Evolutionary paleoecology and the biology of extinction

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Introduction and theory

Brachiopods, environmental preference, and extinction

Ecology and survival in Cenozoic mammals

Community connectedness in Cenozoic mammals

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Framework

Questions

- Why do certain taxa go extinct while others do not?
- How is emergence "formed?" When should it be invoked?
- Is extinction risk taxon–age independent?
- When should we expect global, regional, or local processes to dominate?

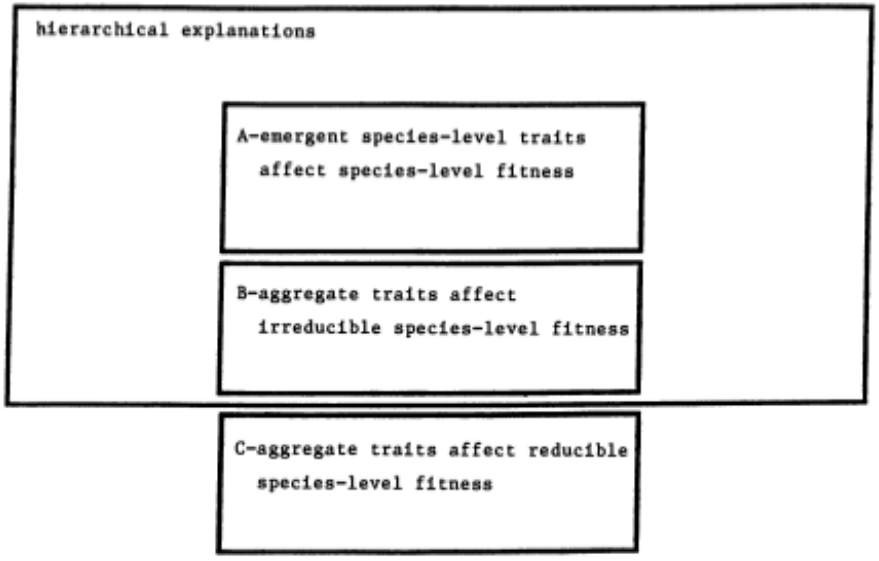
Evolutionary paleoecology

. . . the consequences of distinct ecological factors on differential rate dynamics, particularly rates of faunal turnover and diversification.

(Kitchell 1985 Paleobiology)

environmental interactions $\rightarrow$ macroevolution

Emergent properties



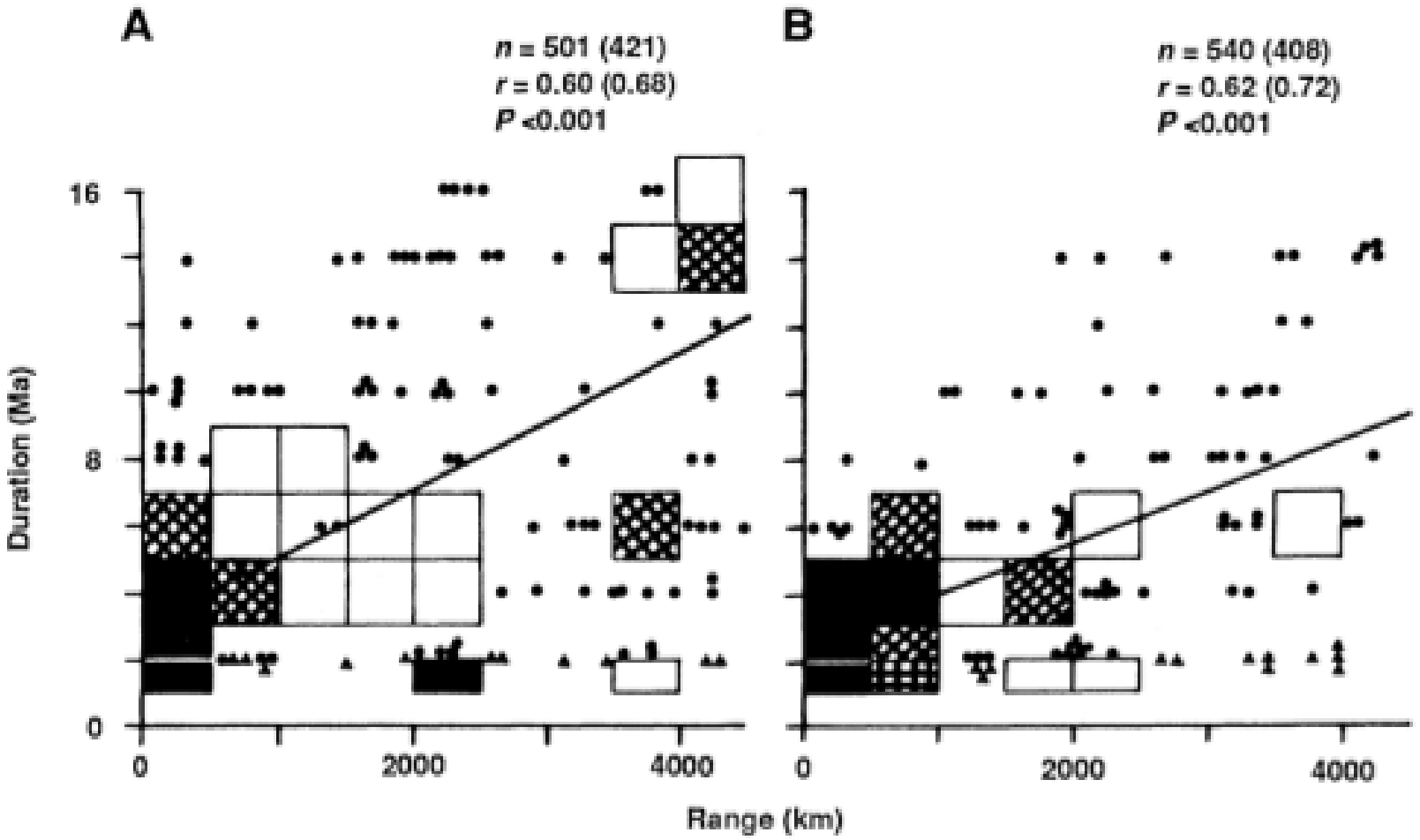
(Grantham 1995 *Ann. Rev. Ecol. Syst.*)

Species level

Trait that cannot be reduced to organismal level

Product of one or more traits/factors

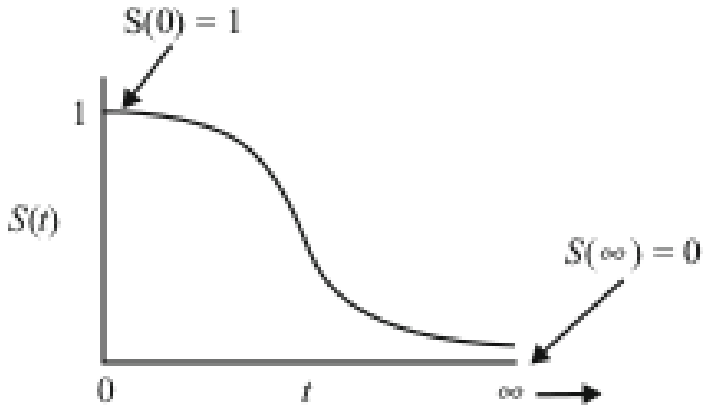
Range size



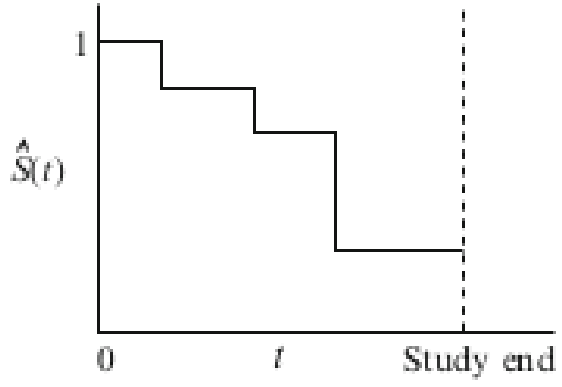
(Jablonski 1987 *Science*)

Probability of survival

Theoretical $S(t)$:



$\hat{S}(t)$ in practice:



(Kleinbaum and Klein 2012)

Survival function

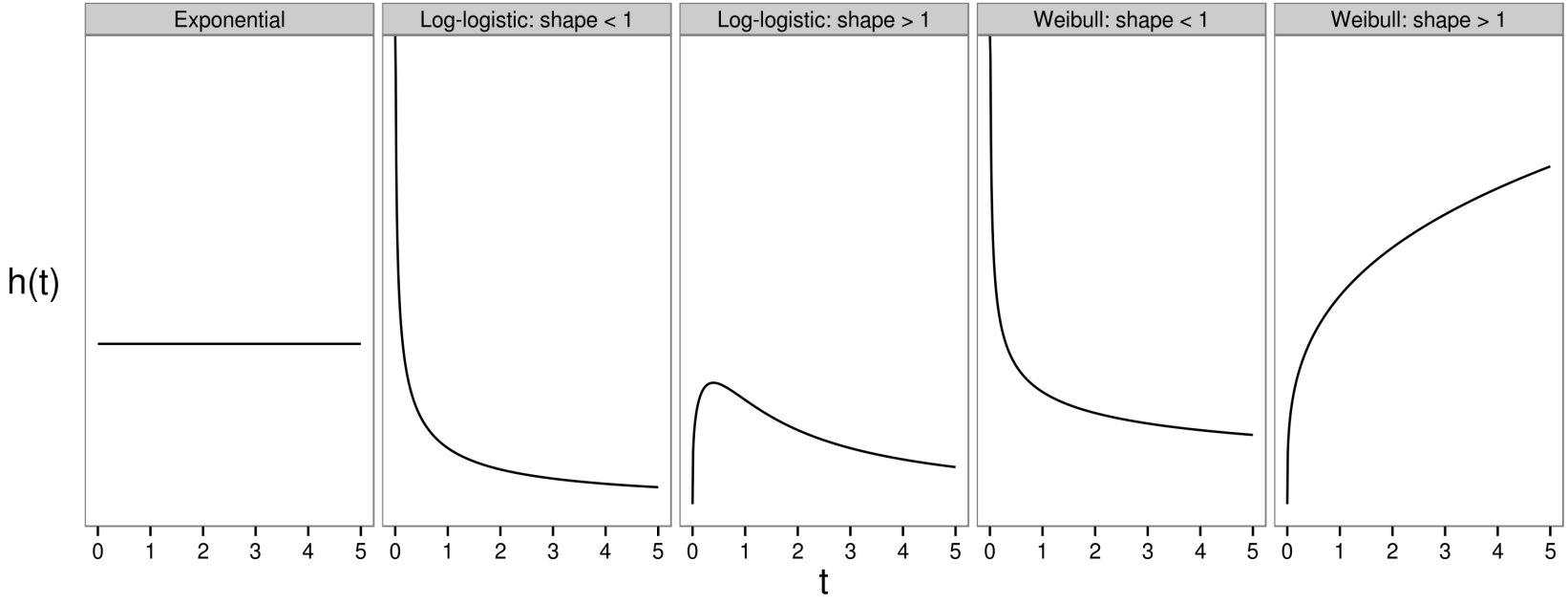
$$S(t) = P(T > t)$$

- T: survival time (≥ 0)
- t: specified time

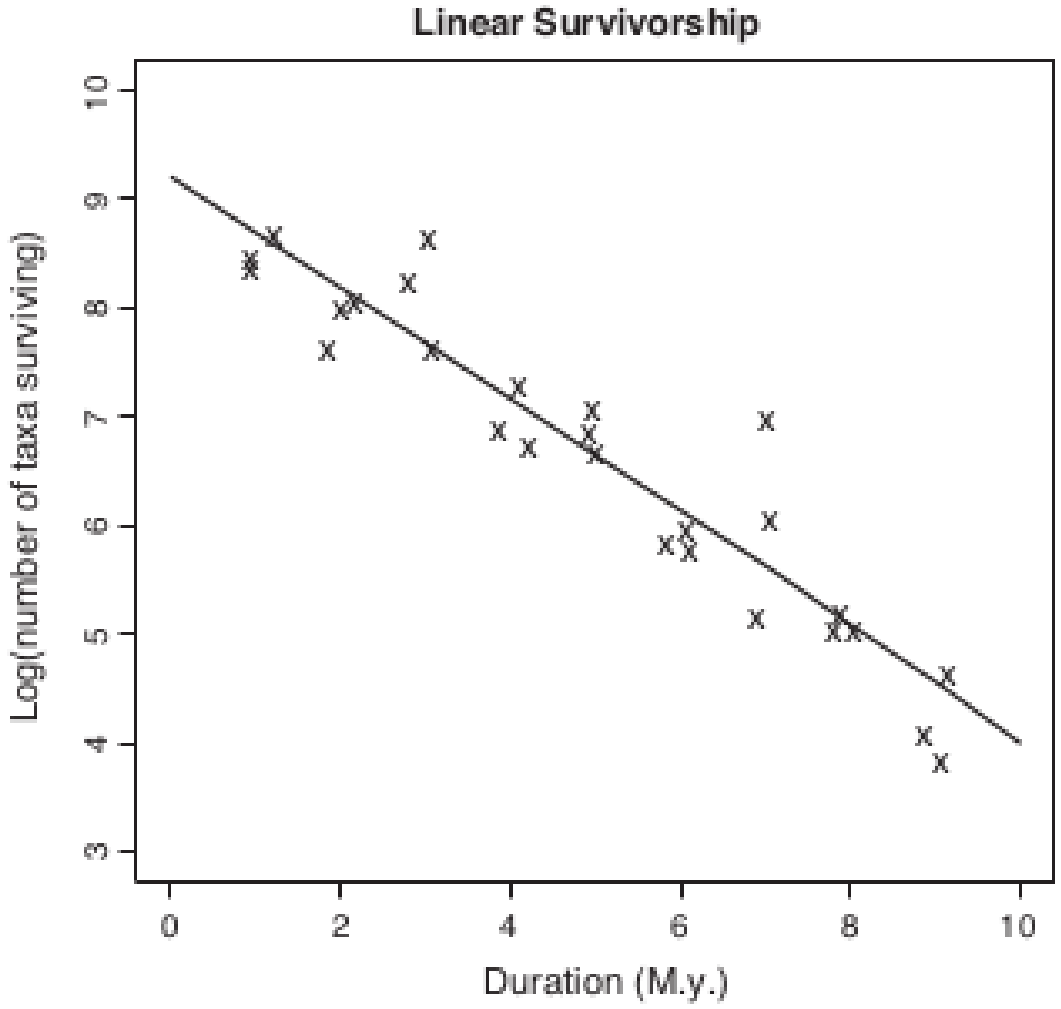
Instantaneous potential of failure (extinction)

Hazard function $\equiv$ conditional failure rate

$$h(t) = \lim_{\Delta t \to 0} \frac{P(t \leq T < t + \Delta t | T \geq t)}{\Delta t}$$



Van Valen's observation of survival



(Liow et al. 2011 *TREE*)

Law of Constant Extinction

Definition

Extinction risk in a given adaptive zone is taxon–age independent.

(Van Valen 1973 *Evol. Theory*)

translation: hazard is constant with respect to time
(exponential survival)

$$h(t) = \lambda \iff S(t) = \exp^{-\lambda t}$$

Brachiopods and mammals: a comparison

brachiopods

- marine
- sessile
- Permian ($\sim$ 47 My)
- Australasia
- global warming

mammals

- terrestrial
- motile
- Cenozoic ($\sim$ 65 My)
- North America, Europe, South America
- global cooling

Series of related questions

- generic level survival in brachiopods
  - ecological traits re. environmental pref. (emergence)
  - survival distribution
- specific level survival in mammals
  - ecological traits re. range size (emergence)
  - generic versus specific survival
  - anagenesis/species:genus simulation
  - survival distribution
- community connectedness in mammals
  - global versus regional versus local scale processes
  - ecological traits (trophic/locomotion)

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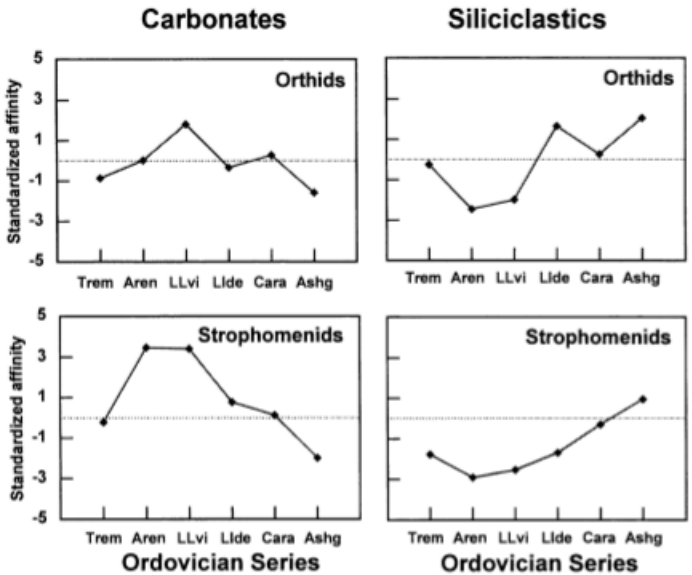
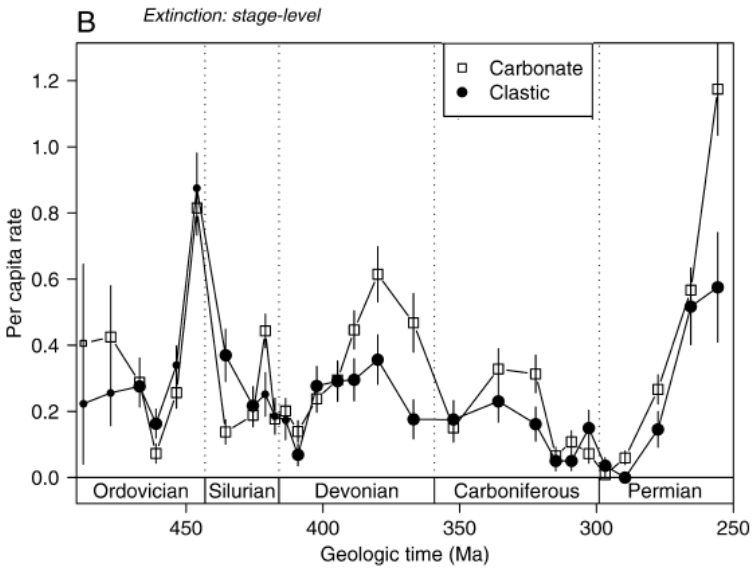
Substrate affinity



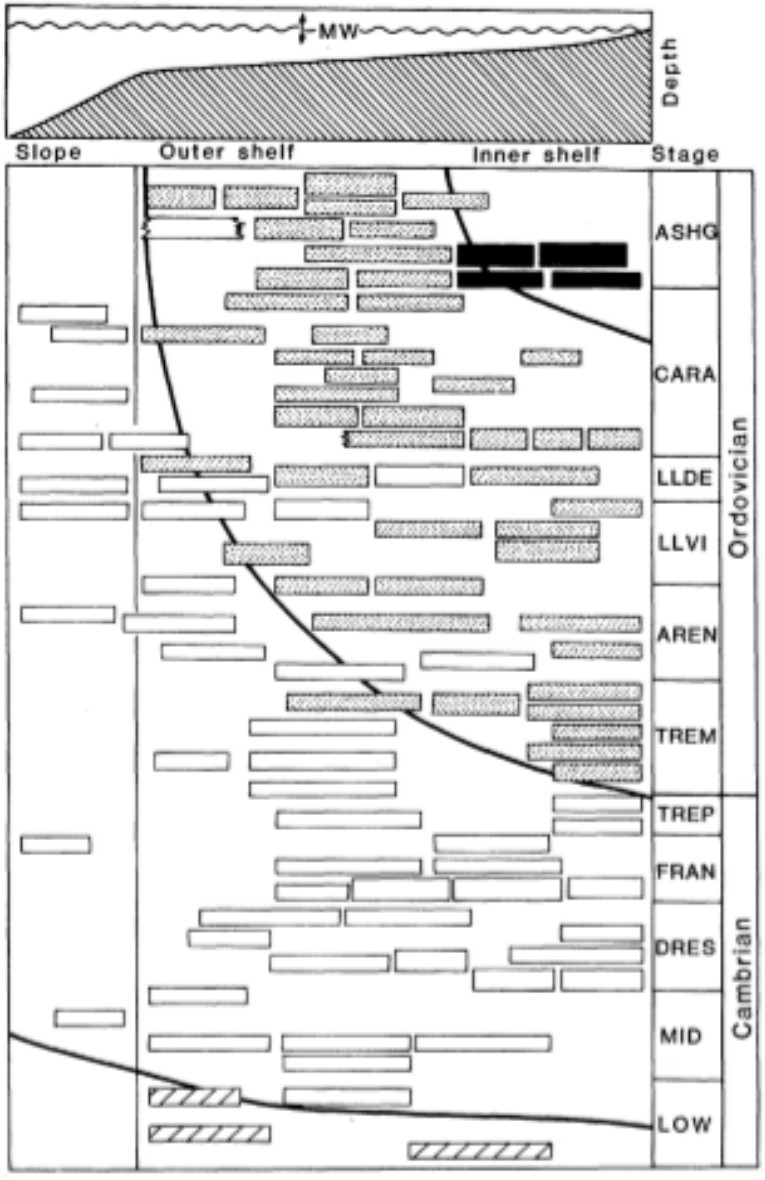
(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

- carbonates, clastics, mixed
- lithology/deposition environment
- Pharenozoic decrease in carbonates:clastics
- predictions
  - clastics $>$ carbonates

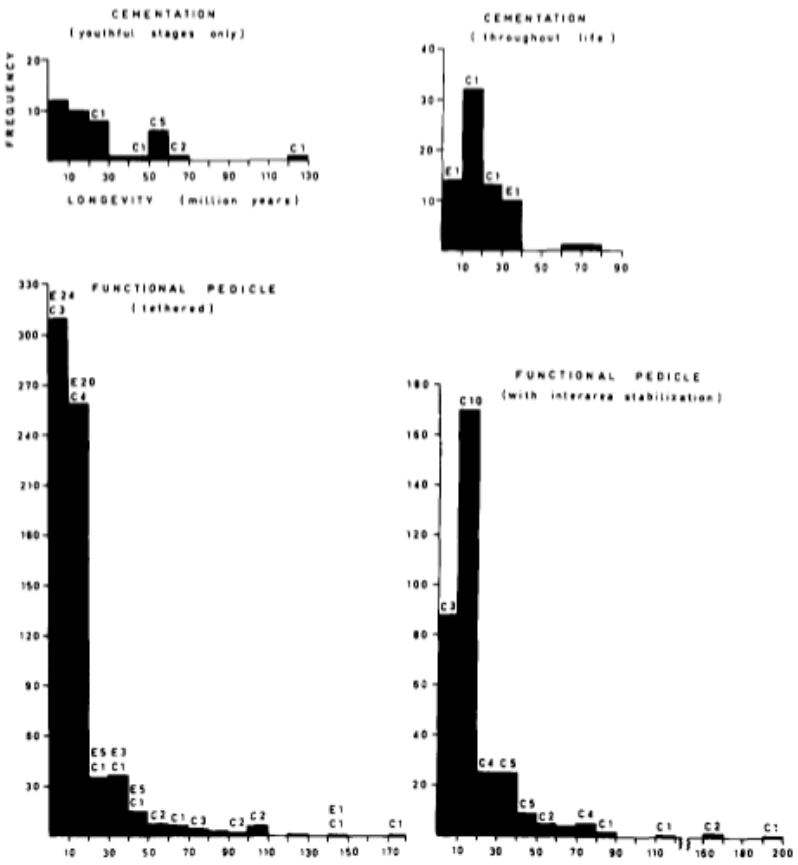
Habitat preference



(Jablonski *et al.* 1983 *Science*)

- classically invoked re. diversification of higher taxa
  - onshore $\rightarrow$ offshore
- on-shore, off-shore, none
  - above/below storm wave base

Affixing strategy



(Alexander 1977 *Paleo*[3])

- pedunculate, reclining, cementing
  - endemics duration: reclining $>$ others
  - cosmopolitan duration: ped./cement $>$ others
- pedunculate:on-shore, reclining:off-shore

Assigning substrate and habitat

Probability of assignment

$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

$$P(E|H) = \binom{n}{k} p^k (1-p)^{n-k}$$

- n: total # of occ
- k: # (e.g.) carbonate occ

(Simpson and Harnik 2009 *Paleobiology*)

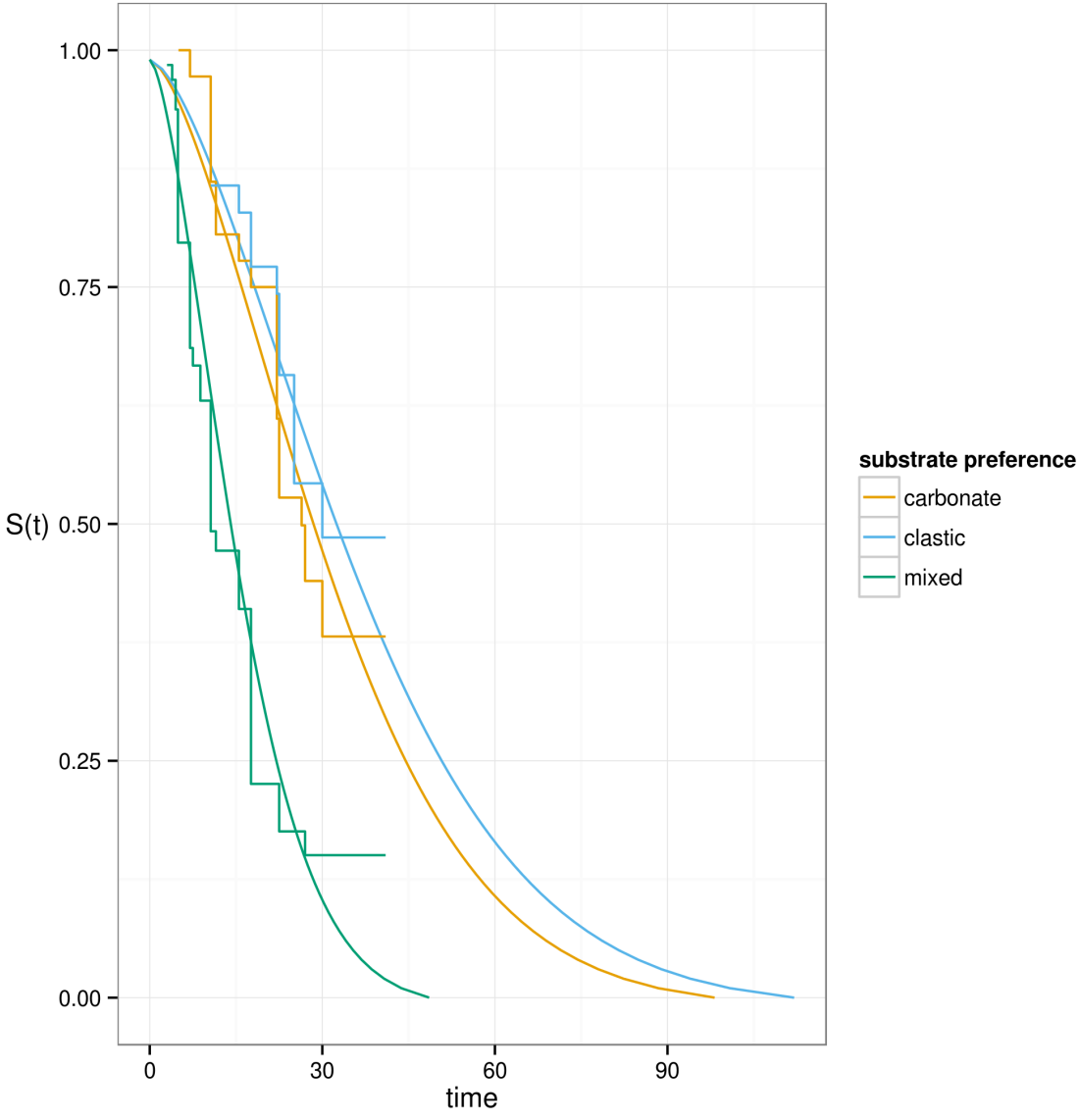
Analysis

- data: genus FAD–LAD
  - Australiasia
  - all taxa occurring in and ranging into/out of Permian
  - PBDB (h/t Clapham)
- traits: time-indep. covariate
  - substrate following Foote 2006 *Paleobio.*
  - habitat following Kiessling *et al.* 2007 *Paleo*^{3}
- climate: time-dep. covariate
  - continuous or Heaviside step function
- distributions of survival: $\exp(\lambda)$, *Weibull*(λ, k), *etc.*

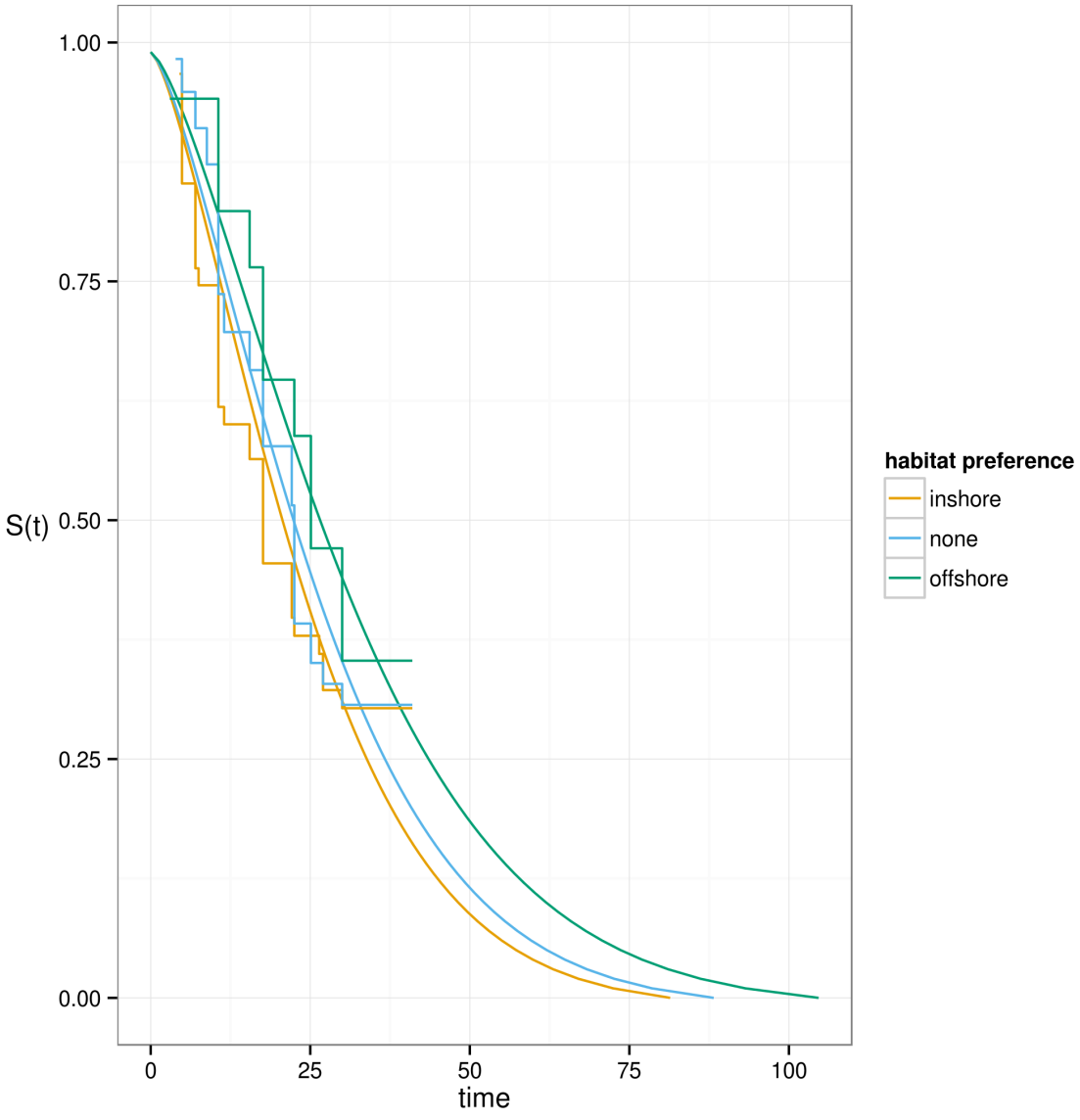
Preliminary results: model comparison

formula	distribution	shape	df	logLik	AICc
~ aff	weibull	1.91	4	-497.5745	1003.4543
~ aff + hab	weibull	1.92	6	-496.8553	1006.3618
~ aff * hab	weibull	1.94	10	-495.7702	1013.3003
~ aff:hab	weibull	1.94	11	-495.7702	1015.6693
~ 1	weibull	1.76	2	-515.1666	1034.4234
~ hab	weibull	1.76	4	-513.9591	1036.2236
~ aff	exponential		3	-532.8690	1071.9199
~ aff + hab	exponential		5	-532.5798	1075.6211
~ 1	exponential		1	-540.9218	1083.8734
~ aff * hab	exponential		9	-532.3099	1084.0485
~ aff:hab	exponential		10	-532.3099	1086.3799
~ hab	exponential		3	-540.2811	1086.7439

Preliminary results: best substrate



Preliminary results: best habitat



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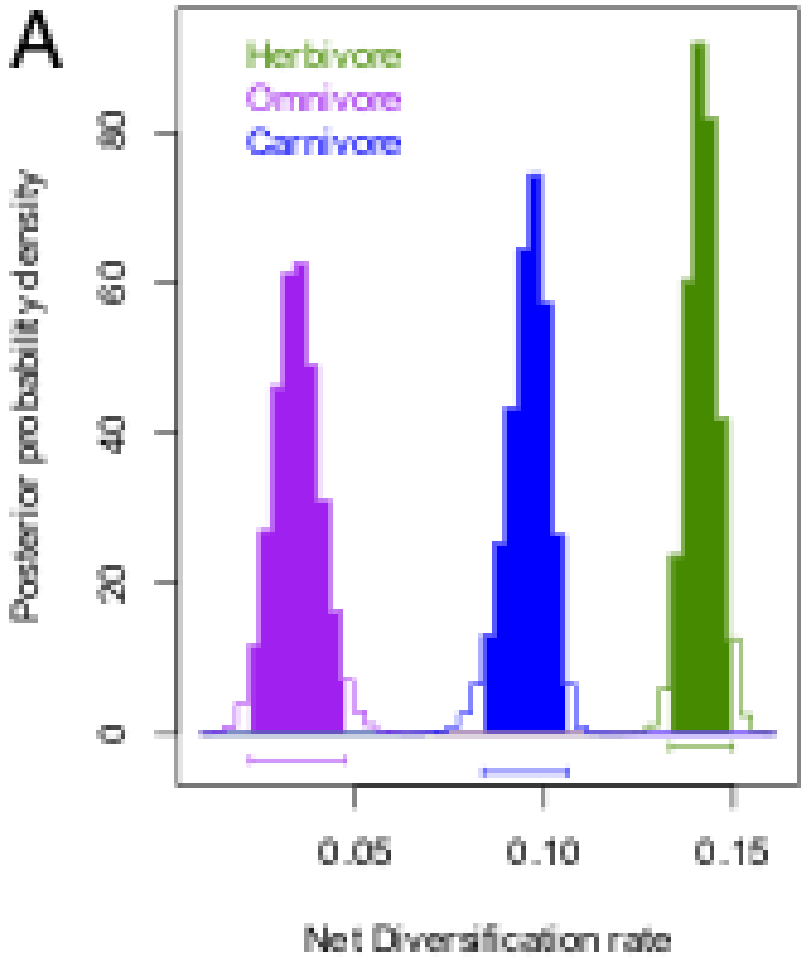
Predictions: dietary category



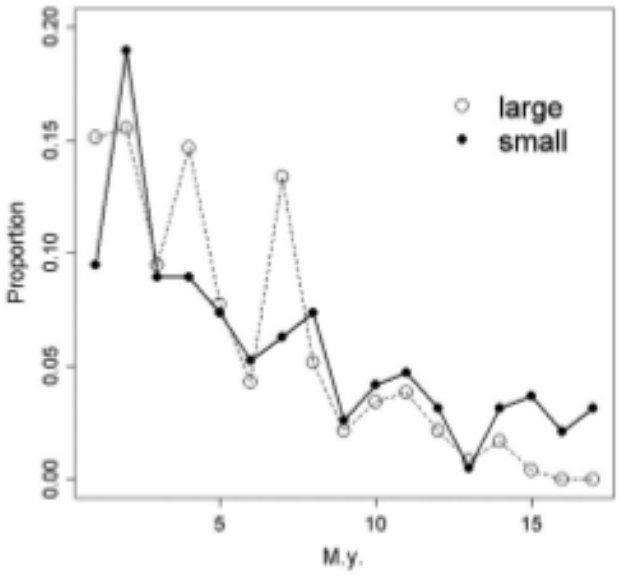
(Price *et al.* 2012 *PNAS*)

- trophic hierarchy (stability $\rightarrow$ duration)
  - herb: most stable, longest duration
  - carni: least stable, shortest duration
  - omni: avg. stability, avg. duration
- $\uparrow$ diversification
  - $\uparrow$ origination; $\simeq$ extinction
  - $\simeq$ origination; $\downarrow$ extinction

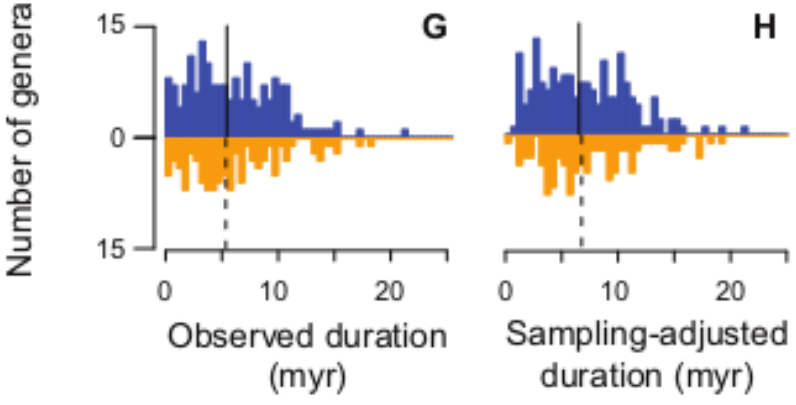
Predictions: locomotor category

- Paleogene $\rightarrow$ Neogene
  - open $\rightarrow$ closed environment
  - arboreal: Paleogene $>$ Neogene
  - ground dwelling: Paleogene $<$ Neogene
  - scansorial: Paleogene $\approx$ Neogene

Predictions: body size



(Liow *et al.* 2008 *PNAS*)



(Tomiya 2013 *Am. Nat.*)

- $\uparrow$ body size, $\uparrow$ energy req, $\uparrow$ range size, $\downarrow$ extinction
- Europe
  - lrg body size genera: $\uparrow$ extinction
- North America
  - generic body size: $\simeq$ extinction

Analysis

- data: genus and species FAD–LAD
  - NA: PBDB (h/t Alroy)
  - Europe: PBDB, NOW
  - SA: collections, compilations
- traits: time-indep. covariates
- climate: time-dep. covariate
  - continuous δO^{18} isotope
    Zachos *et al.* 2008 *Nature*
- Paleogene versus Neogene
- distributions of survival: $\exp(\lambda)$, *Weibull*(λ, k), *etc.*

Biases to survival: a simulation study

- bias away from $h(t) = \lambda$
  - species:genus
  - anagenesis/cryptic speciation
- time-homogeneous birth-death model
  - common phylogenetic model
  - constant p, b
  - expected $S(t) = \exp^{-\lambda t}$
  - vary (cryptic) anagenesis

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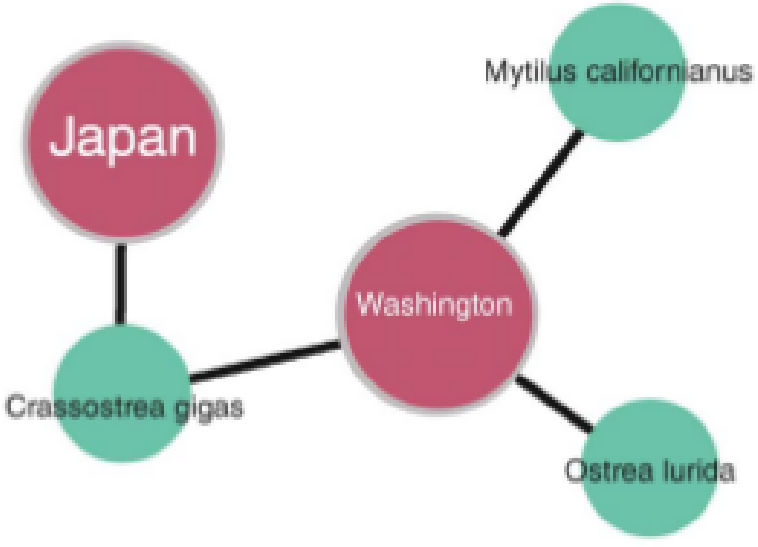
Community connectedness

Definition

The degree to which localities are composed of endemic versus cosmopolitan taxa, and how similar this ratio is across localities.

Biogeographic networks



(Vilhena *et al.* 2013 *Sci. Reports*)

- taxa: species
- locality: 2x2 equal–area map projection grid
- 2 My intervals
- PBDB, NOW, museum collections, compilations

Average relative number of endemics

$$E = \frac{\sum_{i=1}^{L} \frac{u_i}{n_i}}{L}$$

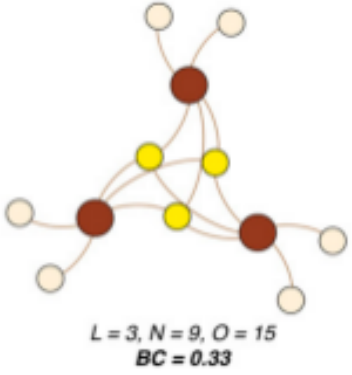
- L: number of localities
- u: number of taxa unique to a locality
- n: number of taxa at a locality
- $0 \leq E \leq 1$

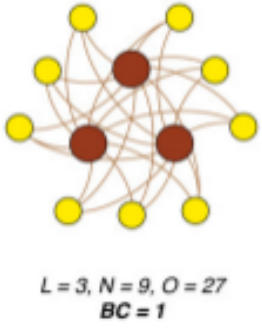
Average relative occupancy per taxon

$$Occ = \frac{\sum_{i=1}^{N} \frac{l_i}{L}}{N}$$

- N: total number of taxa
- l: number of localities a taxon occurs at
- L: number of localities
- $0 \leq Occ \leq 1$

Biogeographic connectedness



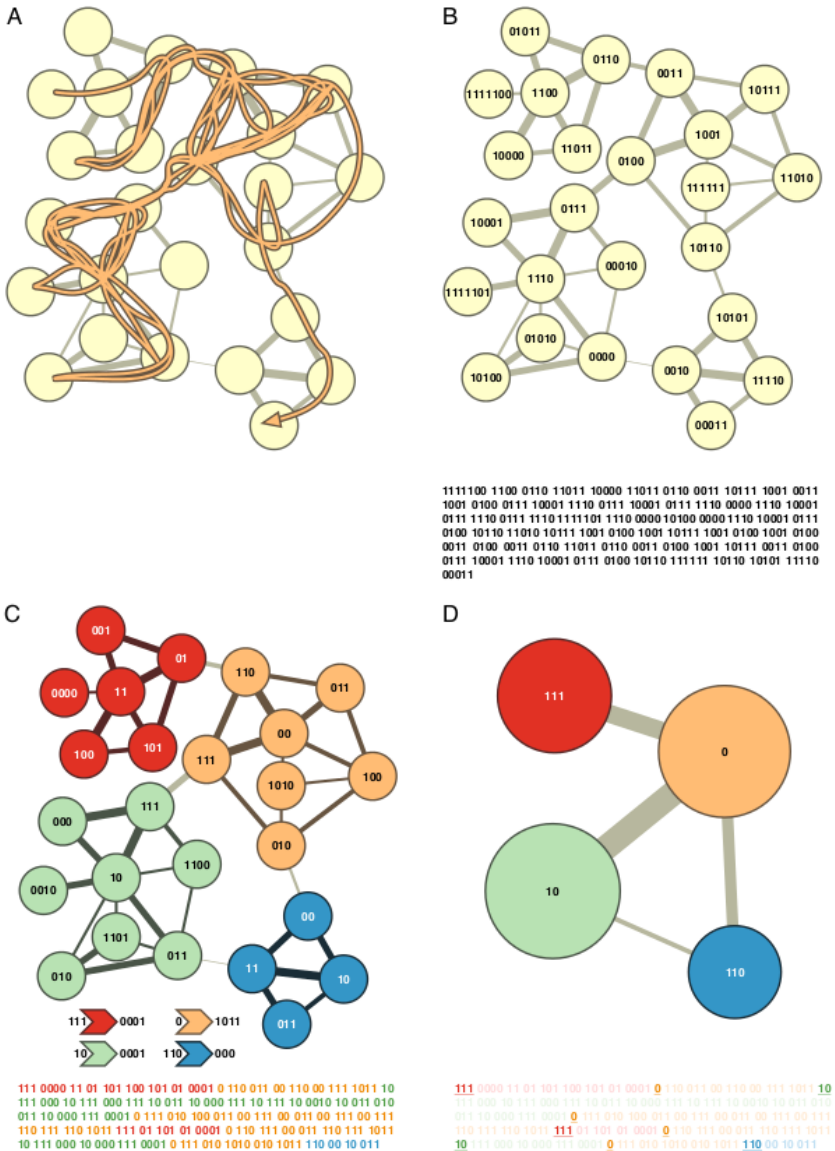


(Sidor et al. 2013 *PNAS*)

$$BC = \frac{O - N}{LN - N}$$

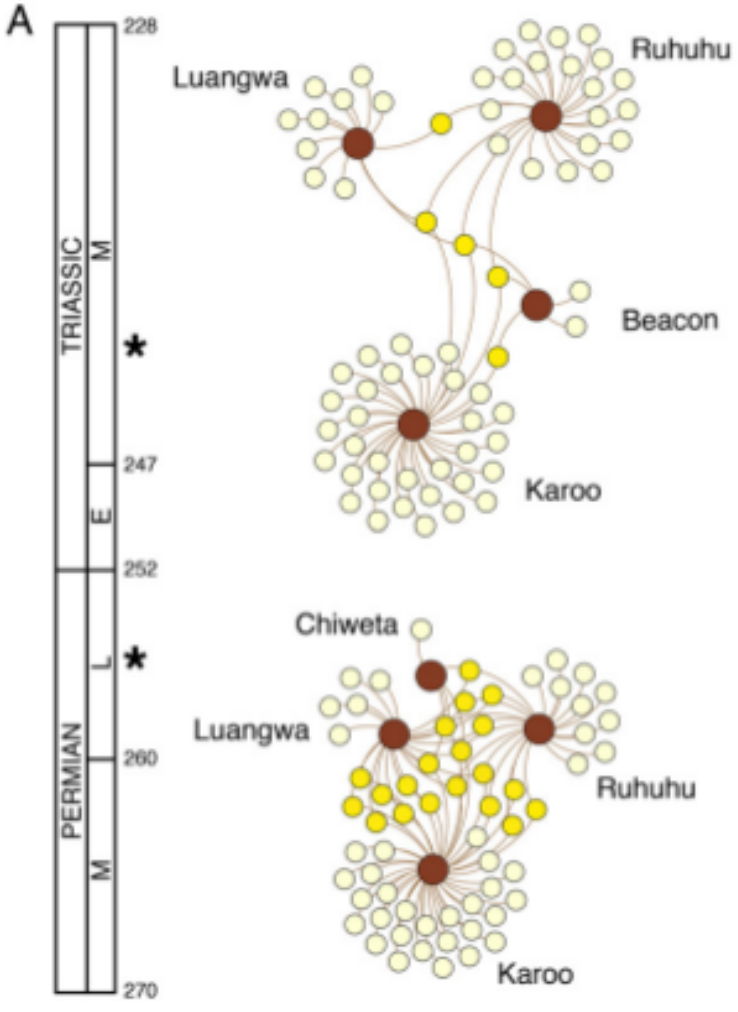
- O: number of occurrences
- N: total number of taxa
- L: number of localities
- $0 \leq BC \leq 1$

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

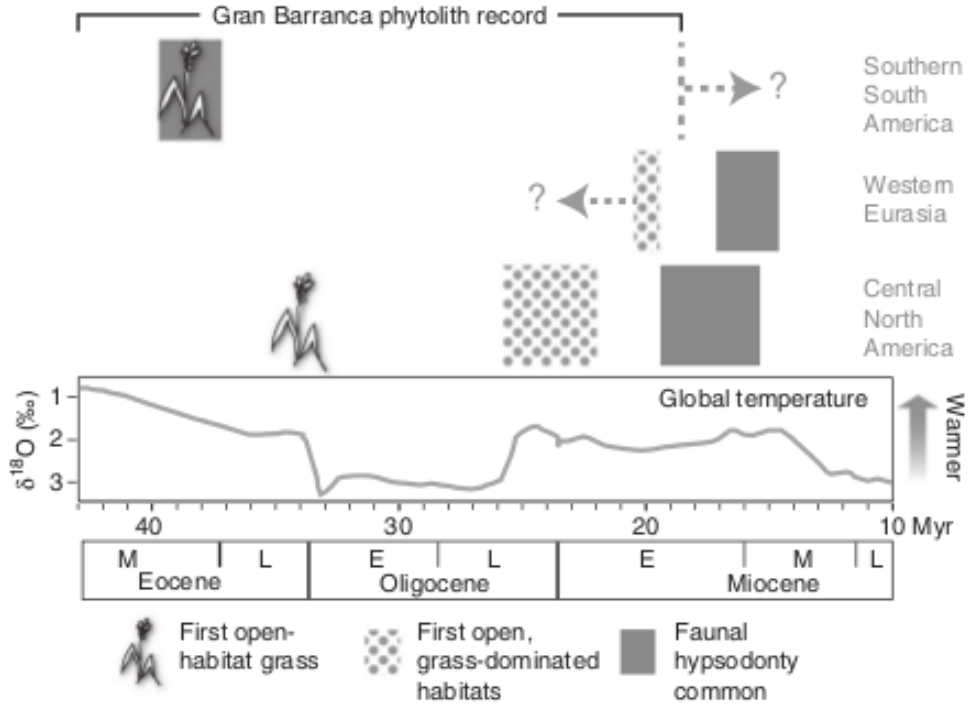
Global versus regional versus local scale processes



(Sidor et al. 2013 *PNAS*)

- global
  - corr w/ global climate
  - multiple regions corr
- regional
  - $\downarrow E$, $\uparrow Occ$, $\uparrow BC$, $\uparrow$ code
- local
  - $\uparrow E$, $\downarrow Occ$, $\downarrow BC$, $\downarrow$ code
- not mutually exclusive

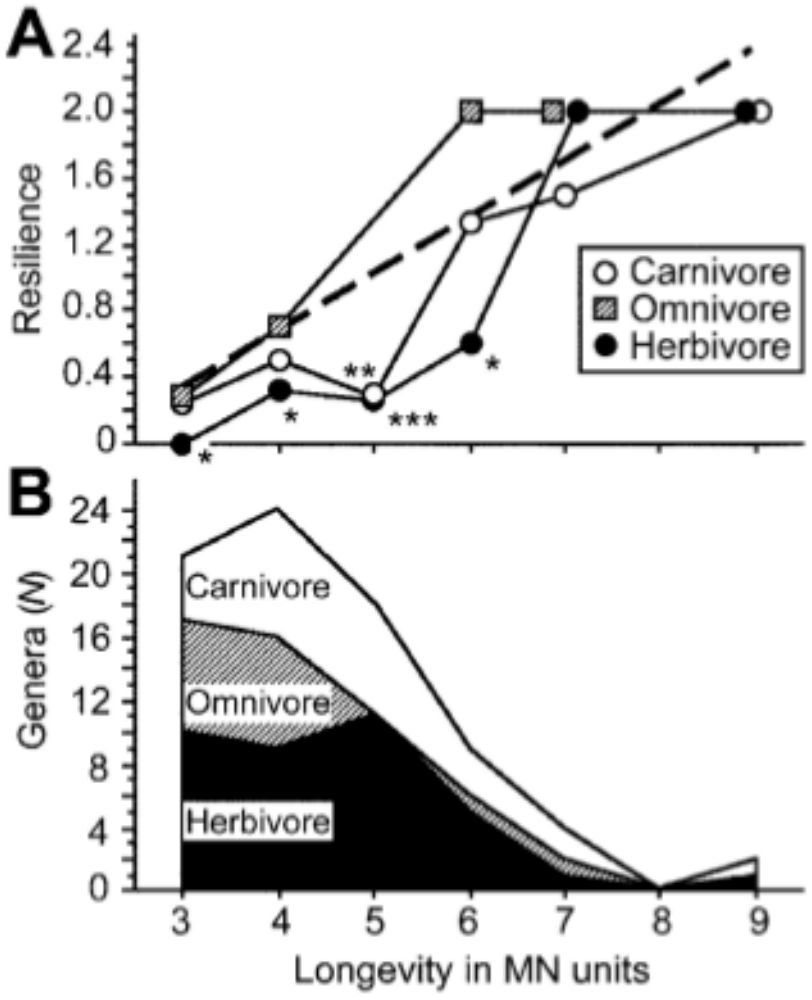
Expectations: locomotor category



(Strömberg *et al.* 2013 *Nature Com.*)

- arboreal
  - $\uparrow E$, $\uparrow$ code
  - $\downarrow BC$, $\downarrow Occ$
- ground dwelling
  - $\downarrow E$, $\downarrow$ code
  - $\uparrow BC$, $\uparrow Occ$
- scansorial
  - constant $\vee$ random

Expectations: dietary category



(Jernvall and Fortelius 2004 *Am. Nat.*)

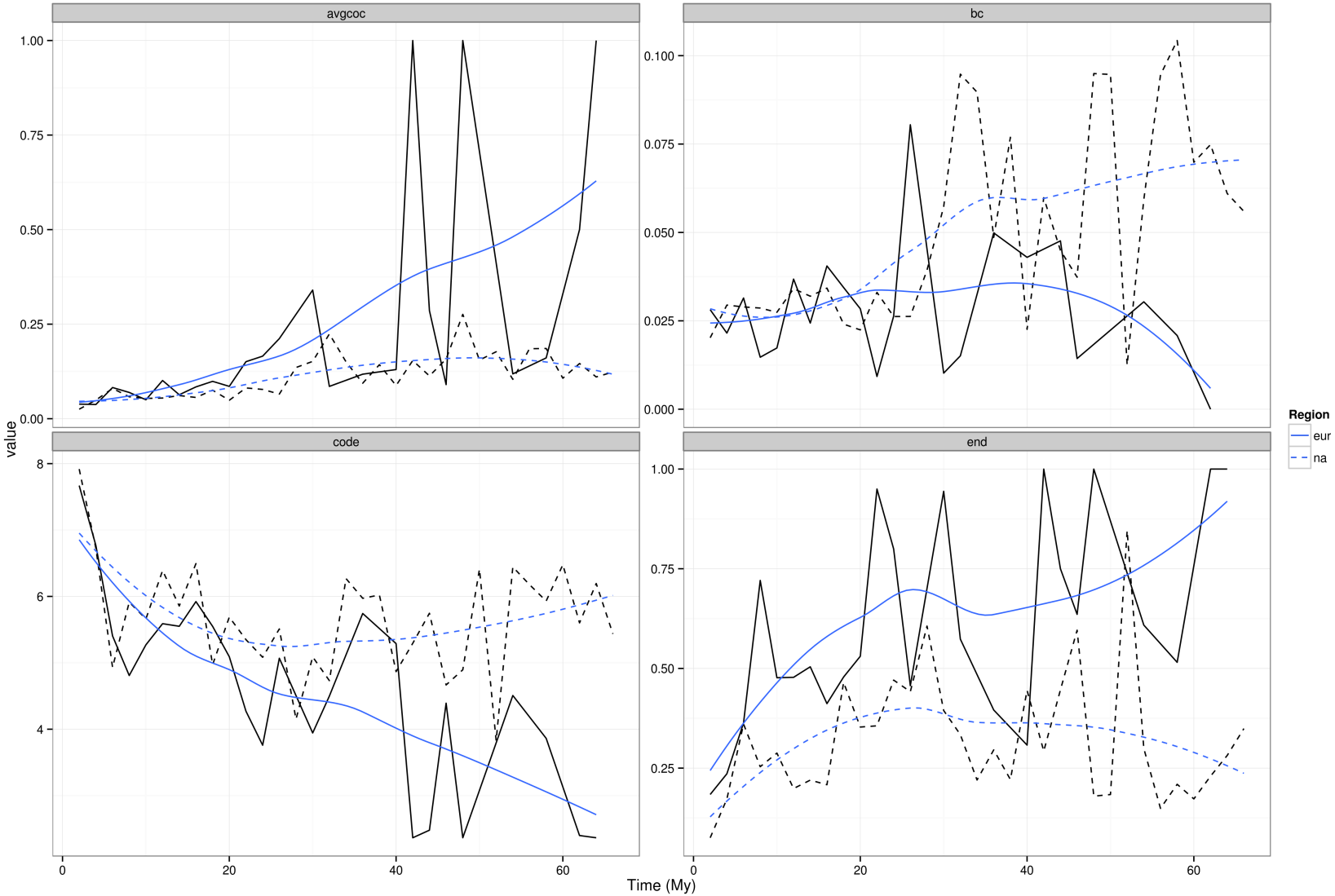
- herbivore
  - most like all taxa
- carnivore
  - constant $\vee$ corr w/ herbivores
- omnivore
  - constant $\vee$ random

Community connectedness of North America

Community connectedness of Europe

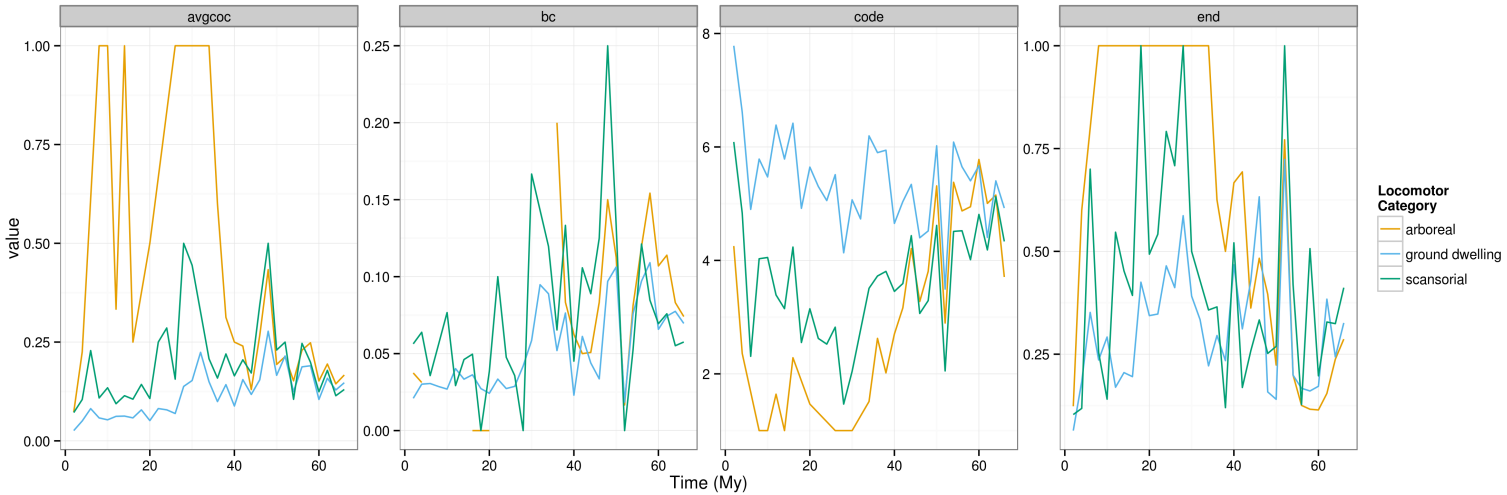
Community connectedness of South America

Preliminary results: NA, Eur

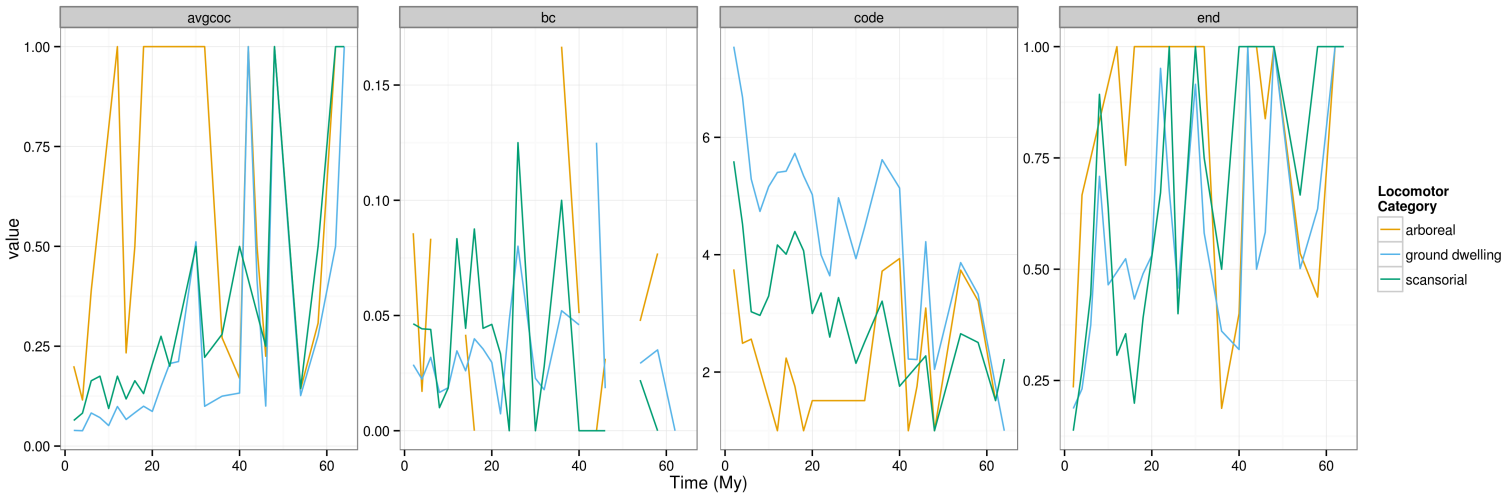


Preliminary results: locomotor category

North America

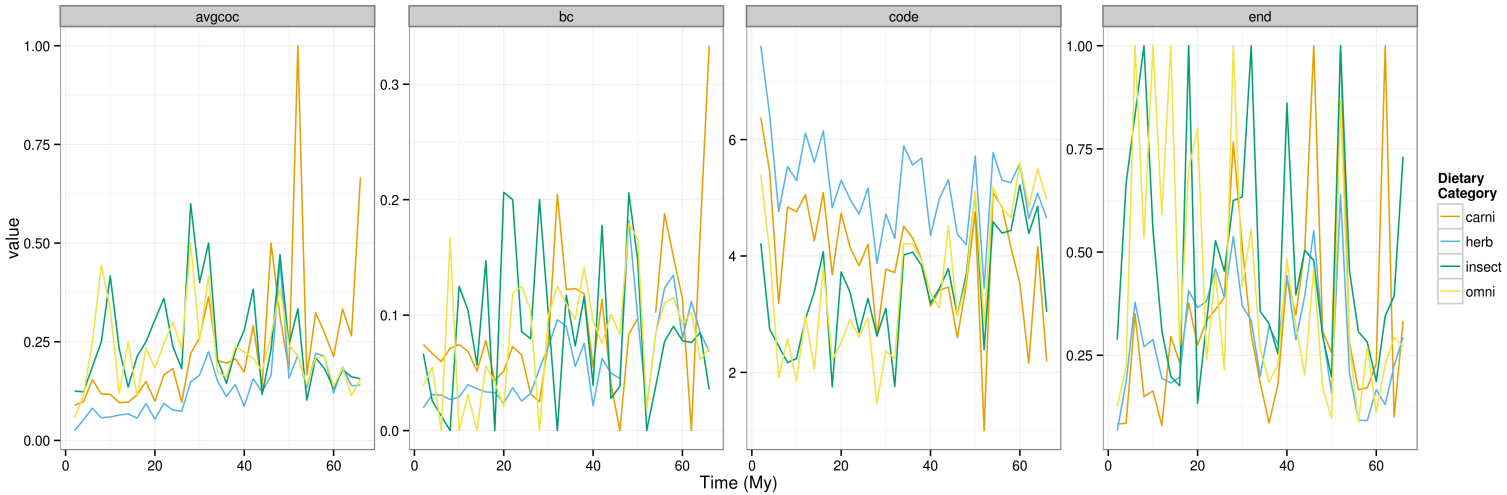


Europe

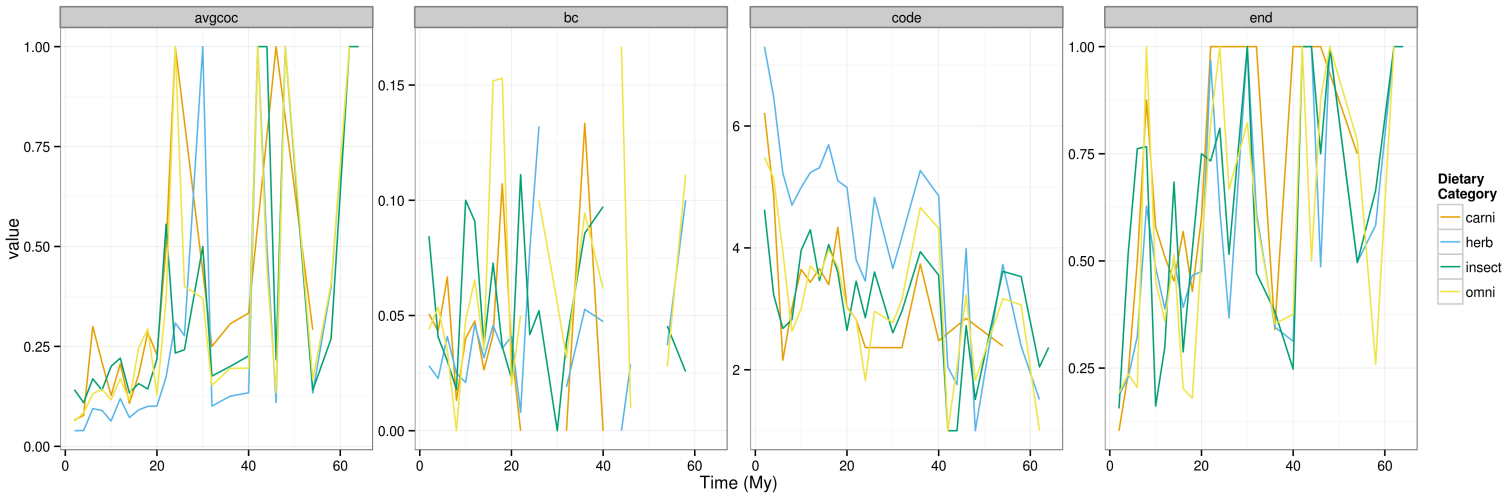


Preliminary results: dietary category

North America



Europe



Questions

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Summary of proposed research

Studies

- Permian brachiopod trait based survival
- Cenozoic mammal trait based survival
- Cenozoic mammal community connectedness

Acknowledgements

- **Committee**
  - Kenneth D. Angielczyk (co-advisor)
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The Field Museum