

*O species, stunned by your terror of chill death, why
fear the Styx, why fear the ghosts and empty names, the
stuff of poets, the spectres of a phantom world? [...]]
Everything changes, nothing dies: the spirit wanders,
arriving here or there, and occupying whatever body it
pleases, passing from a wild beast into a human being,
from our body into a beast, but is never destroyed. As
pliable wax, stamped with new designs, is no longer what
it was; does not keep the same form; but is still one and
the same.*

(Ovid, Metamorphoses, book XV: 143-175)

Evolutionary paleoecology and the biology of extinction

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February 2, 2014

Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

Theory

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Extinction

All species that have ever lived are, to a first approximation, dead.

(Raup 1986 The Nemesis Affair)

Foundation

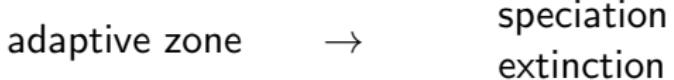
Question

Why do certain taxa go extinct while others do not?

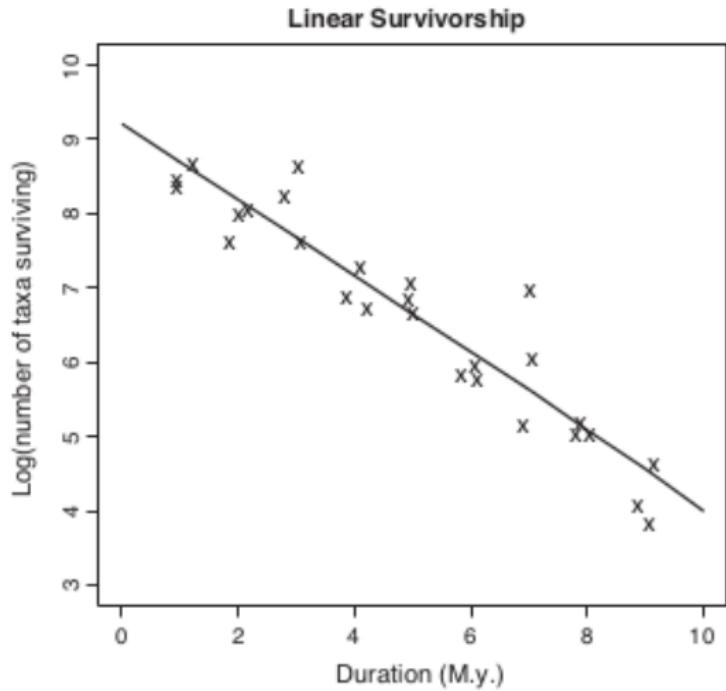
Evolutionary paleoecology

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

(Kitchell 1985 *Paleobiology*)



Van Valen's observation



(Liow et al. 2011 *TREE*)

Law of Constant Extinction

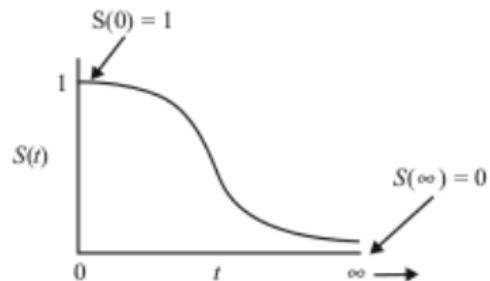
Definition

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

(Van Valen 1973 *Evol. Theory*)

Probability of survival

Theoretical $S(t)$:

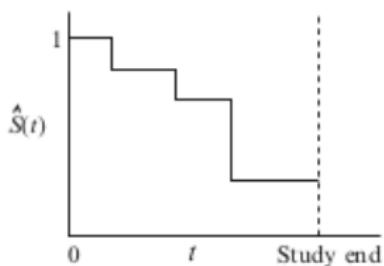


Survival function

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

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

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

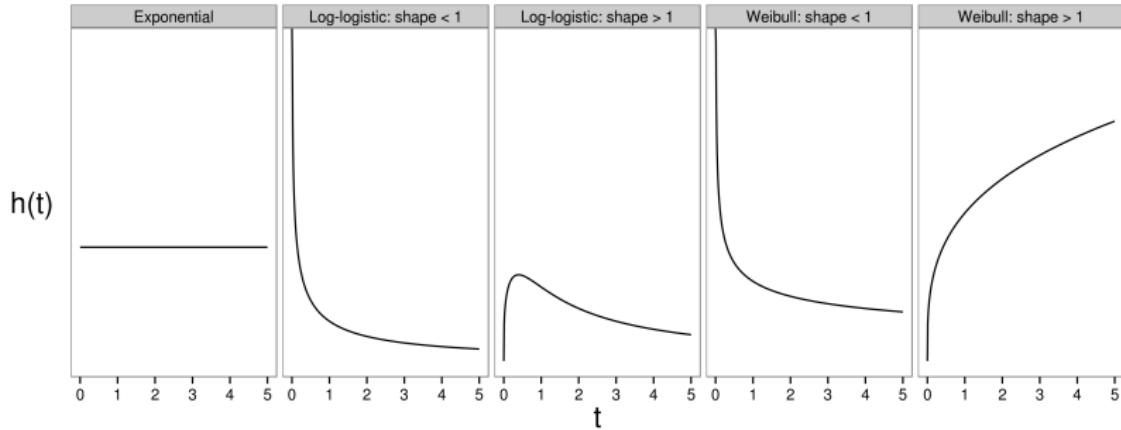


(Kleinbaum and Klein 2012)

Instantaneous potential of failure (extinction)

Hazard function \equiv conditional failure rate

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



Formalization of Van Valen

Law of Constant Extinction

Hazard is constant with respect to time (**exponential survival**).

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

Framework for analysis

Framework and setup

- ▶ background extinction
 - ▶ non-random with respect to biology
- ▶ traits related to habitat selection and range size
 - ▶ “bound” adaptive zone
- ▶ model non-organism mediated environmental change
 - ▶ which/what processes dominate: global, regional, local
 - ▶ how does this change over time?

Taxa and contexts

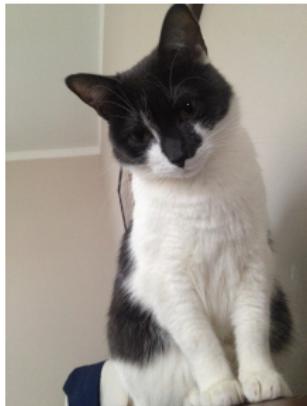
brachiopods

- ▶ marine
- ▶ sessile
- ▶ Permian (~ 47 My)
- ▶ global warming
- ▶ Australasia



mammals

- ▶ terrestrial
- ▶ motile
- ▶ Cenozoic (~ 65 My)
- ▶ global cooling
- ▶ North America, Europe, South America



Proposed studies

- ▶ Permian brachiopod trait based survival
 - ▶ generic level
 - ▶ necessity of emergence?
- ▶ Cenozoic mammal trait based survival
 - ▶ generic, specific level
 - ▶ necessity of emergence?
- ▶ Cenozoic mammal community connectedness
 - ▶ global versus regional versus local
 - ▶ differences across traits?

Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

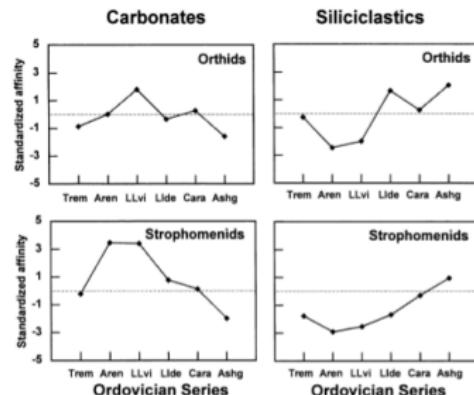
Brachiopods, environmental preference, and extinction

Australasian, Permian brachiopods

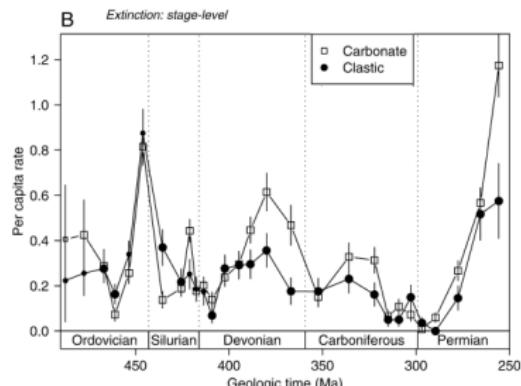
Questions

- ▶ Are traits related to environmental preference correlated with survival?
- ▶ Which trait(s) best model extinction? One or more?
- ▶ Is global climate change important to extinction?

Substrate affinity



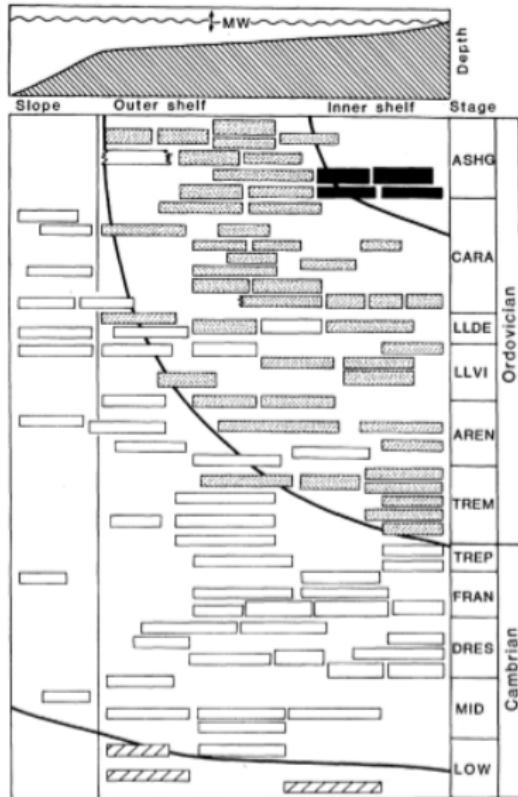
(Miller and Connolly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

- ▶ carbonates, clastics, mixed
 - ▶ physio-chemical
 - ▶ availability
 - ▶ weak proxy for larval dispersal?
- ▶ Phanerozoic decrease carbonates:clastics
 - ▶ predicted longevity: clastics > carbonates

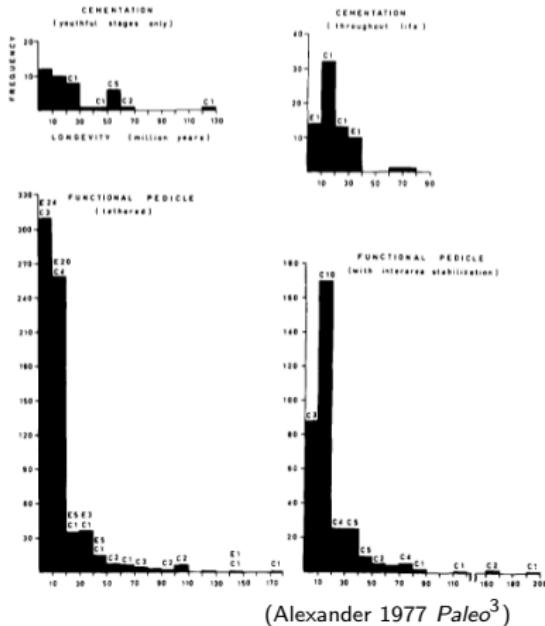
Habitat preference



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

- ▶ on-shore, off-shore, none
 - ▶ above/below storm wave base
 - ▶ energetics, availability
- ▶ classically invoked re. diversification of higher taxa
 - ▶ onshore → offshore

Affixing strategy



- ▶ environmental energetics and material (mud)
- ▶ pedunculate, reclining, cementing
 - ▶ endemics duration: reclining > others
 - ▶ cosmopolitan duration: ped./cement > others
- ▶ pedunculate:on-shore, reclining:off-shore

Assigning substrate and habitat

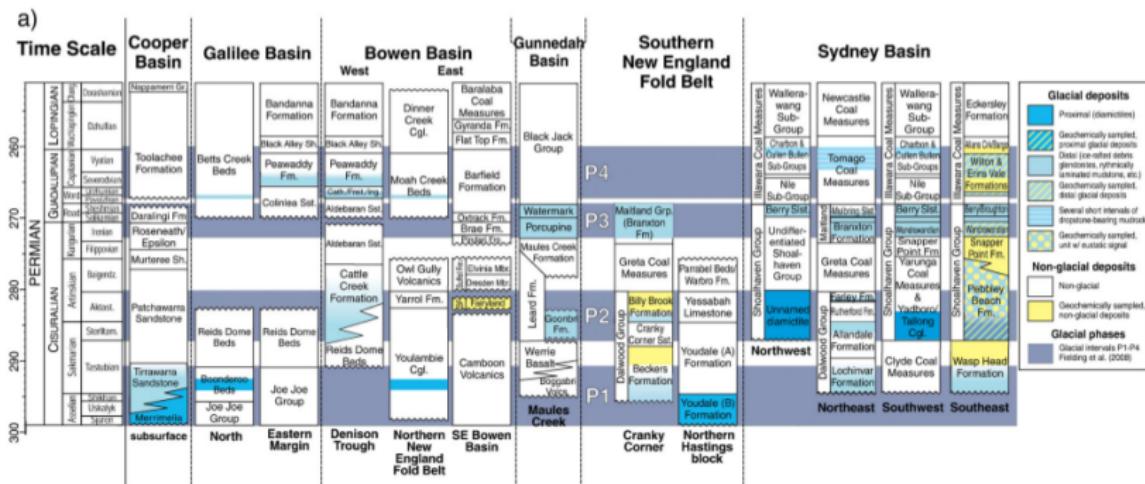
Probability of assignment

$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$
$$P(E|H) = \binom{n}{k} p^k (1-p)^{n-k}$$

- ▶ p : proportion of all collections (e.g.) carbonate
- ▶ n : total # taxon occurrences
- ▶ k : of n , # (e.g.) carbonate occurrences

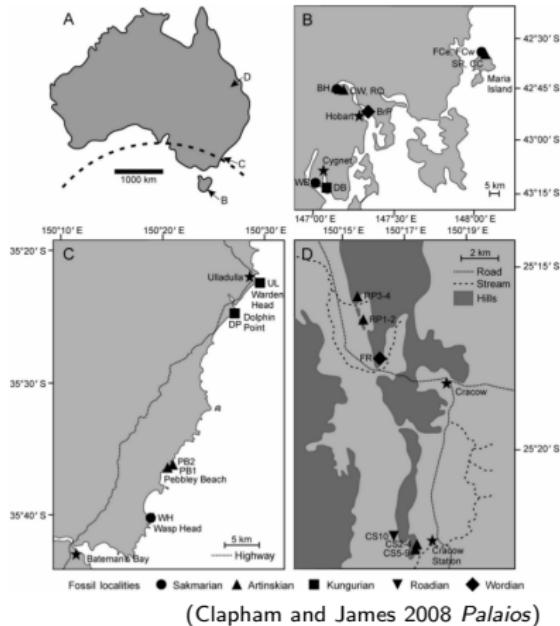
(Simpson and Harnik 2009 *Paleobiology*)

Permian climate



(Birgenheier *et al.* 2010 *Paleo*³)

Analysis

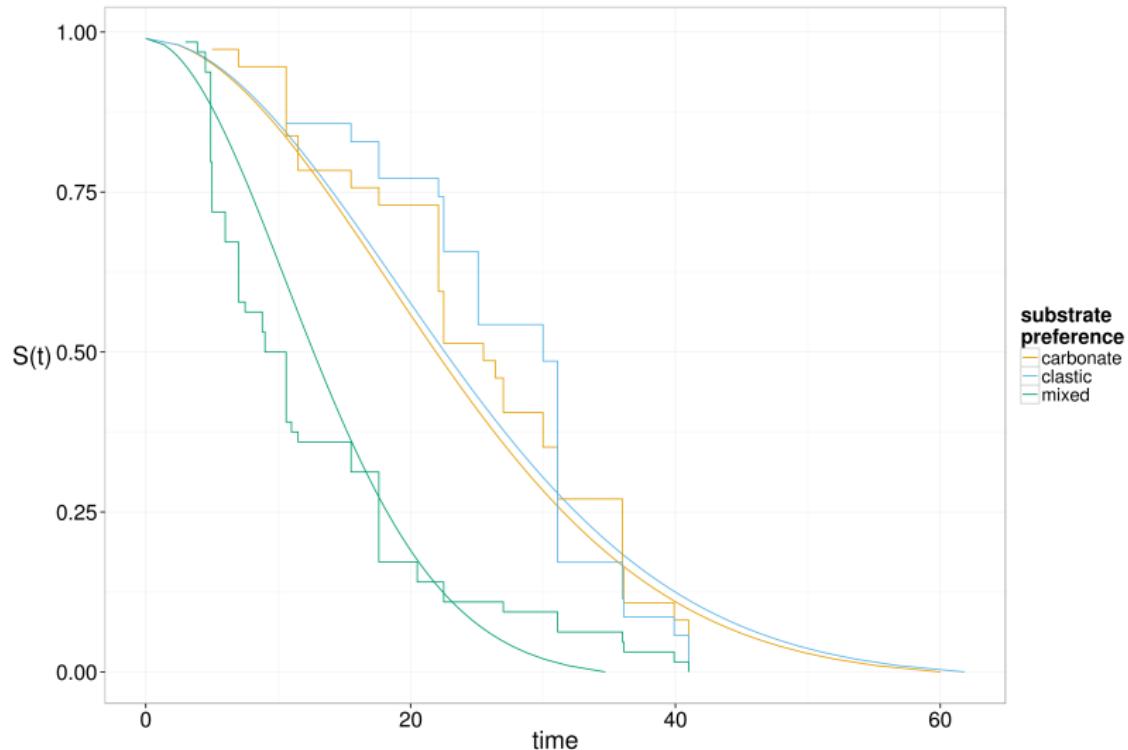


- ▶ genus FAD–LAD
 - ▶ Permian
- ▶ time-independent traits
 - ▶ preliminary substrate following Foote 2006 *Paleobio*.
 - ▶ preliminary habitat following Kiessling *et al.* 2007 *Paleo*³
- ▶ time-dependent climate
- ▶ survival distributions: $\exp(\lambda)$, $Weibull(\lambda, k)$, etc.

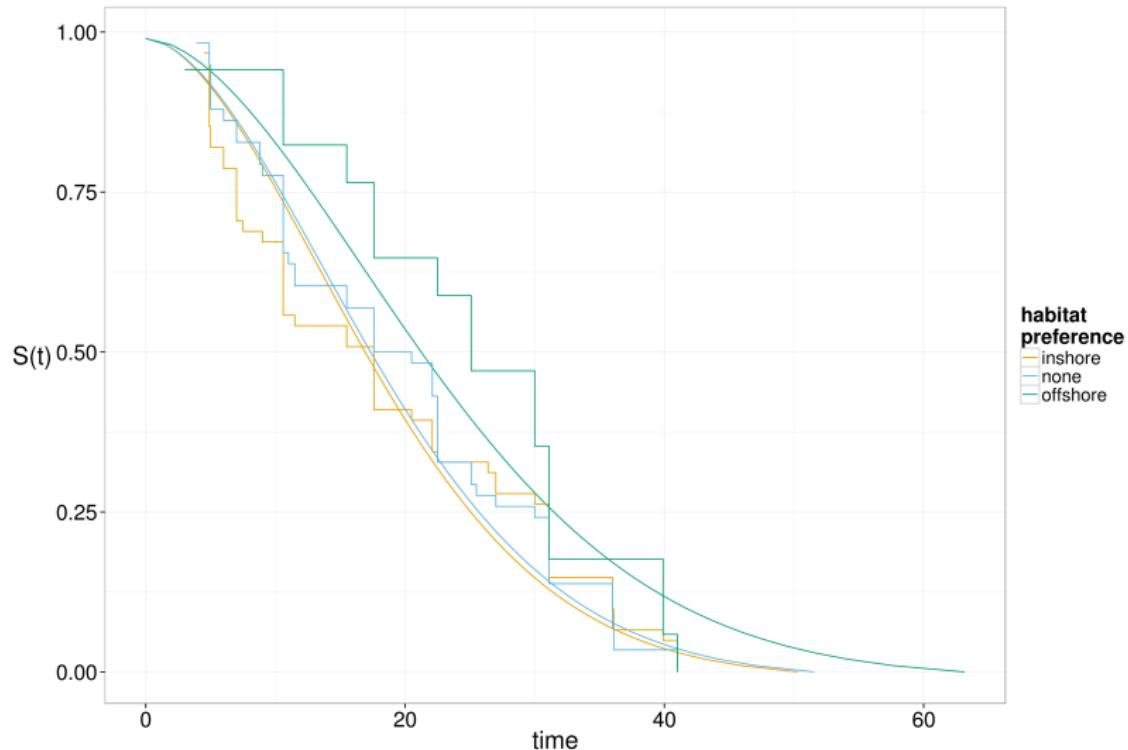
Preliminary results: model comparison

| formula | distribution | shape | df | AICc | weight |
|-------------|--------------|-------|----|-----------|--------|
| ~ aff | weibull | 1.91 | 4 | 1003.4543 | 0.81 |
| ~ aff + hab | weibull | 1.92 | 6 | 1006.3618 | 0.19 |
| ~ aff * hab | weibull | 1.94 | 10 | 1013.3003 | 0.01 |
| ~ 1 | weibull | 1.76 | 2 | 1034.4234 | 0.00 |
| ~ hab | weibull | 1.76 | 4 | 1036.2236 | 0.00 |
| ~ aff | exponential | | 3 | 1071.9199 | 0.00 |
| ~ aff + hab | exponential | | 5 | 1075.6211 | 0.00 |
| ~ 1 | exponential | | 1 | 1083.8734 | 0.00 |
| ~ aff * hab | exponential | | 9 | 1084.0485 | 0.00 |
| ~ hab | exponential | | 3 | 1086.7439 | 0.00 |

Preliminary results: best substrate



Preliminary results: best habitat



Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

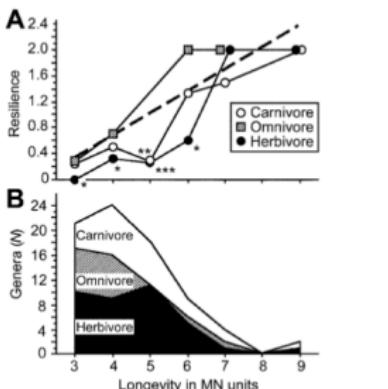
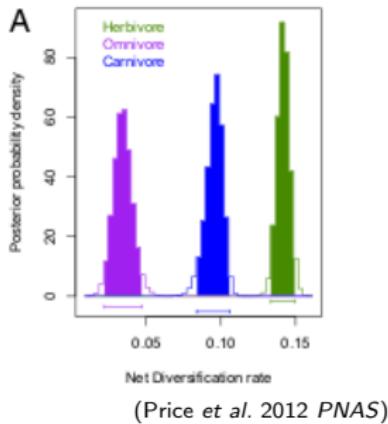
Ecology and survival in Cenozoic mammals

North America, South America, Europe

Questions

- ▶ How do traits related to range size relate to survival?
- ▶ Which trait(s) best model survival? One or more?
- ▶ Is climatic change important for modeling survival?
- ▶ Are patterns of survival different between genera and species?

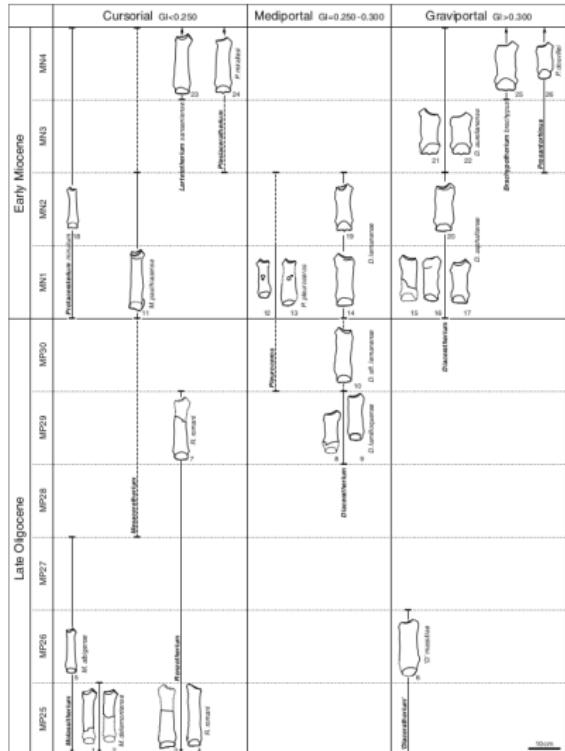
Dietary category



(Jernvall and Fortelius 2004 Am. Nat.)

- ▶ trophic hierarchy (stability → duration)
 - ▶ herb: most stable, longest duration
 - ▶ carni: least stable, shortest duration
 - ▶ omni: avg. stability, avg. duration
- ▶ ↑ diversification
 - ▶ ↑ origination; ≈ extinction
 - ▶ ≈ origination; ↓ extinction

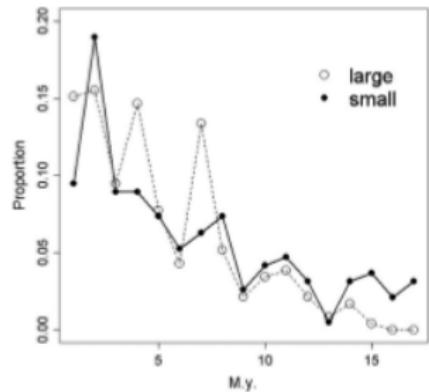
Locomotor category



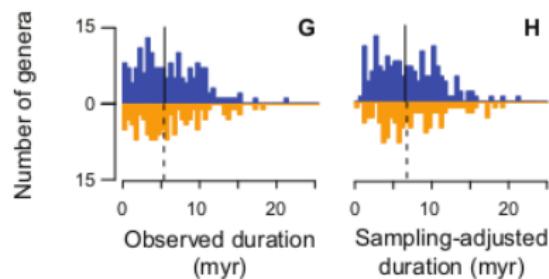
(Scherler et al. 2013 Swiss. J. Geosci.)

- ▶ Paleogene → Neogene
 - ▶ open → closed environment
- ▶ predictions
 - ▶ arboreal:
Paleogene > Neogene
 - ▶ ground dwelling:
Paleogene < Neogene
 - ▶ scansorial:
Paleogene ≈ Neogene

Body size



(Liow et al. 2008 PNAS)



(Tomiya 2013 Am. Nat.)

- ▶ ↑ body size, ↑ energy req,
↑ range size, ↓ extinction
- ▶ or ↑ body size, ↑ extinction
- ▶ Europe
 - ▶ lrg body size genera:
↑ extinction
- ▶ North America
 - ▶ generic body size:
 \simeq extinction

Analysis

- ▶ data: genus, 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
- ▶ survival distributions: $\exp(\lambda)$, $Weibull(\lambda, k)$, etc.

Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

Community connectedness in Cenozoic mammals

Questions

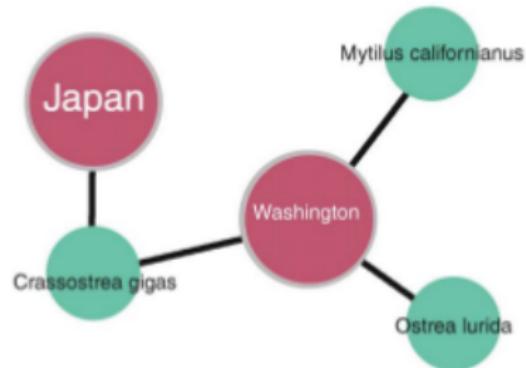
- ▶ How does the ratio between endemic and cosmopolitan taxa change over time?
- ▶ Is there a single global pattern or does each regions have a different patterns?
- ▶ Do these patterns differ between ecological categories?
- ▶ Is global climate change an important predictor of these patterns?

Community connectedness

Definition

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

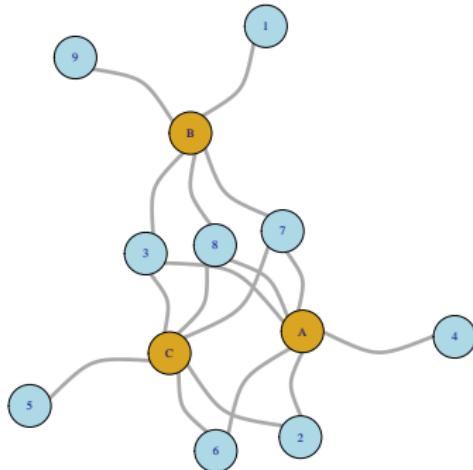
Biogeographic networks



(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



$$u = \{1, 2, 1\}$$

$$n = \{6, 5, 6\}$$

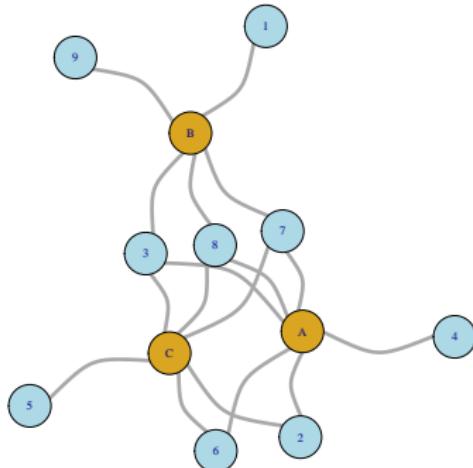
$$L = 3$$

$$E \approx 0.24$$

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

- ▶ 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



$$I = \{1, 2, 3, 1, 1, 2, 3, 3, 1\}$$

$$L = 3$$

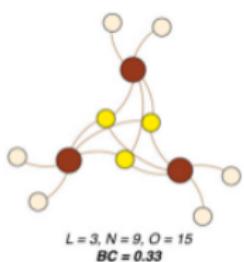
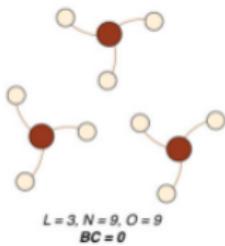
$$N = 9$$

$$Occ \approx 0.63$$

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

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

Biogeographic connectedness

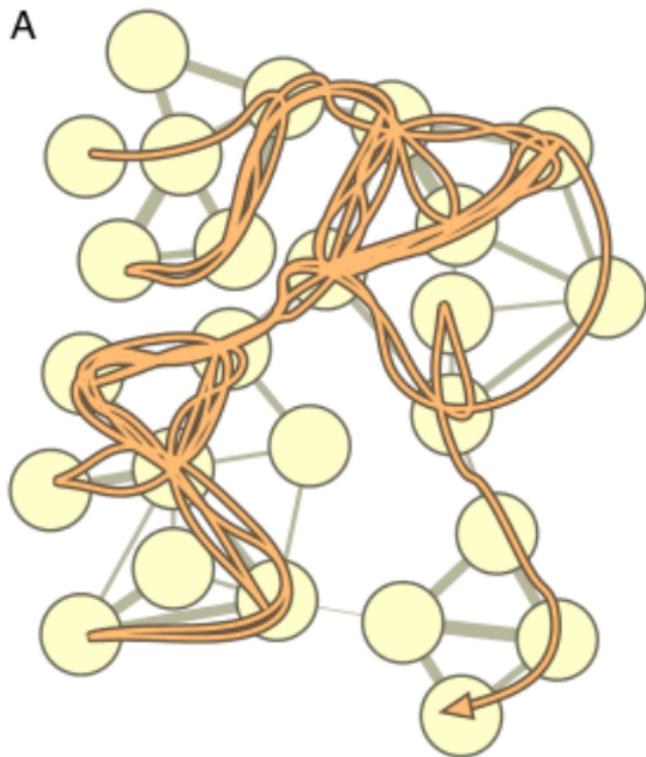


$$BC = \frac{O - N}{LN - N}$$

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

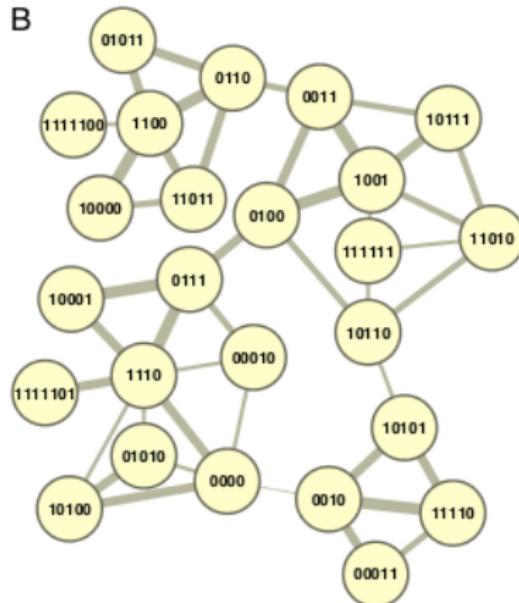
(Sidor et al. 2013 PNAS)

Code length



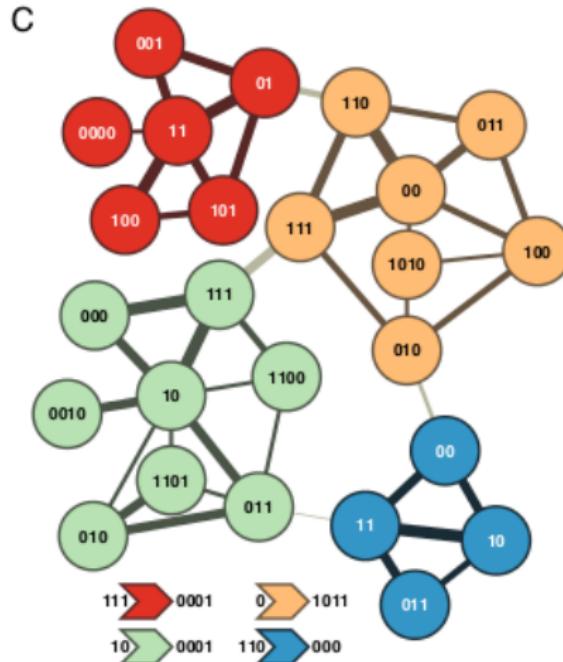
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



```
1111100 1100 0110 11011 10000 11011 0110 0011 10111 1001 0011  
1001 0100 0111 10001 1110 0111 10001 0111 1110 0000 1110 10001  
0111 1110 0111 1110 1111101 1110 0000 10100 0000 1110 10001 0111  
0100 10110 11010 10111 1001 0100 1001 10111 1001 0100 1001 0100  
0011 0100 0011 0110 11011 0110 0011 0100 1001 10111 0011 0100  
0111 10001 1110 10001 0111 0100 10110 111111 10110 10101 11110  
00011
```

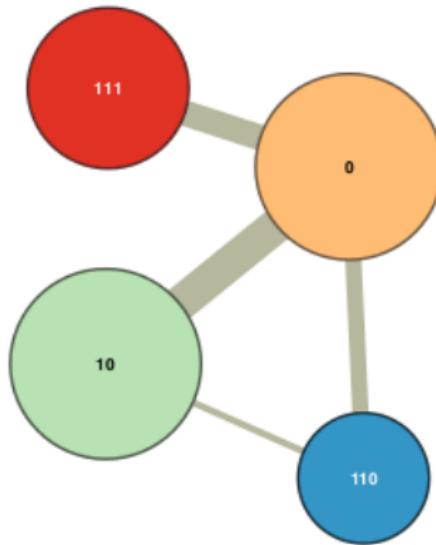
Code length



111 0000 11 01 101 100 101 01 0001 0 110 011 00 110 00 111 1011 10
111 000 10 111 000 111 10 011 10 000 111 10 111 10 0010 10 011 010
011 10 000 111 0001 0 111 010 100 011 00 111 00 011 00 111 00 111
110 111 110 1011 111 01 101 01 0001 0 110 111 00 011 110 111 1011
10 111 000 10 000 111 0001 0 111 010 1010 010 1011 110 00 10 011

Code length

D



111 0000 11 01 101 100 101 01 0001 0 110 011 00 110 00 111 1011 10
011 000 10 111 000 111 10 011 10 000 111 10 111 10 0010 10 011 010
011 10 000 111 0001 0 111 010 100 011 00 111 00 011 00 111 00 111
110 111 110 1011, 111 01 101 01 0001 0 110 111 00 011 110 111 1011
10 111 000 10 000 111 0001 0 111 010 1010 010 1011 110 00 10 011

(Rosvall and Bergstrom 2008 PNAS)

Compressing a network

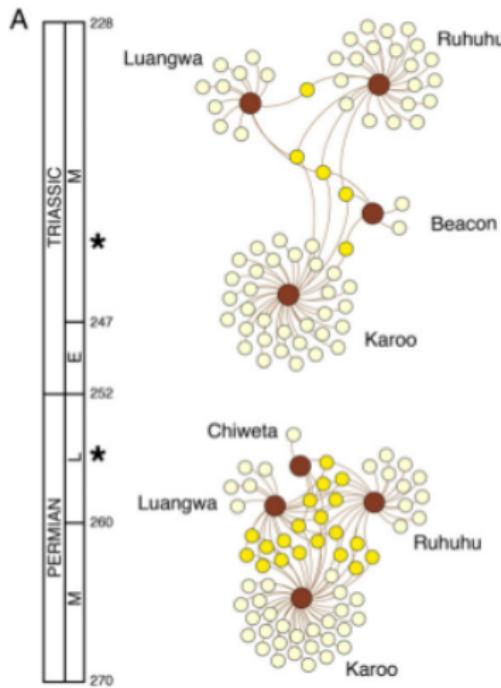
Map equation

(Rosvall and Bergstrom 2008 PNAS)

$$L(\mathbf{M}) = q_{\curvearrowright} H(\mathcal{Q}) + \sum_{i=1}^m p_{\circlearrowleft}^i H(\mathcal{P}^i)$$

- ▶ \mathbf{M} : module partition of n nodes in m partitions
- ▶ $L(\mathbf{M})$: network code length
- ▶ q_{\curvearrowright} : P(walk switches modules)
- ▶ $H(\mathcal{Q})$: entropy module codewords
- ▶ $H(\mathcal{P}^i)$: entropy within-module
- ▶ p_{\circlearrowleft}^i : rate within-module use

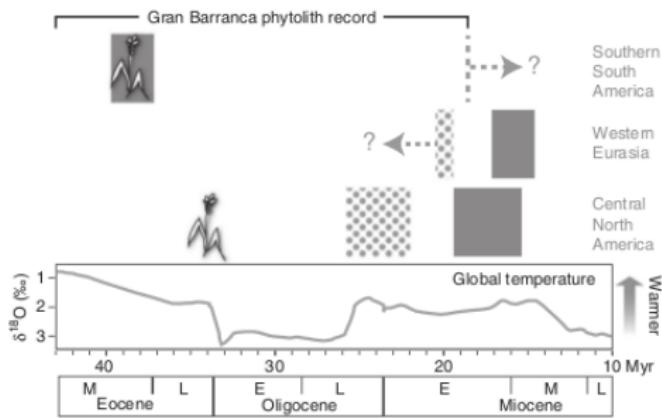
Global versus regional versus local scale



- ▶ 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

(Sidor et al. 2013 PNAS)

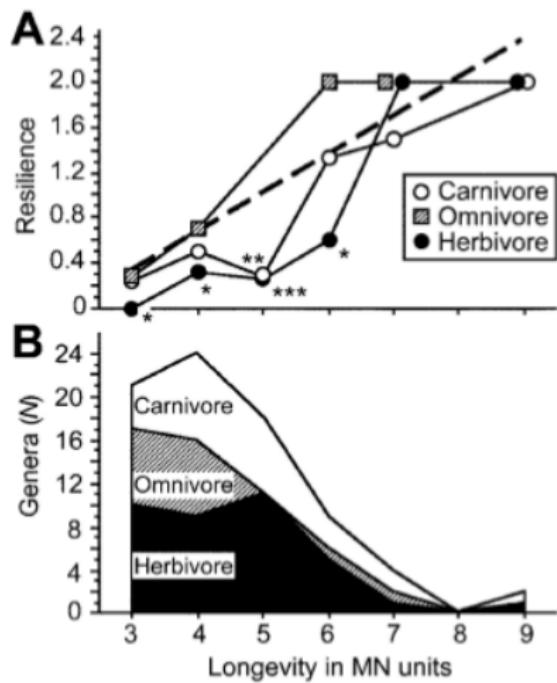
Global expectations: locomotor category



(Strömberg et al. 2013 *Nature Com.*)

- ▶ arboreal
 - ▶ ↑ E , ↑ code
 - ▶ ↓ BC, ↓ Occ
- ▶ ground dwelling
 - ▶ ↓ E , ↓ code
 - ▶ ↑ BC, ↑ Occ
- ▶ scansorial
 - ▶ constant ∨ random

Global expectations: dietary category



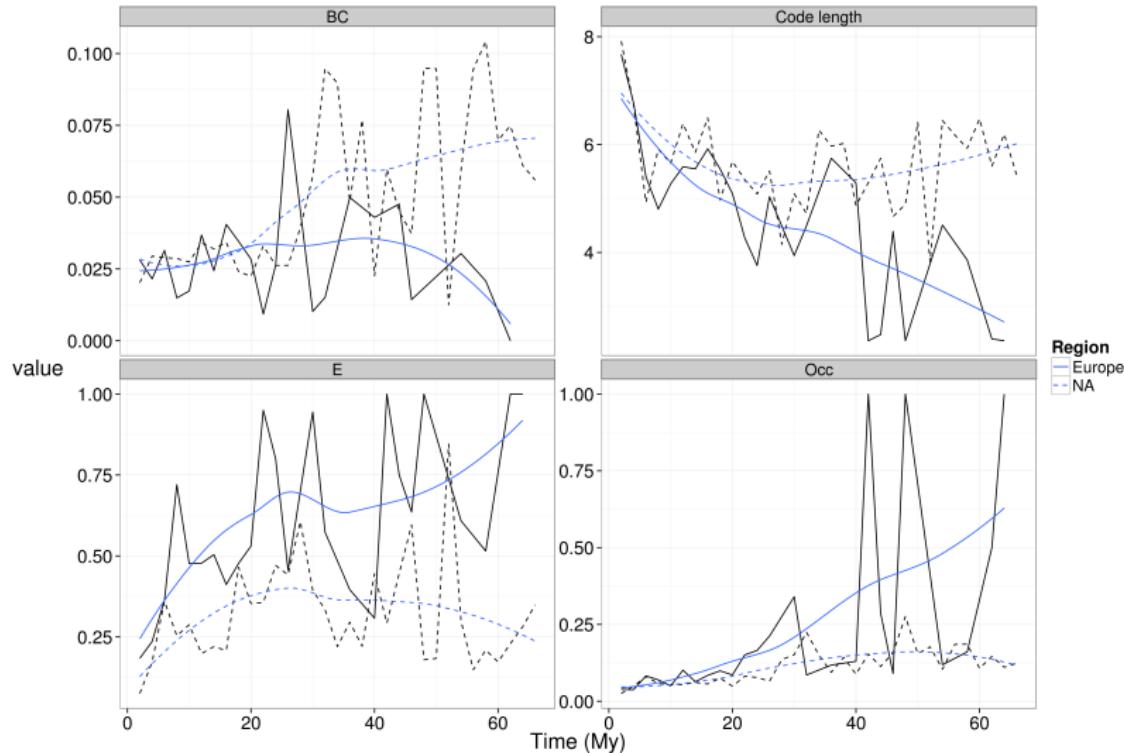
- ▶ herbivore
 - ▶ most like all taxa
- ▶ carnivore
 - ▶ constant ∨ corr w/ herbivores
- ▶ omnivore
 - ▶ constant ∨ random

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

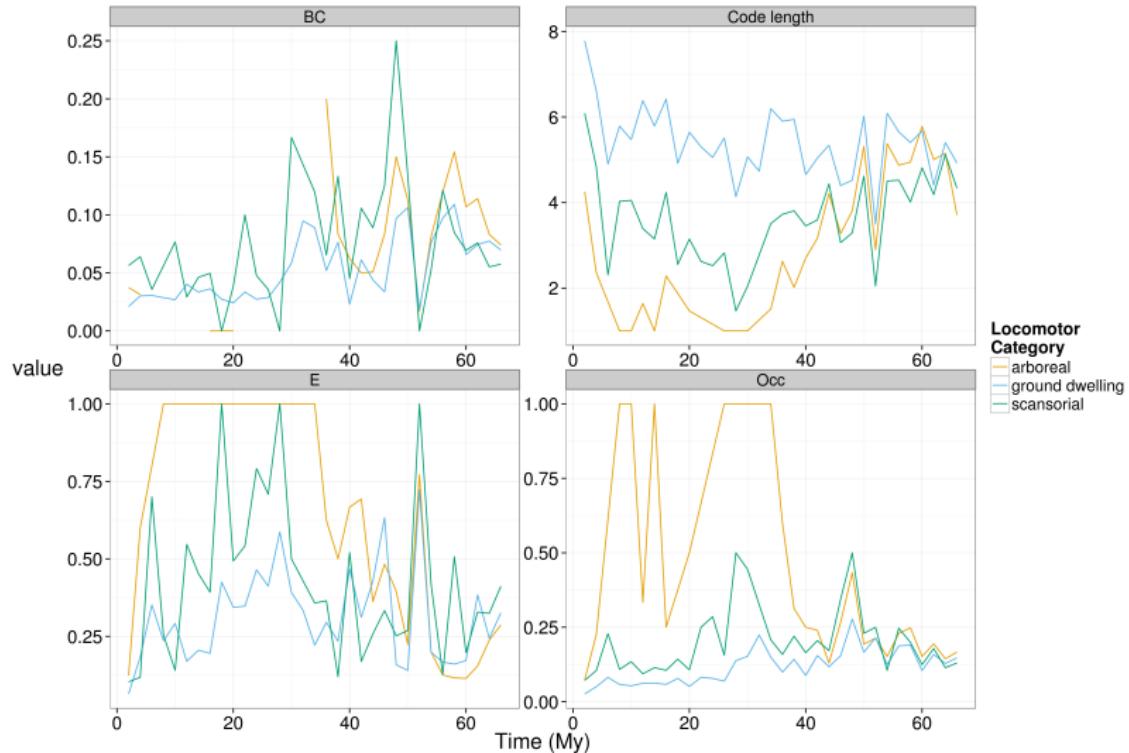
Regional variation

- ▶ North America
 - ▶ similar to global predictions
- ▶ Europe
 - ▶ stable trophic diversity
- ▶ South America
 - ▶ high provincialism (North/South)
 - ▶ early expansion of ground dwelling taxa

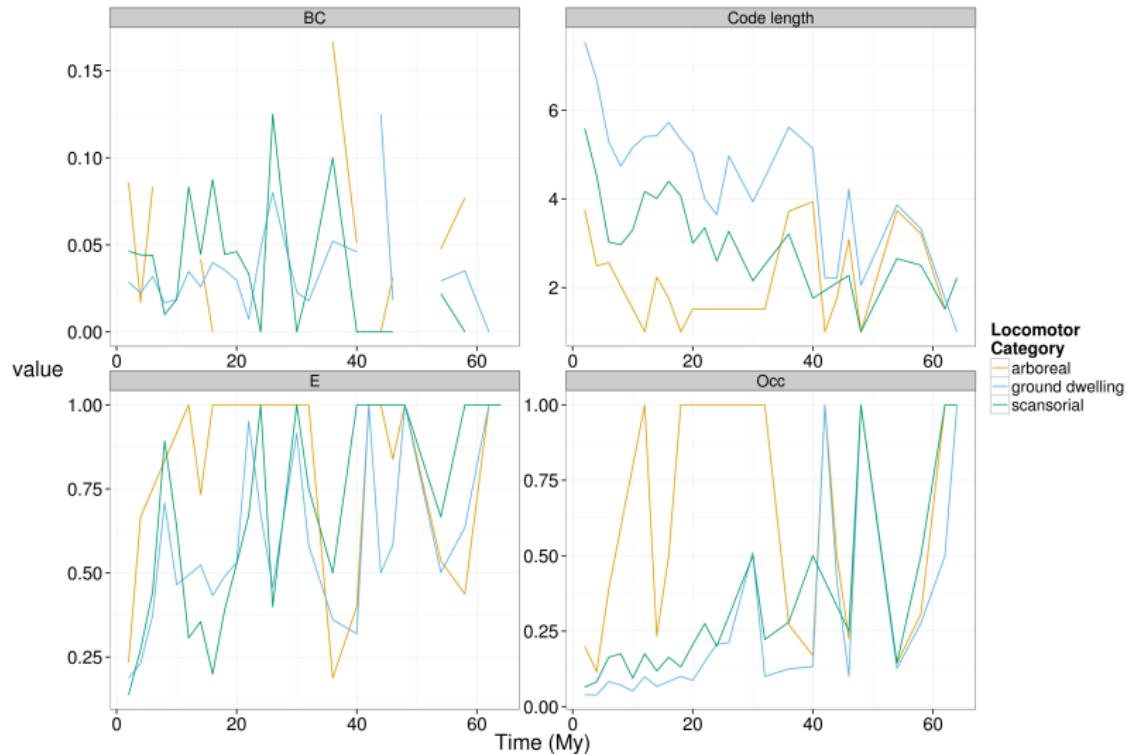
Preliminary results: NA, Eur



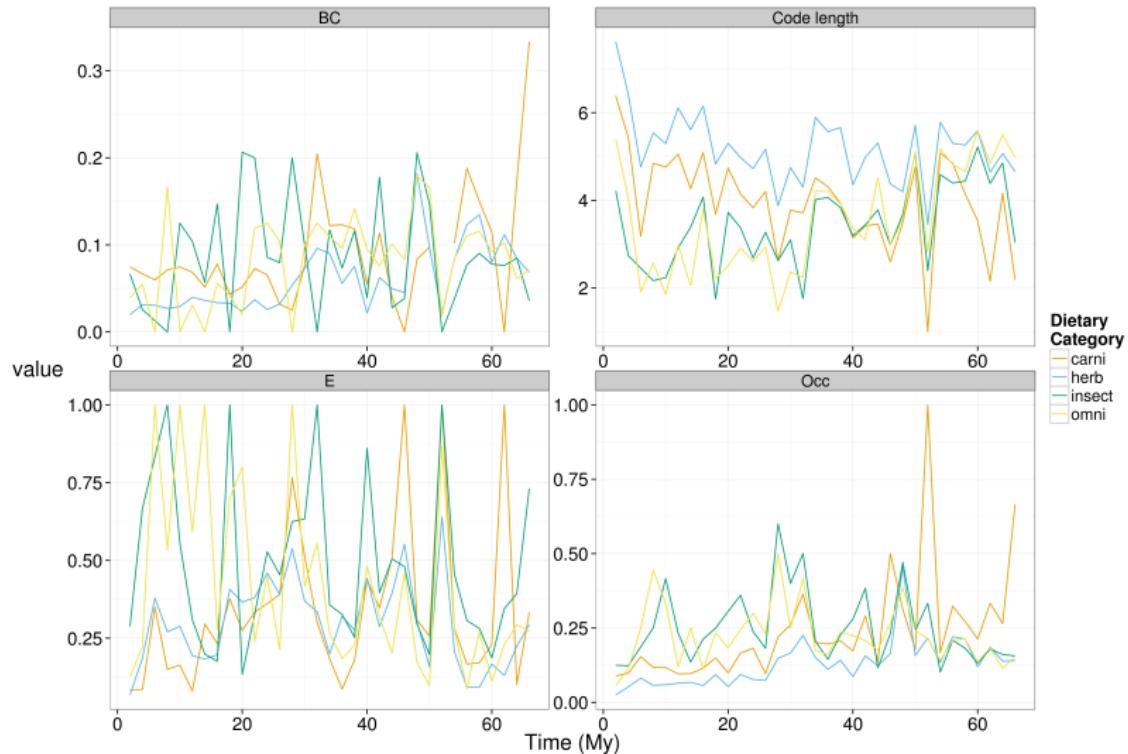
Preliminary results: locomotor category NA



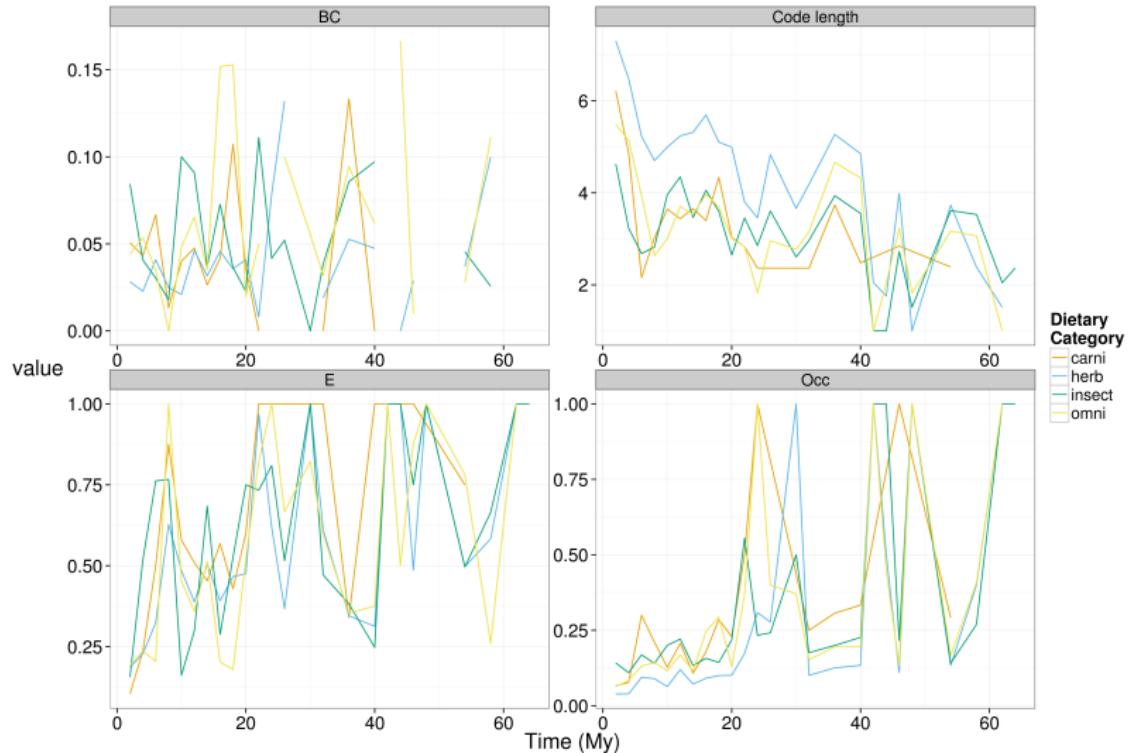
preliminary results: locomotor category Eur



Preliminary results: dietary category NA



Preliminary results: dietary category Eur



Fundamental

Question

Why do some taxa go extinct while others do not?

Evolutionary paleoecological rephrasing

Question

How does a taxon's adaptive zone affect extinction risk?

“Testing” the Law of Constant Extinction

Liow et al. 2011 *TREE*

Only applies during periods of relatively **constant** environment.

Measure, analyze, model changing environment.

Ask the following . . .

Is there a **general pattern** of extinction?

What traits matter for extinction and **when**?

How do they matter?

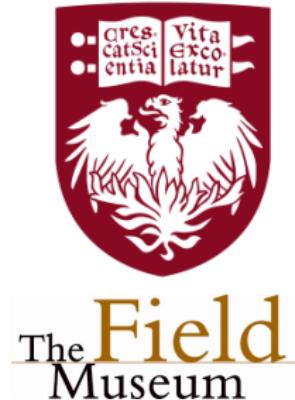
Acknowledgements

► Committee

- ▶ Kenneth D. Angielczyk
(co-advisor)
- ▶ Michael J. Foote
(co-advisor)
- ▶ P. David Polly
- ▶ Richard H. Ree

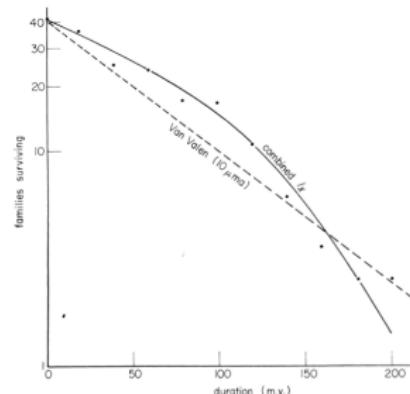
► Discussion

- ▶ David Bapst, Megan Boatright, Ben Frable, Colin Kyle, Darcy Ross, Liz Sander
- ▶ John Alroy, Graeme Lloyd, Carl Simpson, Graham Slater

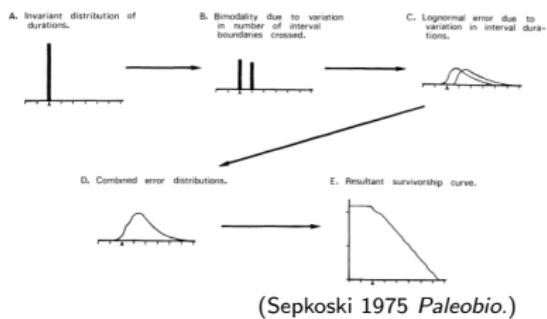


Further concerns

Theseus' ship: simulations and survival



(Raup 1975 *Paleobio.*)

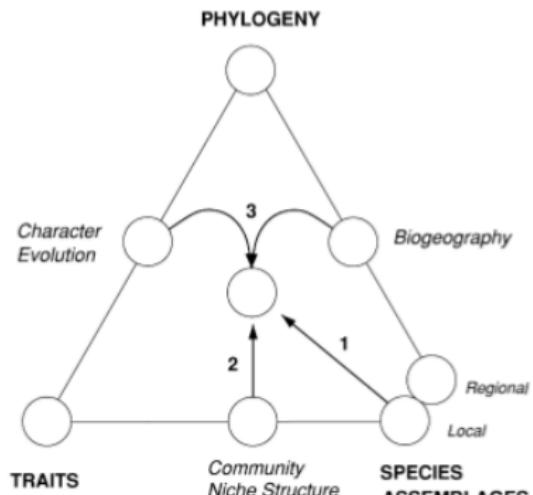


(Sepkoski 1975 *Paleobio.*)

- ▶ heterogeneous preservation
 - ▶ $P(\phi|A) \neq P(\phi|B)$
- ▶ cryptic speciation/anagenesis

- ▶ longer duration than expected
- ▶ proxy generic level?
- ▶ time-homogeneous birth-death model
 - ▶ constant p, b
 - ▶ expected $S(t) = \exp^{-\lambda t}$

Phylogenetic similarity of communities



(Webb *et al.* 2002 *Ann. Rev. Ecol. Syst.*)

- ▶ informal phylogeny (taxonomy tree)
 - ▶ PBDB, EoL, etc.
 - ▶ unit branch length
- ▶ measures
 - ▶ relative mean pairwise distance between taxa at locality
 - ▶ mean locality phylogenetic species variability (Helmus *et al.* 2007 *Am. Nat.*)