# Modeling changes to the functional composition of North American mammal diveristy

multi-level dynamics of a regional species pool

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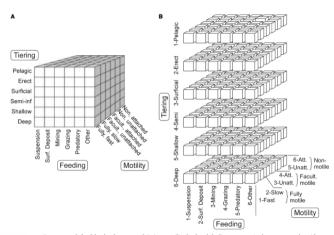
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#### Question

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.

(Bambach et al., 2007, Palaeontology)

## Species pool concept

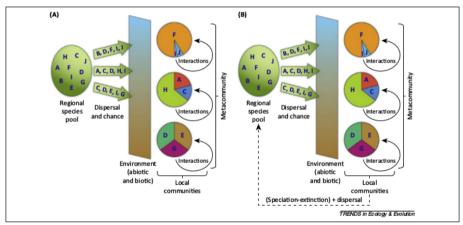
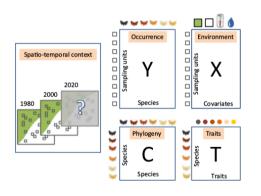
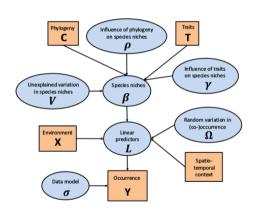


Figure 1. Two models of community assembly. (A) Local communities comprise a subset of species from the regional species pool that have passed through environmental filters. There is no feebback from the metacommunity (collection of local communities) to the regional species pool. Adapted from [5]. (B)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

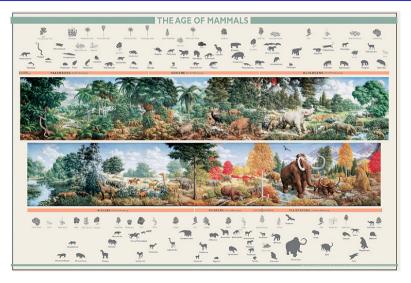
# Structured, multi-level data in biology



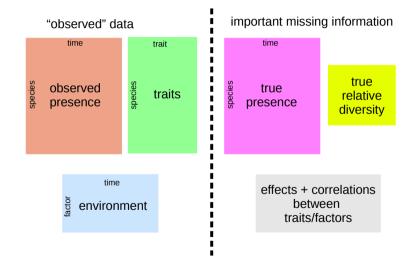


(Ovaskainen et al. 2017 Ecology Letters)

## Cenozoic mammals of North America



## Conceptualizing the knowns and unknows



## Covariates of interest, temporal structure

#### species occurrence (~1400 species) per NALMA

#### observation

- individual-level: species
  - functional group
  - mean mass
- time of observation

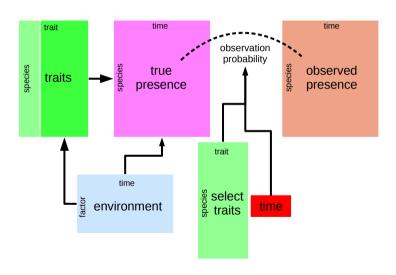
#### origination

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

#### survival

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

# Conceptualizing the analysis



# Hidden Markov Model with absorbing state

## Jolly-Seber CMR/Restricted occupancy model

$$egin{aligned} y_{i,t} &\sim \mathsf{Bernoulli}ig(z_{i,t}p_{i,t}ig) \ z_{i,t=1} &\sim \mathsf{Bernoulli}ig(\phi_{i,t=1}ig) \ z_{i,t} &\sim \mathsf{Bernoulli}igg(z_{i,t-1}\pi_{i,t} + \sum_{x=1}^t (1-z_{i,x})\phi_{i,t}igg) \end{aligned}$$

y observed state; z estimated state.

p observation;  $\phi$  origination;  $\pi$  survival.

i in N; t in T.

## Modeling the probabilities; individual-level

## Multi-level logistic regression

$$p_{i,t} \sim \operatorname{logit}^{-1}(b_t + e_{j[i]} + \beta^p \operatorname{mass}_i)$$
 $\phi_{i,t} \sim \operatorname{logit}^{-1}(f_{j[i],t}^{\phi} + o_{k[i]}^{\phi} + \beta^{\phi} \operatorname{mass}_i)$ 
 $\pi_{i,t} \sim \operatorname{logit}^{-1}(f_{j[i],t}^{\pi} + o_{k[i]}^{\pi} + \beta^{\pi} \operatorname{mass}_i)$ 

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

origination:  $f^{\phi}_{j[i],t}$  time/FG-varying intercept;  $o^{\phi}_{j[i]}$  order eff;  $\beta^{\phi}$  mass eff.

survival:  $f^{\pi}_{j[i],t}$  time/FG-varying intercept;  $o^{\pi}_{j[i]}$  order eff;  $\beta^{\pi}$  mass eff.

# Modeling the probabilities; group-level

## Multivariate regression of time/FG-varying intercept

$$f^{\phi} \sim \mathsf{MVN} egin{pmatrix} U\gamma_{j=1}^{\sigma} \ dots & , \mathsf{diag}( au_{f^{\phi}})\Omega_{f^{\phi}}\mathsf{diag}( au_{f^{\phi}}) \end{pmatrix} \ f^{\pi} \sim \mathsf{MVN} egin{pmatrix} U\gamma_{j=1}^{\pi} \ dots & , \mathsf{diag}( au_{f^{\pi}})\Omega_{f^{\pi}}\mathsf{diag}( au_{f^{\pi}}) \end{pmatrix} \ U\gamma_{i=J}^{\pi} \end{pmatrix}$$

U matrix group-level covariates;  $\gamma^\phi,\,\gamma^\pi$  vectors group-level reg coefs.

 $\Omega_\phi$  ,  $\Omega_\pi$  corr matrix of FG by time;  $\tau_\phi$  ,  $\tau^\pi$  scale of FG by time.

# Modeling the probabilities; final details

#### Comments on priors, implementation

- Random-walk priors for time-varying intercepts
- Regularizing priors predict
  - 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

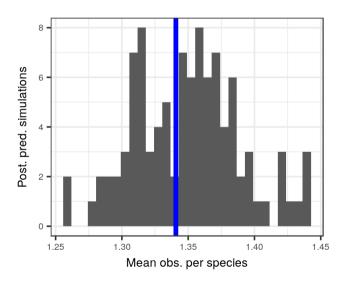
#### Parameter estimation and inference

- 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

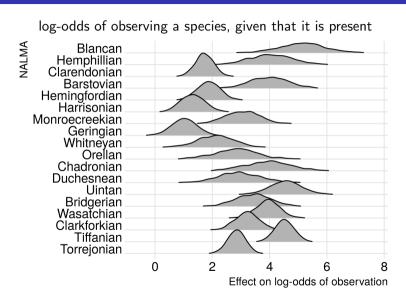


Stan

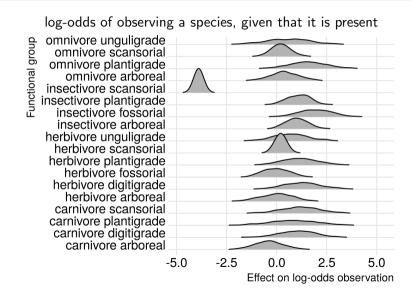
## Model adequate? Posterior predictive check



## Observation; NALMA

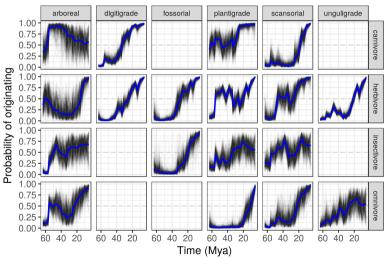


## Observation; functional group



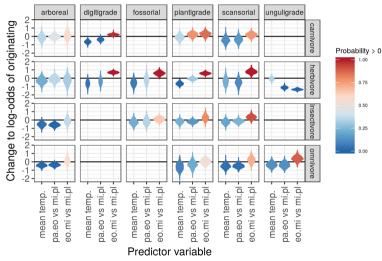
# Origination; individual-level

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



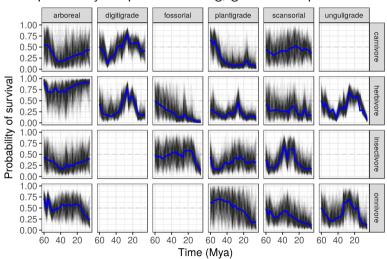
## Origination; group-level

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

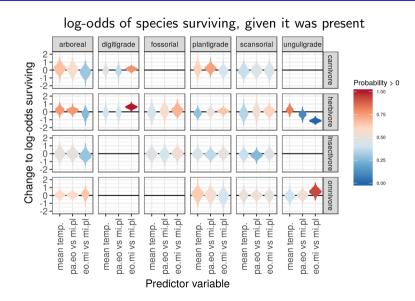


## Survival; individual-level

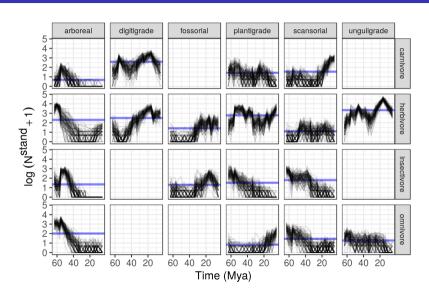
probability of species surviving, given it was present



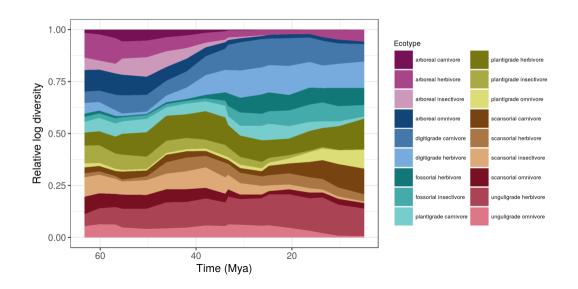
## Survival; group-level



# 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 in P(observation) much larger than effects of functional group
- increases in P(origination) often met with decreases in P(survival), but not 1-to-1
- environment estimated to effect origination of functional groups more often than survival
- ▶ no correlation between functional group origination, survival not accounted for by RW prior
  - ▶ does not preclude short similarity, just no long term correlation
  - ► HMC/MCMC might tweak these results b/c ADVI assumptions

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The Paleobiology Database revealing the history of life