

Modeling changes to the functional composition of North American mammal diversity

multi-level dynamics of a regional species pool

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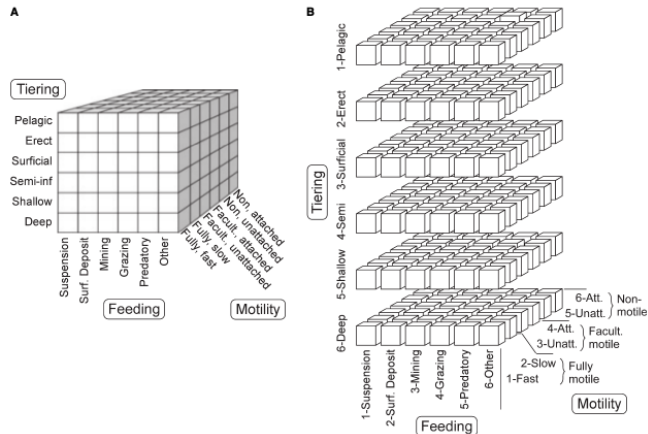
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Question

Why do the relative diversities of functional groups change within a species pool?

- ▶ function of **species traits** and **environmental context**

Eco-cube and 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.

Species pool concept

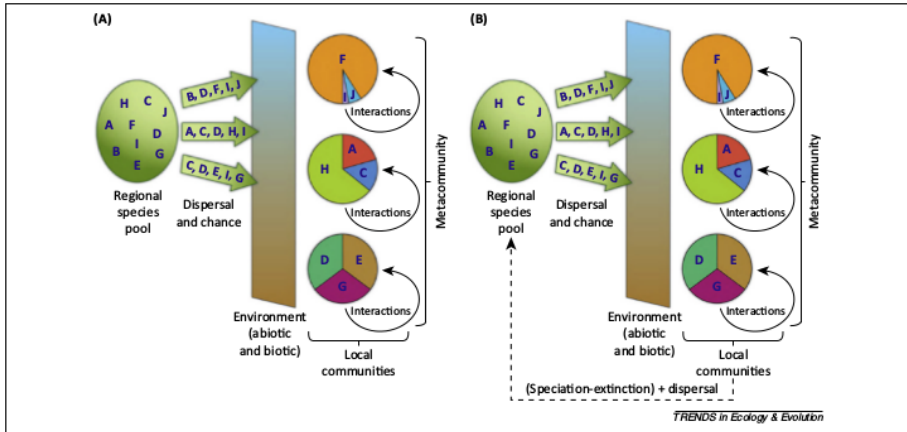
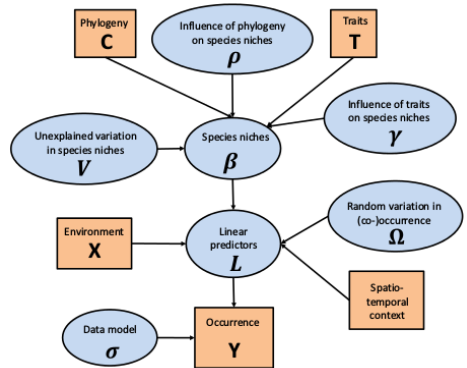
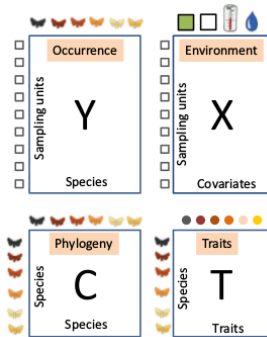
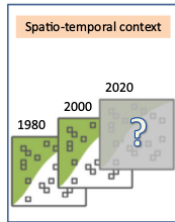


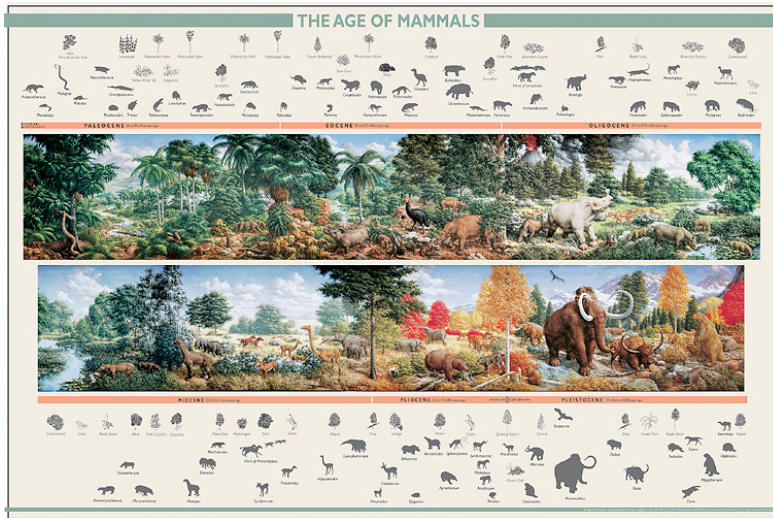
Figure 1. Two models of community assembly. **(A)** Local communities comprise a subset of species from the regional species pool that have passed through environmental filters. There is no feedback from the metacommunity (collection of local communities) to the regional species pool. Adapted from [5]. **(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.

Structured, multi-level data in biology



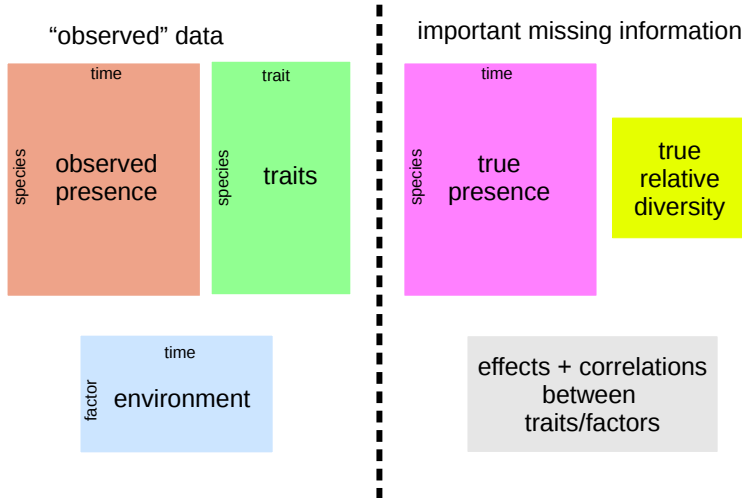
(Ovaskainen *et al.* 2017 *Ecology Letters*)

Cenozoic mammals of North America



(Rudolph Zallinger)

Conceptualizing the knowns and unknowns



Covariates of interest, temporal structure

species occurrence (~ 1400 species) per NALMA

functional group

- ▶ dietary category:
carnivore, herbivore, insectivore,
omnivore
- ▶ locomotor category:
arboreal, digitigrade, fossorial,
plantigrade, scansorial, unguligrade

observation

- ▶ indiv-level: species
 - ▶ functional group
 - ▶ mean mass
- ▶ time of observation

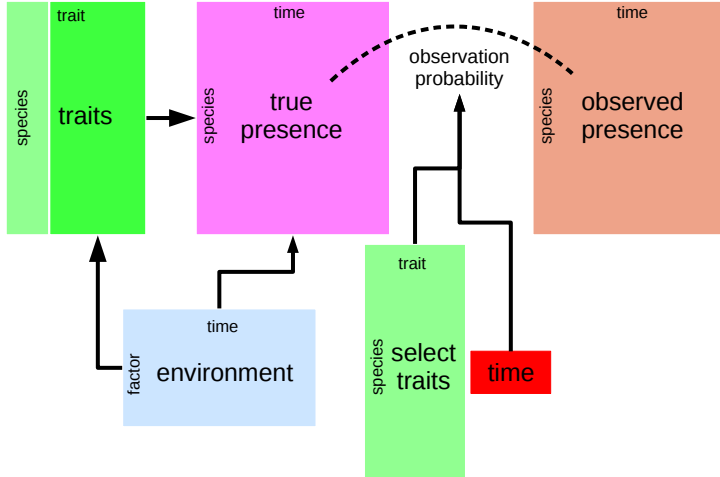
origination

- ▶ indiv-level: species
 - ▶ functional group
 - ▶ taxon order
 - ▶ mean mass
- ▶ group-level: FG/time
 - ▶ temperature est
Mg/Ca
 - ▶ plant phase
(Pa-Eo, Eo-Mi, Mi-Pi)

survival

- ▶ indiv-level: species
 - ▶ functional group
 - ▶ taxon order
 - ▶ mean mass
- ▶ group-level: FG/time
 - ▶ temperature est
Mg/Ca
 - ▶ plant phase
(Pa-Eo, Eo-Mi, Mi-Pi)

Conceptualizing the analysis



Hidden Markov Model with absorbing state

Jolly-Seber CMR/Restricted occupancy model

$$y_{i,t} \sim \text{Bernoulli}(z_{i,t}p_{i,t})$$

$$z_{i,t=1} \sim \text{Bernoulli}(\phi_{i,t=1})$$

$$z_{i,t} \sim \text{Bernoulli} \left(z_{i,t-1}\pi_{i,t} + \sum_{x=1}^t (1 - z_{i,x})\phi_{i,t} \right)$$

y observed state; z estimated state

p observation; ϕ origination; π survival

i in N ; t in T

Modeling the probabilities; individual-level

Multi-level logistic regression

$$p_{i,t} \sim \text{logit}^{-1}(b_t + e_{j[i]} + \beta^p \text{mass}_i)$$

$$\phi_{i,t} \sim \text{logit}^{-1}(f_{j[i],t}^{\phi} + o_{k[i]}^{\phi} + \beta^{\phi} \text{mass}_i)$$

$$\pi_{i,t} \sim \text{logit}^{-1}(f_{j[i],t}^{\pi} + o_{k[i]}^{\pi} + \beta^{\pi} \text{mass}_i)$$

observation: b_t time-varying intercept; $e_{j[i]}$ functional group eff; β^p mass eff

origination: $f_{j[i],t}^{\phi}$ time/FG-varying intercept; $o_{k[i]}^{\phi}$ order eff; β^{ϕ} mass eff

survival: $f_{j[i],t}^{\pi}$ time/FG-varying intercept; $o_{k[i]}^{\pi}$ order eff; β^{π} mass eff

Modeling the probabilities; group-level

Multivariate regression of time/FG-varying intercept

$$f^{\phi} \sim \text{MVN} \left(\begin{pmatrix} U\gamma_{j=1}^{\phi} \\ \vdots \\ U\gamma_{j=J}^{\phi} \end{pmatrix}, \text{diag}(\tau_{f\phi})\Omega_{f\phi}\text{diag}(\tau_{f\phi}) \right)$$
$$f^{\pi} \sim \text{MVN} \left(\begin{pmatrix} U\gamma_{j=1}^{\pi} \\ \vdots \\ U\gamma_{j=J}^{\pi} \end{pmatrix}, \text{diag}(\tau_{f\pi})\Omega_{f\pi}\text{diag}(\tau_{f\pi}) \right)$$

U matrix group-level covariates; γ^{ϕ} , γ^{π} vectors group-level reg coefs

Ω_{ϕ} , Ω_{π} corr matrix of FG by time; τ_{ϕ} , τ^{π} scale of FG by time

Modeling the probabilities; final details

Comments on priors, implementation

- ▶ random-walk priors on time-varying intercepts
- ▶ regularizing priors with some specific predictions
 - ▶ very weak/no effect of mass e.g. $\mathcal{N}(0, 0.5)$
 - ▶ very weak/no effect of group-level covariates e.g. $\mathcal{N}(0, 0.5)$
 - ▶ very weak/no correlation b/w functional groups e.g. LKJ(2)
- ▶ marginalization problem b/c gradient based estimation

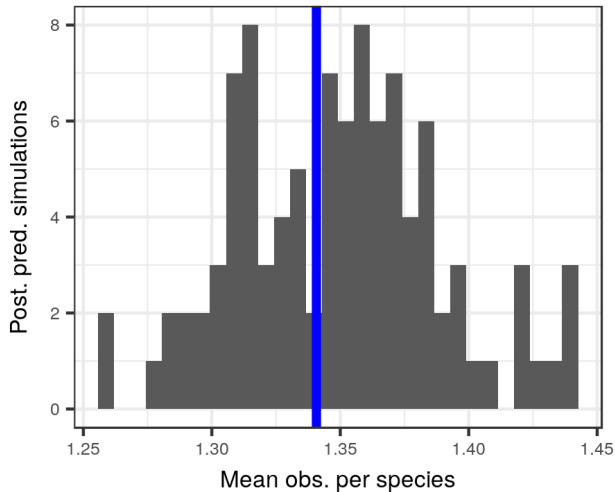
- ▶ **Bayesian inference**
 - ▶ intuitive and expressive
 - ▶ regularization/partial pooling
 - ▶ external information
- ▶ **Automatic Differentiation Variational Inference (ADVI)**
 - ▶ when full HMC/MCMC slow
 - ▶ approx Bayesian inference; assumes posterior is Gaussian
 - ▶ true Bayesian posterior



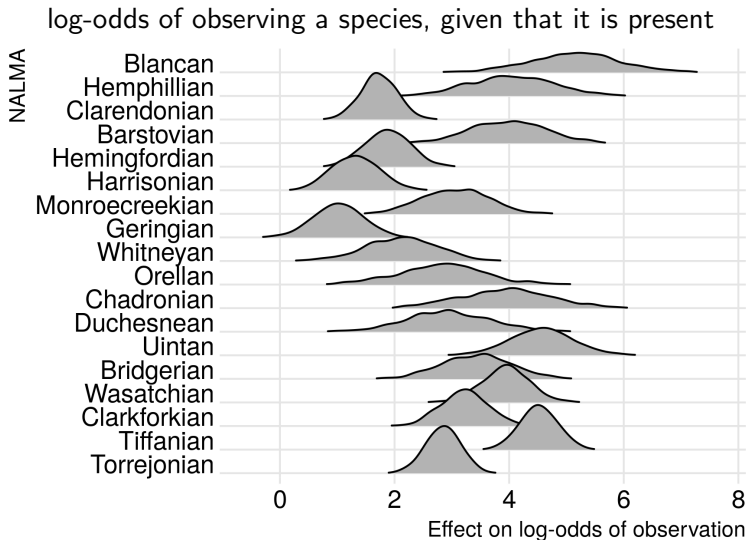
Stan

Model adequate? Posterior predictive check

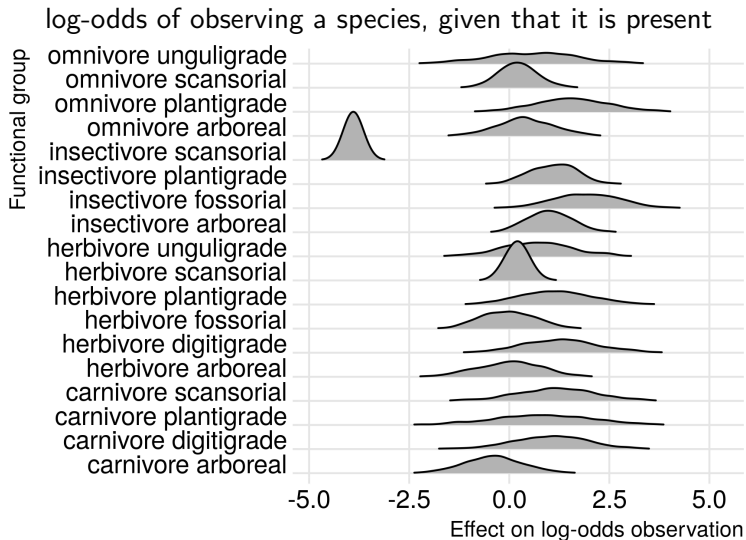
mean # occurrences per species from datasets simulated from posterior



Observation; NALMA

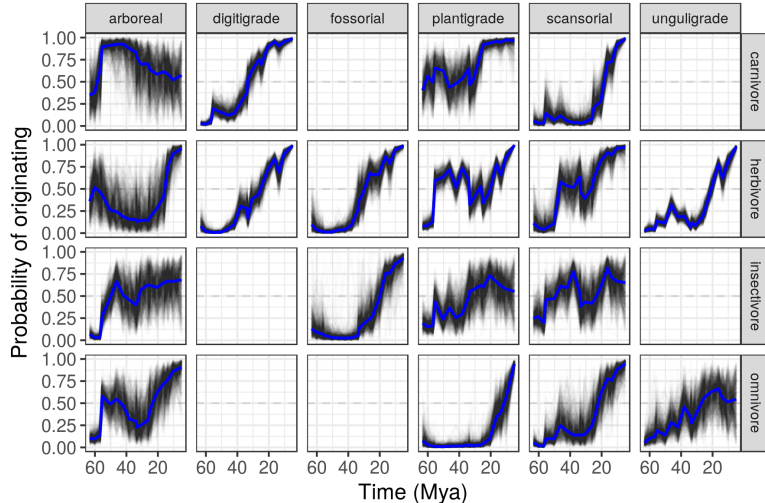


Observation; functional group



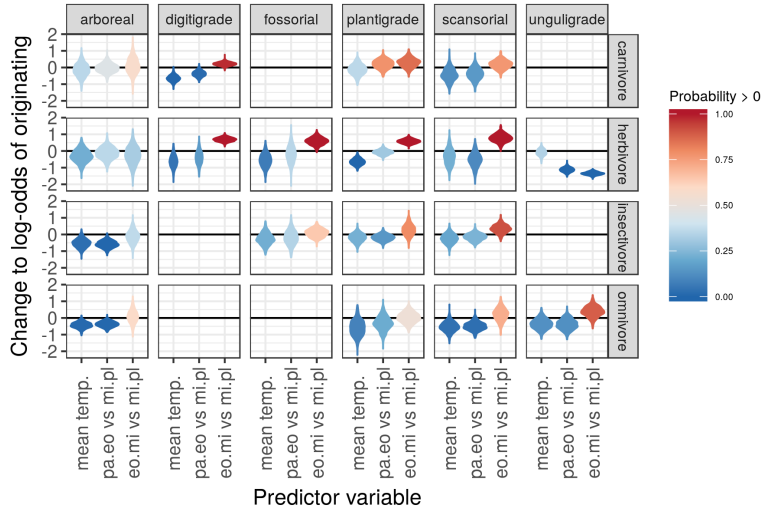
Origination; individual-level

probability of species originating, given it hasn't originated yet



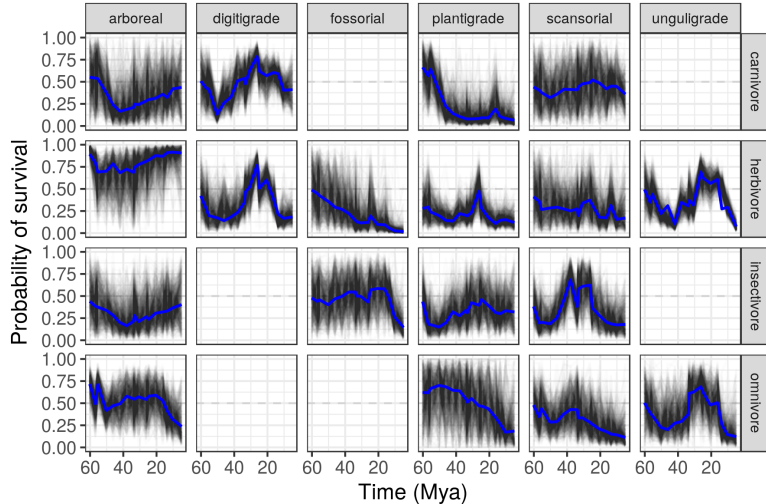
Origination; group-level

change to log-odds of species originating, given it hasn't originated yet



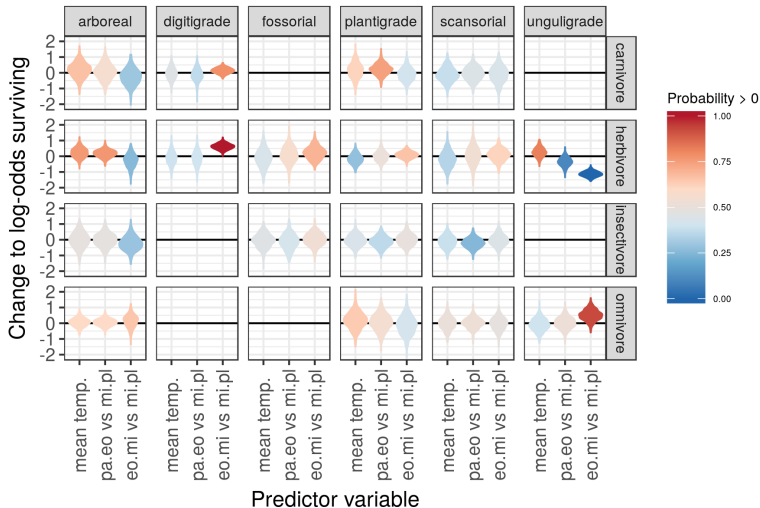
Survival; individual-level

probability of species surviving, given it was present

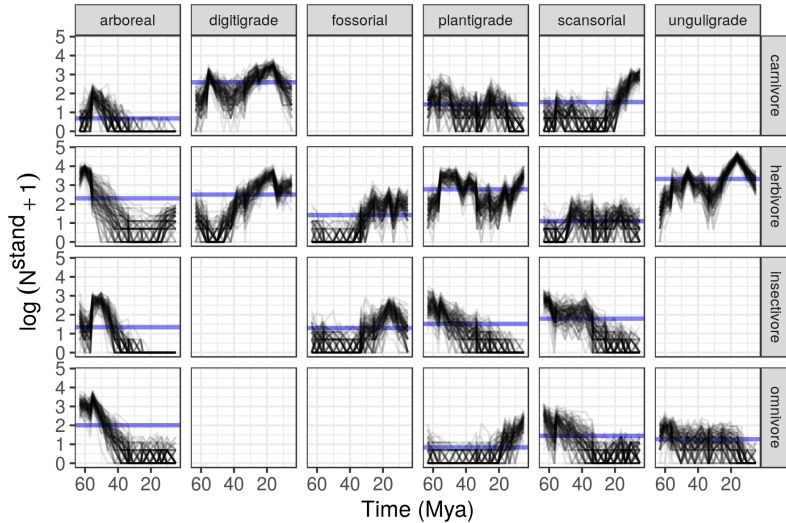


Survival; group-level

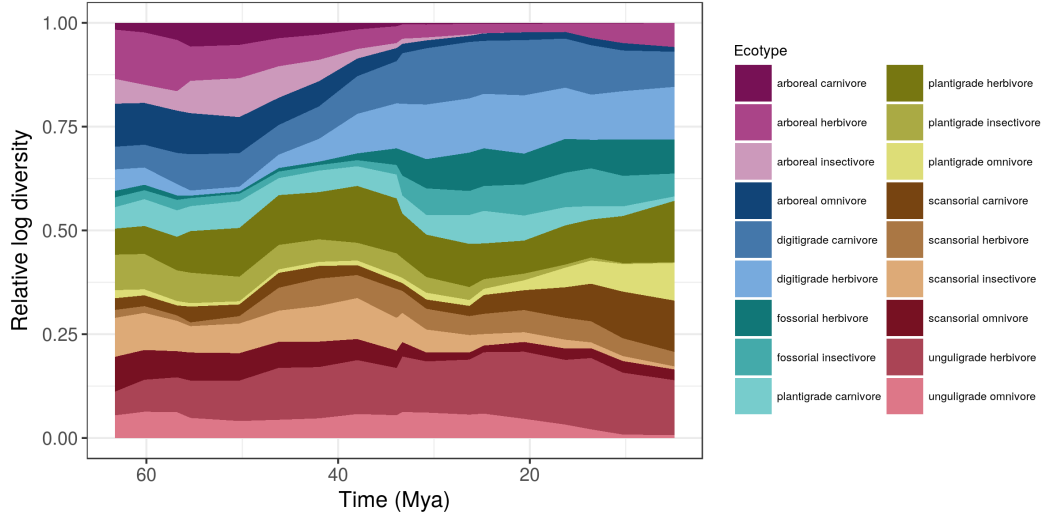
change to log-odds of species surviving, given it was present



Standing diversity of functional groups through time



Relative diversity of functional groups through time



Changes to relative diversity between Neogene/Paleogene

- ▶ increase
 - ▶ digitigrade, plantigrade, unguligrade herbivores
 - ▶ fossorial functional groups
 - ▶ plantigrade omnivores
- ▶ decrease
 - ▶ near total loss of arboreal functional groups
 - ▶ plantigrade, scansorial insectivores
 - ▶ unguligrade omnivores

Conclusions

- ▶ temporal differences have larger effect on $P(\text{observation})$ than effect of FG
- ▶ increase in $P(\text{origination})$ often met with decrease in $P(\text{survival})$, but not 1-to-1
- ▶ environmental covariates effect origination within FG more often than survival
- ▶ no evidence for correlation in origination or survival of functional groups over time that is not accounted for by RW prior
 - ▶ potential for short-term similarity, just no long-term correlation
 - ▶ HMC/MCMC might tweak these results b/c ADVI assumptions (Gaussian posterior)

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Graham Slater



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The Paleobiology Database
revealing the history of life