Remodeling the fossil record

analysis of emergent evolutionary and ecological patterns

Peter D Smits

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The Paleobiology Database
revealing the history of life

Macroevolution and macroecology

Structured data and modelling emergent patterns

Patterns in survival

- Background extinction and expected differences in species survival
- Interplay between extinction intensity and extinction selectivity

Patterns in functional diversity

- Mammal species pool functional composition

Conclusions and commentary

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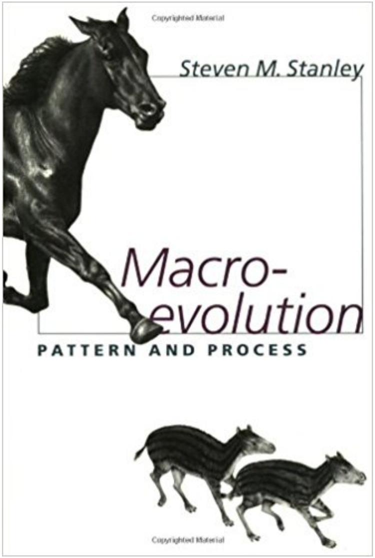
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evolution
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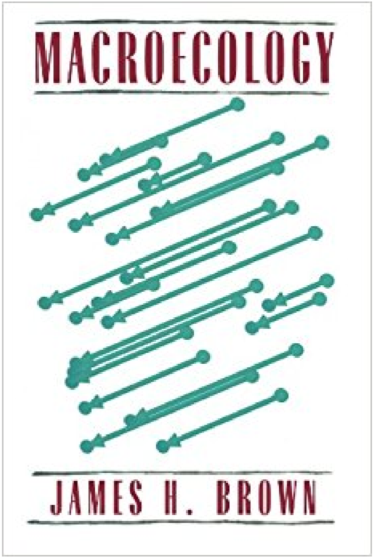

MACROECOLOGY
JAMES H. BROWN

Definition

- macroevolution: study of patterns which emerge when considering the evolutionary history of multiple species.
- macroecology: study of patterns which emerge when considering the ecology of multiple species.
- *in both time and space*

Traits as conceptual and operational link

Definition

- trait: identifiable property of an organism
  e.g. pelage color, body mass, beak depth, tooth shape
- functional trait: trait that strongly influences performance/means of interacting with environment
- species trait: identifiable property assignable to a species

Species selection

Rabosky and McCune 2010 *TREE*

> *Species selection is the outcome of heritable variation in speciation and extinction rates among taxa.*

- avoids selection versus sorting,
  "strict" species selection versus effect macroevolution

Species fitness

Cooper 1984 *J. Theoretical Biology*

Expected time till extinction.

- logic: if more fit, more likely to be present
- distribution based definition (population)
- other definitions can be derived based on definition of extinction

Law of Constant Extinction

Van Valen 1973 *Evol. Theory*

Extinction risk (species fitness), in a given adaptive zone, is taxon–age independent.

Survival of the unspecialized

Simpson 1944 *Tempo and Mode in Evolution p. 143*

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.**

Species pool concept

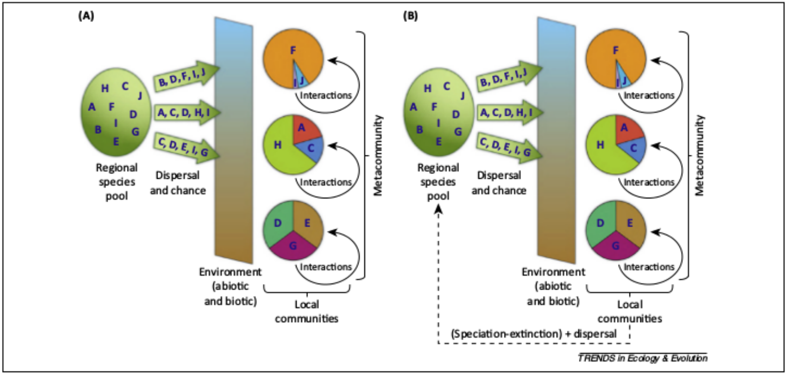
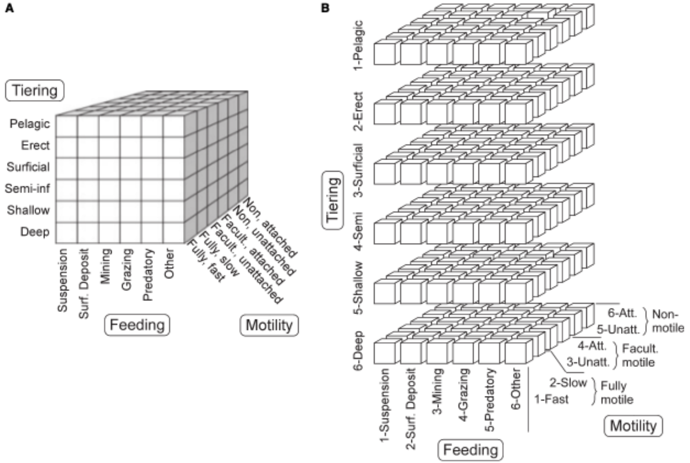


Figure 1. Two models of community assembly. **(A)** Local communities comprise a subset of species from the regional species pool that have passed through environmental filters. There is no feedback from the metacommunity (collection of local communities) to the regional species pool. Adapted from [5]. **(B)** Local communities are assembled as in (A), but speciation adds new species to the pool, extinction removes others, and dispersal allows the persistence of species that might otherwise go extinct.

(Mittelbach and Schemske 2015 *TREE*)

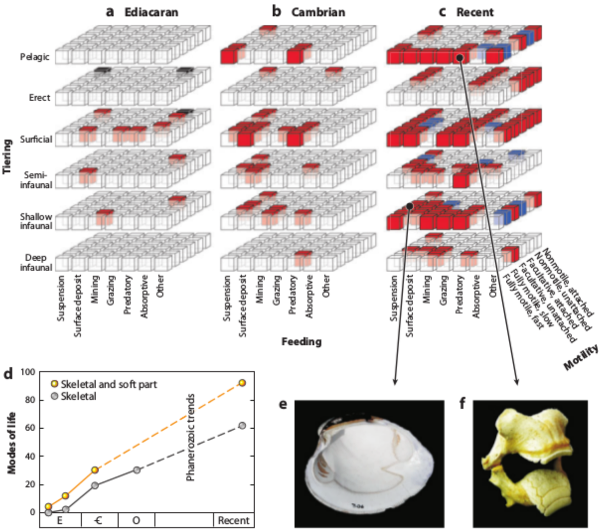
Functional groups



TEXT-FIG. 1. Ecospace as defined by the three axes of tiering, motility level and feeding strategy. A, the ecospace cube with categories on each axis labelled. B, the ecospace cube 'exploded', showing 216 'bins' or modes of life specified by the combination of the categories on each ecospace axis.

(Bambach *et al. 2007* Palaeontology)

Functional groups over time



(Bush and Bambach 2011 *Annu. Rev. Earth Planet Sci.*)

Structured data in biology and paleontology

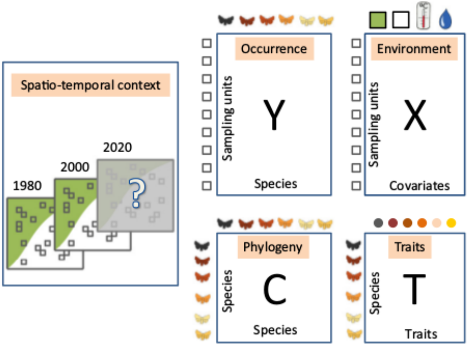
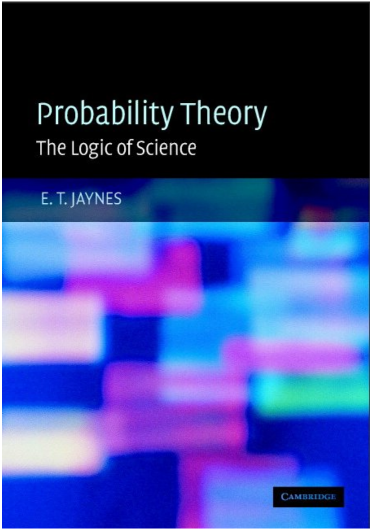


Figure 3 Data typically collected in community ecology. The occurrence data (denoted as the **Y** matrix) includes the occurrences of the species recorded in a set of temporal and/or spatial sampling units. The environmental data (denoted as the **X** matrix) consists of the environmental covariates measured over the sampling units. The traits data (denoted as the **T** matrix) consists of a set of traits measured for the species present in the **Y** matrix. To account for the phylogenetic dependencies among the species, we can include a fourth matrix consisting of the phylogenetic correlations among the species (denoted as the **C** matrix). The spatiotemporal context includes location and time information about the samples.

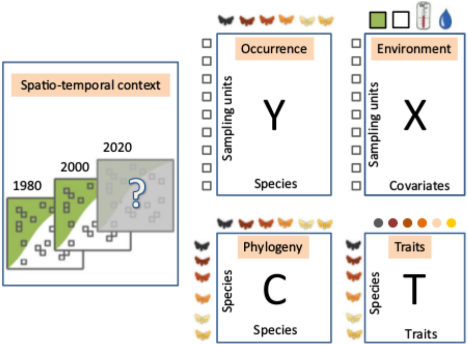
(Ovaskainen *et al.* 2017 *Ecology Letters*)

Inference



The theory of probability is the only mathematical tool available to help map the unknown and the uncontrollable.
(Mandelbrot)

Structured data in biology and paleontology



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(Ovaskainen *et al.* 2017 *Ecology Letters*)

Models of structured data

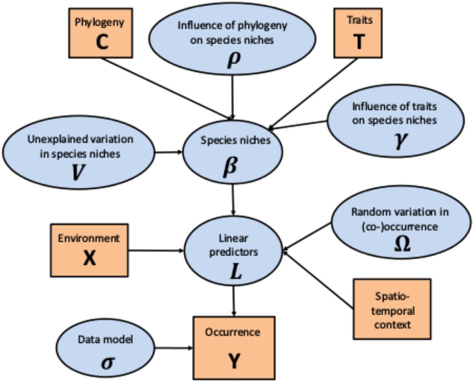
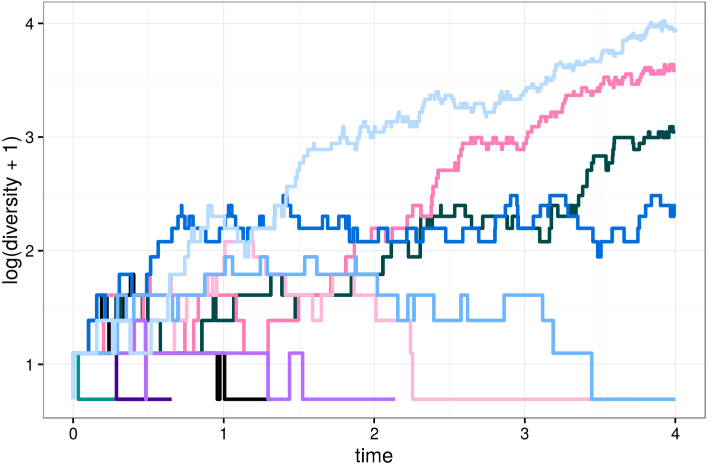


Figure 4 A graphical summary of the HMSC statistical framework. In this Directed Acyclic Graph (DAG), the orange boxes refer to data, the blue ellipses to parameters to be estimated, and the arrows to functional relationships described with the help of statistical distributions.

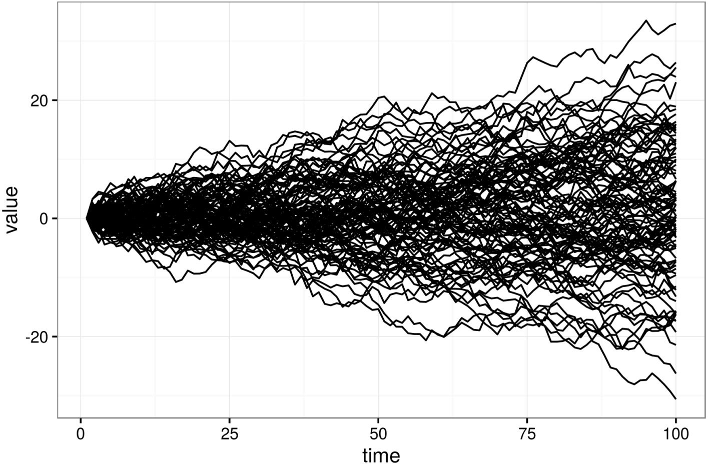
(Ovaskainen *et al.* 2017 *Ecology Letters*)

Models in macroevolution: birth-death



$$m_t = ae^{(\lambda-\mu)t}$$

Models in macroevolution: Brownian motion

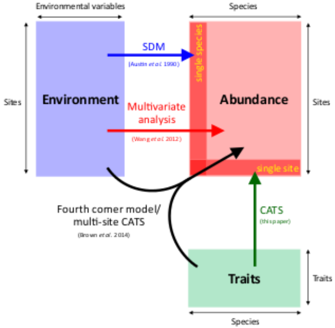


$$x_t - x_s \sim \mathcal{N}(\mu, \sigma)$$

Models in macroecology: species distribution models

Goal

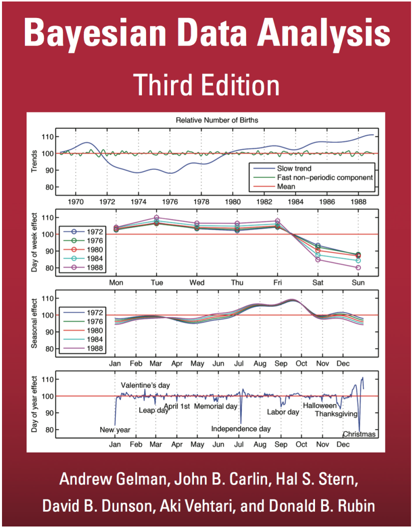
Understand species distribution in space (and time) as function of that species' environmental context or species trait values.



(Warton *et al.* 2015 *Methods Ecol. Evol.*)

Bayesian inference and statistics

- flexible, expressive, intuitive
- regularize, partial pooling, external information
- Stan probabilistic programming language
  - Hamiltonian Monte Carlo
  - Automatic Differentiation Variational Inference



Mammals and brachiopods

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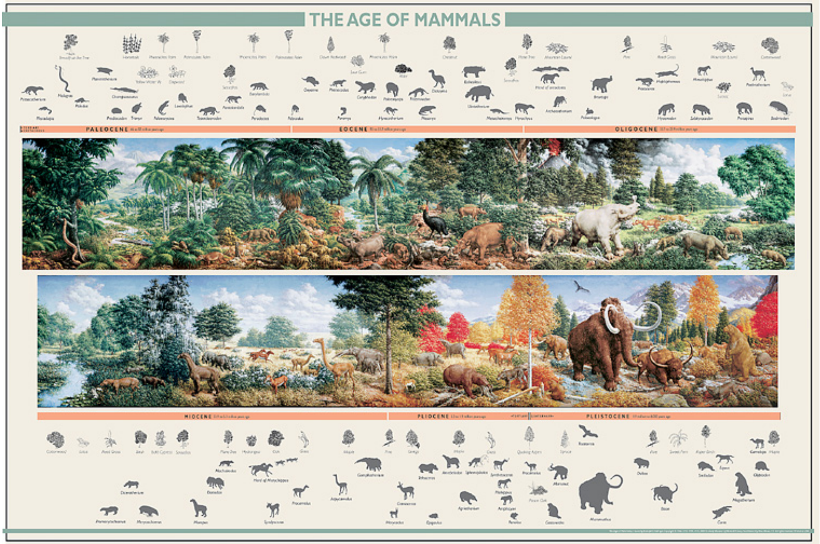
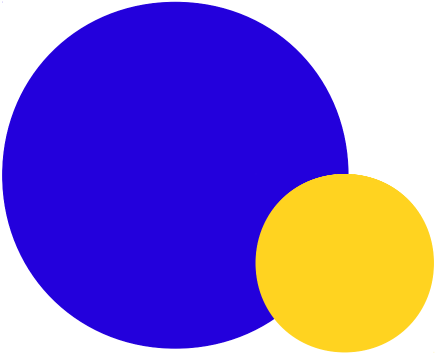
Age of Mammals



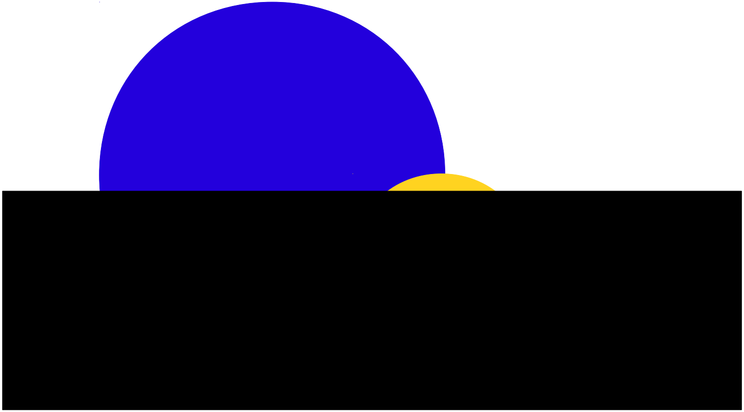
Motivating questions

- How do mammal species traits affect extinction risk?
  - How do shared time of origination or evolutionary history relate to extinction risk?
- How do my findings compare to current risk factors?
- Is species extinction risk age-independent?

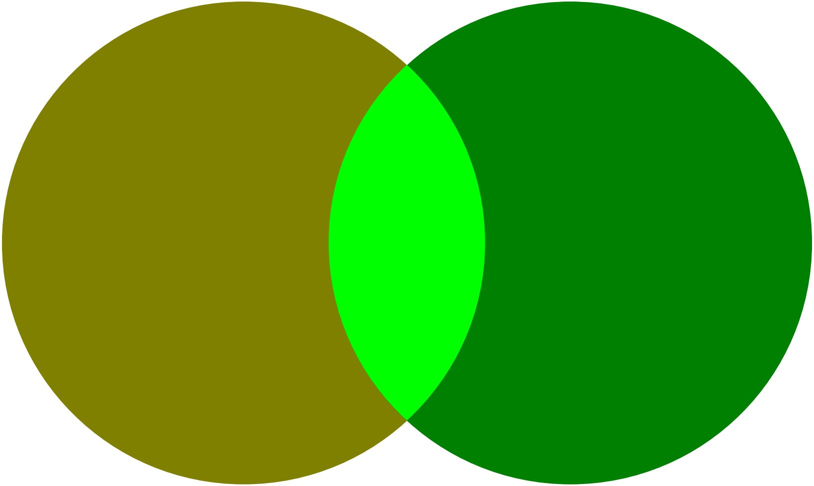
Relationship between range size and extinction risk



Relationship between range size and extinction risk



Hypotheses of effects of locomotor category



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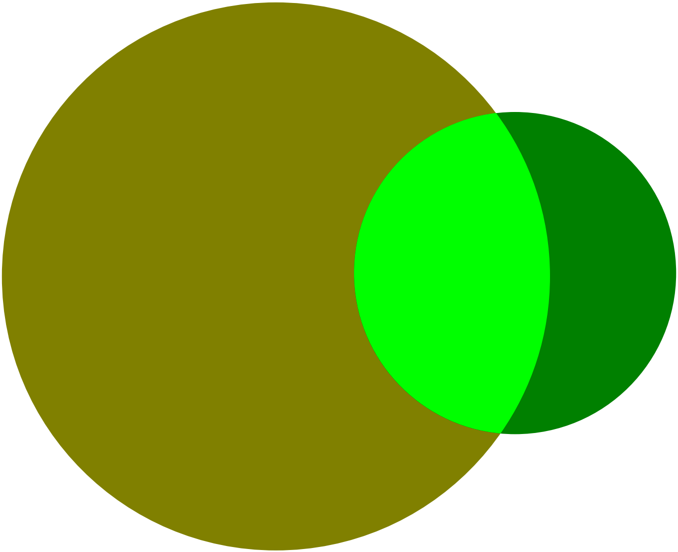
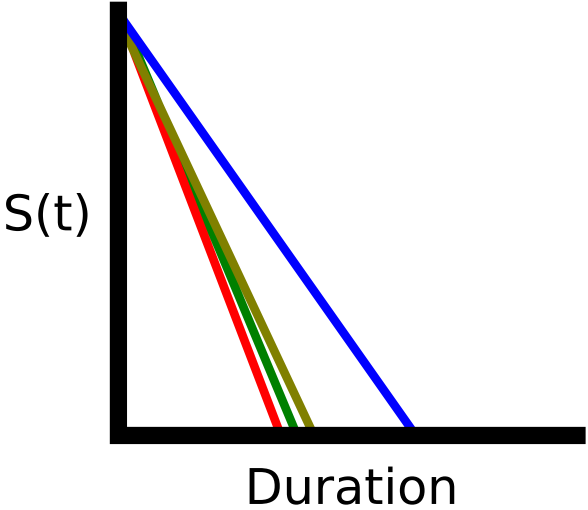
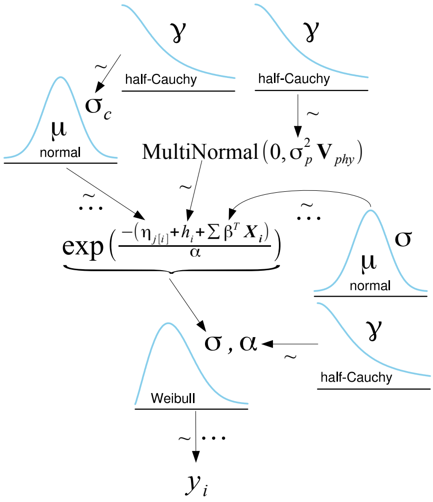


Hypotheses of effects of dietary category

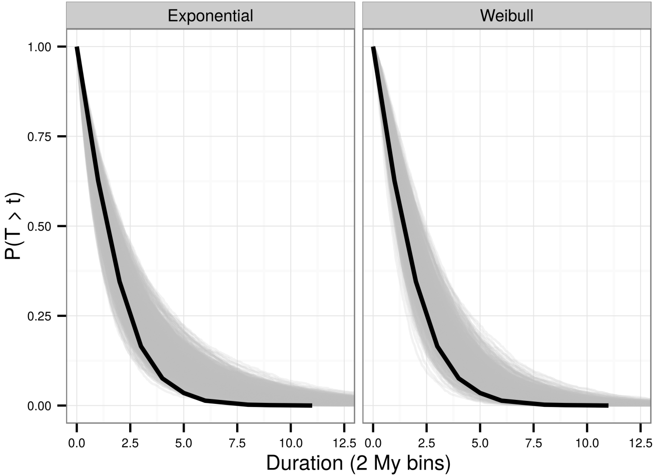


Survival model diagram



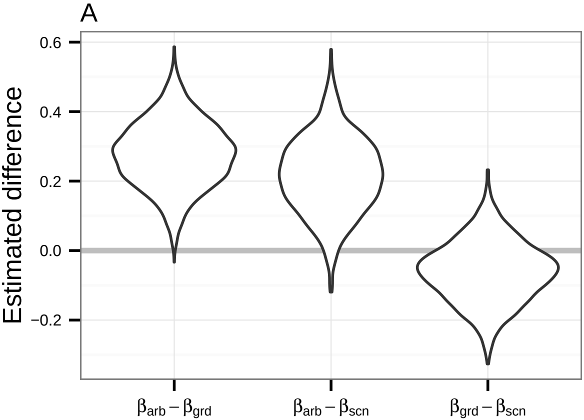
$$y_i \sim \text{Weibull}(\sigma, \alpha)$$
$$\eta_{j[i]} \sim \text{Normal}(0, \sigma_c)$$
$$\sigma_c \sim \text{half-Cauchy}(2.5)$$
$$h_i \sim \text{MultiNormal}(0, \Sigma)$$
$$\Sigma = \sigma_p^2 \mathbf{V}_{phy}$$
$$\sigma_p \sim \text{half-Cauchy}(2.5)$$
$$\beta \sim \text{Normal}(0, 10)$$
$$\alpha \sim \text{half-Cauchy}(2.5)$$

Pattern of species survival under two models



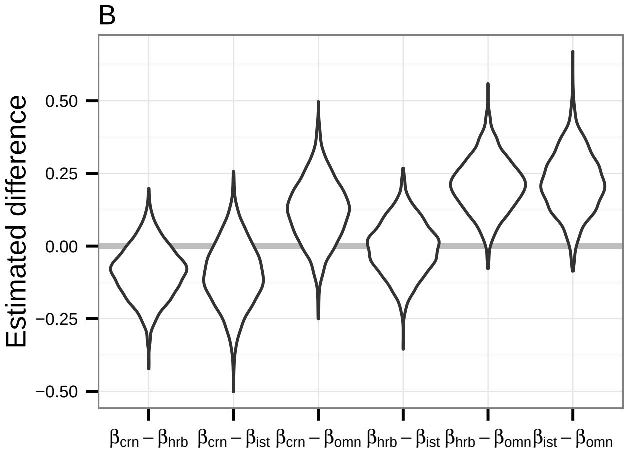
(Smits 2015 *PNAS*)

Effect of locomotor category on extinction risk



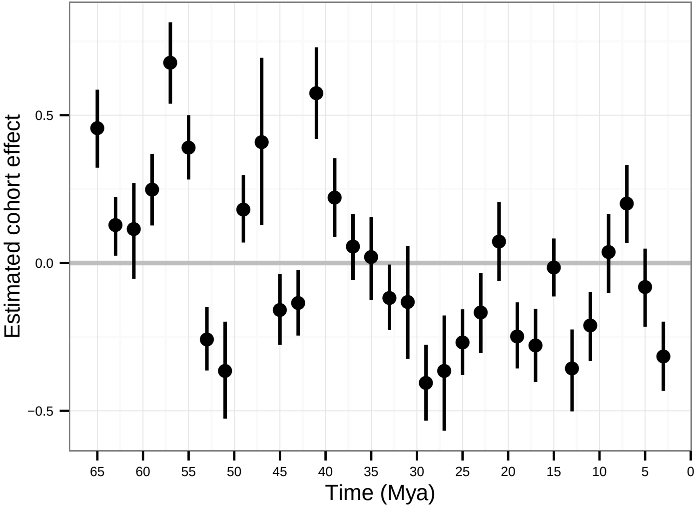
(Smits 2015 *PNAS*)

Effect of dietary category on extinction risk



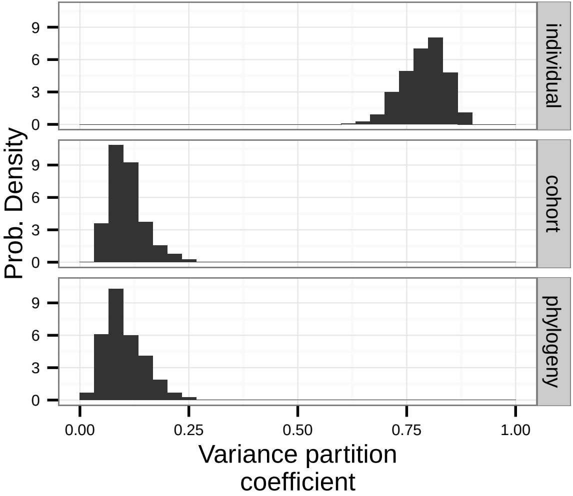
(Smits 2015 *PNAS*)

Difference in risk between origination cohorts



(Smits 2015 *PNAS*)

Three sources of variance



(Smits 2015 *PNAS*)

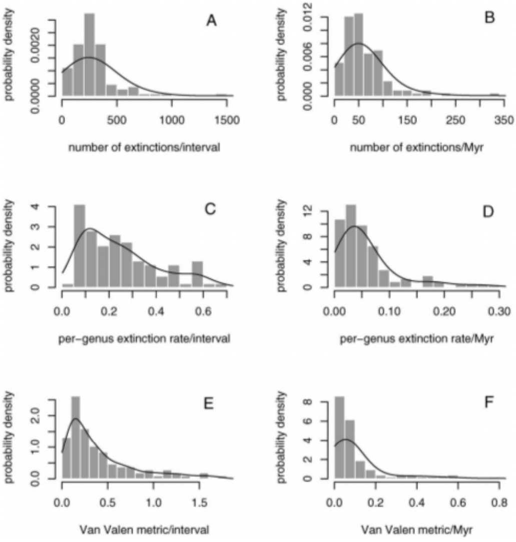
Summary of results

- Survival of the unspecialized as time-invariant generalization.
- Decrease in extinction risk with time.
  - Both cohort/temporal and phylogenetic effect.
- Some incongruence with risk factors in the Recent.
  - e.g. effect of body size, trophic category, phylogenetic clustering.

Jablonski 1986 *Science*

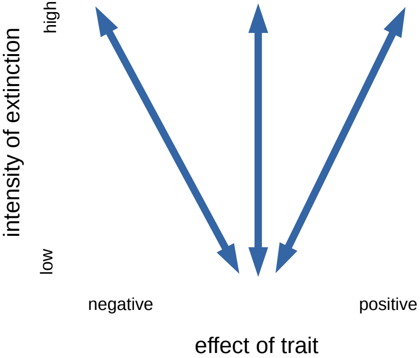
At K/Pg mass extinction, biological traits (except geographic range) have no effect on bivalve taxonomic survival.

Variation in extinction rate



(Wang 2003 *Paleobio.*)

Intensity and selectivity



Questions and analysis

How do the effect of traits on duration (extinction selectivity) vary with expected duration (extinction intensity)?

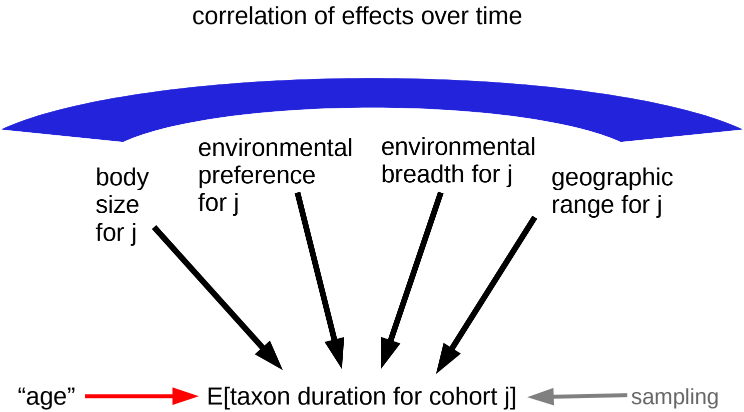
Brachiopods

(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)
- effect of traits varies 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*

Hierarchical survival model



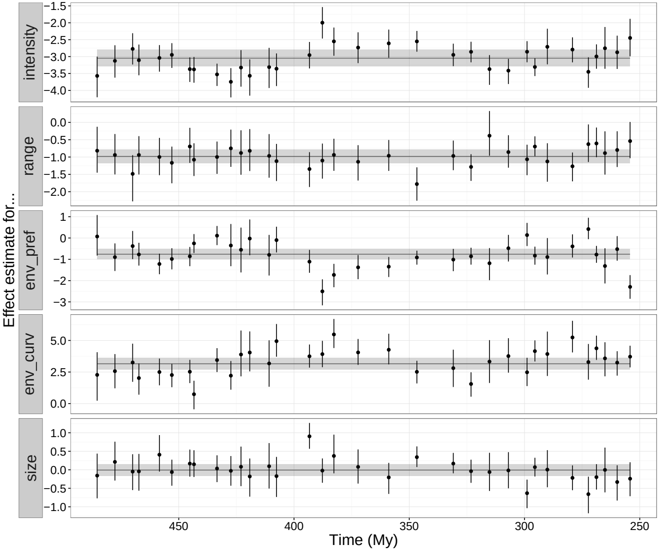
Sampling statement for the joint posterior probability

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

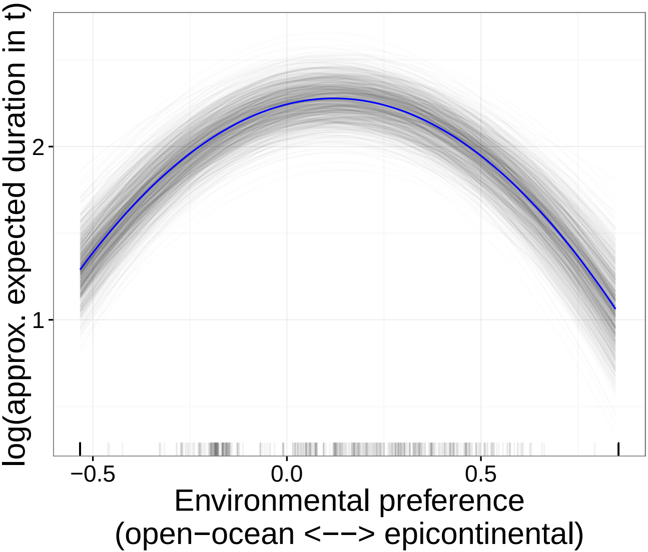
$$
\begin{aligned}
\mu_{intensity} &\sim \mathcal{N}(0, 5) \\
\mu_{range} &\sim \mathcal{N}(-1, 1) \\
\mu_{envpref} &\sim \mathcal{N}(0, 1) \\
\mu_{envcurve} &\sim \mathcal{N}(1, 1) \\
\mu_{size} &\sim \mathcal{N}(0, 1) \\
\delta &\sim \mathcal{N}(0, 1) \\
\tau &\sim \text{C}^{+}(1) \\
\Omega &\sim \text{LKJ}(1)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

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

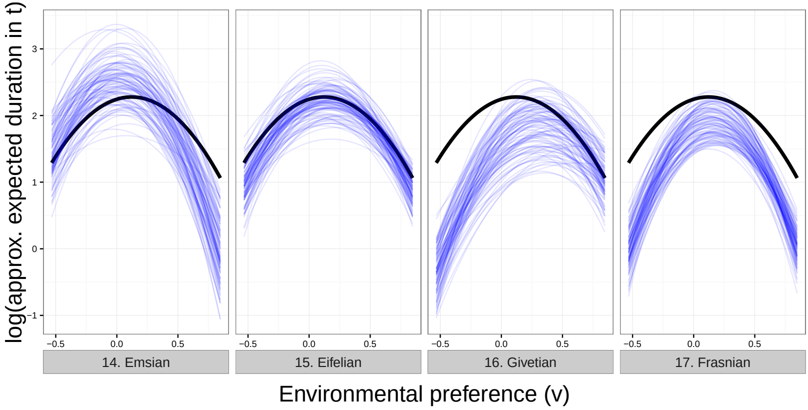
Variation in trait effects between cohorts



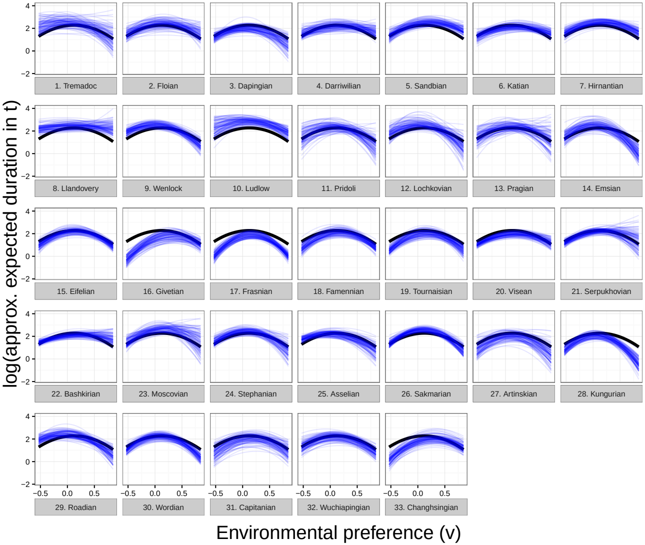
Overall effect of environmental preference



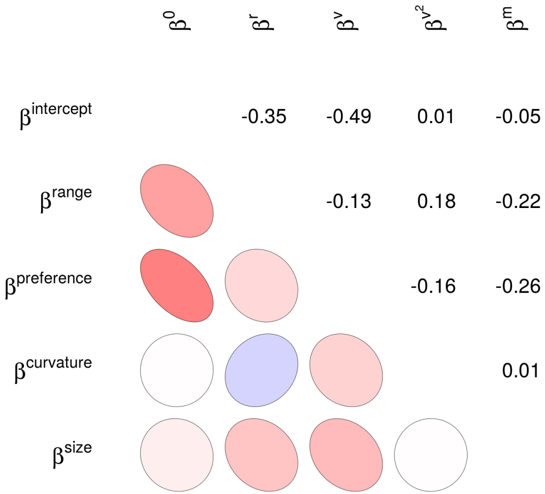
Change in effect of environment between cohorts



Change in effect of environment between cohorts



Correlation of effects between cohorts



Summary of results

- Effect of geographic range consistent with prior expectations; low variance.
- No effect of body size; low variance.
- Epicontinental environmental preference slightly favored on average; 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.
- Evidence for qualitative difference between mass and background extinction.

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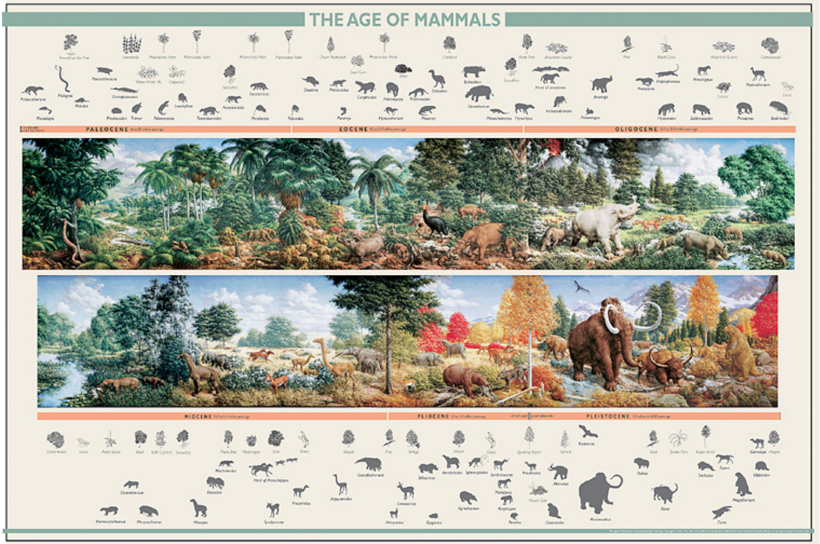
Conclusions and commentary

Question

When are certain ecologies, ecotypes, or functional groups enriched or depleted in a species pool?

Age of Mammals



relative expected species duration

short ⟷ long

locomotor	short	long
	arboreal	ground dwelling, scansorial

diet	short		long
	insectivore, herbivore	carnivore	omnivore

(Smits 2015 *PNAS*)

Fourth-corner modelling problem

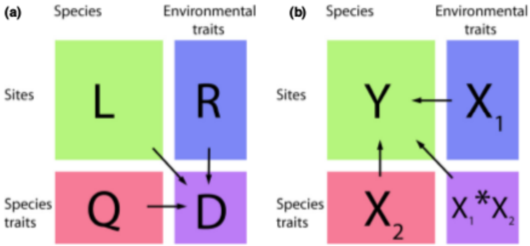
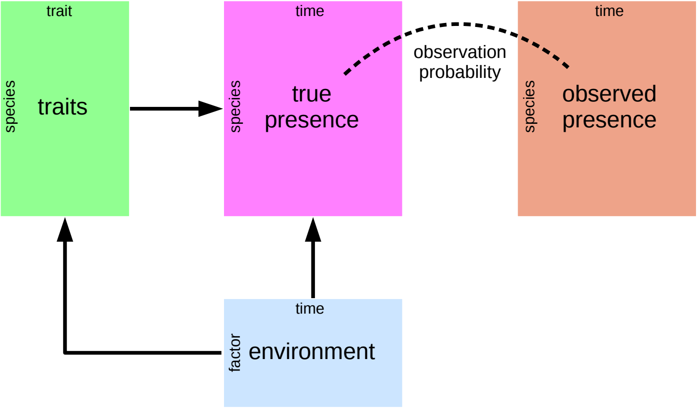


Fig. 1. Graphical representation of the fourth-corner problem and its solution. (a) The problem as posed by Legendre, Galzin & Harmelin-Vivien (1997), where the goal is to combine abundance (**L**), trait (**Q**) and environment (**R**) data in some way, to determine a matrix describing the trait–environment relationship (**D**). (b) The proposed model-based solution to the fourth-corner problem, where the goal is to predict abundance (**Y**) as a function of predictor variables for environment ($\mathbf{X}_1$), species traits ($\mathbf{X}_2$) and their interaction ($\mathbf{X}_1 * \mathbf{X}_2$). The matrix of coefficients for the interaction between $\mathbf{X}_1$ and $\mathbf{X}_2$ is the fourth corner.

(Brown *et al. 2014* Methods Ecol. Evol.)

Paleontological fourth-corner model



Covariates of interest

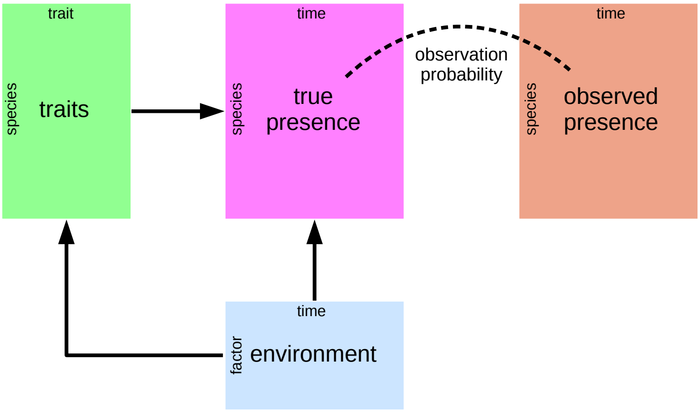
individual-level
(species i at time unit t)

- ecotype: combination diet and locomotor categories
  - effect is function of group-level covariates
- body size
  (rescaled log body mass)

group-level (2 My time unit t)

- temperature record based on Mg/Ca estimates
  - mean and range
    (rescaled log degrees)
- plant community phase following Graham 2011

Paleontological fourth-corner model

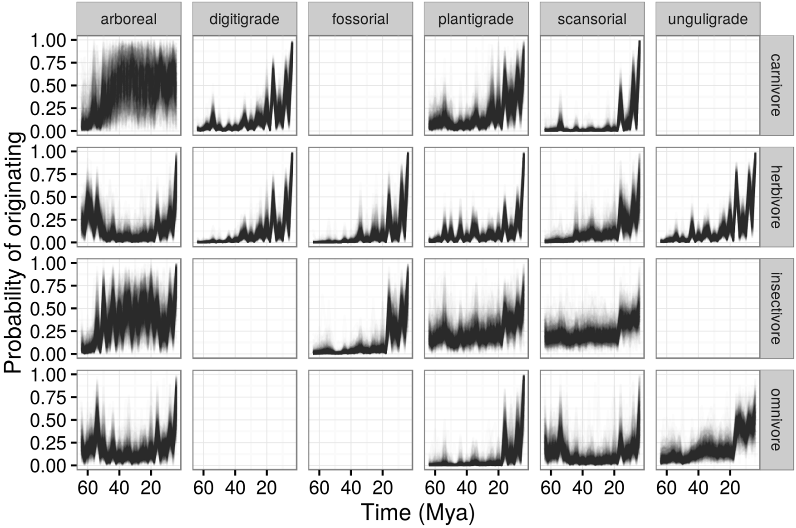


Model and sampling statement definition

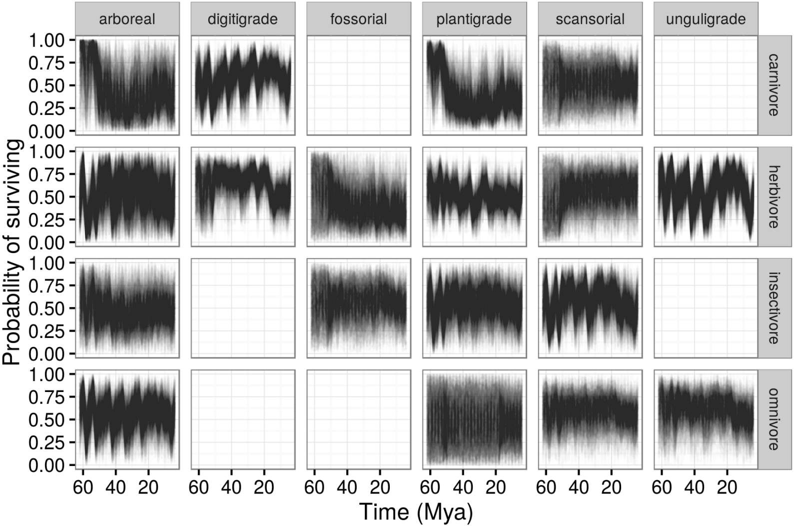
$$
\begin{aligned}
y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) \\
p_{i,t} &= \text{logit}^{-1}(\alpha_0 + \alpha_1 m_i + r_t) \\
r_t &\sim \mathcal{N}(0, \sigma) \\
\alpha_0 &\sim \mathcal{N}(0, 1) \\
\alpha_1 &\sim \mathcal{N}(1, 1) \\
\sigma &\sim \mathcal{N}^+(1) \\
z_{i,1} &\sim \text{Bernoulli}(\phi_{i,1}) \\
z_{i,t} &\sim \text{Bernoulli}\left(z_{i,t-1}\pi_{i,t} + \sum_{x=1}^{t}(1 - z_{i,x})\phi_{i,t}\right) \\
\phi_{i,t} &= \text{logit}^{-1}(a^{\phi}_{t,j[i]} + b^{\phi}_1 m_i + b^{\phi}_2 m_i^2) \\
\pi_{i,t} &= \text{logit}^{-1}(a^{\pi}_{t,j[i]} + b^{\pi}_1 m_i + b^{\pi}_2 m_i^2) \\
a^{\phi} &\sim \text{MVN}(U\gamma^{\phi}, \Sigma^{\phi}) \\
a^{\pi} &\sim \text{MVN}(U\gamma^{\pi}, \Sigma^{\pi})
\end{aligned}
$$

$$
\begin{aligned}
\Sigma^{\phi} &= \text{diag}(\tau^{\phi})\Omega^{\phi}\text{diag}(\tau^{\phi}) \\
\Sigma^{\pi} &= \text{diag}(\tau^{\pi})\Omega^{\pi}\text{diag}(\tau^{\pi}) \\
\rho &\sim \text{U}(0, 1) \\
b^{\phi}_1 &\sim \mathcal{N}(0, 1) \\
b^{\pi}_1 &\sim \mathcal{N}(0, 1) \\
b^{\phi}_2 &\sim \mathcal{N}(-1, 1) \\
b^{\pi}_2 &\sim \mathcal{N}(-1, 1) \\
\gamma^{\phi} &\sim \mathcal{N}(0, 1) \\
\gamma^{\pi} &\sim \mathcal{N}(0, 1) \\
\tau^{\phi} &\sim \mathcal{N}^+(1) \\
\tau^{\pi} &\sim \mathcal{N}^+(1) \\
\Omega^{\phi} &\sim \text{LKJ}(2) \\
\Omega^{\pi} &\sim \text{LKJ}(2).
\end{aligned}
$$

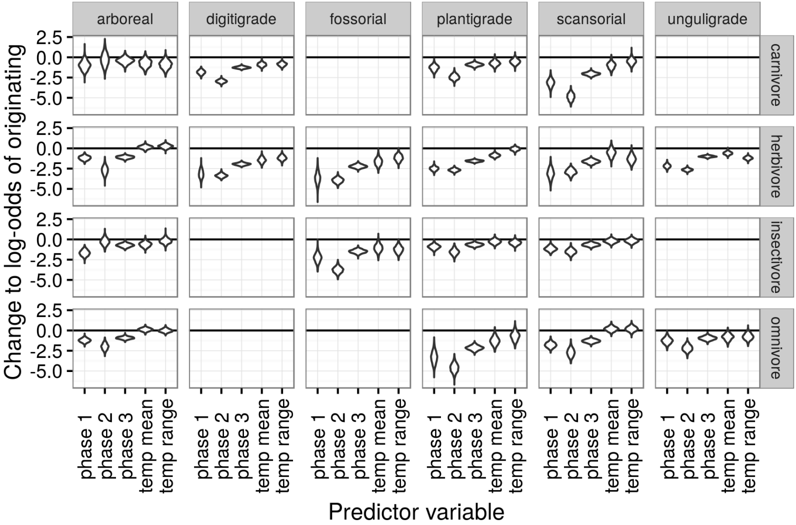
Probability of ecotype origination



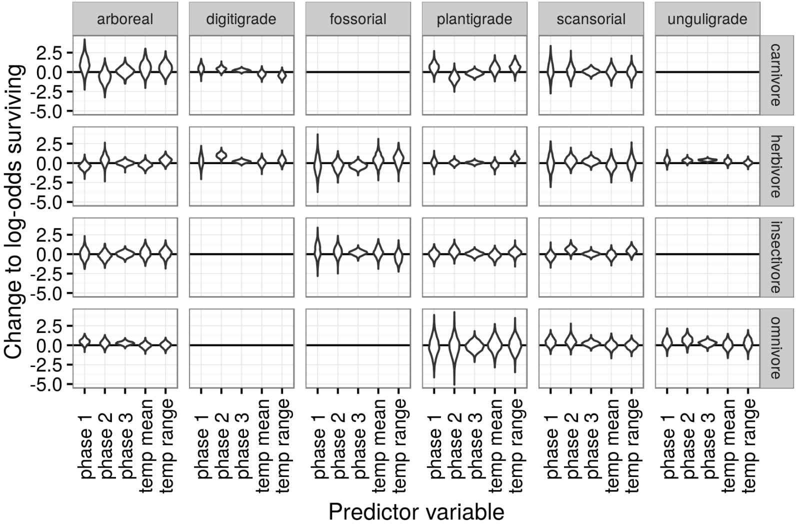
Probability of ecotype survival



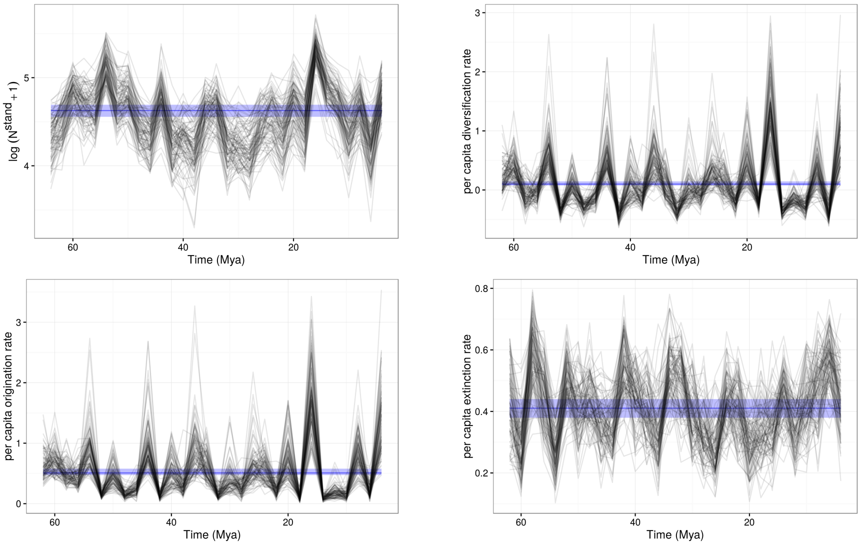
Group-level effects (plant phase, climate) on origination



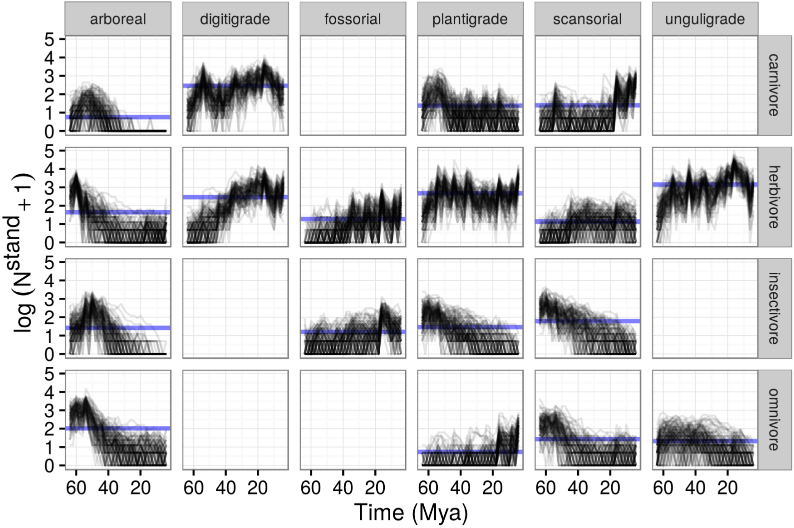
Group-level effects (plant phase, climate) on survival



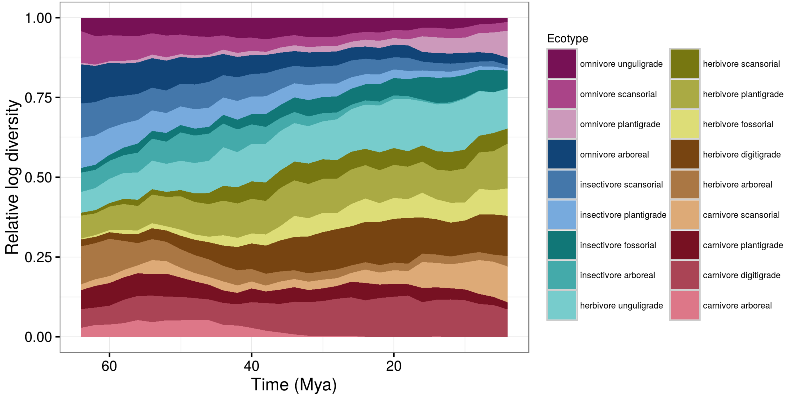
Total species pool diversity and diversification



Ecotype-specific diversity



Relative ecotype diversity



Summary of results

- changes to ecotype composition driven by origination, not extinction
  - specific ecotypes source of most variation in overall origination
- arboreal taxa decrease through Paleogene, all but absent by Neogene
- digitigrade and unguligrade herbivores only groups with sustained increase
- environmental covariates virtually always affect origination, not survival

Macroevolution and macroecology

Structured data and modelling emergent patterns

Patterns in survival

Background extinction and expected differences in species survival

Interplay between extinction intensity and extinction selectivity

Patterns in functional diversity

Mammal species pool functional composition

Conclusions and commentary

High level review

- macroevolution and macroecology devoted to explaining emergent patterns in evolution and ecology

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- Gelman: “big data are messy. messy data need large models. large models need Bayesian inference.”

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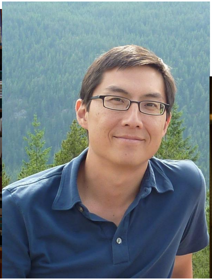
- functional diversity
  - hypotheses from macroevolution can inspire macroecological study
  - model unifies macroevolutionary and macroecological frameworks

Acknowledgements

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The Paleobiology Database
revealing the history of life

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