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 14, 2014

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.

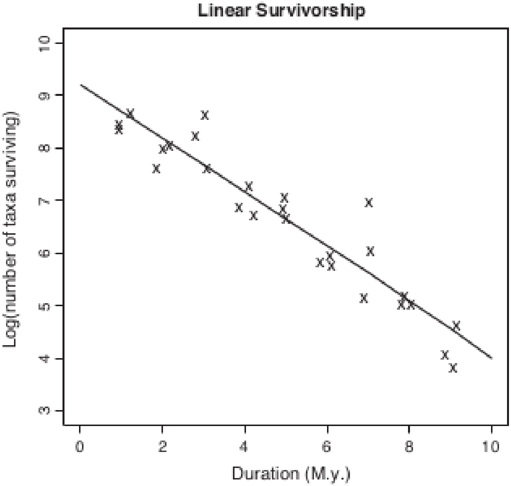
(Kitchell 1985 Paleobiology)

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 ($\sim$ 47 My)
- global warming
- Australia

mammals

- terrestrial
- motile
- Cenozoic ($\sim$ 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

Survival analysis framework

Definition

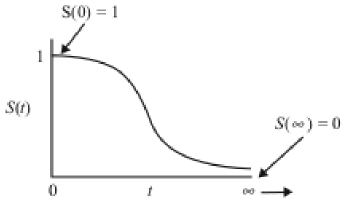
Analysis of time till event data.

Time is taxon duration or age.

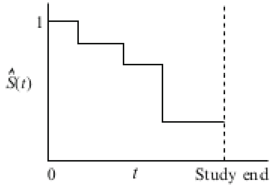
Event is an occurrence of interest (extinction).

Probability of survival

Theoretical $S(t)$:



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



(Kleinbaum and Klein 2012)

Survival function

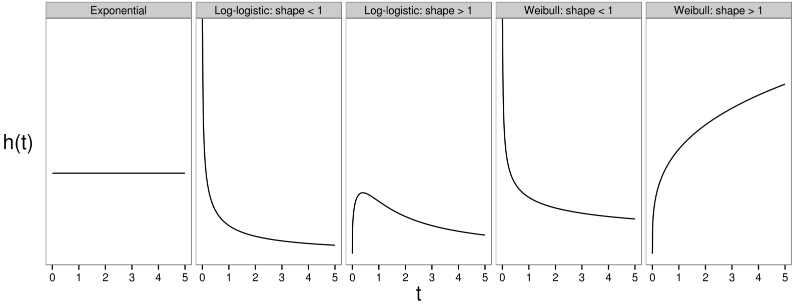
$$S(t) = Pr(T > t)$$

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

Instantaneous potential of failure (extinction)

Hazard function $\equiv$ conditional failure rate

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



Formalization of Van Valen

Law of Constant Extinction

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

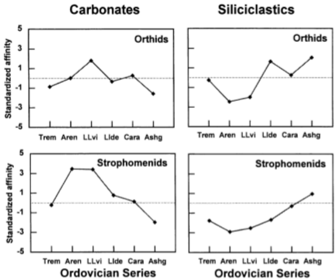
$$h(t) = \lambda \iff S(t) = \exp^{-\lambda t}$$

Brachiopods, environmental preference, and extinction

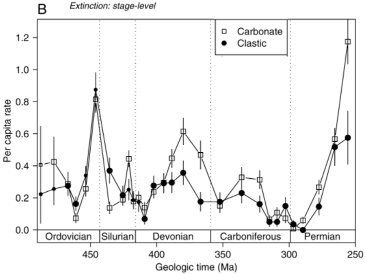
Questions

- 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



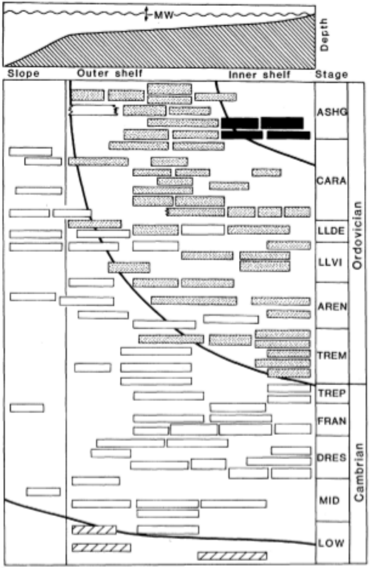
(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

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

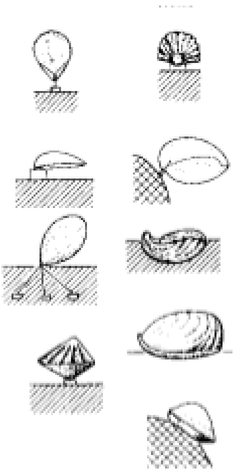
Habitat preference



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

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

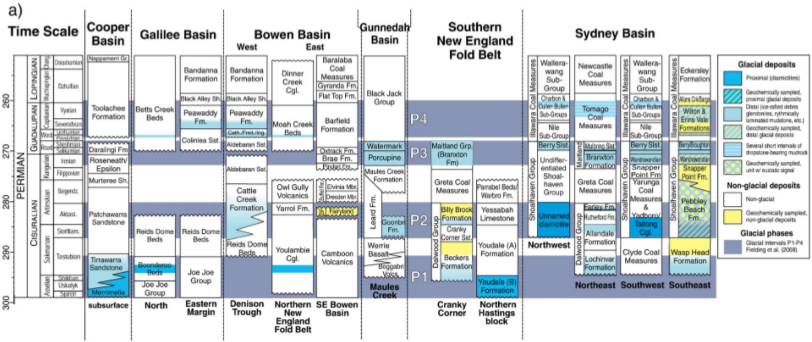
Affixing strategy



(Johansen 1989 *Paleo*[3])

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

Permian climate



(Birgenheier *et al.* 2010 *Paleo*[3])

Assigning substrate and habitat

Probability of assignment

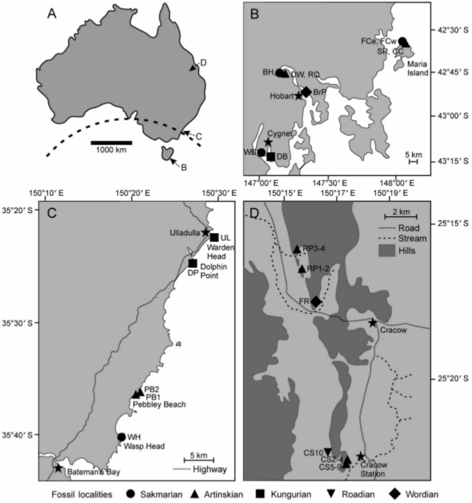
$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

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

- 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



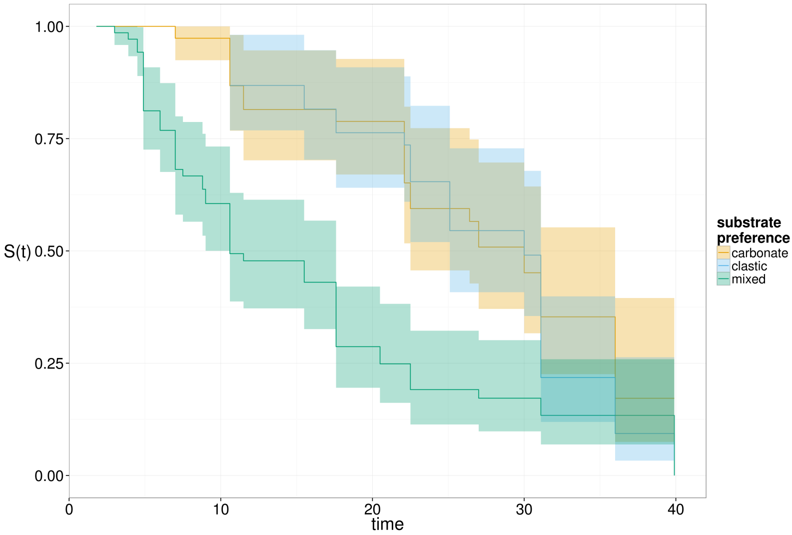
(Clapham and James 2008 *Palaios*)

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

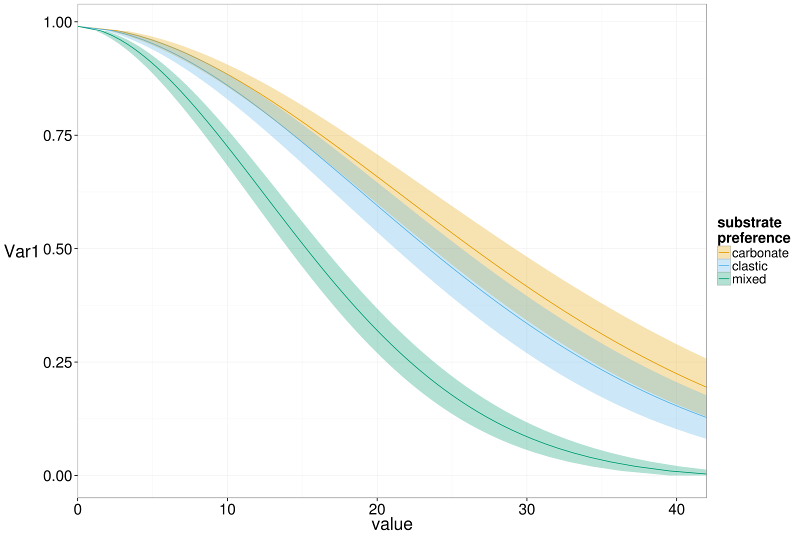
Preliminary results: model comparison

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

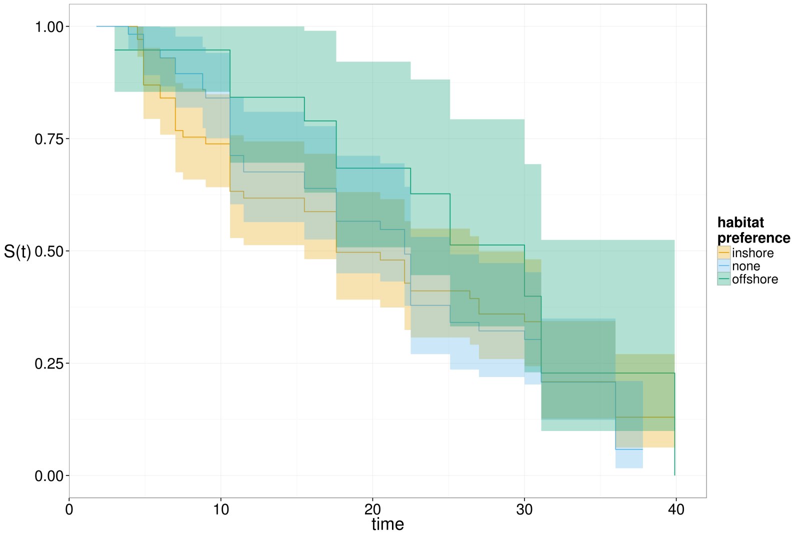
K-M curve substrate



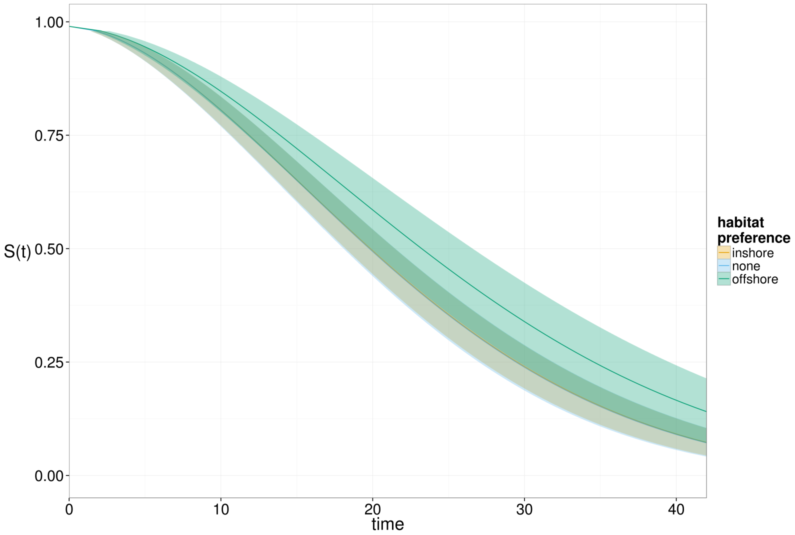
Estimated survival curve substrate



K-M curve habitat



Estimated survival curve habitat

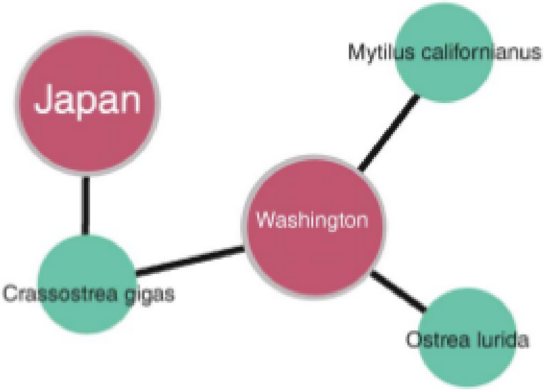


Community connectedness

Definition

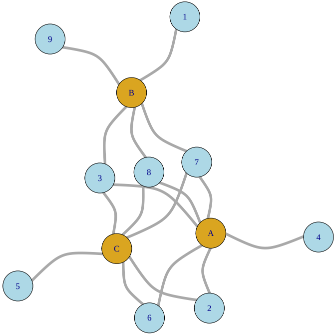
The degree to which localities are composed of endemic versus cosmopolitan taxa, and how similar this ratio is across localities.

Biogeographic networks



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

Average relative number of endemics

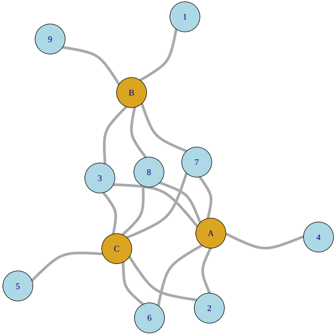


$$u = \{1, 2, 1\}$$
$$n = \{6, 5, 6\}$$
$$L = 3$$
$$E \approx 0.24$$

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

- 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

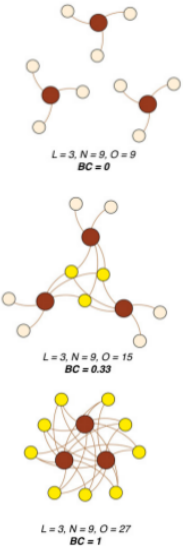


$$I = \{1, 2, 3, 1, 1, 2, 3, 3, 1\}$$
$$L = 3$$
$$N = 9$$
$$Occ \approx 0.63$$

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

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

Biogeographic connectedness

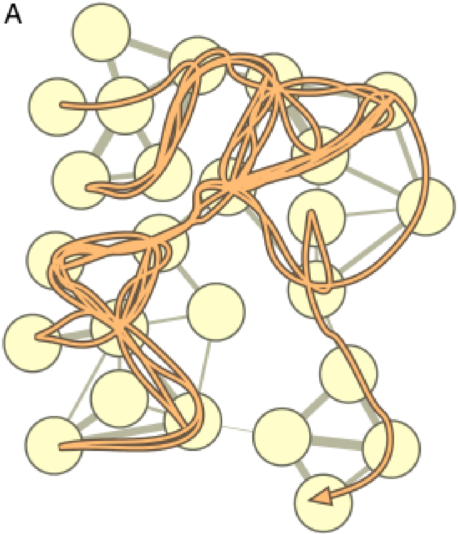


(Sidor et al. 2013 *PNAS*)

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

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

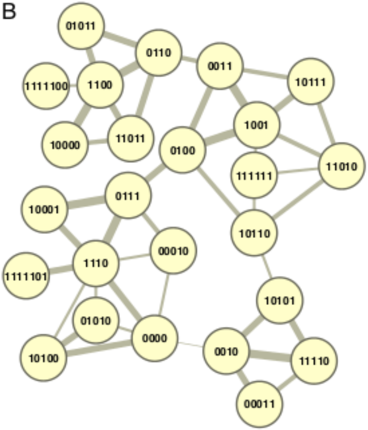
Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Code length

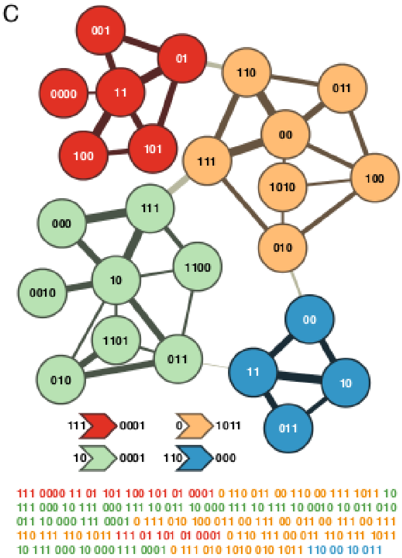
B



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

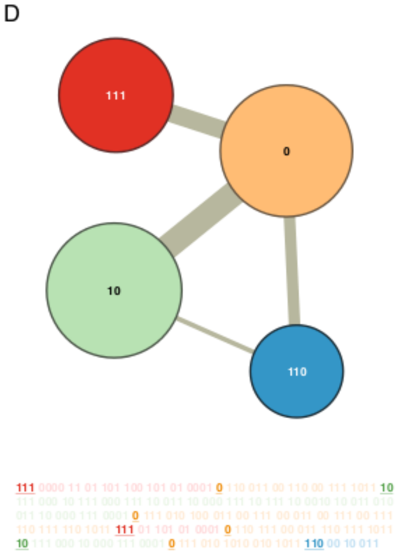
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



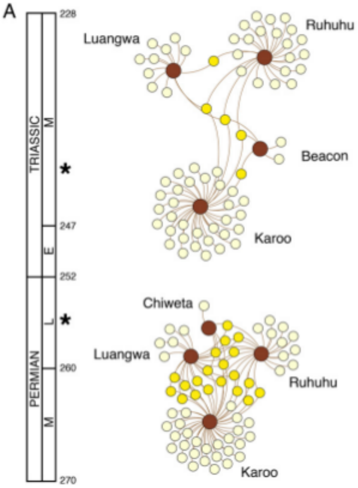
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Global versus regional versus local scale



(Sidor et al. 2013 *PNAS*)

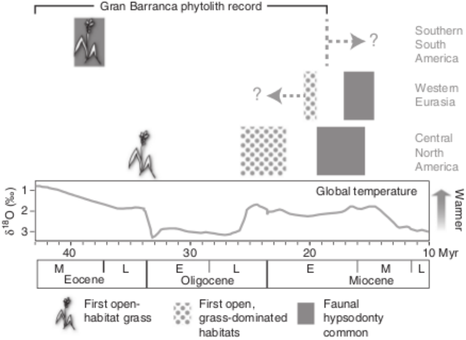
- global
  - corr w/ global climate
  - multiple regions corr
- regional
  - $\downarrow E$, $\uparrow Occ$, $\uparrow BC$, $\uparrow$ code
- local
  - $\uparrow E$, $\downarrow Occ$, $\downarrow BC$, $\downarrow$ code
- not mutually exclusive

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 very in relation to phylogenetic similarity?
- When would we expect global, regional, and/or local processes to most strongly shape taxonomic patterns?

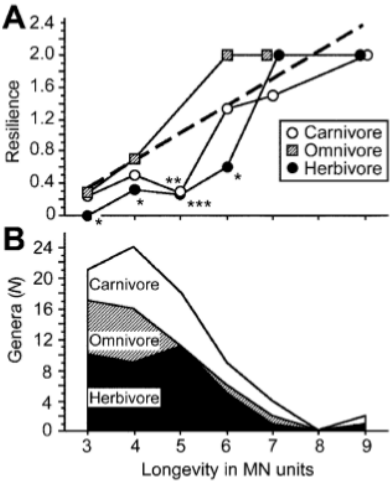
Global expectations: locomotor category



(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

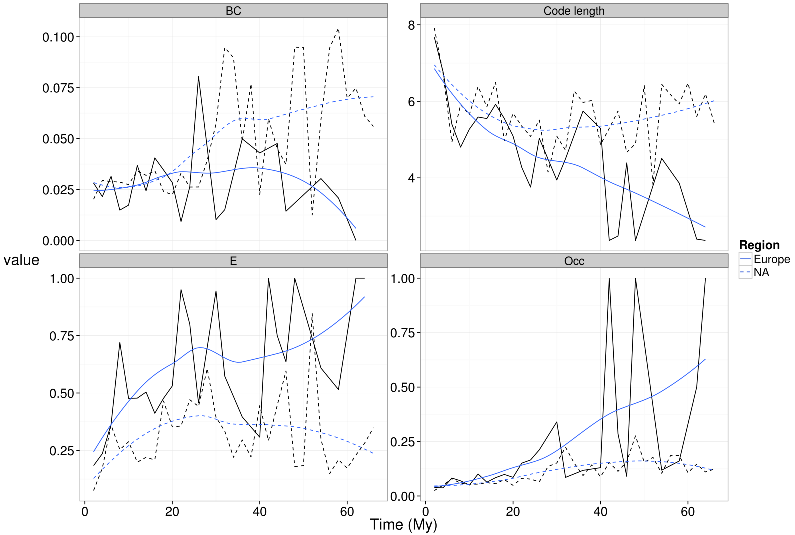
Global expectations: dietary category



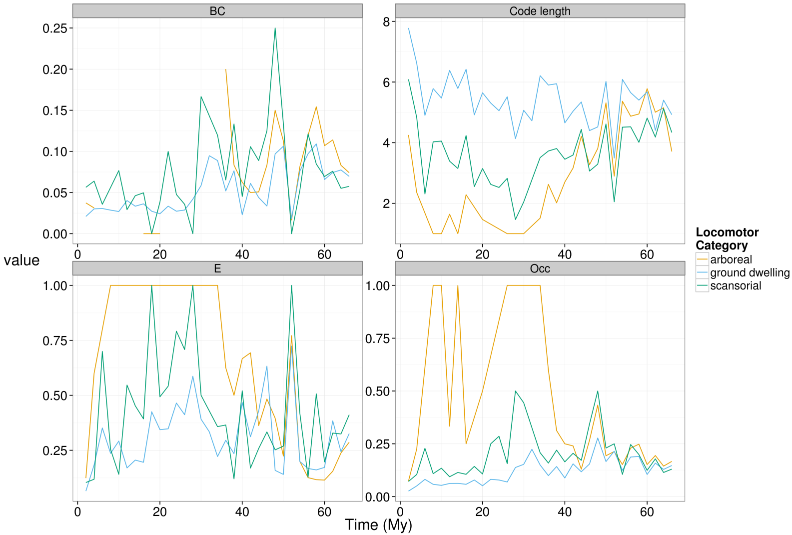
(Jernvall and Fortelius 2004 *Am. Nat.*)

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

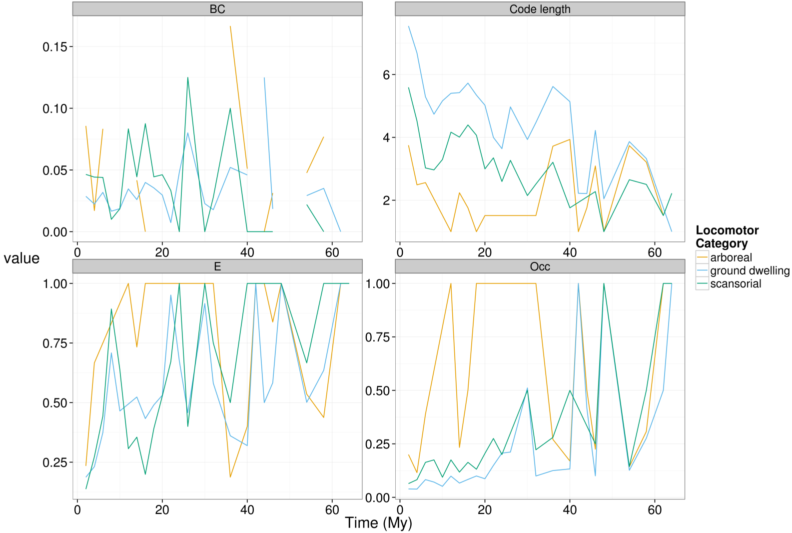
Preliminary results: NA, Eur



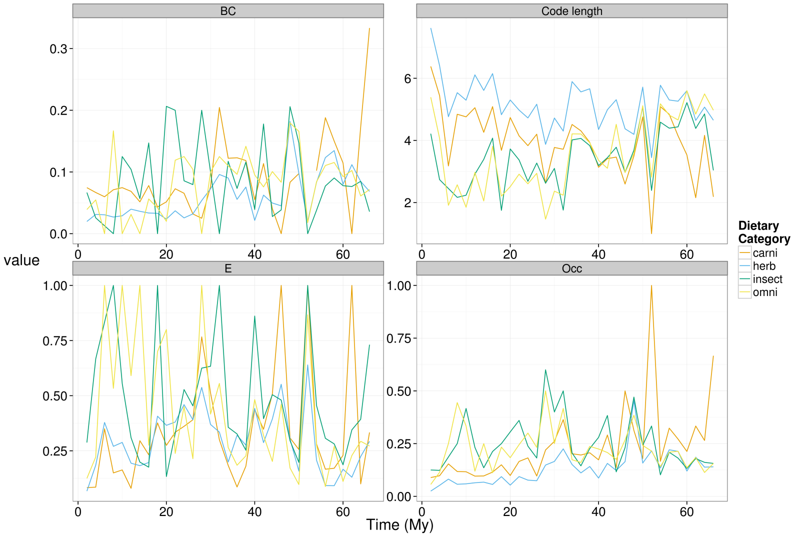
Preliminary results: locomotor category NA



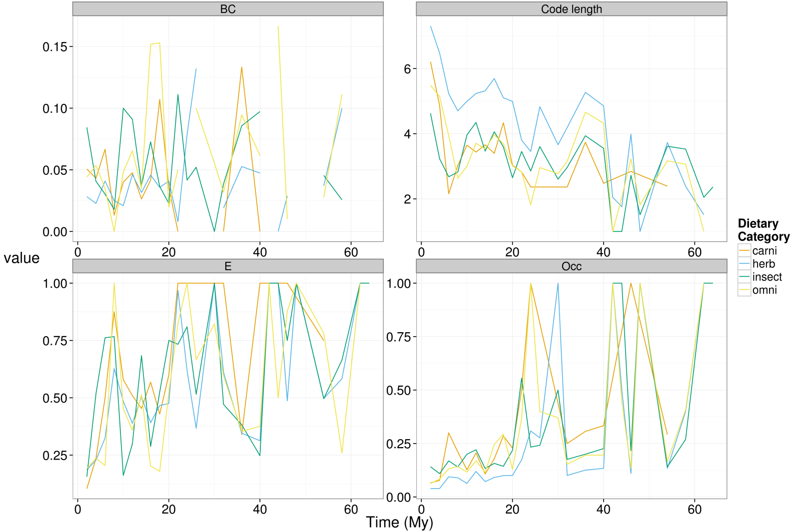
preliminary results: locomotor category Eur



Preliminary results: dietary category NA



Preliminary results: dietary category Eur



Theory

Survival

Communities

Summary

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?

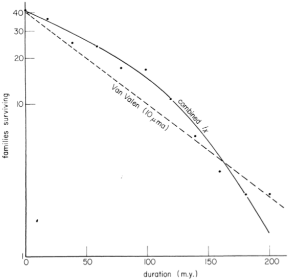
How do they matter?

Acknowledgements

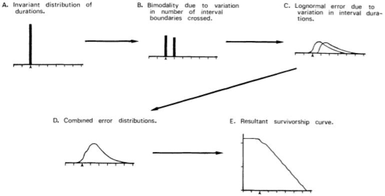
- **Committee**
  - Kenneth D. Angielczyk (co-advisor)
  - Michael J. Foote (co-advisor)
  - P. David Polly
  - Richard H. Ree
- Discussion
  - David Bapst, Megan Boatright, Ben Frable, Colin Kyle, Darcy Ross, Liz Sander
  - John Alroy, Graeme Lloyd, Carl Simpson, Graham Slater

Further concerns

Differential preservation and survival



(Raup 1975 *Paleobio.*)



(Sepkoski 1975 *Paleobio.*)

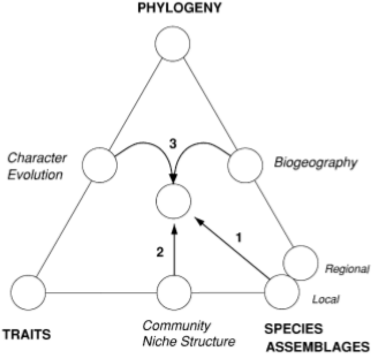
Models

Sampling: Poisson process (ϕ)

Diversification: birth-death (λ, μ)

1. $=$ birth, death; $=$preservation
2. $=$ birth, death; ! $=$preservation
3. ! $=$ birth, death; $=$ preservation
4. ! $=$ birth, death; ! $=$preservation

Phylogeneic 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 Bargstrom 2008 *PNAS*)

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

- $\mathbf{M}$: module partion 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
- $p_{\circlearrowright}^{i}$: rate within–module use