### 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.

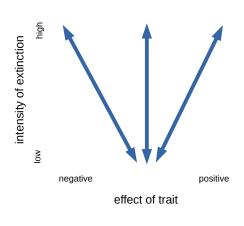
(Jablonski, 1986, Science)

### Questions and analysis

and each other?

- ► How do the effect of emergent traits on duration (extinction selectivity) vary with expected duration (extinction intensity)
  - ► 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.

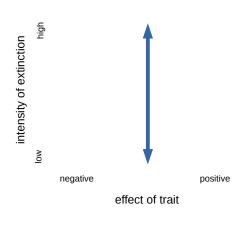
# Intensity and selectivity



# 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, x²)
  - 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

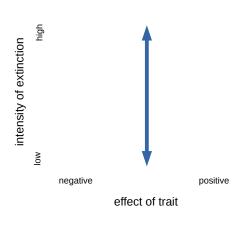


### Hypotheses of effect of environmental preference

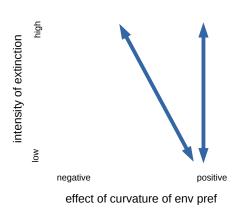
When related phyla die out ... more specialized phyla tend to become extinct before less specialized. This phenomenon is also far from universal, but it is so common that it does deserve recognition as a rule or principle in evolutionary studies: the rule of the survival of the relatively unspecialized.

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

## Hypothesis of effect environmental preference and intensity



## Hypotheses of effect of environmental breadth and intensity



### 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)

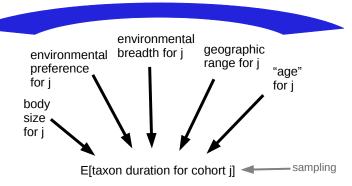
Can only be estimated for taxa with duration of three or more. Have to impute (e.g. fill-in) the values for all other taxa  $r^*$ .

$$s \sim \mathsf{Beta}(\phi, \lambda)$$
  
 $\phi = \mathsf{logit}^{-1}(W\gamma)$   
 $s^* \sim \mathsf{Beta}(\phi^*, \lambda)$   
 $\phi^* = \mathsf{logit}^{-1}(W^*\gamma)$ 

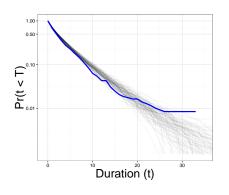
Note: Beta distribution parameterized in terms of mean  $\phi$  and total count  $\lambda$ . Also, this presentation excludes final (hyper)priors.

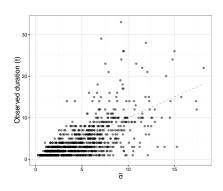
### Hierarchical survival model

#### correlation of effects over time

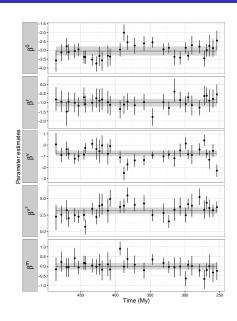


# Model adequacy

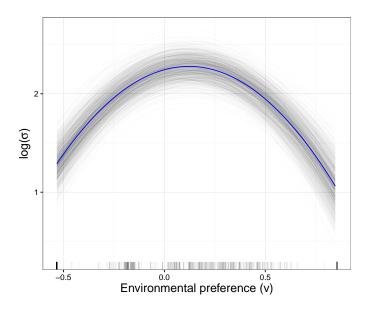




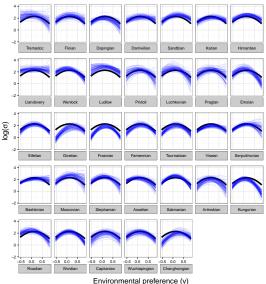
# Change in trait effects between cohorts



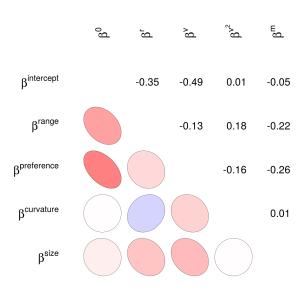
## Overall effect of environmental preference



### Change in effect of environment between cohorts



### Correlation of effects between cohorts



### Effect summary

- ► Effect of geographic range consistent with prior expectations; 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.

### 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



# New measure of taxon's environmental affinity

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

- $\bullet$   $\alpha$  is the # epicontinental background occurrences (+ 1).
  - $\blacktriangleright$   $\beta$  is the # open ocean background (+ 1).

## Sampling statement for the joint posterior probability

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

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

