The changing functional composition of the North American species pool

modeling species origination-extinction as a function of functional group and environmental context

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The Paleobiology Database
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Question

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

Species pool concept

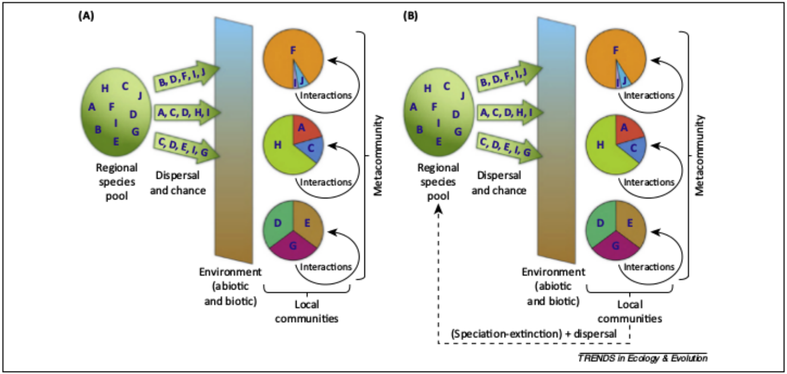
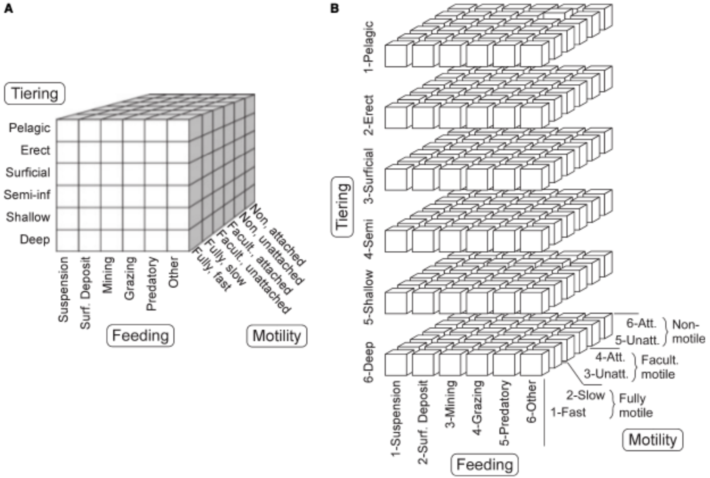


Figure 1. Two models of community assembly. **(A)** Local communities comprise a subset of species from the regional species pool that have passed through environmental filters. There is no feedback from the metacommunity (collection of local communities) to the regional species pool. Adapted from [5].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

Structured data in biology; the fourth-corner problem

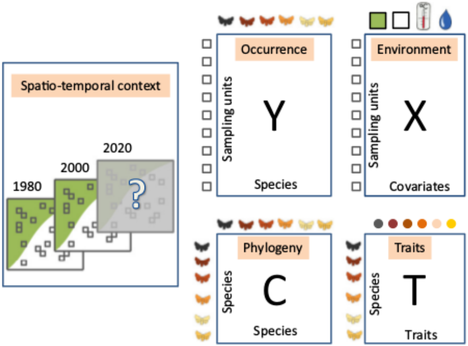
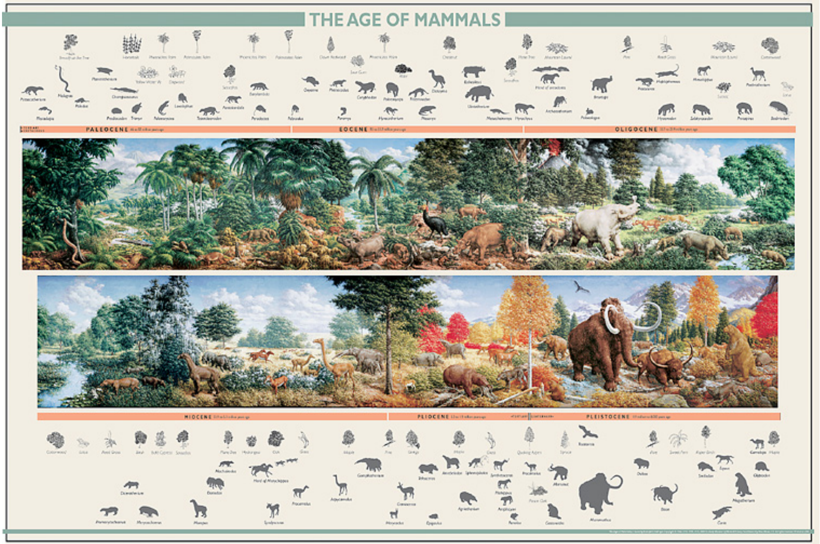


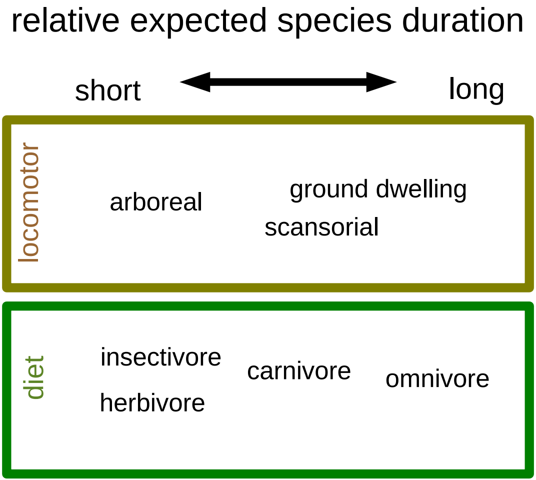
Figure 3 Data typically collected in community ecology. The occurrence data (denoted as the **Y** matrix) includes the occurrences of the species recorded in a set of temporal and/or spatial sampling units. The environmental data (denoted as the **X** matrix) consists of the environmental covariates 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*)

Age of Mammals



Differences in extinction risk



(Smits 2015 *PNAS*)

Covariates of interest

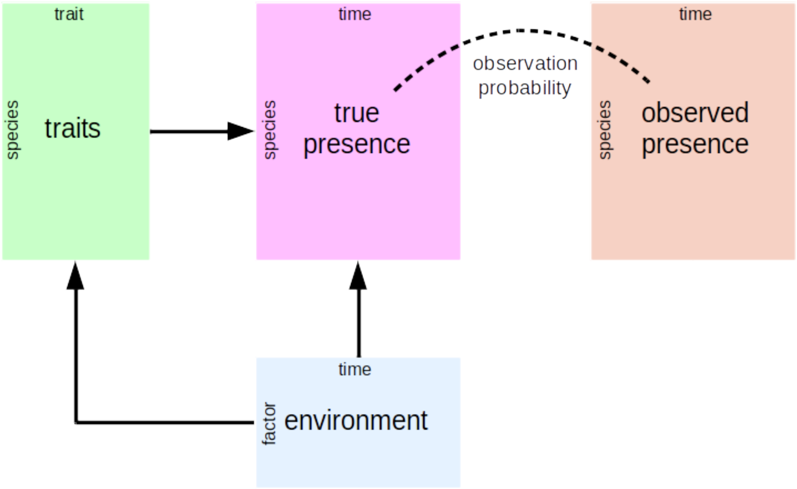
individual-level
(species i at time unit t)

- effect of locomotor type
  - arboreal, digitigrade, plantigrade, unguligrade, fossorial, scansorial
- effect of dietary type
  - carnivore, herbivore, insectivore, omnivore
- effect 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

Paleo-fourth corner model



Model and sampling statement definition

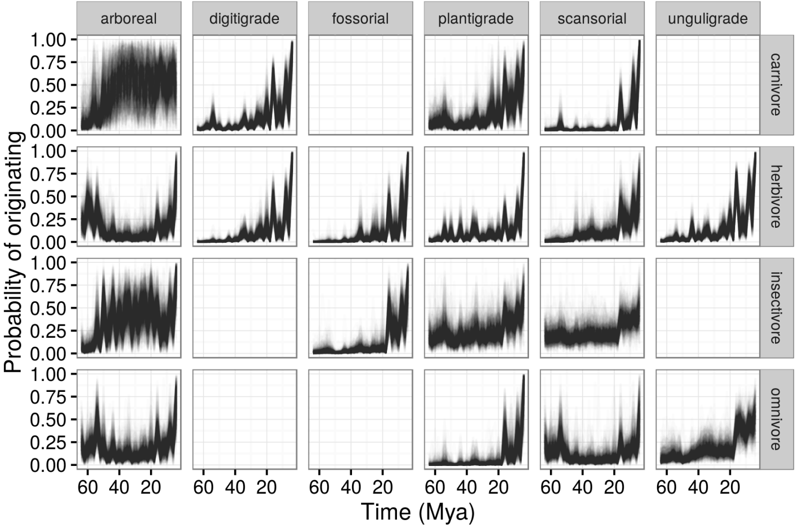
$$
\begin{aligned}
y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) \\
p_{i,t} &= \text{logit}^{-1}(\alpha_0 + \alpha_1 m_i + r_t) \\
r_t &\sim \mathcal{N}(0, \sigma) \\
\alpha_0 &\sim \mathcal{N}(0, 1) \\
\alpha_1 &\sim \mathcal{N}(1, 1) \\
\sigma &\sim \mathcal{N}^+(1) \\
z_{i,1} &\sim \text{Bernoulli}(\phi_{i,1})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

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

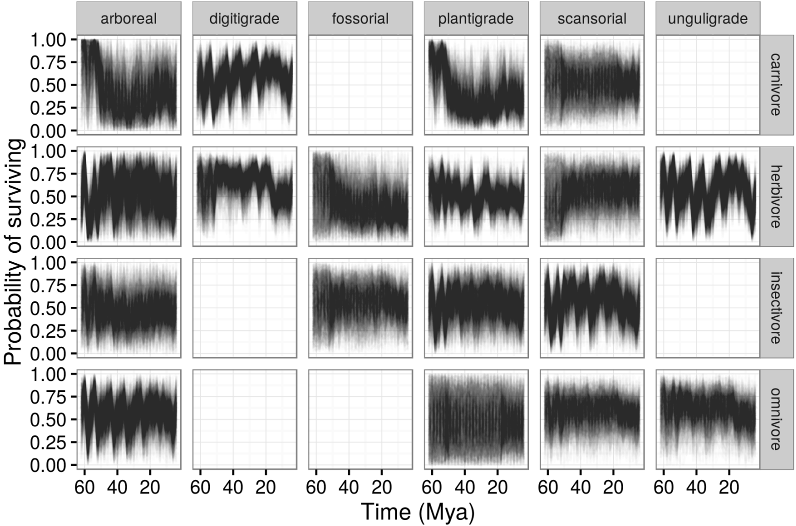
Bayesian inference and statistics

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

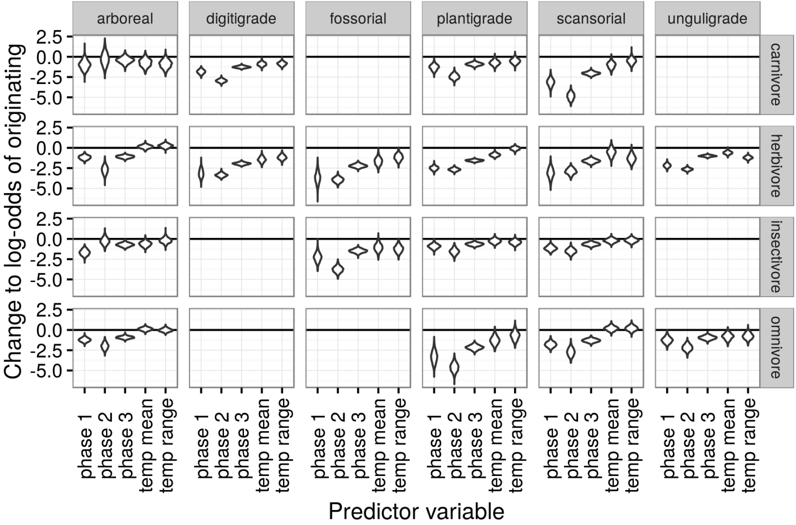
Probability of ecotype origination



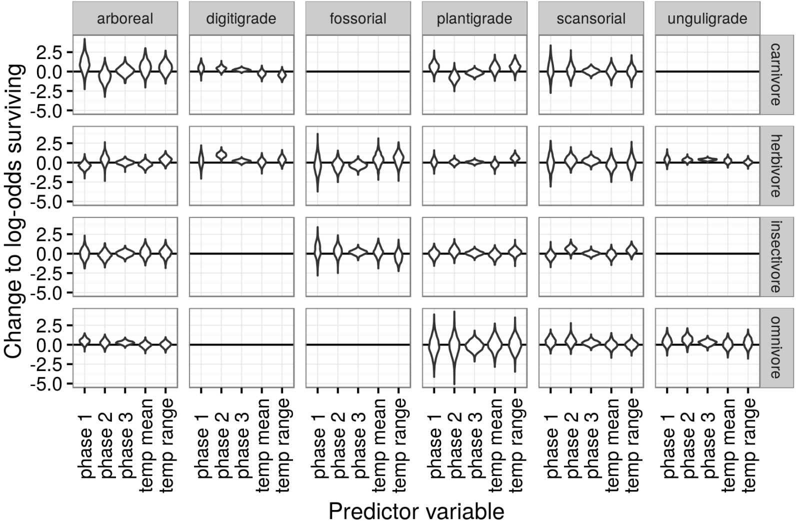
Probability of ecotype survival



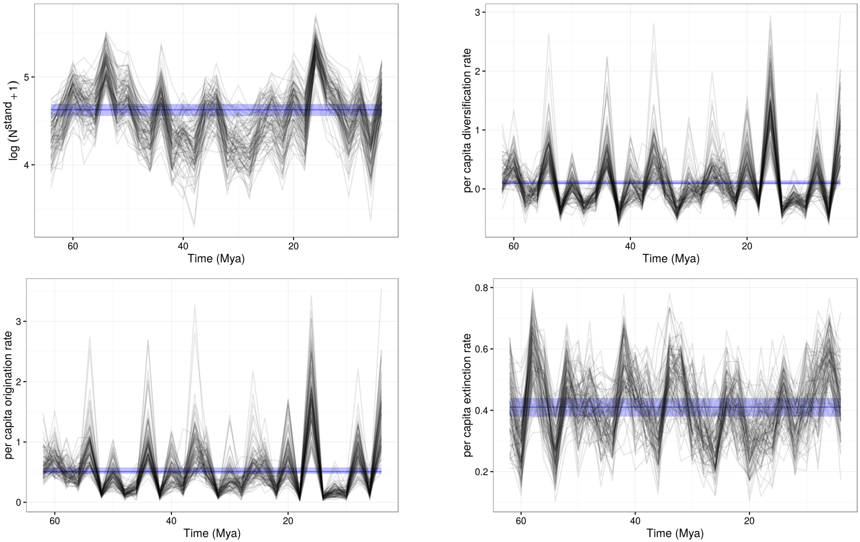
Group-level effects (plant phase, climate) on origination



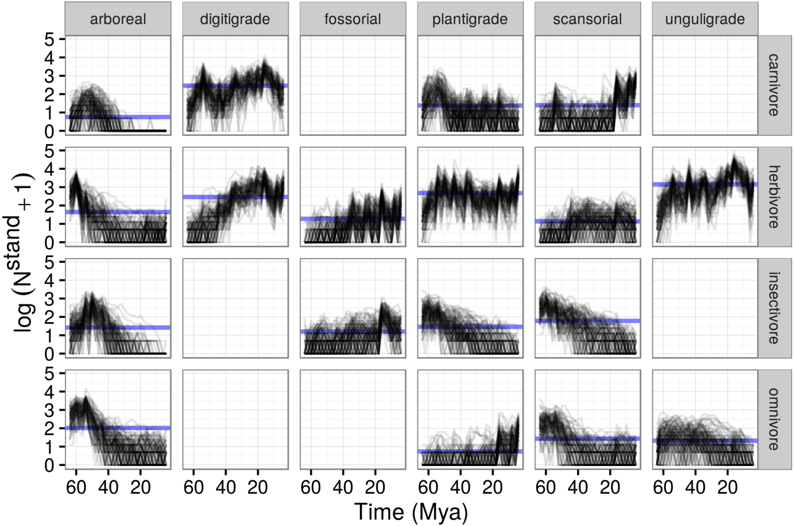
Group-level effects (plant phase, climate) on survival



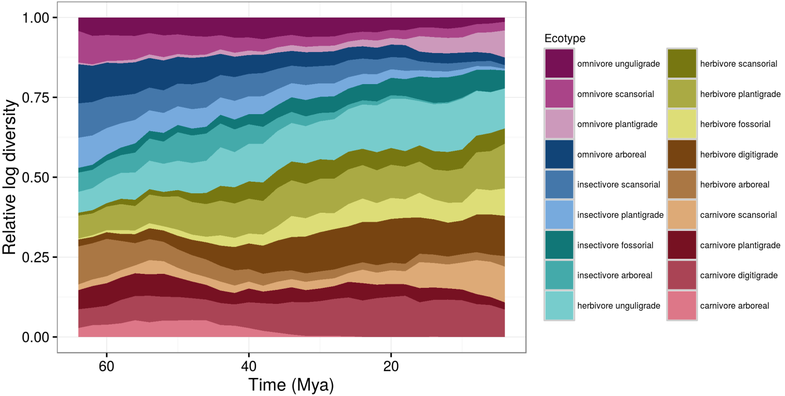
Total species pool diversity and diversification



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

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