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

The Paleobiology Database
revealing the history of life

Selection on species traits

- A species with a beneficial trait should persist for longer, on average, than a species without that beneficial trait (Jablonski 2008 *Paleobio*, Rabosky and McCune 2010 *TREE*).
- Taxon survival an aspect of taxon fitness (Cooper 1984 *J. Theo. Biol.*, Palmer and Feldman 2012 *PLoS One*).

Trait-dependent extinction

- Extinction is second only to speciation in shaping diversity (Raup 1994 *PNAS*, Stanley 1975 *PNAS*).
- two major approaches: phylogenetic comparative and paleobiological
- difficult to estimate from phylogenies alone (Rabosky 2010 *Evolution*, Liow et al 2010 *Syst Biol*, Quental and Marshall 2008 *Evolution*).
- fossil record is (imperfect) observation of extinction

Observation

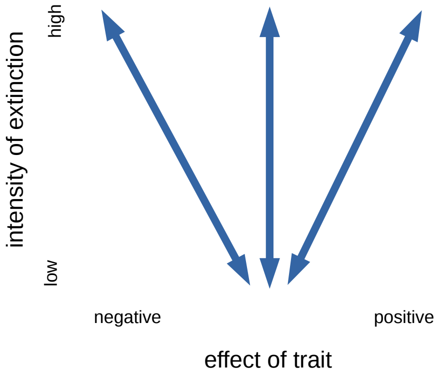
At K/Pg mass extinction, biological traits (except geographic range) have no effect on bivalve taxonomic survival.

(Jablonski, 1986, *Science*)

Questions and analysis

- How do the effect of emergent traits on duration (extinction selectivity) vary with expected duration (extinction intensity)?
- **Approach:** hierarchical Bayesian survival model;
  effect estimates vary with origination cohort;
  correlation btw effects modeled.

Intensity and selectivity



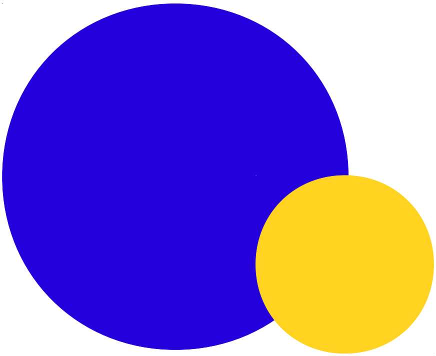
Brachiopods

(ComputerHotline, wikimedia CC BY 2.5; Dwergenpaartje, wikimedia CC BY-SA 3.0)

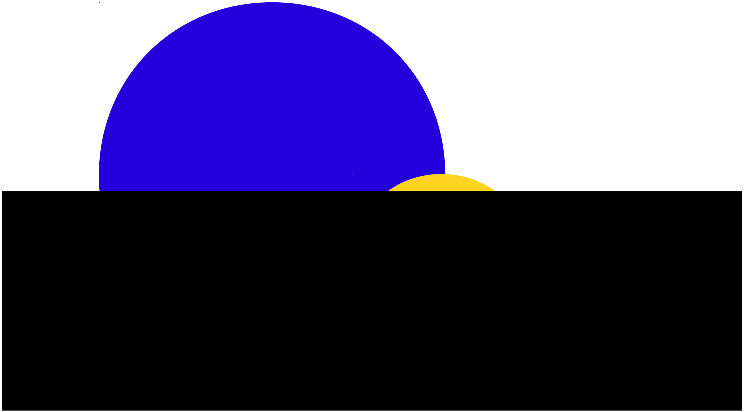
Post-Cambrian Paleozoic brachiopod genera and covariates

- time range approx. 488-252 Mya.
- stage as time unit; duration measured in stages (2-5 My each)
- multiple emergent traits analyzed; estimates vary by origination cohort
  - geographic range
  - body size
  - environmental preference (v, v^2)
- gap statistic as measure of sampling (Foote and Raup 1996 *Paleobio*)
  imputed for taxa with short durations

Hypothesis of effect of geographic range



Hypothesis of effect of geographic range

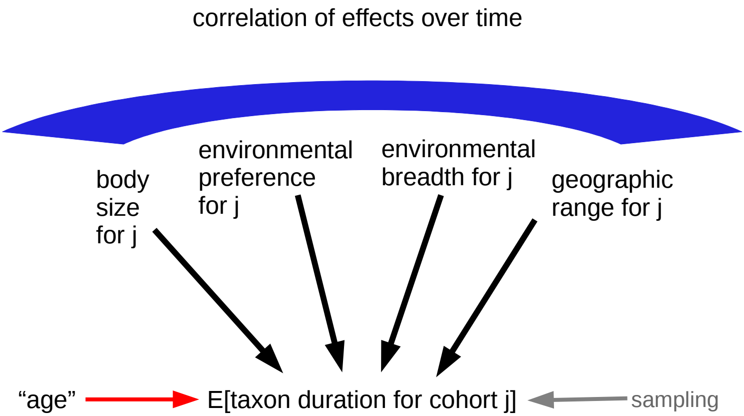


Hypotheses of effect of environmental preference

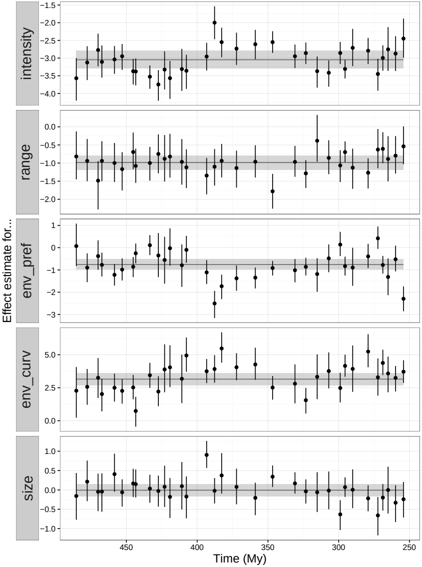
When related phyla die out . . . more specialized phyla tend to become extinct before less specialized. This phenomenon is also far from universal, but it is so common that it does deserve recognition as a rule or principle in evolutionary studies: **the rule of the survival of the relatively unspecialized.**

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

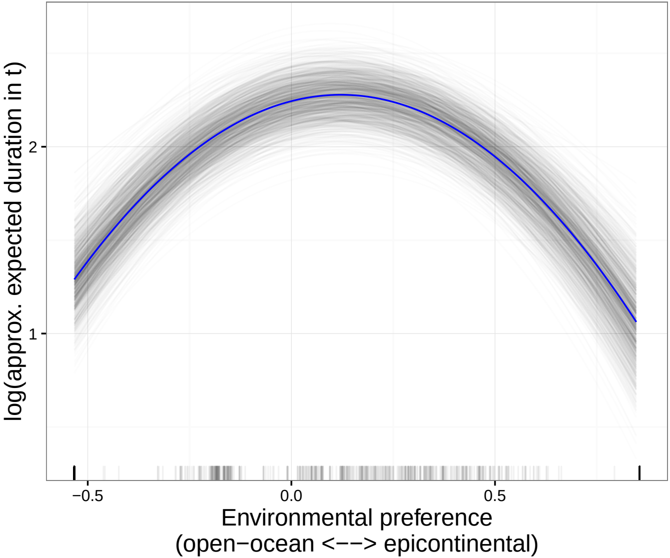
Hierarchical survival model



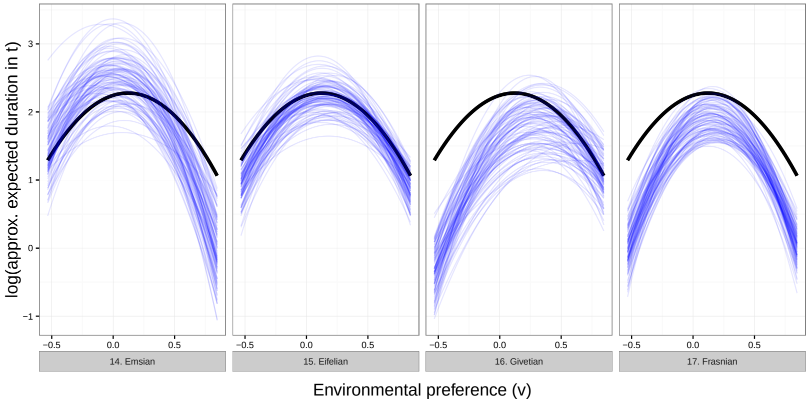
Variation in trait effects between cohorts



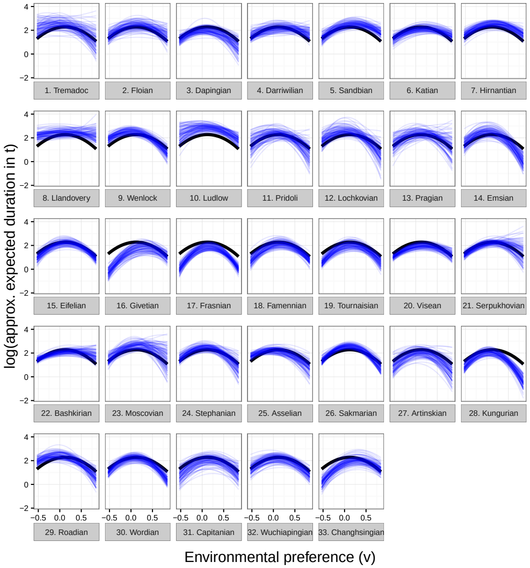
Overall effect of environmental preference



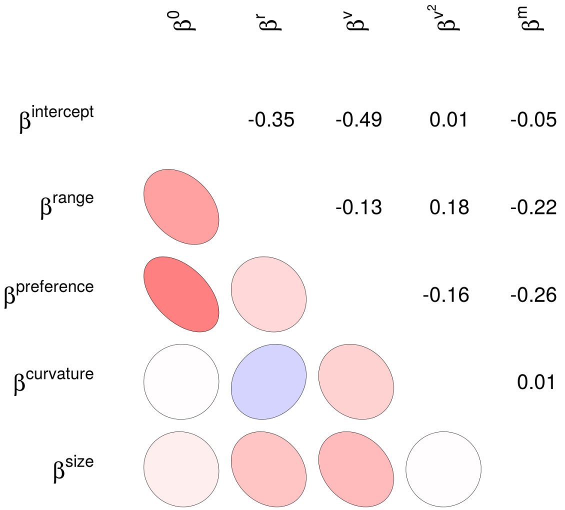
Change in effect of environment between cohorts



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

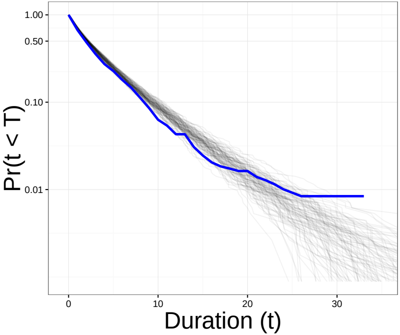
- Magnitude of effect of geographic range and environmental preference increase with extinction intensity.
- As extinction risk decreases, the differences between taxa matter less.

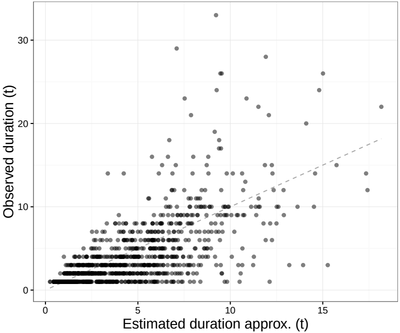
Acknowledgements

- Advising
  - Kenneth D. Angielczyk, Michael J. Foote, P. David Polly, Richard H. Ree, Graham Slater
- Angielczyk Lab
  - David Grossnickle, Dallas Krentzel, Jackie Lungmus
- Foote lab
  - Marites Villarosa Garcia, Nadia Pierrehumbert
- Stewart Edie, Elizabeth Sander, Laura Southcott, Courtney Stepien
- David Bapst, Ben Frable, **Arnold Miller**, Peter Wagner
- UChicago CEB, Sandy Carlson

The Paleobiology Database
revealing the history of life

Model adequacy





New measure of taxon's environmental affinity

(# epicontinental / total # occurrences) is what quantile of the distribution of all other background occurrences Beta(α, β).

- 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^*.

$$
\begin{aligned}
s &\sim \text{Beta}(\phi, \lambda) \\
\phi &= \text{logit}^{-1}(W\gamma) \\
s^* &\sim \text{Beta}(\phi^*, \lambda) \\
\phi^* &= \text{logit}^{-1}(W^*\gamma)
\end{aligned}
$$

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

Sampling statement for the joint posterior probability

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

$$
\begin{aligned}
\mu_{intensity} &\sim \mathcal{N}(0, 5) \\
\mu_{range} &\sim \mathcal{N}(-1, 1) \\
\mu_{envpref} &\sim \mathcal{N}(0, 1) \\
\mu_{envcurve} &\sim \mathcal{N}(1, 1) \\
\mu_{size} &\sim \mathcal{N}(0, 1) \\
\delta &\sim \mathcal{N}(0, 1) \\
\tau &\sim \text{C}^{+}(1) \\
\Omega &\sim \text{LKJ}(1) \\
\lambda &\sim \text{Pareto}(0.1, 1.5) \\
\gamma &\sim \mathcal{N}(0, 1)
\end{aligned}
$$

Note: Calculation of log probability of right and left censored observations is modified from the above

Inspecting the imputations