

How macroecology affects macroevolution

the interplay between extinction intensity and trait-dependent extinction in brachiopods

Peter D Smits

Committee on Evolutionary Biology, University of Chicago



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Observation

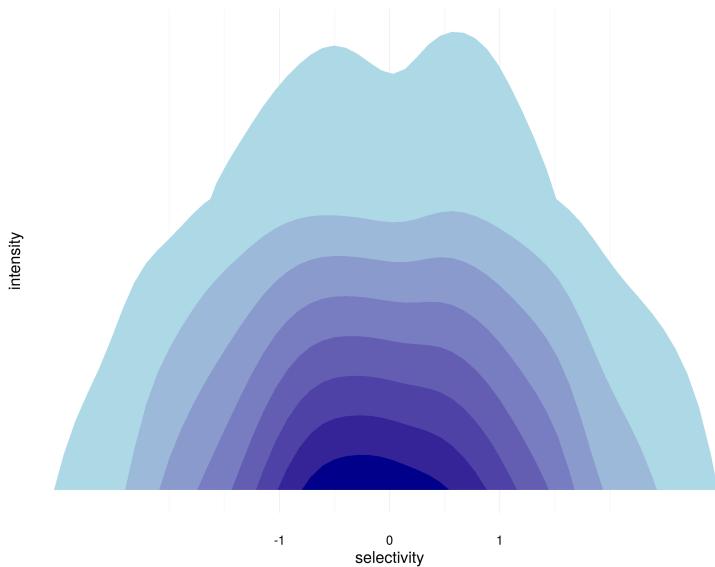
At K/Pg mass extinction, biological traits (except geographic range) have no effect on **bivalve** taxonomic survival.

(Jablonski, 1986, *Science*)

Questions and analysis

- ▶ How do the effect of emergent traits on duration (**extinction selectivity**) vary with expected duration (**extinction intensity**) and each other?
- ▶ What is the relationship between environmental affinity and duration wrt specialists versus generalists?
- ▶ **Approach:** hierarchical Bayesian survival model, varying intercepts and slopes, Weibull distribution, imputed gap statistic for taxa with duration < 3 .

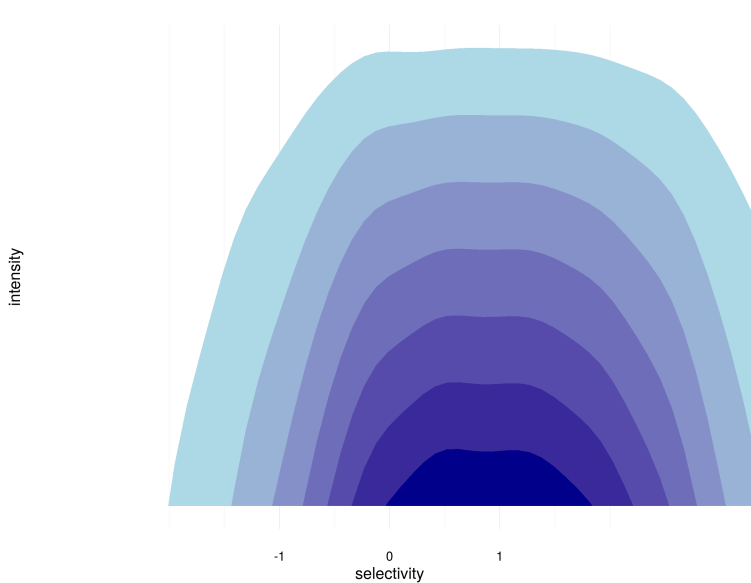
Intensity and selectivity



Analysis of post-Cambrian Paleozoic brachiopod genus durations

- ▶ stage as time unit; duration measured in stages
- ▶ multiple emergent traits analyzed
 - ▶ geographic range
 - ▶ transformed using **JADE** fo biased sampling (Chao et al. 2015 *Ecology*)
 - ▶ body size
 - ▶ from Payne et al from the *Treatise on Invertebrate Paleontology*
 - ▶ environmental preference (x , x^2)
 - ▶ gap statistic as measure of sampling (Foote and Raup 1996 *Paleobio*)
- ▶ factors vary by cohort (except gap statistic)

Hypothesis of range size, extinction risk and intensity

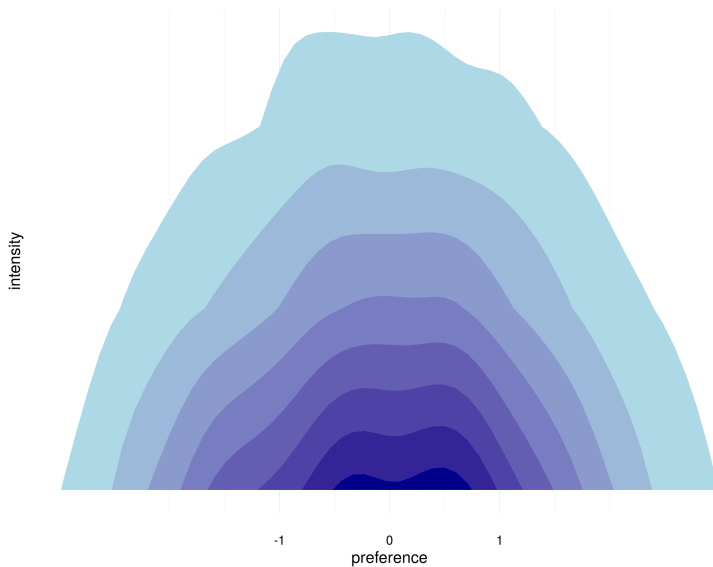


Hypotheses of effect of environmental preference

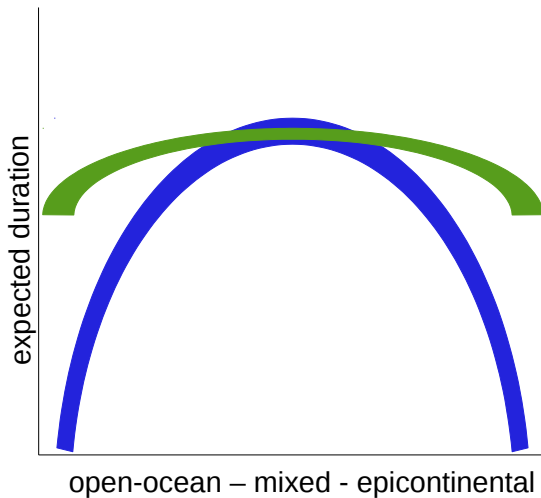
*When related phyla die out . . . more specialized phyla tend to become extinct before less specialized. This phenomenon is also far from universal, but it is so common that it does deserve recognition as a rule or principle in evolutionary studies: **the rule of the survival of the relatively unspecialized.***

(Simpson, 1944, Tempo and Mode of Evolution, p. 143)

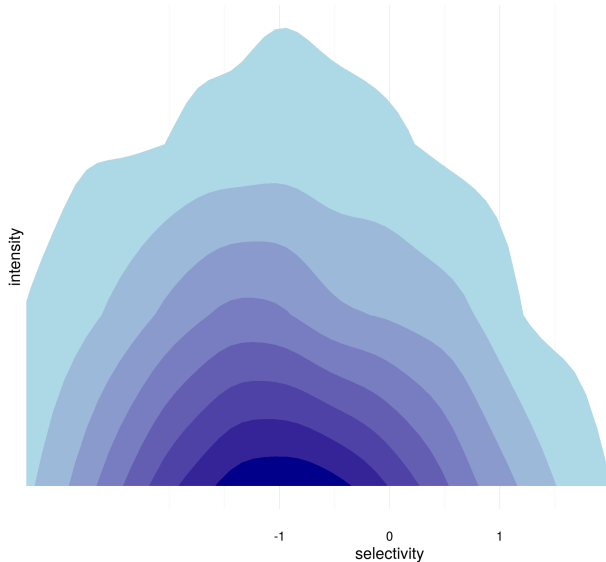
Hypothesis of effect of environmental preference



Hypotheses of effect of environmental breadth



Hypothesis of relationship environmental breadth with extinction intensity



New measure of taxon's environmental affinity

(# epicontinental / total # occurrences) is what quantile of the distribution of all other background occurrences $\text{Beta}(\alpha, \beta)$.

- ▶ α is the # epicontinental background occurrences (+ 1).
- ▶ β is the # open ocean background (+ 1).

Measure of sampling and imputed values

Sampling is measured as the gap statistic r :

(number of bins with an occurrence - 2) / (duration in bins - 2)

Can only be estimated for taxa with duration of three or more.

Have to impute (e.g. fill-in) the values for all other taxa r^* .

$$s \sim \text{Beta}(\phi, \lambda)$$

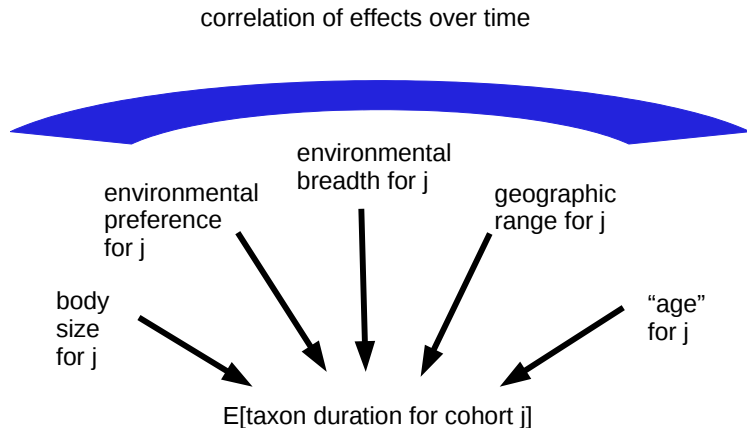
$$\phi = \text{logit}^{-1}(W\gamma)$$

$$s^* \sim \text{Beta}(\phi^*, \lambda)$$

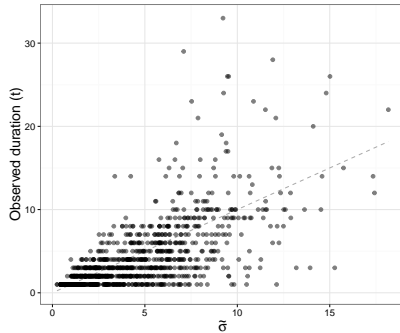
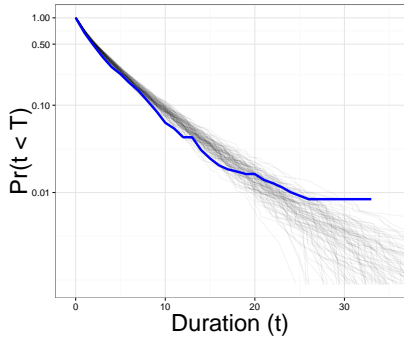
$$\phi^* = \text{logit}^{-1}(W^*\gamma)$$

Note: Beta distribution parameterized in terms of mean ϕ and total count λ .
Also, this presentation excludes final (hyper)priors.

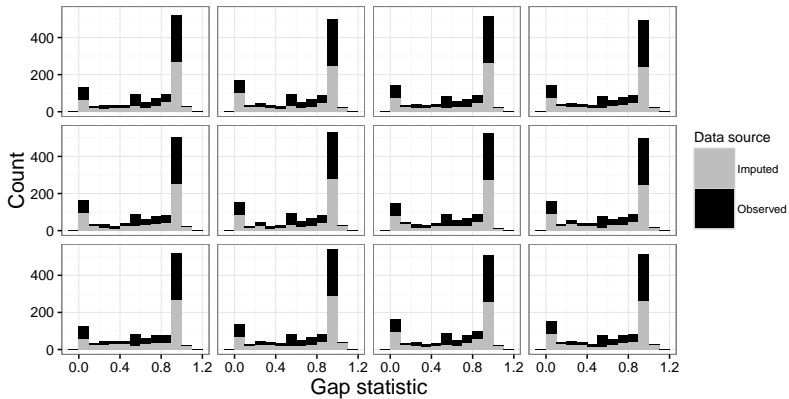
Hierarchical survival model



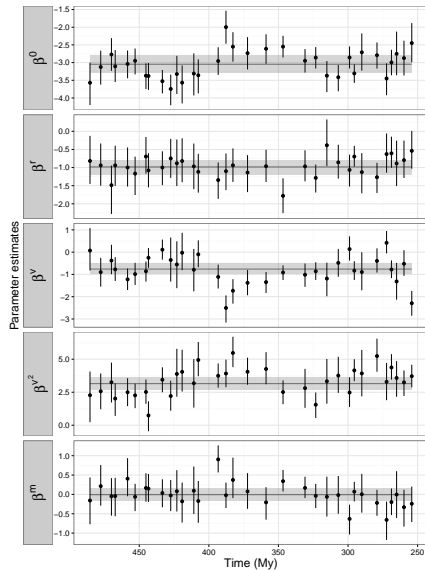
Model adequacy



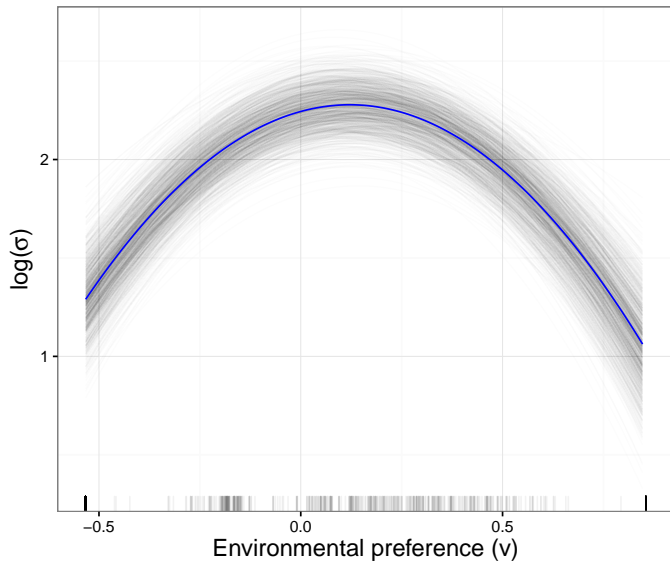
Inspecting the imputations



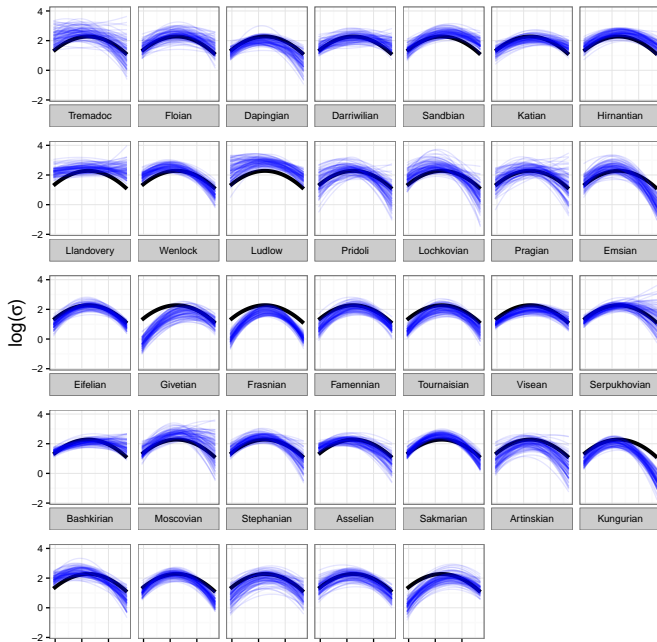
Change in trait effects between cohorts



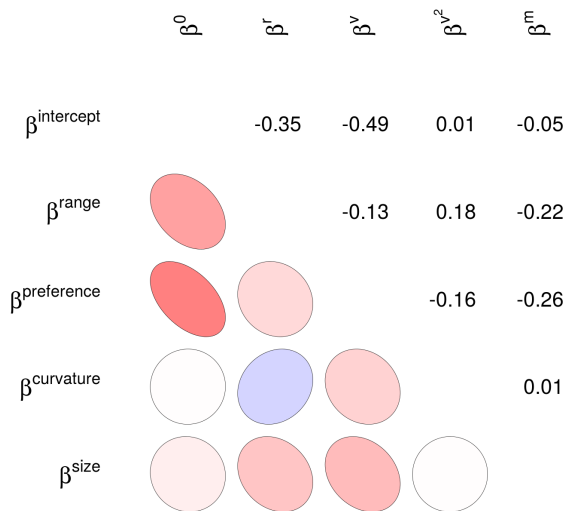
Overall effect of environmental preference



Change in effect of environment between cohorts



Correlation of effects between cohorts



Effect summary

- ▶ Effect of geographic range consistent with prior expectations.
- ▶ No effect of body size; either environmental preference approximately equal.
- ▶ Strong support for survival of unspecialized as generalization wrt environmental preference.

Macroevolutionary process

- ▶ As extinction risk increases, the effect of geographic range “washes out” the effects of other traits.
 - ▶ Support for hypotheses presented in Jablonski 1986 *Science*, Raup 1994 *PNAS*.

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