$  and  $\beta^v$  are positively  
 correlated. This lack of cross-correlation may be due in part to the much higher  
 500 between-cohort variance of the effect of environmental preference  $\tau^v$  than the  
 very small between-cohort variance in the effect of geographic range  $\tau^r$  (Table  
 502 1); the effect of geographic range might simply not vary enough relative to the  
 much noisier environmental preference.
- 504 Comparison of observed values of sampling, as measured by the gap statistic, to  
 random draws from the posterior estimates of the imputed sampling values  
 506 indicate that they are very similar (Fig. 11. This result is very encouraging as  
 this is the ultimate goal of multiple imputation: to fill in missing data with  
 508 values similar to the observed while taking into account the randomness of that  
 variable (Gelman and Hill, 2007, Rubin, 1996). The estimates of  $\delta$  are based on

510 the set of observed values and the entire posterior of imputed values.

Sampling was found to have a negative effect (positive  $\delta$ ) on duration: greater  
512 sampling, shorter duration (Table 1). While potentially counter intuitive, this  
result is most likely due to some long lived taxa only be sampled in the stages of  
514 the first and last appearance. Also, longer lived taxa have more opportunities to  
not be sampled than shorter lived taxa. These two factors will lead to this result.

516 While the effect of sampling appears large compared to the other regression  
coefficients, this is only because sampling was not standardized like the other  
518 covariates. To make the coefficients comparable,  $\delta$  is multiplied by twice the  
posterior mean of the standard deviation of sampling probability; the  
520 transformed value of  $\delta$  is then 0.642 ( $\pm 0.1$  SD). This effect is relatively small  
compared to the other covariate effects (Table 1). There is then a 98.6%  
522 probability that the effect of geographic range  $\mu^r$  has a greater magnitude than  
 $\delta$ . Similarly,  $\mu^v$  has a 71.8% probability of having a greater magnitude of effect  
524 than  $\delta$ . Finally,  $\mu^{v^2}$  has a 100% probability of having a greater magnitude of  
effect than  $\delta$ .

526 The Weibull shape parameter  $\alpha$  was found to be approximately 1.36 ( $\pm 0.05$  SD)  
with a 100% probability of being greater than 1. This result is not consistent  
528 with the Law of Constant Extinction (Van Valen, 1973) and is instead  
consistent with accelerating extinction risk with taxon age. This may indicate  
530 that older taxa are out-competed by younger taxa, a result consistent with some  
empirical results (Quental and Marshall, 2013, Smits, 2015, Wagner and  
532 Estabrook, 2014) and (ironically) with a recently proposed Red Queen-like  
model of evolution (Rosindell et al., 2015). This results, however, is not  
534 consistent with other empirical results (Crampton et al., 2016, Finnegan et al.,  
2008) and could potentially be caused by the minimum resolution of the fossil  
536 record (Sepkoski, 1975). It is thus unclear if a strong biological inference can be

made from this result, which means that further work is necessary on the effect  
538 of taxon age on extinction risk.

## 4 Discussion

540 The generating observation behind this study was that for bivalves at the end  
Cretaceous mass extinction event, the only biological trait that was found the  
542 affect extinction risk was geographic range while traits that had previously been  
beneficial had no effect (Jablonski, 1986). This observation raises two linked  
544 questions: how does the effect of geographic range change with changing  
extinction intensity, and how does the effect of other biological traits change  
546 with changing extinction intensity?

I find that as intensity increases ( $\beta^0$  decreases), the magnitude of the effect of  
548 geographic range increases. I also find that as intensity increases, the effect of  
favoring epicontinental environments of open-ocean environments is expected to  
550 be increase; this is consistent with the results of Miller and Foote (2009). There  
is no evidence for a correlation between the effect of geographic range and  
552 environmental preference. Additionally, the between-cohort variance in effect of  
geographic range is much less than the between-cohort variance of the effect of  
554 environmental preference which may underlie the lack of correlation between  
these two effects.

556 Additionally, the lower between-cohort variance in the effect of geographic range  
versus that higher between-cohort variance implies that for cohorts with a  
558 greater than average extinction intensity, the difference in the effect geographic  
range and the group-level effect of geographic range is expected to be smaller  
560 than the difference between the effect of environmental preference and the  
group-level effect of environmental preference.

I find consistent support for the “survival of the unspecialized,” with respect to epicontinental versus open-ocean environmental preference, as a time-invariant generalization of brachiopod survival; taxa with intermediate environmental preferences are expected to have lower extinction risk than taxa specializing in either epicontinental or open-ocean environments (Fig. ??), though the curvature of the relationship varies from rather shallow to very peaked (Fig. ??). However, this relationship is not symmetric about 0, as taxa favoring epicontinental environments are expected to have a greater duration than taxa favoring open-ocean environments. This description of environment only describes one major aspect of a taxon’s environmental context, with factors such as bathymetry and temperature being further descriptors of a taxon’s adaptive zone (Harnik, 2011, Harnik et al., 2012, Heim and Peters, 2011, Nürnberg and Aberhan, 2013); inclusion of these factors in future analyses would potentially improve our understanding of the “survival of the unspecialized” hypothesis (Simpson, 1944).

Hopkins et al. (2014), in their analysis of niche conservatism and substrate lithological preference in marine invertebrates, found that brachiopods were among the least “conservative” groups; taxa were found to easily change substrate preference on short time scales. While substrate preference is not the same as environmental preference (as defined here), a question does arise: are there three classes of environmental preference instead of two? These classes would be taxa with broad tolerance (“true” generalists), inflexible specialists (“true” specialists), and flexible but with a narrow tolerance. A flexible taxon is one with a narrow habitat preference at one time, but with preference that changes over time with changing environmental availability. My analysis assumes that traits are constant over the duration of the taxon meaning that this scenario is not detectable; taxa with broad tolerances and flexible taxa with

narrow per-stage preference end up being treated the same way. Future work  
590 should explore how environmental preference changes over lineage duration in  
relation to environmental availability to estimate if the generalists–specialists  
592 continuum is actually ternary relationship.

An alternative approach for specifically modeling survival that can take into  
594 account imperfect observation than the method used here is the  
Cormack-Jolly-Seber (CJS) model (Liow et al., 2008, Liow and Nichols, 2010,  
596 Royle and Dorazio, 2008, Tomiya, 2013). This model is a type of hidden Markov  
model with an absorbing state (i.e. extinction). In this model, survival is defined  
598 as the probability of surviving from time  $t$  to time  $t + 1$ . Additionally, the effect  
of preservation and sighting is estimated as probability of observing a taxon that  
600 is present; this can extend the duration of a taxon beyond its last occurrence.  
This approach is a fundamentally different from the method used in my analysis:  
602 I am estimating the biasing effect of sampling probability on taxon duration to  
then compare with effects of other covariates, while the CJS model estimates the  
604 pre-sampling fossil record and then estimates per-time unit survival probability.

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

The model used here could be improved through either increasing the number of  
614 analyzed traits, expanding the hierarchical structure of the model to include  
other major taxonomic groups of interest, and the inclusion of explicit

616 phylogenetic relationships between the taxa in the model as an additional  
hierarchical effect. An example trait that may be of particular interest is the  
618 affixing strategy or method of interaction with the substrate of the taxon, which  
has been found to be related to brachiopod survival where, for cosmopolitan  
620 taxa, taxa that are attached to the substrate are expected to have a greater  
duration than those that are not (Alexander, 1977).

622 It is theoretically possible to expand this model to allow for comparisons both  
within and between major taxonomic groups which would better constrain the  
624 brachiopod estimates while also allowing for estimation of similarities and  
differences in cross-taxonomic patterns. The major issue surrounding this  
626 particular expansion involves finding a similarly well sampled taxonomic group  
that is present during the Paleozoic. Potential groups include Crinoidea,  
628 Ostracoda, and other members of the “Paleozoic fauna” (Sepkoski, 1981).

With significant updates, it would also be possible to compare the brachiopod  
630 record with with Modern groups such as bivalves or gastropods (Sepkoski, 1981),  
though remembering that the groups may not necessarily share all cohorts with

632 the brachiopods. This particular model expansion would act as a test of any  
universal cross-taxonomic patterns in the effects of emergent traits on extinction  
634 such as has been proposed for geographic range (Payne and Finnegan, 2007).

Additionally, this expanded model would also act as a test of the distinctness of  
636 the Sepkoski (1981) three-fauna hypothesis in terms of trait-dependent  
extinction.

638 Traits like environmental preference or geographic range (Hunt et al., 2005,  
Jablonski, 1987) are most likely heritable. Without phylogenetic context, this  
640 analysis assumes that differences in extinction risk between taxa are  
independent of the shared evolutionary history of those taxa (Felsenstein, 1985).

642 In contrast, the origination cohorts only capture shared temporal context. For

example, if taxon duration is phylogenetically heritable, then closely related  
644 taxa may have more similar durations as well as more similar biological traits.  
Without taking into account phylogenetic similarity the effects of these  
646 biological traits would be inflated solely due to inheritance. The inclusion of  
phylogenetic context as an additional individual-level hierarchical effect,  
648 independent of origination cohort, would allow for determining how much of the  
observed variability is due to shared evolutionary history versus shared temporal  
650 context versus actual differences associated with biological traits (Smits, 2015).

The combination and integration of the phylogenetic comparative and  
652 paleontological approaches requires both sources of data, something which is not  
possible for this analysis because there is no phylogenetic hypothesis for all  
654 Paleozoic taxa, something that is frequently the case for marine invertebrates  
with a good fossil record. When both data sources are available has been  
656 possible, however, the analysis can more fully address the questions of interest  
in macroevolution (Fritz et al., 2013, Harnik et al., 2014, Raia et al., 2012, 2013,  
658 Simpson et al., 2011, Slater et al., 2012, Slater, 2013, 2015, Smits, 2015, Tomiya,  
2013).

660 In summary, patterns of Paleozoic brachiopod survival were analyzed using a  
fully Bayesian hierarchical survival modelling approach while also eschewing the  
662 traditional separation between background and mass extinction. I find that  
cohort extinction intensity is negatively correlated with both the cohort-specific  
664 effects of geographic range and environmental preference. These results imply  
that as extinction intensity increases ( $\beta^0$ ) increases, it is expected that both  
666 effects will increase in magnitude. However, the change in effect of  
environmental preference is expected to be greater than the change in the effect  
668 of geographic range. Additionally, I find support for greater survival in  
environmental generalists over specialists in all origination cohorts analyzed;

670 this is consistent with the long standing “survival of the unspecialized”  
hypothesis (Baumiller, 1993, Liow, 2004, 2007, Nürnberg and Aberhan, 2013,  
672 2015, Simpson, 1944, 1953, Smits, 2015). The results of this analysis support the  
conclusion that for Paleozoic brachiopods, as extinction intensity increases  
674 overall extinction selectivity is expected to increase as well.

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Table 1: Estimates of various parameters in the model used here. These include group-level estimates of the effects of biological traits on brachiopod generic survival, the standard deviation of the between-cohort effects, as well as the estimates of both the effect of sampling  $\delta$  and the Weibull shape parameter  $\alpha$ . The mean, standard deviation (SD), 10th, 50th, and 90th quantiles of the marginal posteriors are presented.

type	parameter	effect of	mean	SD	10%	50%	90%
Mean	$\mu^i$	intercept	-3.05	0.20	-3.30	-3.05	-2.80
	$\mu\_i$	-3.18	0.20	-3.45	-3.18	-2.93	
	$\mu\_r$	-1.15	0.20	-1.40	-1.14	-0.90	
	$\mu\_v$	-0.69	0.22	-0.97	-0.70	-0.41	
	$\mu\_v2$	3.10	0.41	2.58	3.12	3.61	
	$\mu\_rxv$	0.33	0.43	-0.21	0.32	0.88	
	$\mu\_rxv2$	0.17	0.61	-0.62	0.18	0.94	
	$\mu\_m$	-0.05	0.13	-0.21	-0.05	0.10	
Standard deviation	$\tau^i$	intercept	0.51	0.11	0.38	0.50	0.65
	$\tau\_i$	0.49	0.12	0.35	0.49	0.64	
	$\tau\_r$	0.66	0.19	0.42	0.65	0.90	
	$\tau\_v$	0.93	0.20	0.69	0.91	1.19	
	$\tau\_v2$	1.67	0.47	1.12	1.62	2.31	
	$\tau\_rxv$	1.78	0.46	1.23	1.75	2.36	
	$\tau\_rxv2$	1.90	1.12	0.52	1.79	3.42	
	$\tau\_m$	0.48	0.13	0.32	0.47	0.64	
$\delta$	$\delta$		sampling	0.90	0.15	0.71	0.90
	Other	0.91	0.16	0.71	0.91	1.11	1.09
	$\alpha$	1.41	0.05	1.35	1.41	1.47	

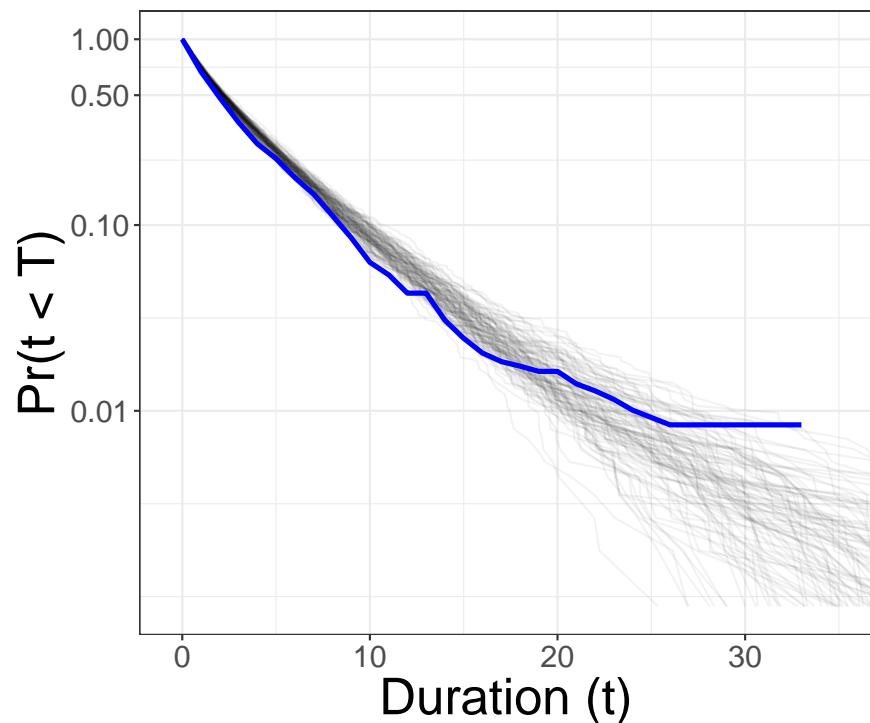


Figure 1: Comparison of the empirical estimate of  $S(t)$  (highlighted) versus estimates from 100 posterior predictive data sets (black).  $S(t)$  corresponds to the probability that the age of a genus  $t$  is less than the genus' ultimate duration  $T$ . The vertical axis is log10 transformed.

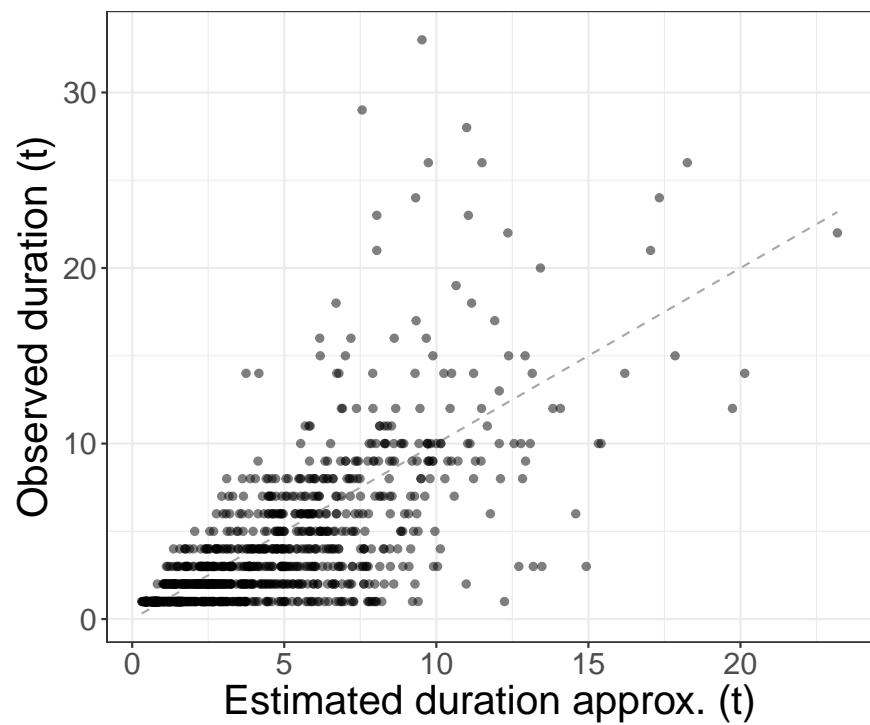


Figure 2: Comparison of all observed genus durations in number of geological stages to the average posterior predictive estimates of  $\log(\sigma)$ . The dashed, diagonal line corresponds to  $x = y$ .

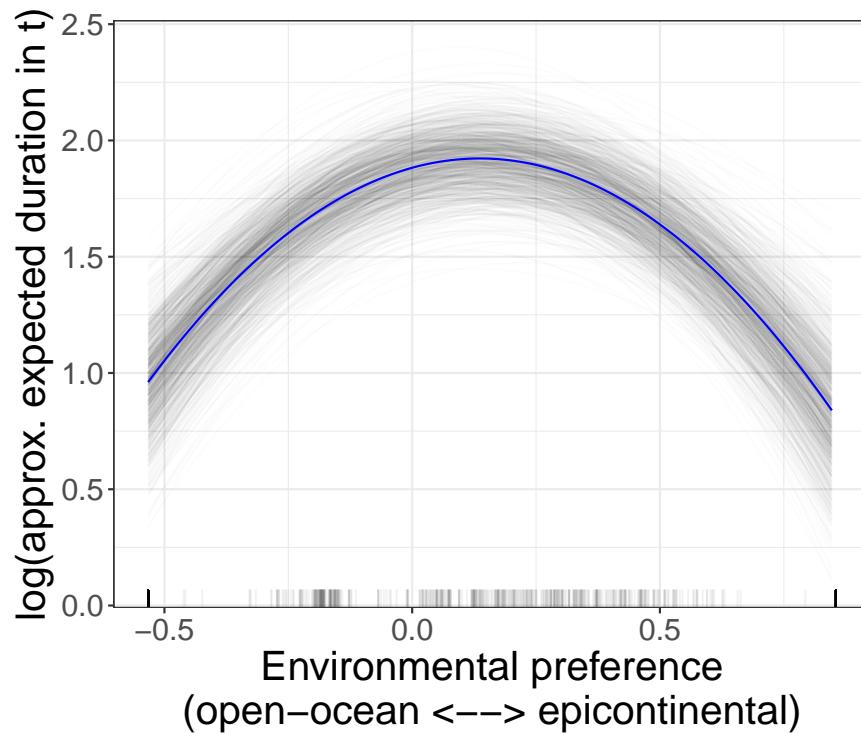


Figure 3: The overall expected relationship between environmental affinity  $v_i$  and a  $\log(\sigma)$  when  $r = 0$  and  $m = 0$ . The 1000 semi-transparent lines corresponds to a single draw from the posterior predictive distribution, while the highlighted line corresponds to the median of the posterior predictive distribution. The overall relationship is concave down with an optimum greater than 0, which means that taxa favoring epicontinental environments are expected to have longer durations than those favoring open-ocean environments. The tick marks along the bottom of the plot correspond to the (rescaled) observed values of environmental preference.

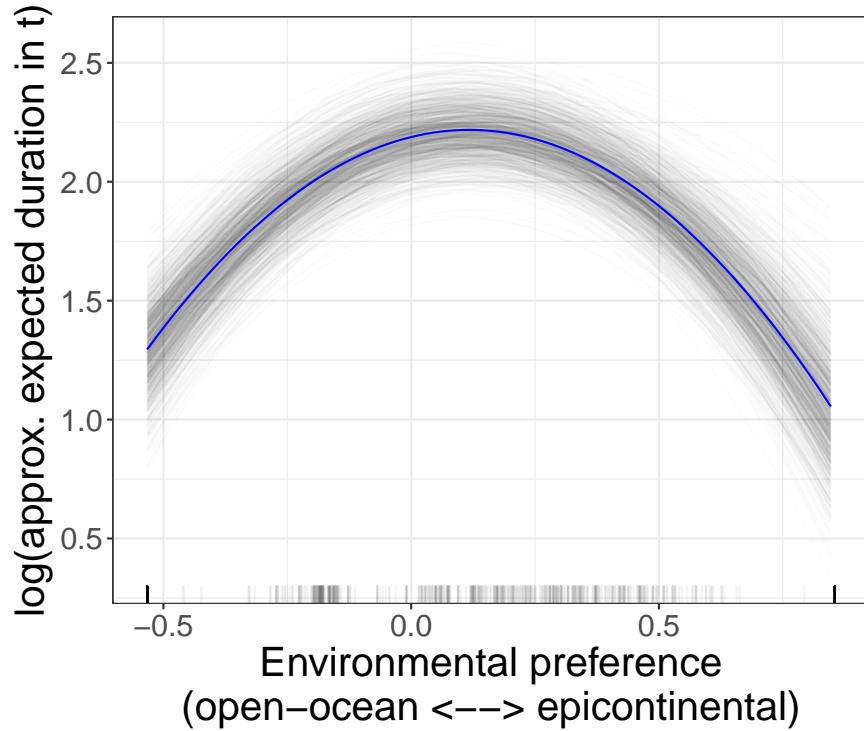


Figure 4: The overall expected relationship between environmental affinity  $v_i$  and a  $\log(\sigma)$  when  $r = 0$  and  $m = 0$ . The 1000 semi-transparent lines corresponds to a single draw from the posterior predictive distribution, while the highlighted line corresponds to the median of the posterior predictive distribution. The overall relationship is concave down with an optimum greater than 0, which means that taxa favoring epicontinental environments are expected to have longer durations than those favoring open-ocean environments. The tick marks along the bottom of the plot correspond to the (rescaled) observed values of environmental preference.

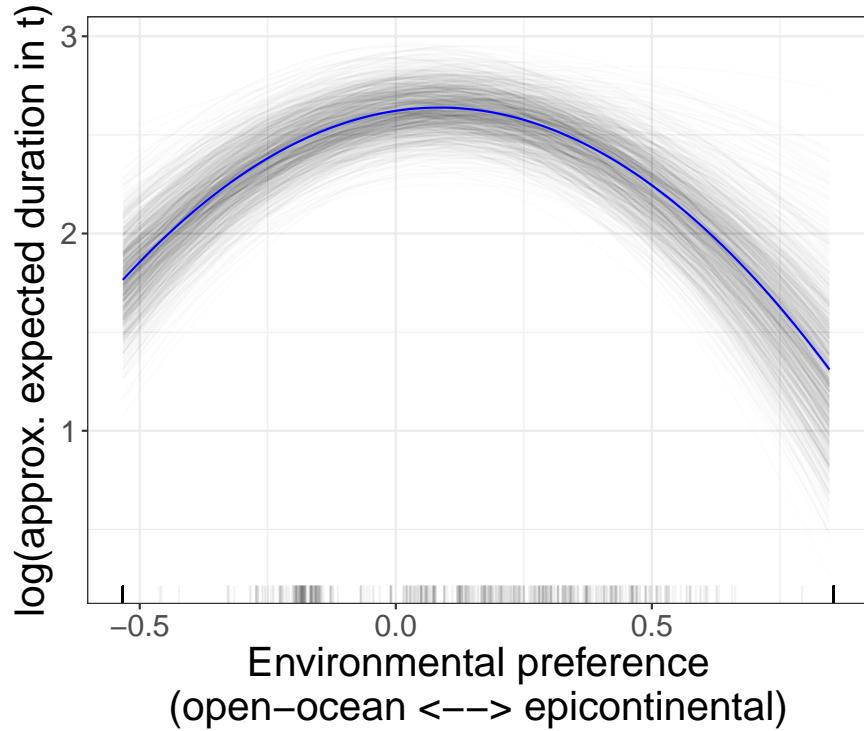


Figure 5: The overall expected relationship between environmental affinity  $v_i$  and a  $\log(\sigma)$  when  $r = 0$  and  $m = 0$ . The 1000 semi-transparent lines corresponds to a single draw from the posterior predictive distribution, while the highlighted line corresponds to the median of the posterior predictive distribution. The overall relationship is concave down with an optimum greater than 0, which means that taxa favoring epicontinental environments are expected to have longer durations than those favoring open-ocean environments. The tick marks along the bottom of the plot correspond to the (rescaled) observed values of environmental preference.

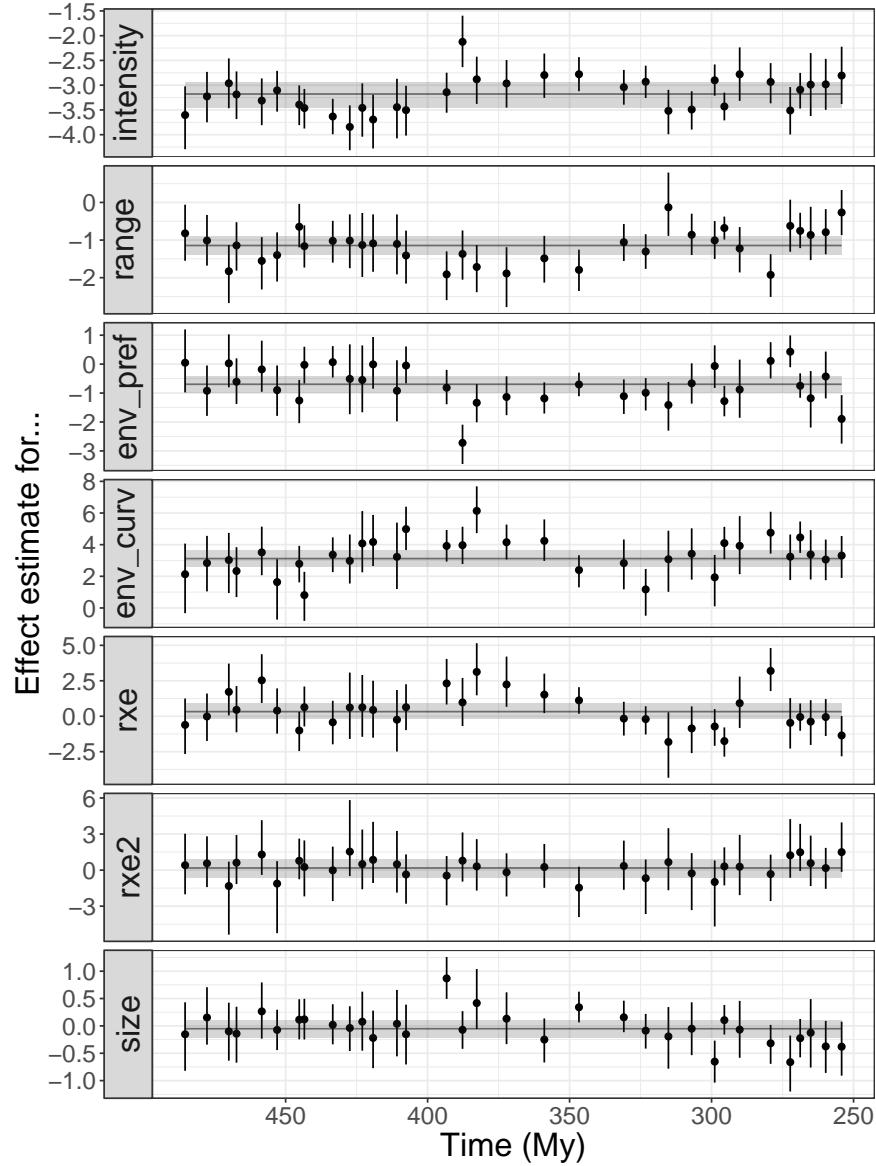


Figure 6: Comparison of cohort-specific estimates of  $\beta^0$ , the effect of geographic range on extinction risk  $\beta^r$ , the effect of environmental preference  $\beta^v$  and  $\beta^{v^2}$ , and body size  $\beta^m$ . Points correspond to the median of the cohort-specific estimate, along with 80% credible intervals. Points are plotted at the midpoint of the cohorts stage of origination in millions of years before present (My). Black, horizontal lines are the overall estimates of covariate effects along with 80% credible intervals (shaded).

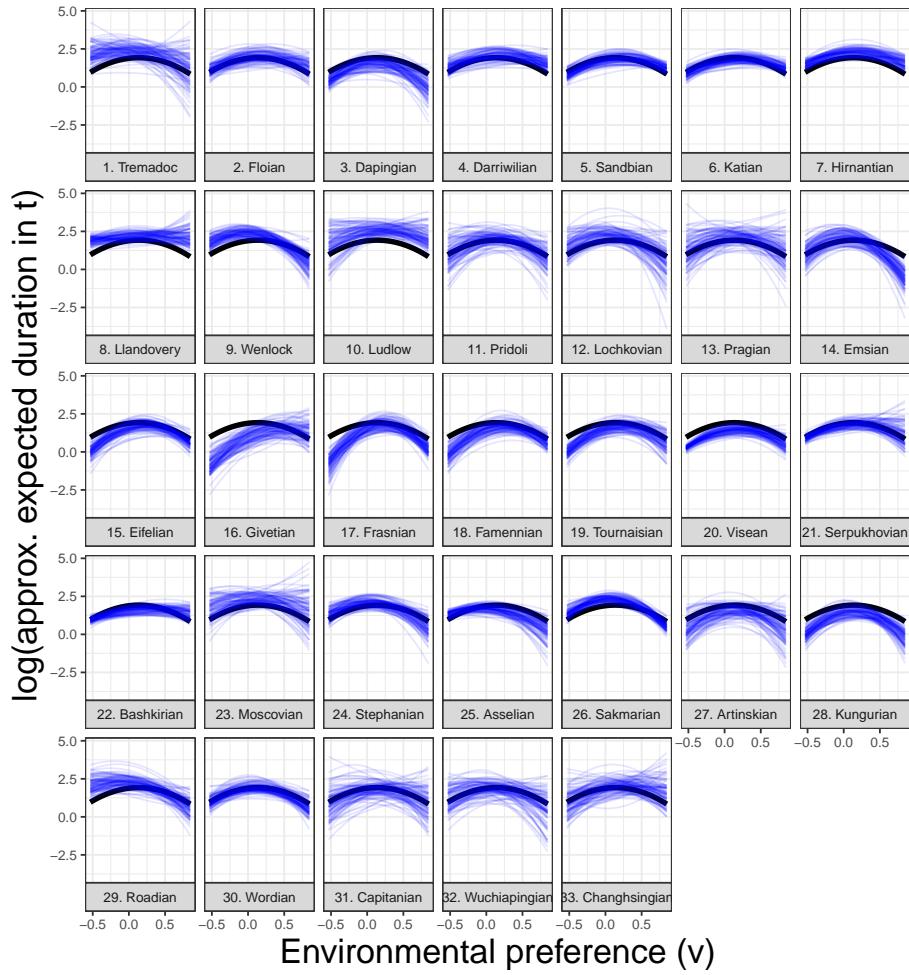


Figure 7: Comparison of origination cohort-specific (posterior predictive) estimates of the effect of environmental preference on  $\log(\sigma)$  to the mean overall estimate of the effect of environmental preference. Cohort-specific estimates are from 100 posterior predictive simulations across the range of (transformed and rescaled) observed values of environmental preference. The oldest cohort is in the top-right and younger cohorts proceed left to right, with the youngest cohort being the right-most facet of the last row. Panel names correspond to the name of the stage in which that cohort originated.

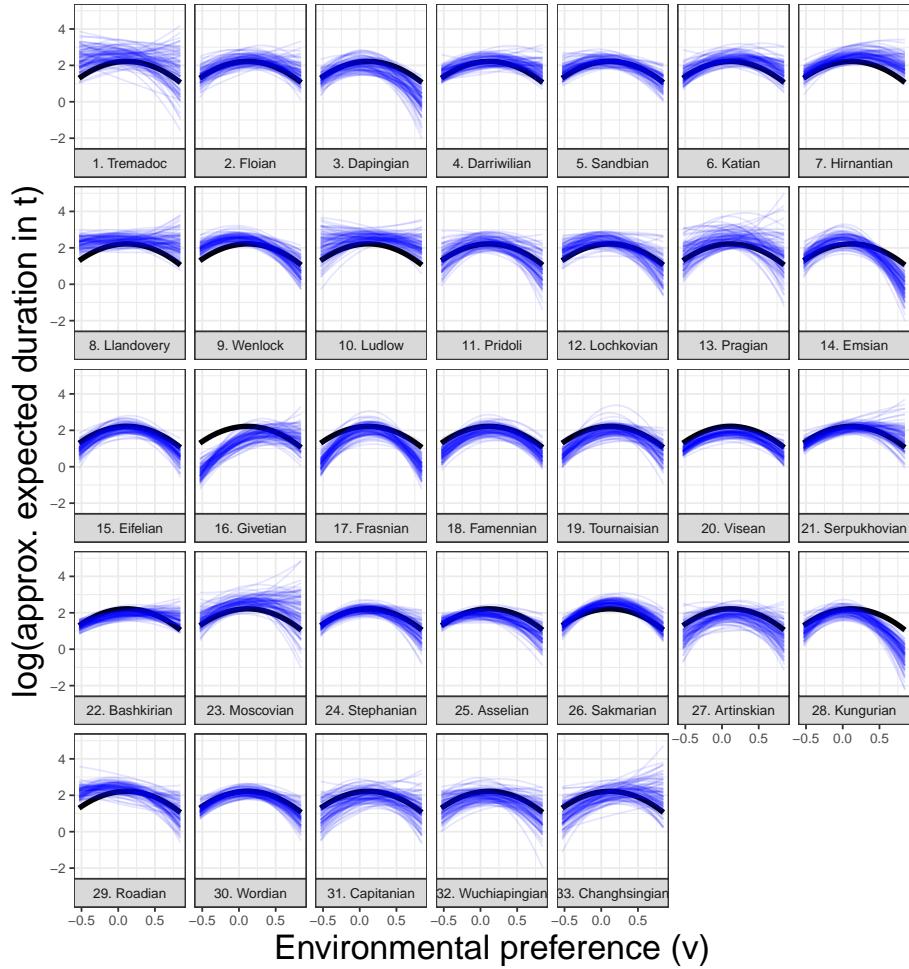


Figure 8: Comparison of origination cohort-specific (posterior predictive) estimates of the effect of environmental preference on  $\log(\sigma)$  to the mean overall estimate of the effect of environmental preference. Cohort-specific estimates are from 100 posterior predictive simulations across the range of (transformed and rescaled) observed values of environmental preference. The oldest cohort is in the top-right and younger cohorts proceed left to right, with the youngest cohort being the right-most facet of the last row. Panel names correspond to the name of the stage in which that cohort originated.

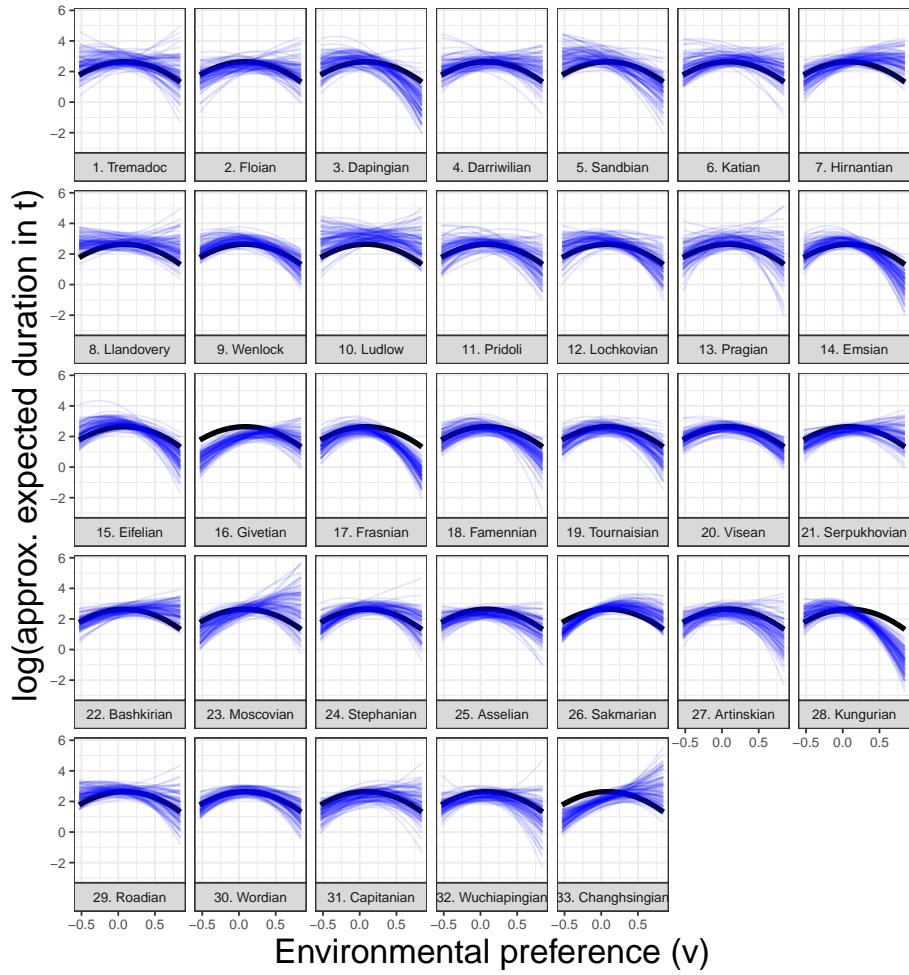


Figure 9: Comparison of origination cohort-specific (posterior predictive) estimates of the effect of environmental preference on  $\log(\sigma)$  to the mean overall estimate of the effect of environmental preference. Cohort-specific estimates are from 100 posterior predictive simulations across the range of (transformed and rescaled) observed values of environmental preference. The oldest cohort is in the top-right and younger cohorts proceed left to right, with the youngest cohort being the right-most facet of the last row. Panel names correspond to the name of the stage in which that cohort originated.

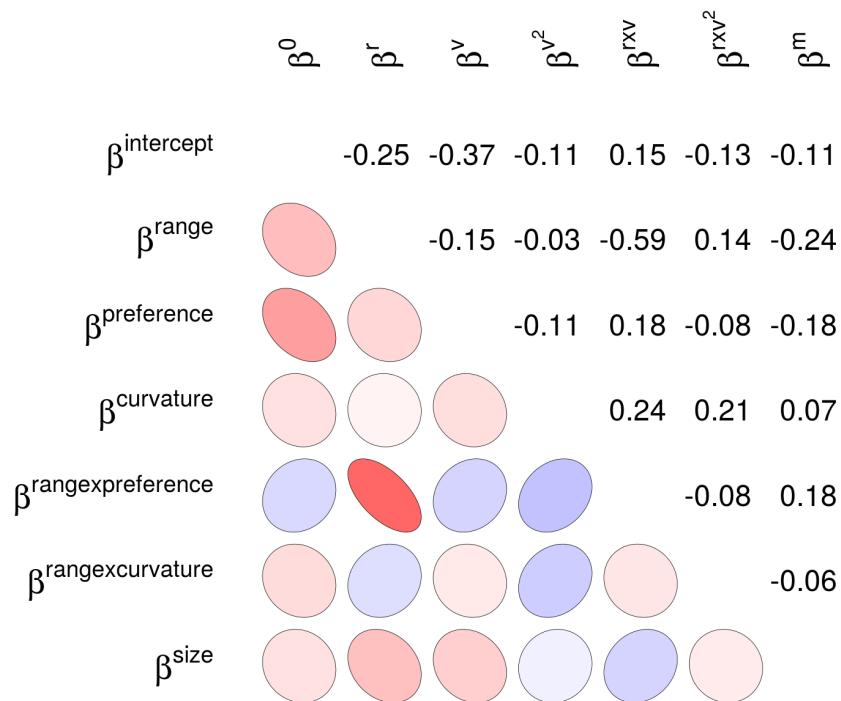


Figure 10: Mixed graphical and numerical representation of the correlation matrix  $\Omega$  of variation in cohort-specific covariate estimates. These correlations are between the estimates of the cohort-level effects of covariates, along with intercept/baseline extinction risk. The median estimates of the correlations are presented numerically (upper-triangle) and as idealized ellipses representing that much correlation (lower-triangle). The darkness of the ellipse corresponds to the magnitude of the correlation.

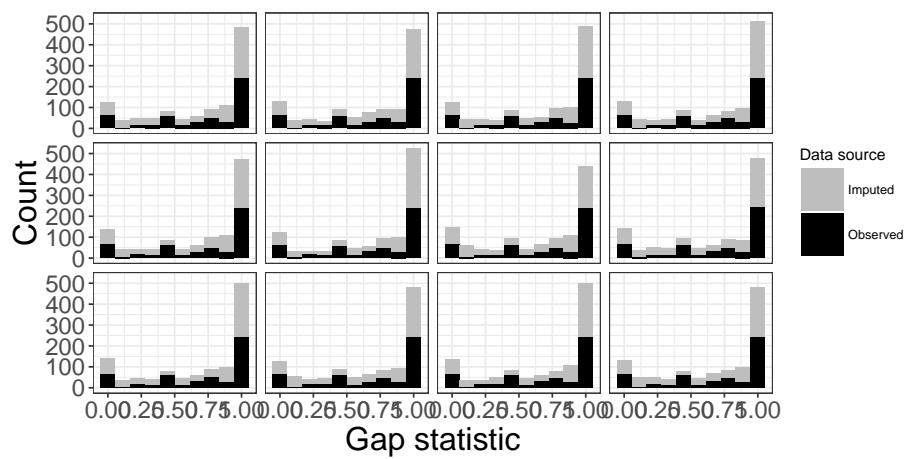


Figure 11: Histograms of the distribution of gap statistic values from both the observed values and the imputed values from 12 unique posterior realizations. For each panel the observed values are identical but the imputed values are from a single set of their posterior estimates.