

# How macroecology affects macroevolution

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

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## Observation

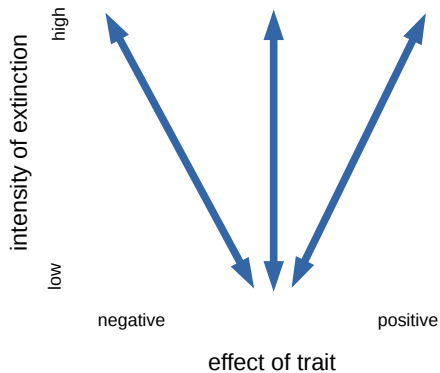
At K/Pg mass extinction, biological traits (except geographic range) have no effect on **bivalve** taxonomic survival.

(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

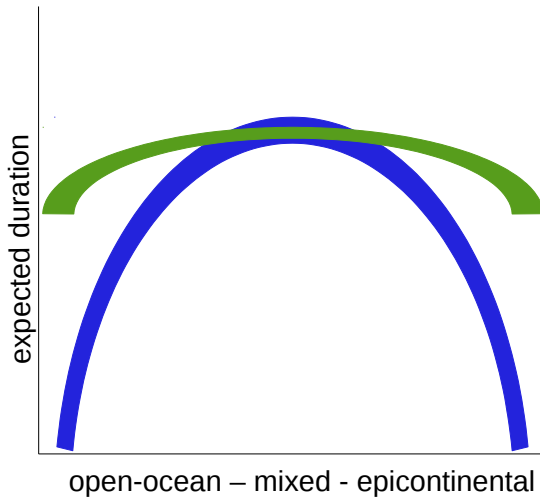
- ▶ stage as time unit; duration measured in stages (2-5 My each)
- ▶ multiple emergent traits analyzed
  - ▶ geographic range
    - ▶ transformed using **JADE** fo biased sampling (Chao et al. 2015 *Ecology*)
  - ▶ body size
    - ▶ from Payne et al from the *Treatise on Invertebrate Paleontology*
  - ▶ environmental preference ( $x$ ,  $x^2$ )
  - ▶ gap statistic as measure of sampling (Foote and Raup 1996 *Paleobio*)
- ▶ factors vary by cohort (except gap statistic)

# Hypotheses of effect of environmental preference

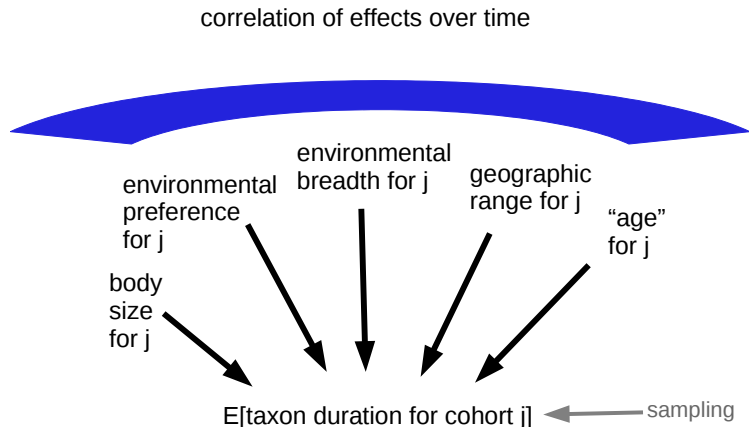
*When related phyla die out . . . more specialized phyla tend to become extinct before less specialized. This phenomenon is also far from universal, but it is so common that it does deserve recognition as a rule or principle in evolutionary studies: **the rule of the survival of the relatively unspecialized.***

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

# Hypothesis of effect of environmental preference

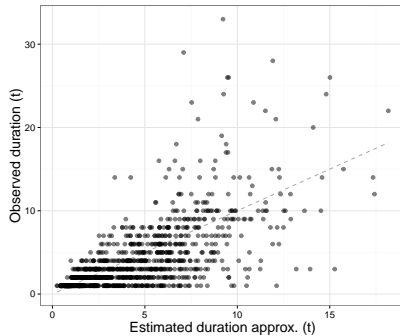
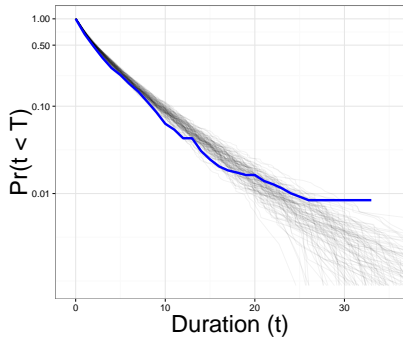


# Hierarchical survival model

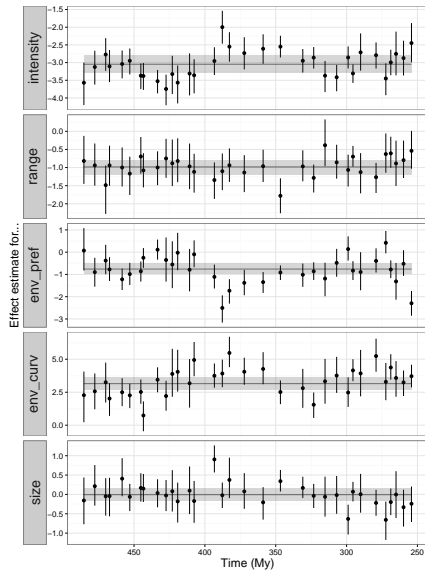




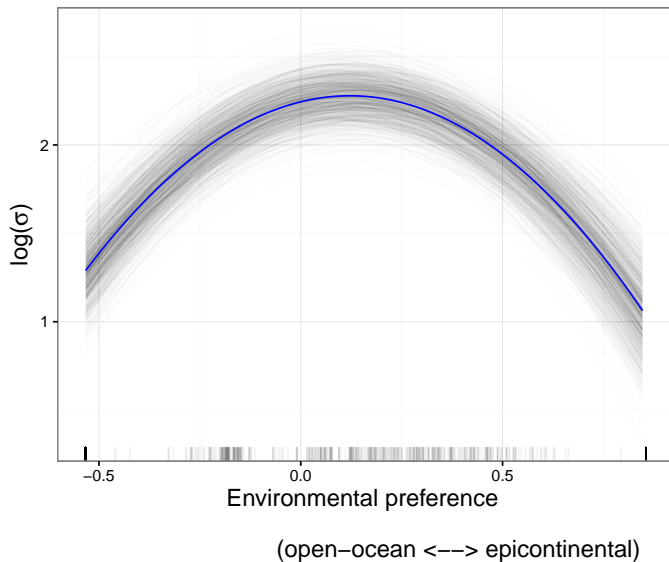
# Model adequacy



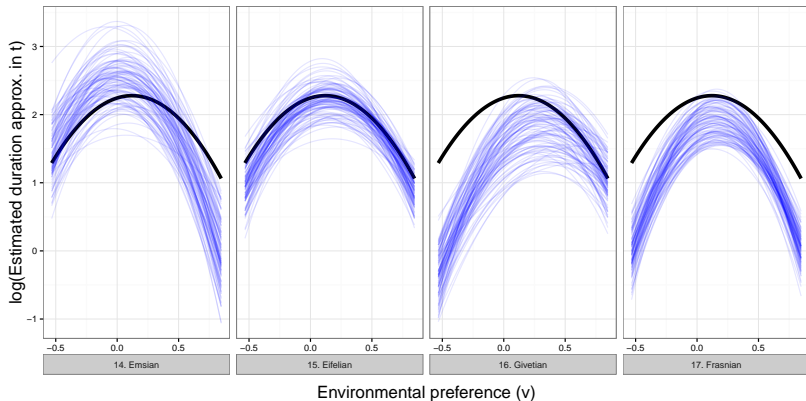
# Change in trait effects between cohorts



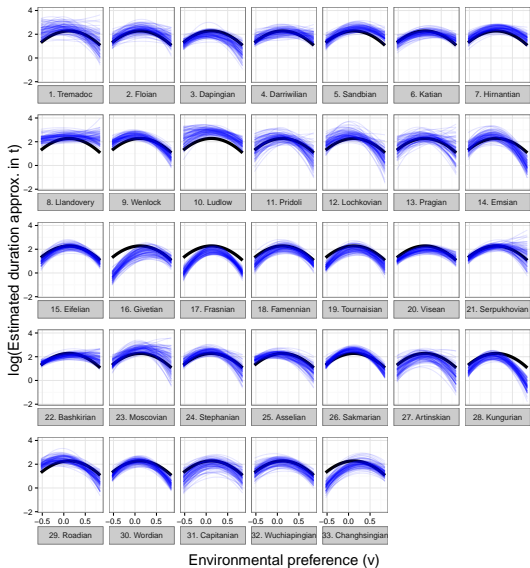
# Overall effect of environmental preference



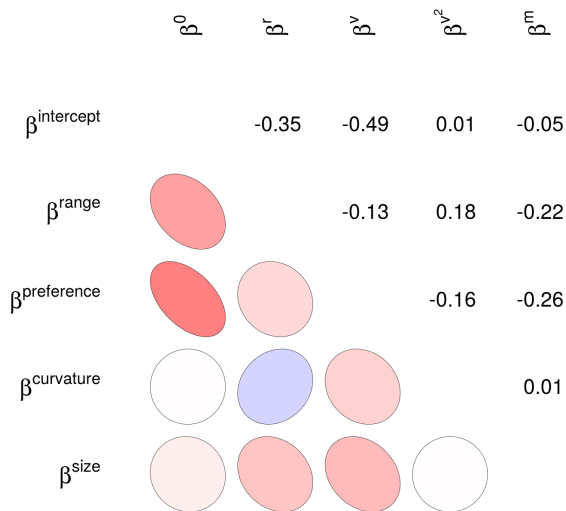
# Change in effect of environment between cohorts



# Change in effect of environment between cohorts



# Correlation of effects between cohorts



## Effect summary

- ▶ Effect of geographic range consistent with prior expectations; low variance.
- ▶ No effect of body size; low variance.
- ▶ Epicontinental environmental preference slightly favored on averaged; high variance.
- ▶ Strong support for survival of unspecialized as generalization wrt environmental preference; medium variance.

## Macroevolutionary process

- ▶ As extinction risk decreases, the differences between taxa matter less.
- ▶ Magnitude of effect of geographic range and environmental preference increase with extinction intensity.



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## New measure of taxon's environmental affinity

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

- ▶  $\alpha$  is the # epicontinental background occurrences (+ 1).
- ▶  $\beta$  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  $\phi$  and total count  $\lambda$ .  
Also, this presentation excludes final (hyper)priors.

# Sampling statement for the joint posterior probability

$$\begin{aligned}y_{i,t} &\sim \text{Weibull}(\sigma_{i,t}, \alpha) \\ \log(\sigma_{i,t}) &= \frac{X_i B_{j[i],t} + \delta s_i}{\alpha} \\ B_j &\sim \text{MVN}(\mu, \Sigma) \\ \Sigma &= \text{diag}(\tau) \Omega \text{diag}(\tau) \\ s_i &\sim \text{Beta}(\phi_i, \lambda) \\ \phi_i &= \text{logit}^{-1}(W_i \gamma)\end{aligned}$$

Note: Calculation of log probability of right and left censored observations is modified from the above. Also, presentation excludes final (hyper)priors.

# Inspecting the imputations

