

*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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April 1, 2014

Theory

Survival

Communities

Summary

Theory

Survival

Communities

Summary

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.

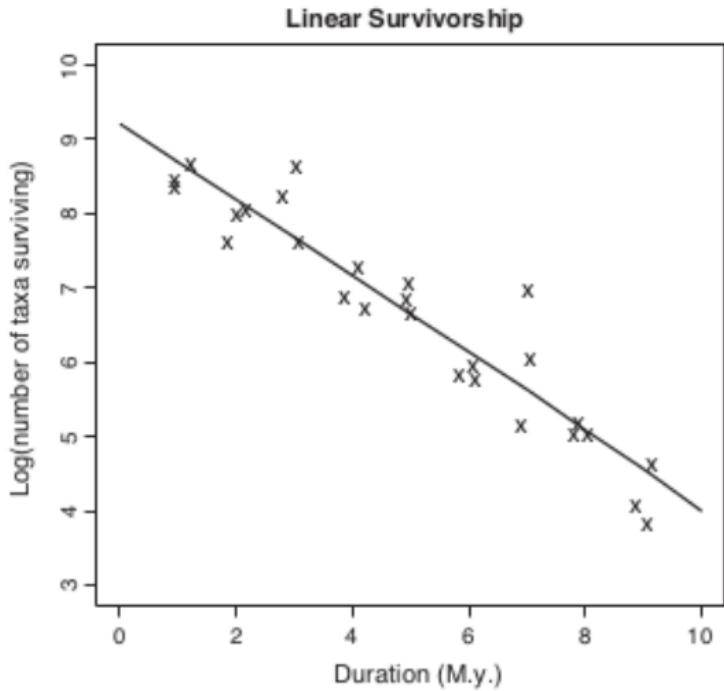
(Kitchell 1985 *Paleobiology*)

In context of this study

Rephrased

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

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*)

Approach

Framework and setup

- ▶ background extinction
- ▶ traits related to environmental preference
 - ▶ “bound” adaptive zone
- ▶ when/which/what processes dominate:
global, regional, local

Systems

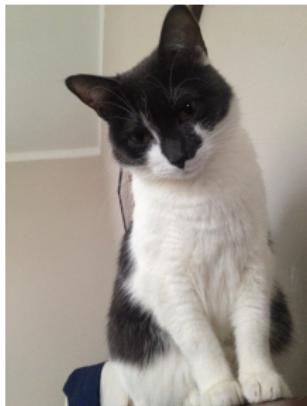
brachiopods

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



mammals

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



Proposed studies

- ▶ Australian Permian brachiopods
 - ▶ survival patterns
 - ▶ community connectedness (not shown)
 - ▶ traits: substrate, habitat, affixing strategy
- ▶ Cenozoic mammals
 - ▶ survival patterns (not shown; come to Evolution2014)
 - ▶ community connectedness
 - ▶ traits: dietary and locomotor categories, body size

Theory

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Survival analysis framework

Definition

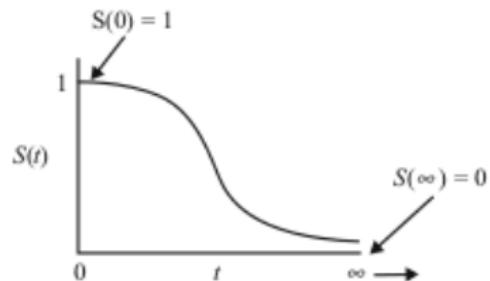
Analysis of time till event data.

Time is duration or age.

Event is an occurrence of interest.

Probability of survival

Theoretical $S(t)$:

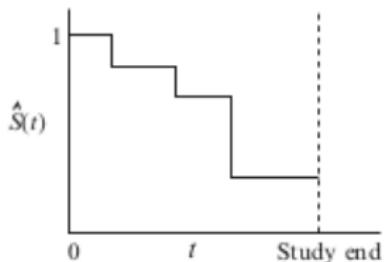


Survival function

$$S(t) = \Pr(T > t)$$

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

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

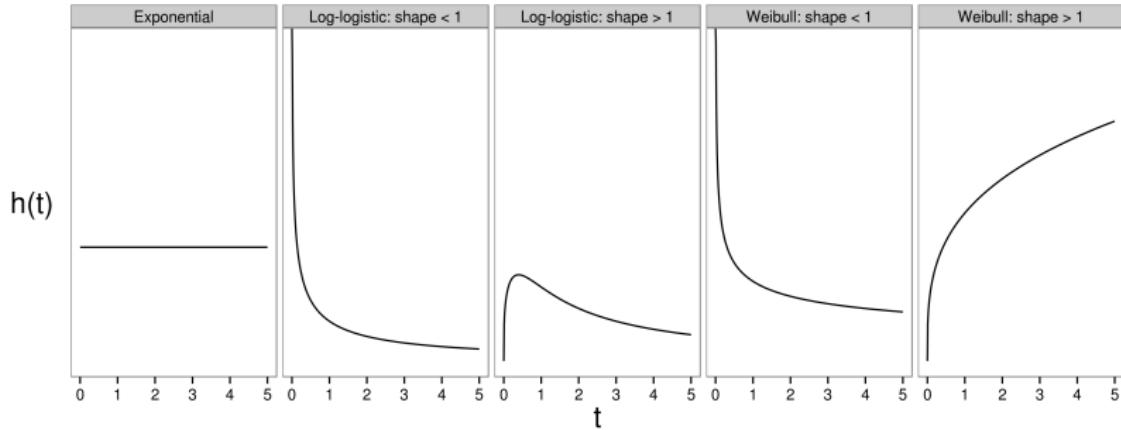


(Kleinbaum and Klein 2012)

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**).

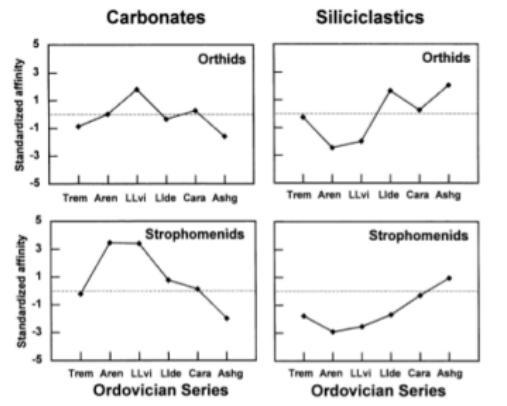
$$h(t) = \lambda \iff S(t) = \exp^{-\lambda t}$$

Brachiopods, environmental preference, and extinction

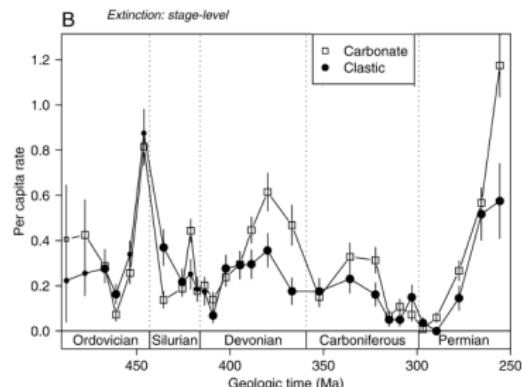
Questions

- ▶ Do traits related to environmental preference have different distributions of taxonomic duration?
 - ▶ Is survival best modeled by a single trait or multiple?
 - ▶ How do other factors, such as climate, affect these patterns?
- ▶ Is extinction taxon-age independent or dependent?

Substrate affinity



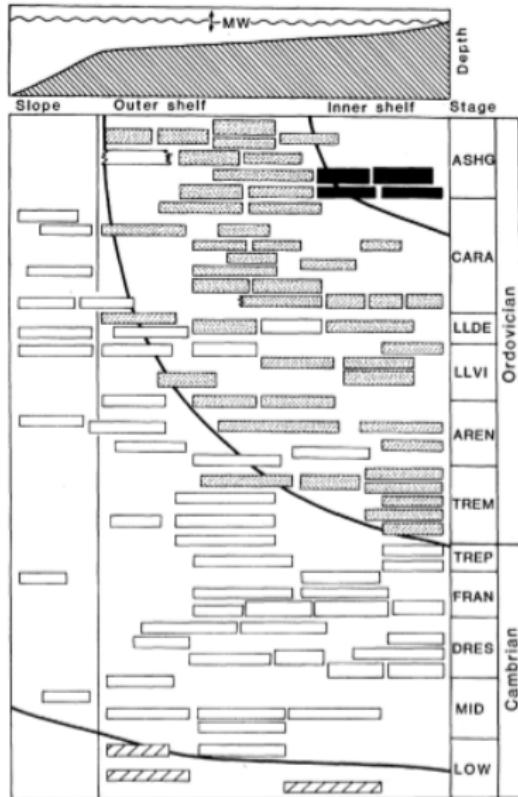
(Miller and Connolly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

- ▶ depositional setting
 - ▶ carbonates, clastics
 - ▶ availability
- ▶ Phanerozoic decrease carbonates:clastics
 - ▶ predicted longevity: clastics > carbonates

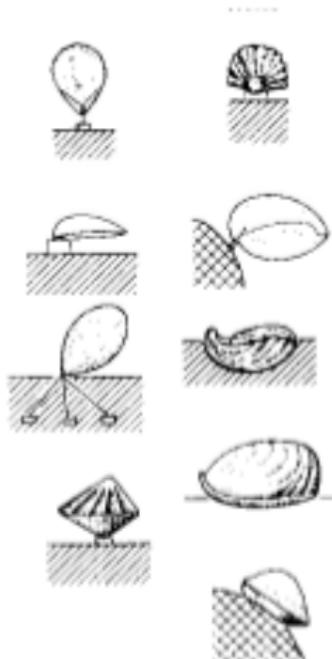
Habitat preference



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

- ▶ storm wave base
 - ▶ on-shore, off-shore, none
 - ▶ availability
 - ▶ stability
- ▶ offshore > onshore

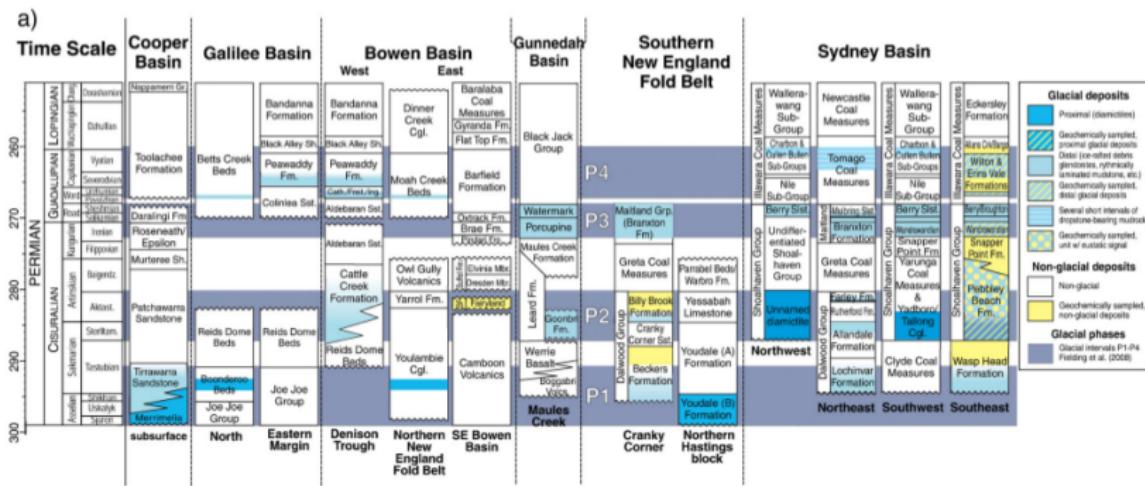
Affixing strategy



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

(Johansen 1989 *Paleo*³)

Permian climate



(Birgenheier *et al.* 2010 *Paleo*³)

Assigning substrate and habitat

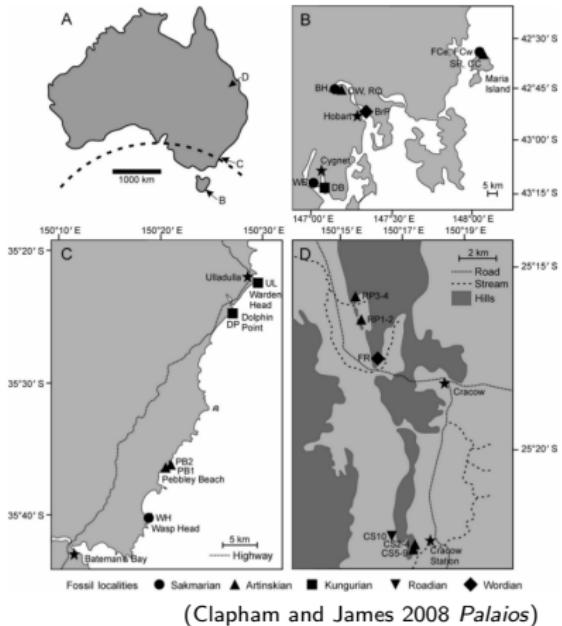
Probability of assignment

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

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

(Simpson and Harnik 2009 *Paleobiology*)

Analysis

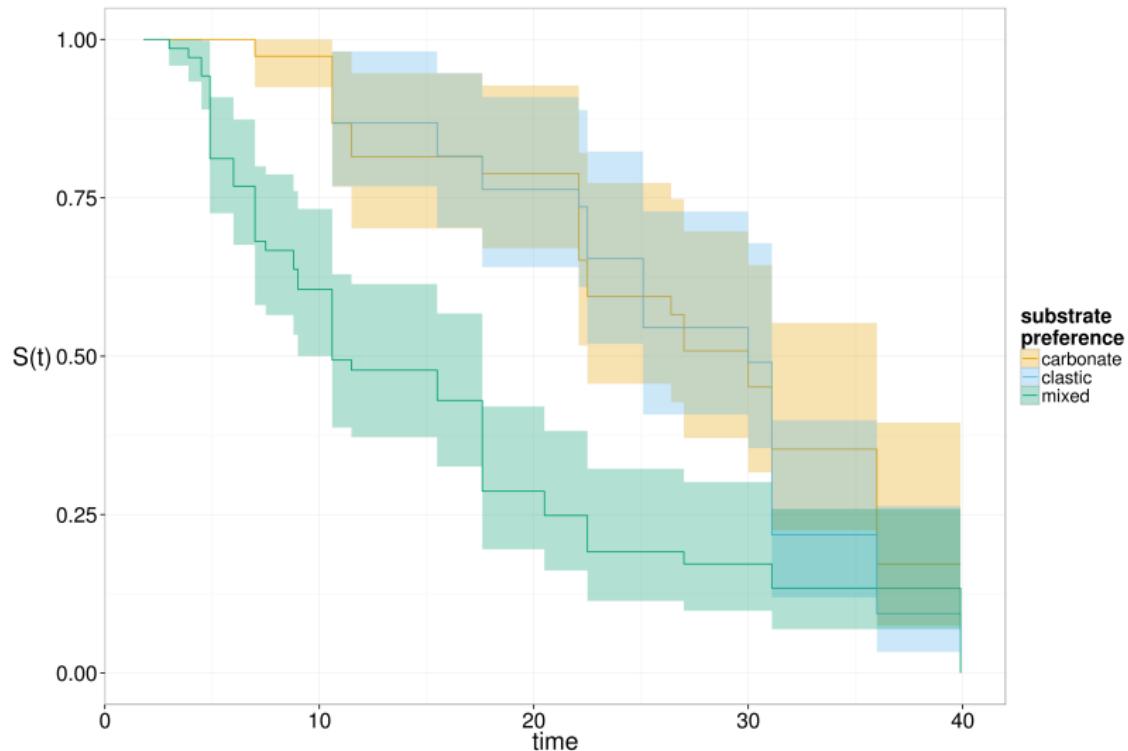


- ▶ genus FAD–LAD
- ▶ time-independent traits
 - ▶ preliminary substrate following Foote 2006 *Paleobio*.
 - ▶ preliminary habitat following Kiessling *et al.* 2007 *Paleo*³
- ▶ time-dependent climate

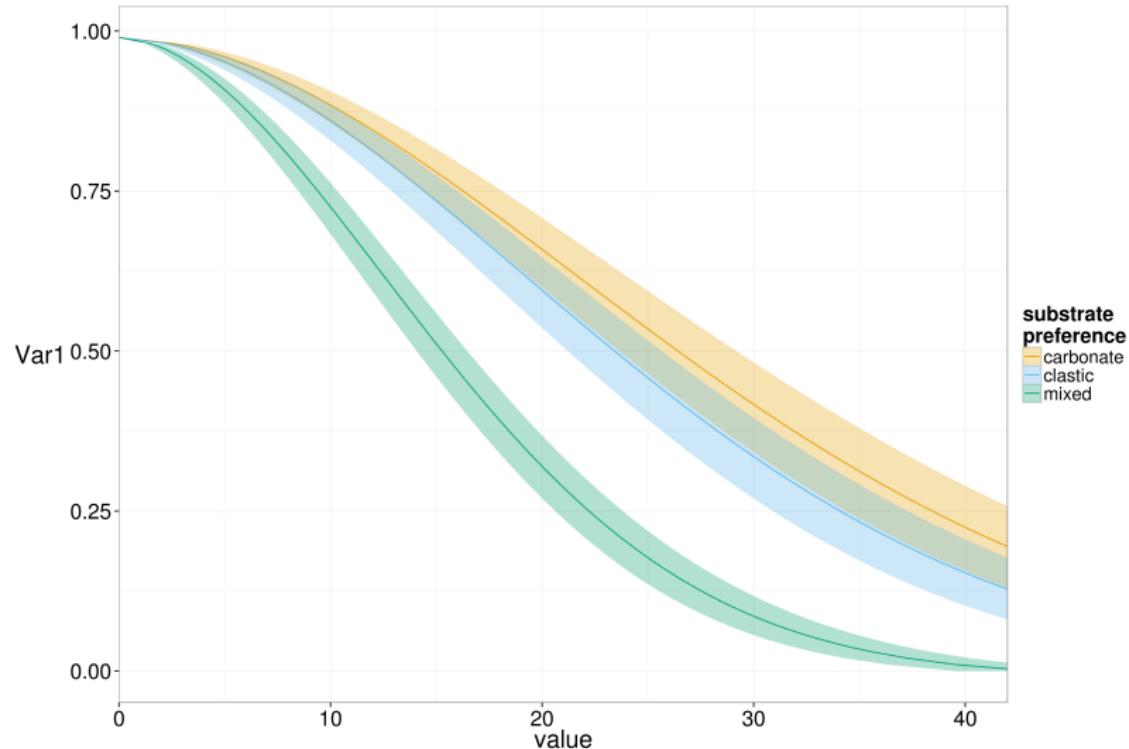
Preliminary results: model comparison

formula	distribution	shape	df	AICc	weight
~ aff	weibull	1.85	4	941.6757	0.65
~ aff + hab	weibull	1.87	6	942.9977	0.34
~ aff * hab	weibull	1.89	10	949.0816	0.02
~ 1	weibull	1.74	2	960.2550	0.00
~ hab	weibull	1.75	4	963.3091	0.00
~ aff	exponential		3	993.1724	0.00
~ aff + hab	exponential		5	996.4089	0.00
~ 1	exponential		1	1000.2592	0.00
~ aff * hab	exponential		9	1003.7639	0.00
~ hab	exponential		3	1003.9227	0.00

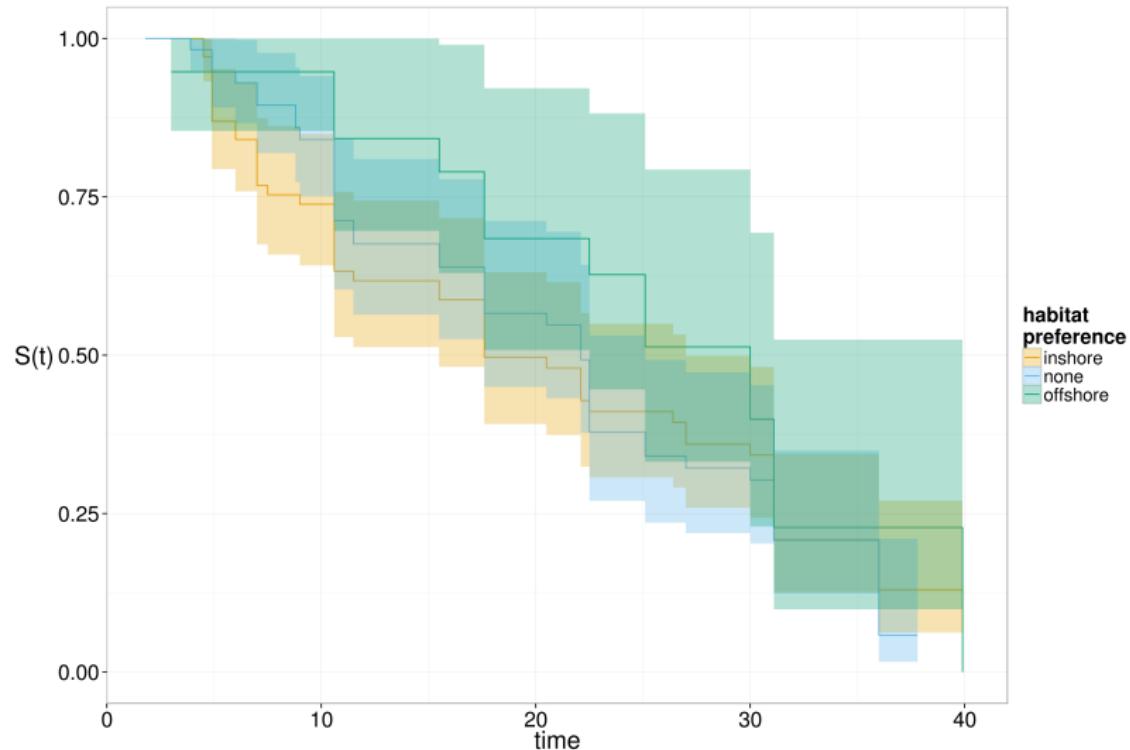
K-M curve substrate



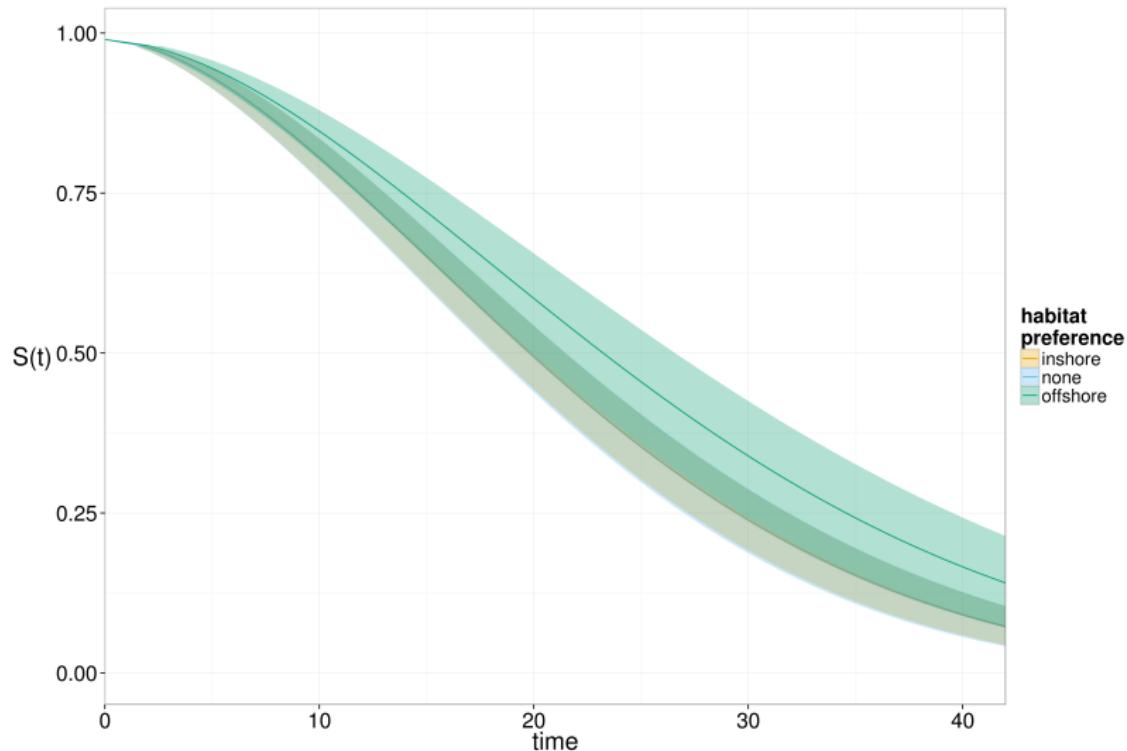
Estimated survival curve substrate



K-M curve habitat



Estimated survival curve habitat



Theory

Survival

Communities

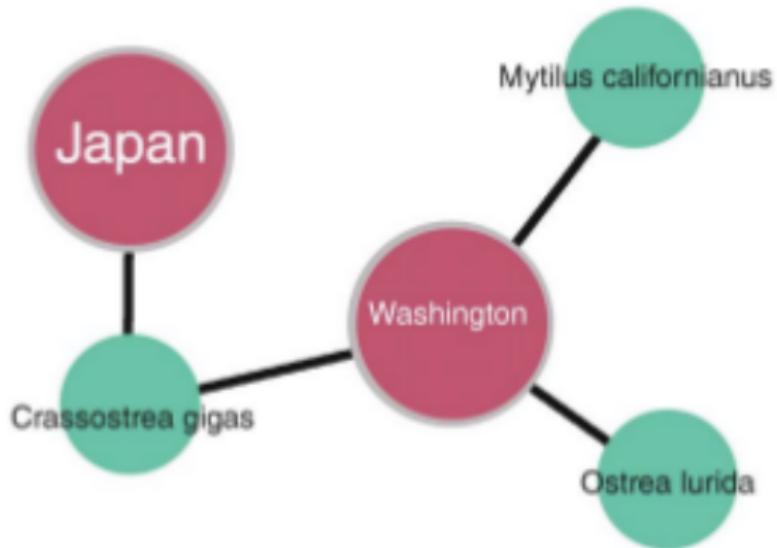
Summary

Community connectedness

Definition

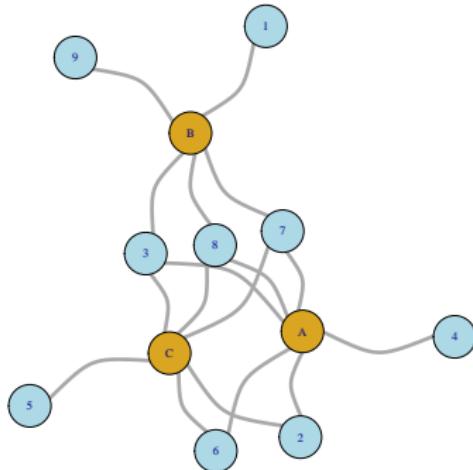
The degree to which localities are composed of endemic versus cosmopolitan taxa, and how similar this ratio is across localities.

Biogeographic networks



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

Average relative number of endemics



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

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

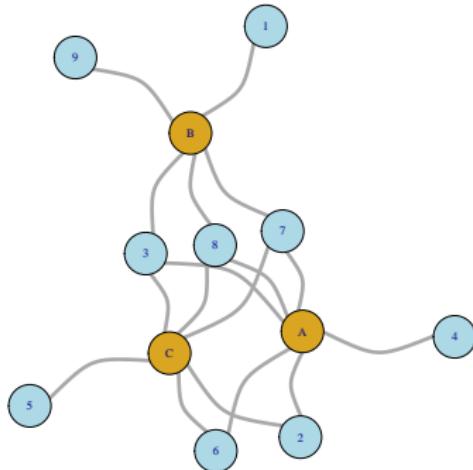
$$L = 3$$

$$E \approx 0.24$$

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

- ▶ 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



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

$$L = 3$$

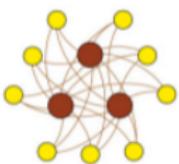
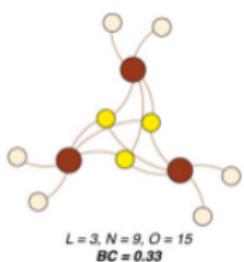
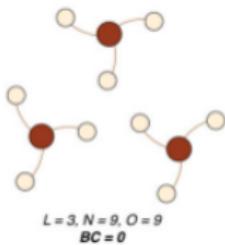
$$N = 9$$

$$Occ \approx 0.63$$

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

- ▶ 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

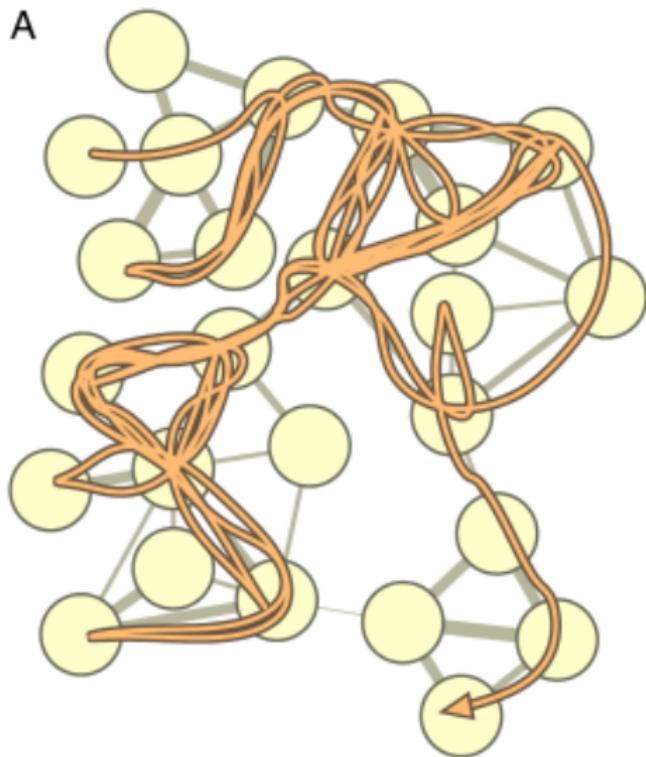


$$BC = \frac{O - N}{LN - N}$$

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

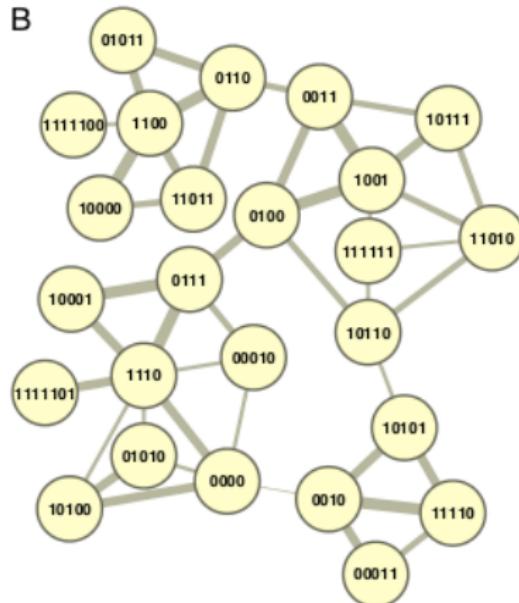
(Sidor et al. 2013 PNAS)

Code length



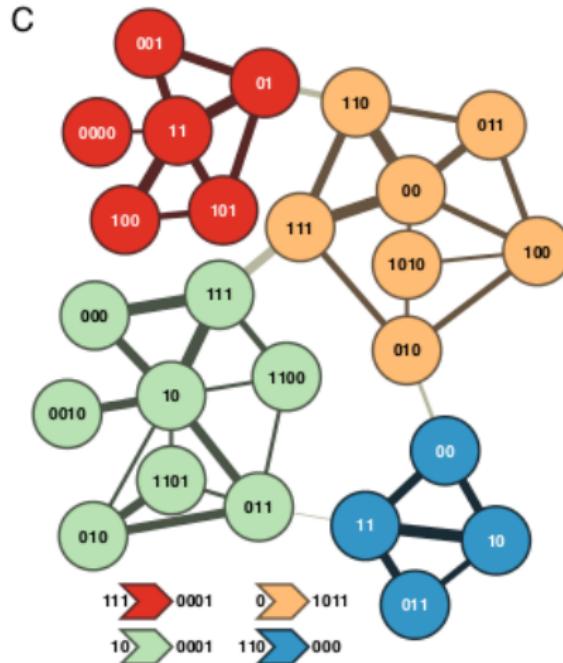
(Rosvall and Bergstrom 2008 *PNAS*)

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
```

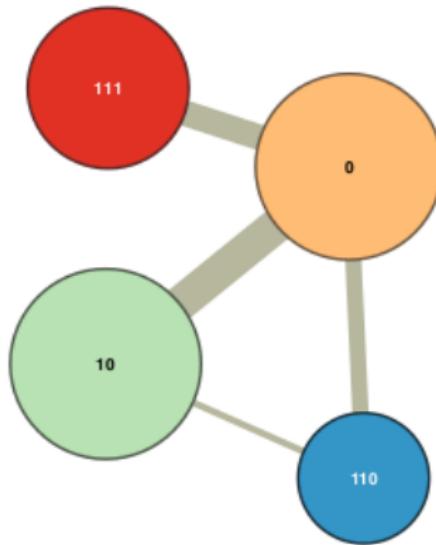
Code length



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

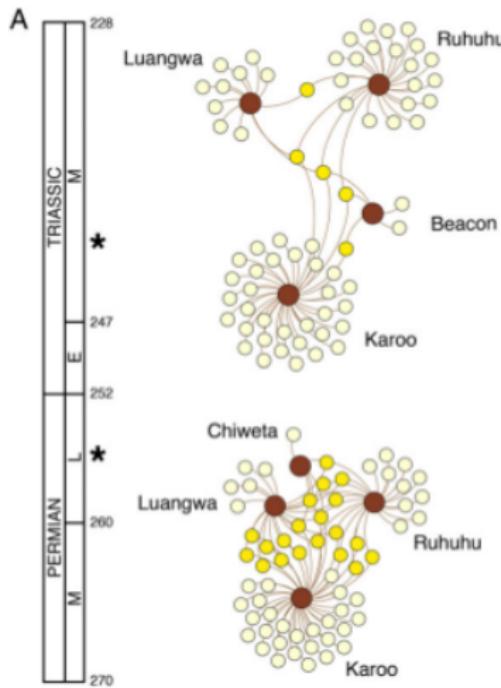
D



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)

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

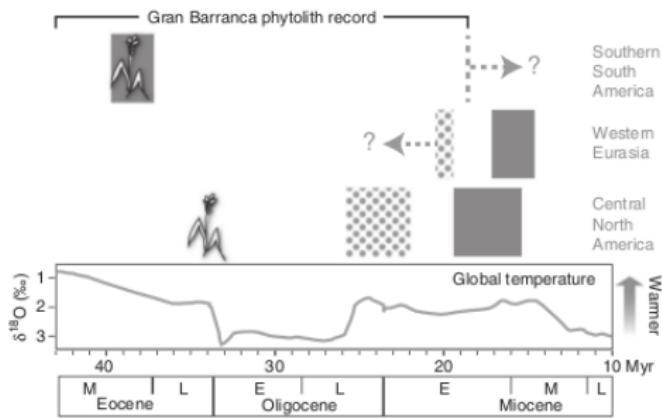
(Sidor et al. 2013 PNAS)

Community connectedness in Cenozoic mammals

Questions

- ▶ How does the ratio of cosmopolitan to endemic taxa, per locality, change over time?
 - ▶ Is this pattern different between taxa exhibiting different traits?
 - ▶ How does this pattern vary in relation to phylogenetic similarity?
- ▶ When would we expect global, regional, and/or local processes to most strongly shape taxonomic patterns?

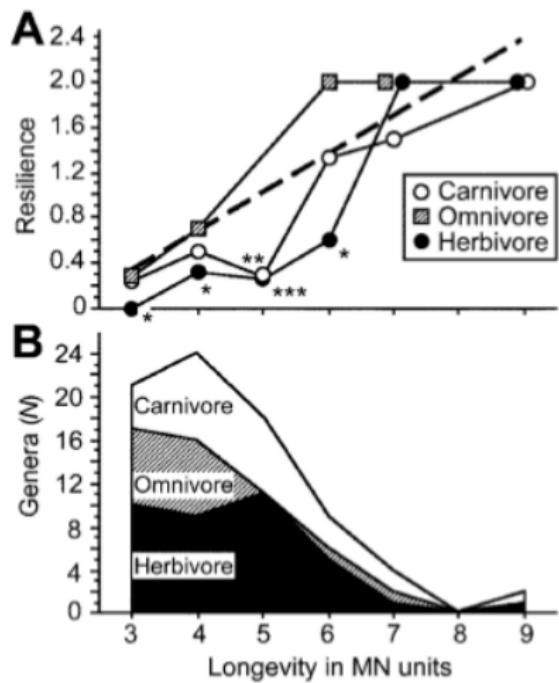
Global expectations: locomotor category



(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/random

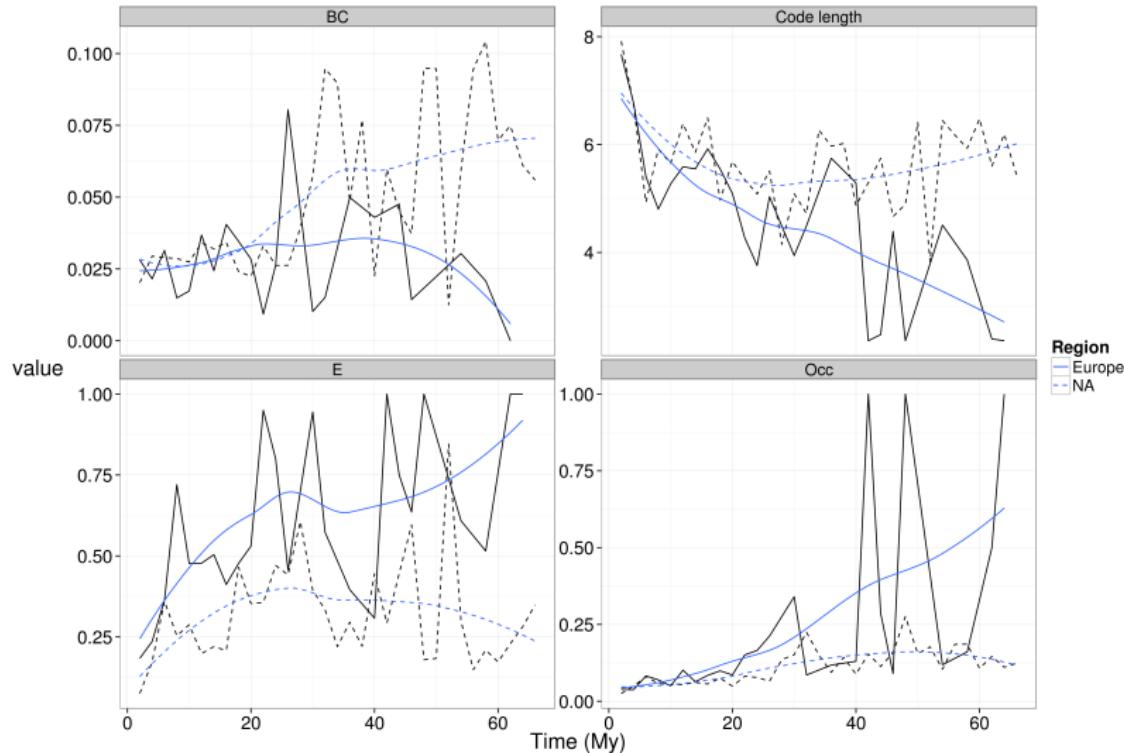
Global expectations: dietary category



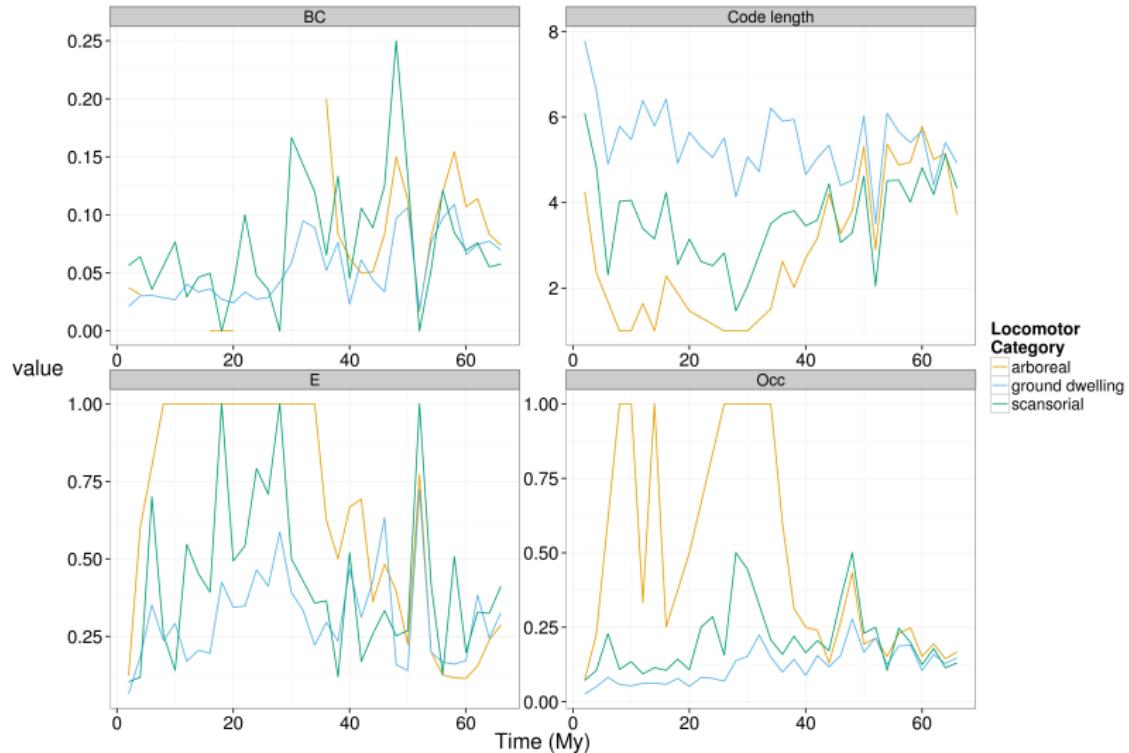
- ▶ herbivore
 - ▶ most like combined
- ▶ carnivore
 - ▶ constant ∨ corr w/ herbivores
- ▶ omnivore
 - ▶ constant ∨ random

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

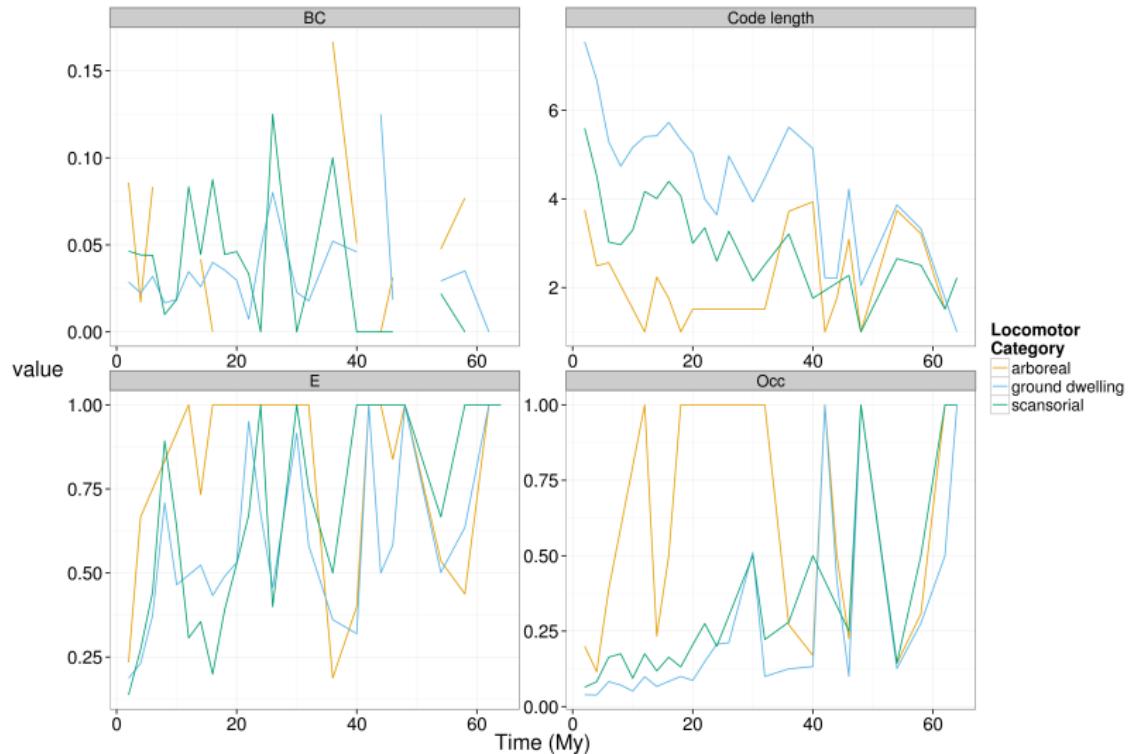
Preliminary results: NA, Eur



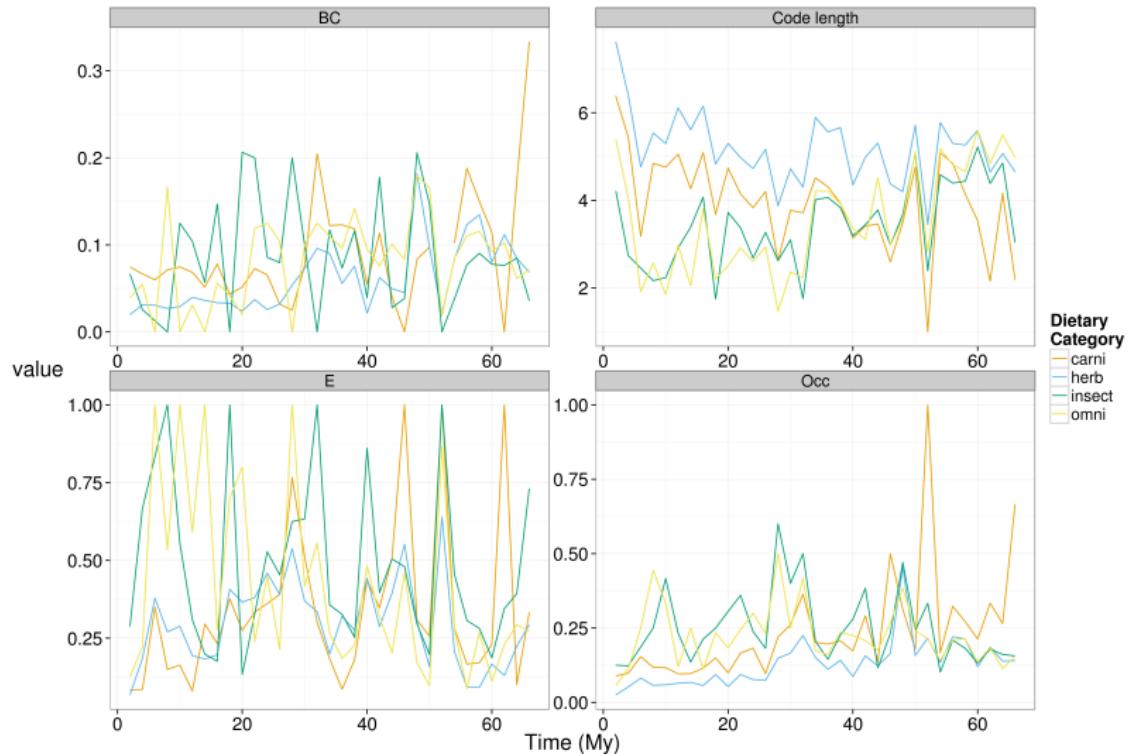
Preliminary results: locomotor category NA



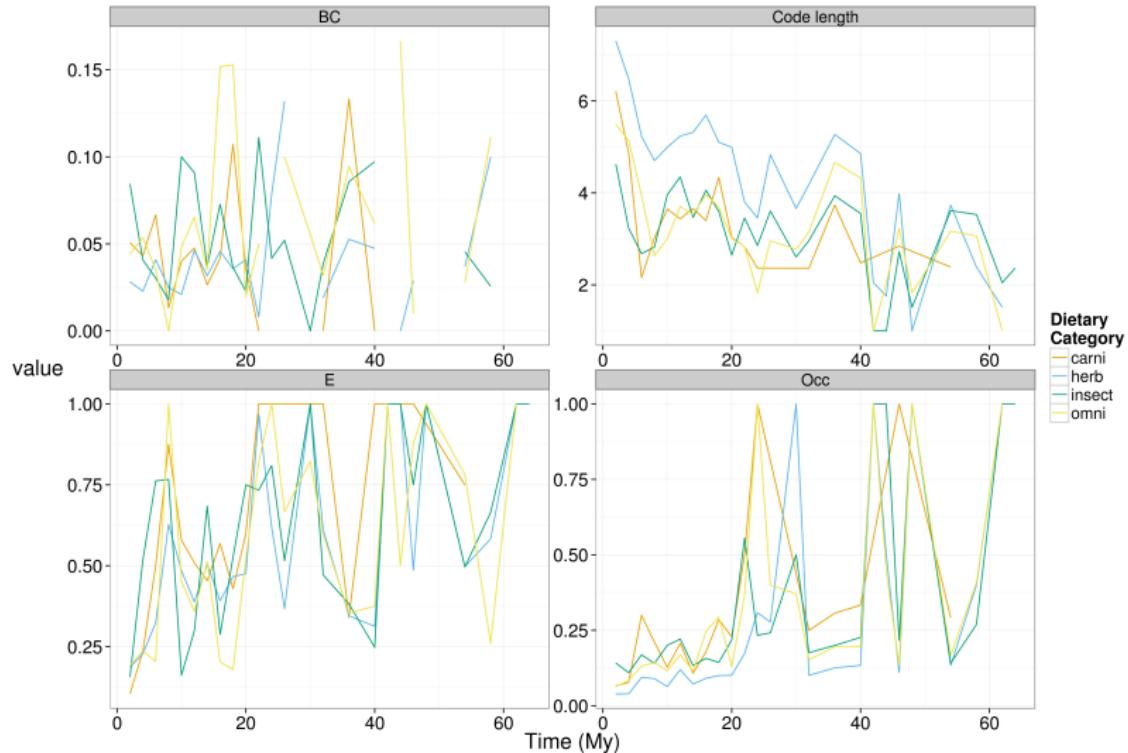
preliminary results: locomotor category Eur



Preliminary results: dietary category NA



Preliminary results: dietary category Eur



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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 environmental context.

Ask the following . . .

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

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

How do they matter?

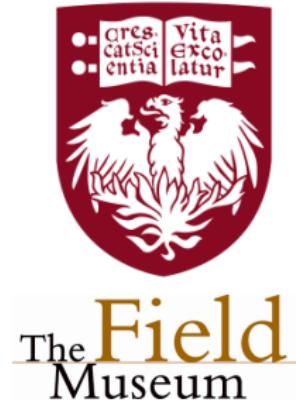
Acknowledgements

► Committee

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

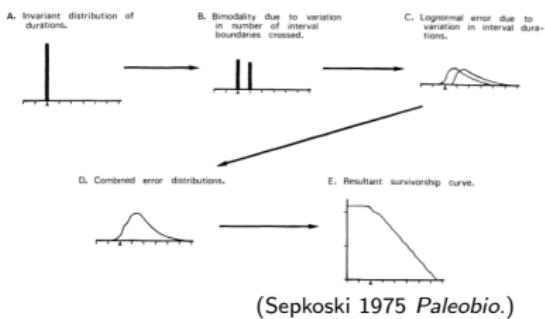
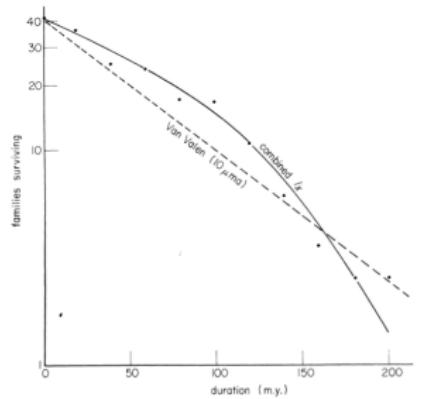
► Discussion

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



Further concerns

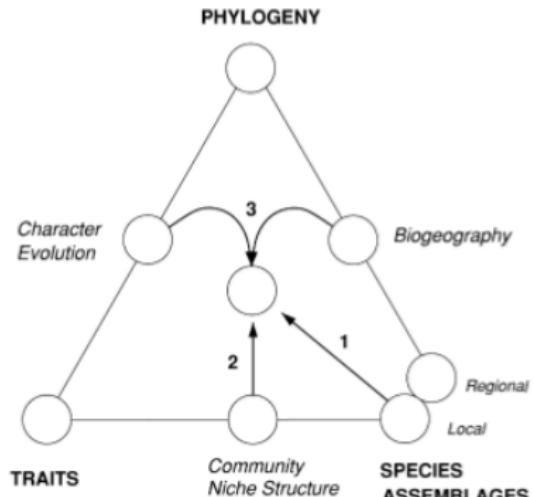
Differential preservation and survival



two groups in four scenarios

- ▶ = birth, death;
- =preservation
- ▶ = birth, death;
- ! =preservation
- ▶ ! = birth, death;
- = preservation
- ▶ ! = birth, death;
- ! =preservation

Phylogenetic similarity of communities



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

- ▶ informal time scaled phylogeny (taxonomy tree)
- ▶ measures
 - ▶ pairwise patristic distance
 - ▶ phylogenetic species variability (Helmus *et al.* 2007 *Am. Nat*)

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