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?

(Ovid, Metamorphoses, book XV: 143-175, A. S. Kline trans.)

Evolutionary paleoecology and the biology of extinction

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May 5, 2014

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?

Modes of extinction

Field of Bullets – Wanton – Fair Game

(Raup 1991 Extinction: Bad Genes or Bad Luck?)

Evolutionary paleoecology

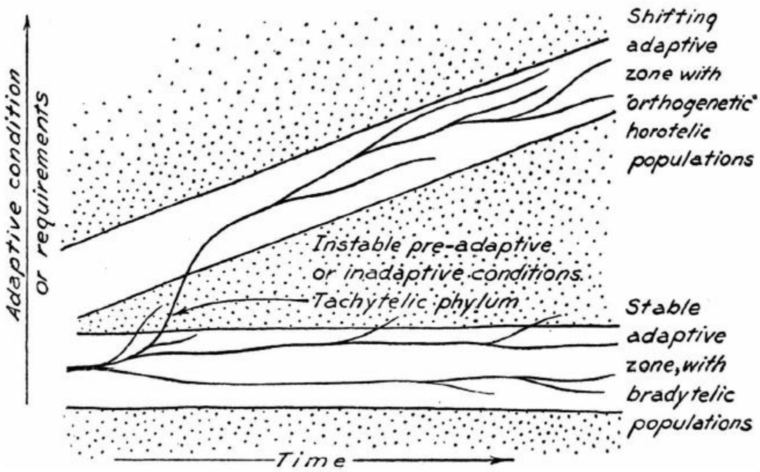
> *. . . the consequences of distinct ecological factors on differential rate dynamics, particularly rates of faunal turnover and diversification.*
>
> *(Kitchell 1985 Paleobiology)*

In context of this study

Rephrased

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

Adaptive zones



(Simpson 1944 Tempo and Mode)

Simpson's terms

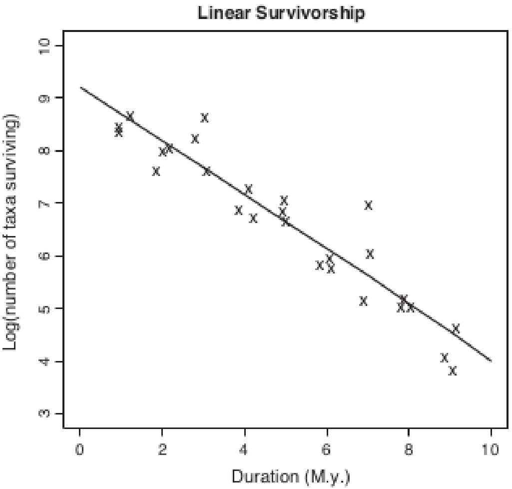
Definition

Environment: The set of all possible interactions, both biotic and abiotic.

Adaptive zone: The set of all interactions, biotic and abiotic, that a individual/taxon is adapted to or experiences in a given environment.

(Simpson 1944 Tempo and Mode, Simpson 1953 Major Features)

Van Valen's observation



(Liow et al. 2011 *TREE*)

Theory

Law of Constant Extinction

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

(Van Valen 1973 *Evol. Theory*)

Approach

Analytical challenge

Model extinction in context of adaptive zone (selective pressures).

Survival

- traits, factors and duration
- extinction mode

Communities

- α, β diversity
- biome distinctiveness

Systems

Brachiopods

Mammals

Proposed studies

Australian Permian brachiopods

- survival patterns
- community connectedness (not shown)
- substrate, habitat, affixing strategy

Cenozoic mammals

- survival patterns (not shown; come to Evolution2014)
- community connectedness
- dietary and locomotor categories, body size

Survival

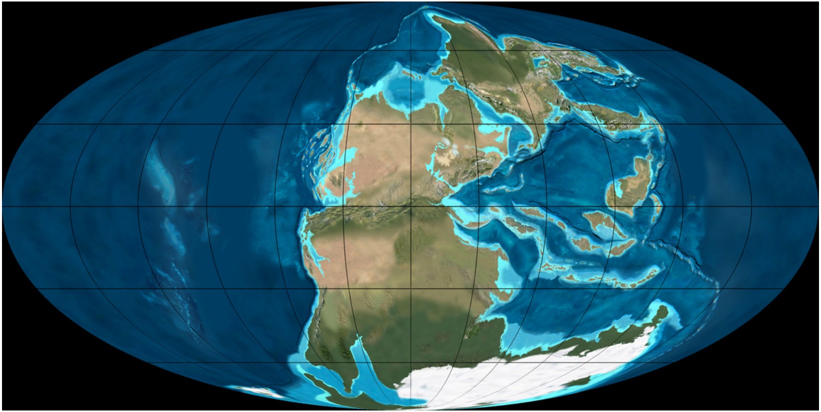
Definition

Time from origination to extintion of a taxon (age).

Brachiopods

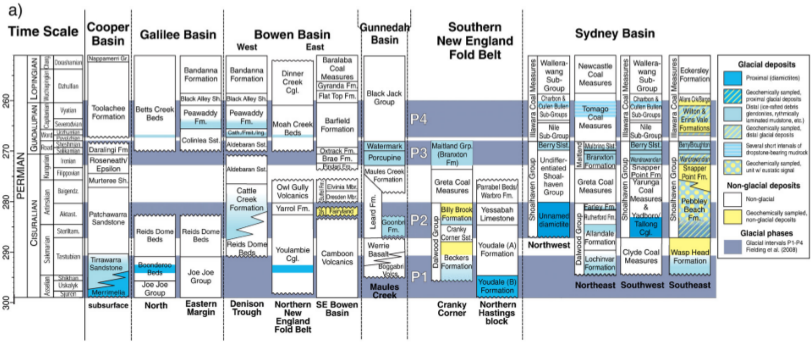
(http://earthphysicsteaching.homestead.com)

Permian



(Blakey `http://cpgeosystems.com/mollglobe.html`)

Permian of Australia



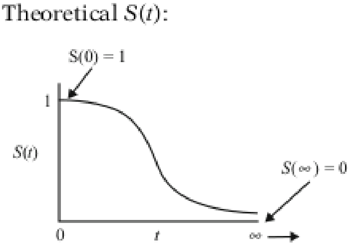
(Birgenheier *et al.* 2010 *Paleo*[3])

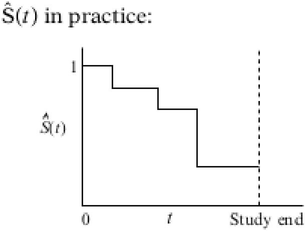
Brachiopods, environmental preference, and extinction

Questions

- Do interactions involved in environmental preference predict differential survival?
  - Is survival best modeled by a single interactor or multiple interactors?
  - How do other factors, such as climate, contribute?
- Is extinction taxon-age independent or dependent?

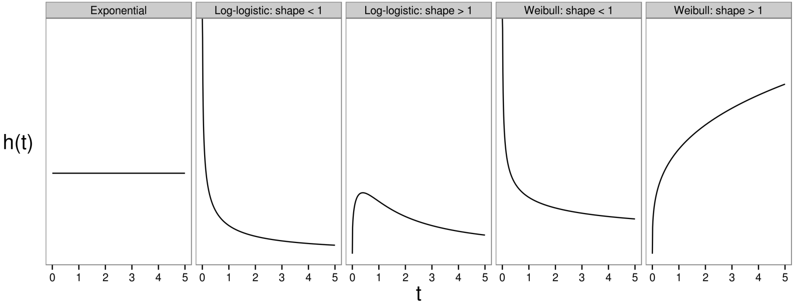
Probability of survival





(Kleinbaum and Klein 2012)

Extinction function



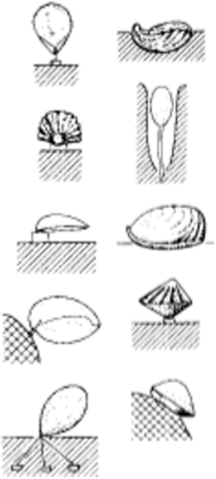
Formalization of Van Valen

Law of Constant Extinction

$$T \sim Exp(\lambda)$$

T: survival time
λ: expected number of extinctions per unit time

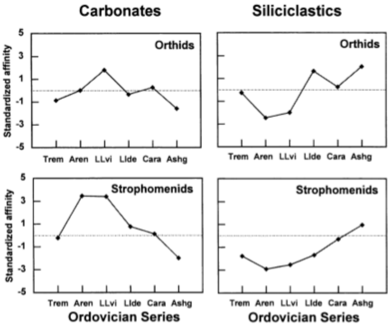
Affixing strategy



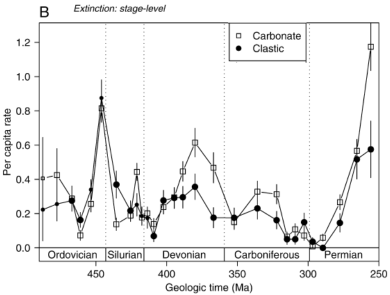
(modified from Johansen 1989 *Paleo*[3])

- Alexander 1977 *Paleo*[3]
  - endemic:
    reclining > others
  - cosmopolitan:
    ped./cement > others
- Clapham and Bottjer 2007 *Paleo*[3]
  - penduncIate: on-shore
  - reclining: off-shore

Substrate affinity

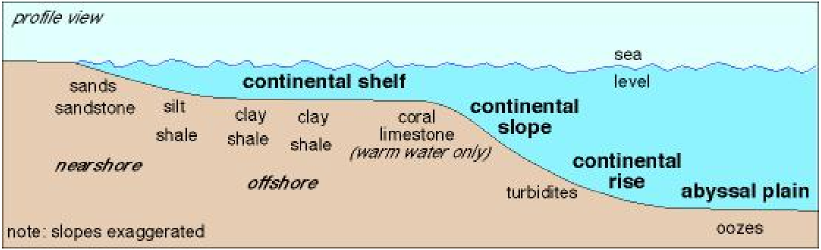


(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

Habitat preference



(http://www.columbia.edu/)

Assigning substrate and habitat

Probability of assignment

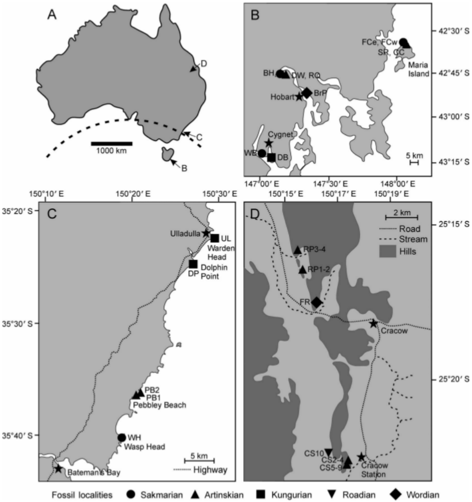
$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

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

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

(Simpson and Harnik 2009 *Paleobiology*)

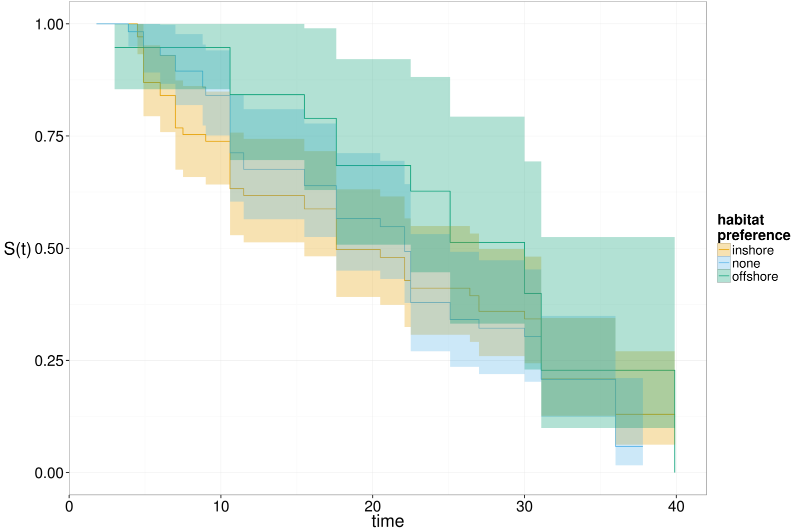
Analysis



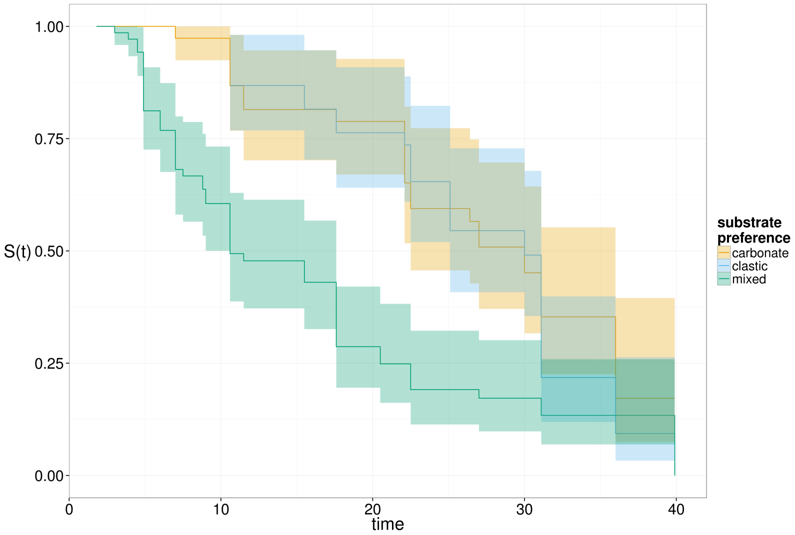
(Clapham and James 2008 *Palaios*)

- age $\sim$ Exponential or Weibull
- $\lambda \propto$ interactions, k constant
- range in/out taxa right censored
- habitat, substrate unedited from PBDB (this analysis)

K-M curve habitat



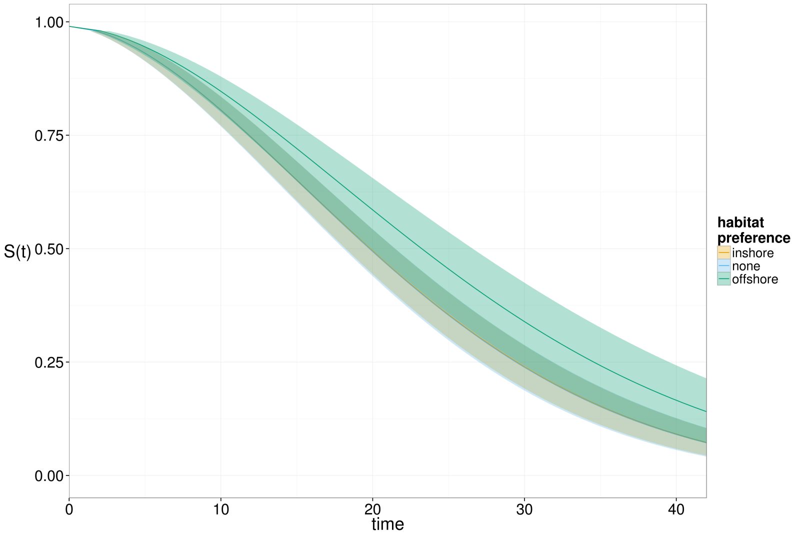
K-M curve substrate



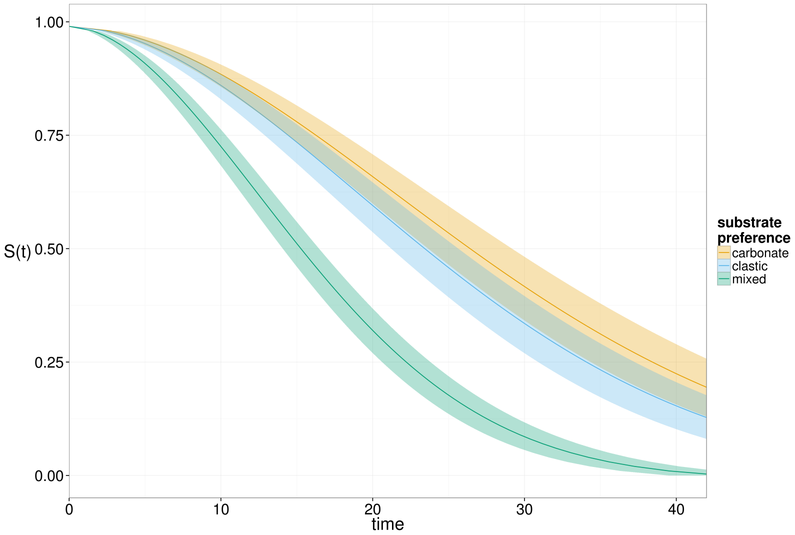
Preliminary results: model comparison

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

Estimated survival curve habitat



Estimated survival curve substrate

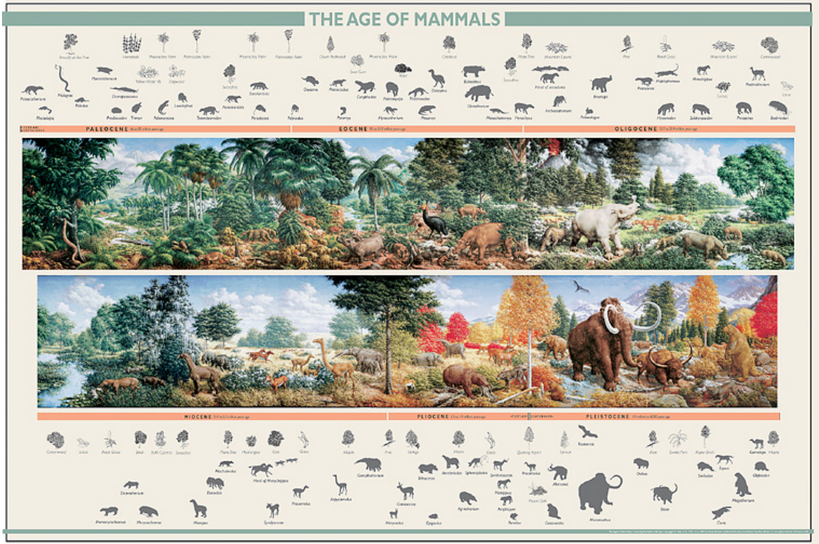


Community connectedness

Definition

The relationship between α, β diversity and provinciality.

Mammals



(Yale Peabody Museum)

Community connectedness in Cenozoic mammals

Questions

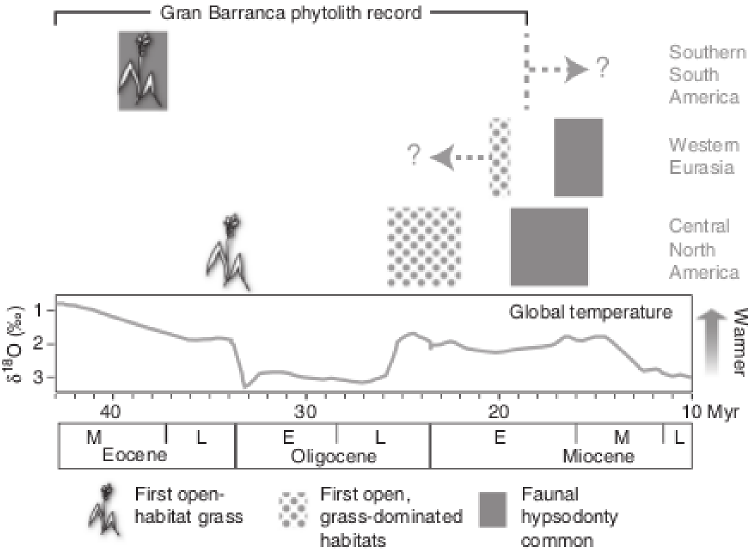
- How does average biome α and β diversity contribution change over time?
  - Do taxa with different traits exhibit different patterns?
  - How does this pattern vary with biome phylogenetic similarity?
- When would we expect global, regional, and/or local processes to shape taxonomic patterns?

Uniformity and distinctiveness

high α, high distinctiveness, difference in selective pressures

high β, high uniformity, similarity in selective pressures

Environments



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

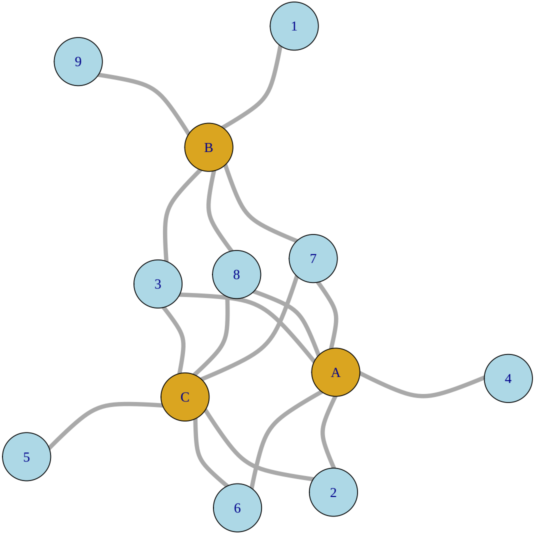
Occurrences

A: 2, 3, 4, 6, 7, 8

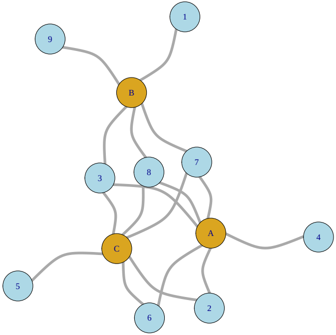
B: 1, 3, 7, 8, 9

C: 3, 5, 6, 7, 8

Biogeographic network



α diversity



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

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

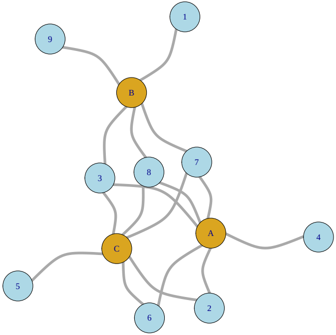
$$L = 3$$

$$E \approx 0.24$$

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

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

β diversity contribution

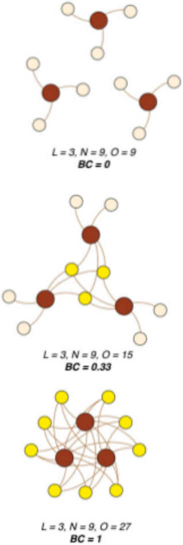


$$I = \{1, 2, 3, 1, 1, 2, 3, 3, 1\}$$
$$L = 3$$
$$N = 9$$
$$Occ \approx 0.63$$

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

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

Uniformity

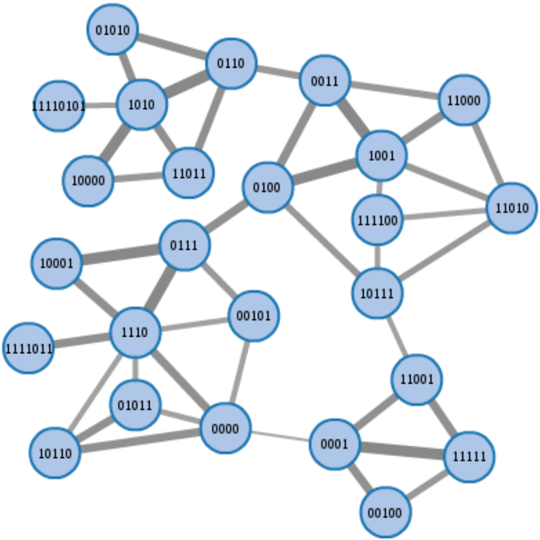


(Sidor et al. 2013 *PNAS*)

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

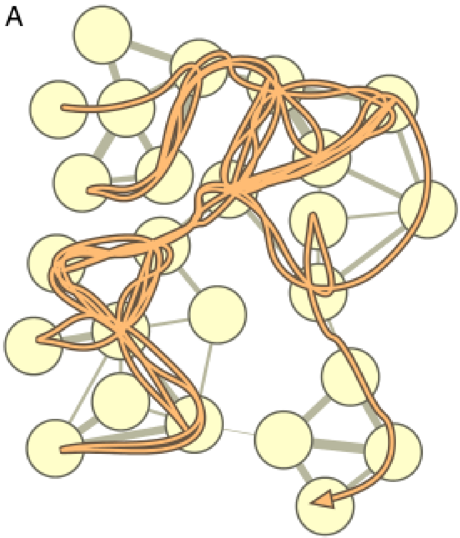
- O: number of occurrences
- N: total number of taxa
- L: number of localities
- $0 \leq BC \leq 1$

Code length



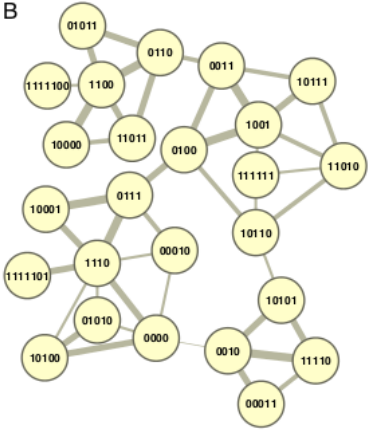
(mapequation.org)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

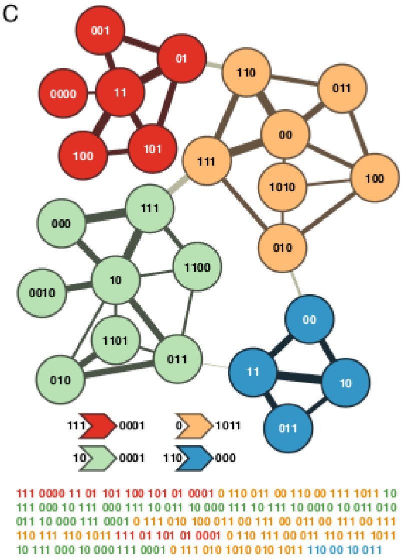
Code length



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

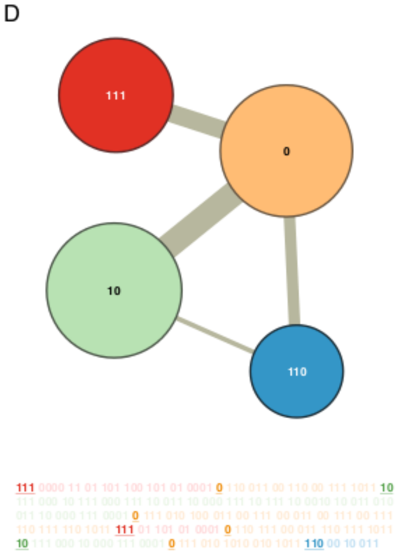
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



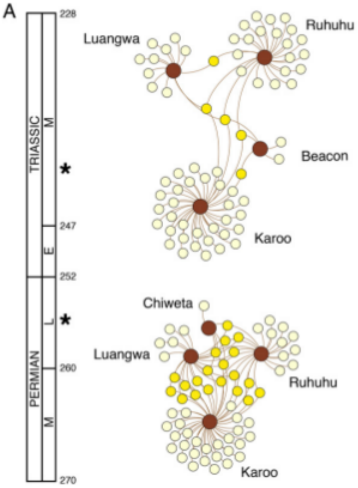
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Process 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

Scenario

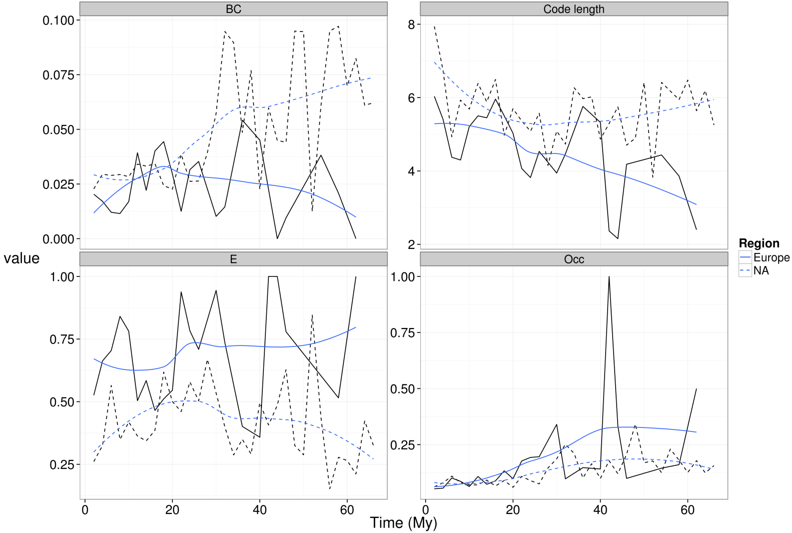
Locomotor

- ground dwelling, arboreal, scansorial

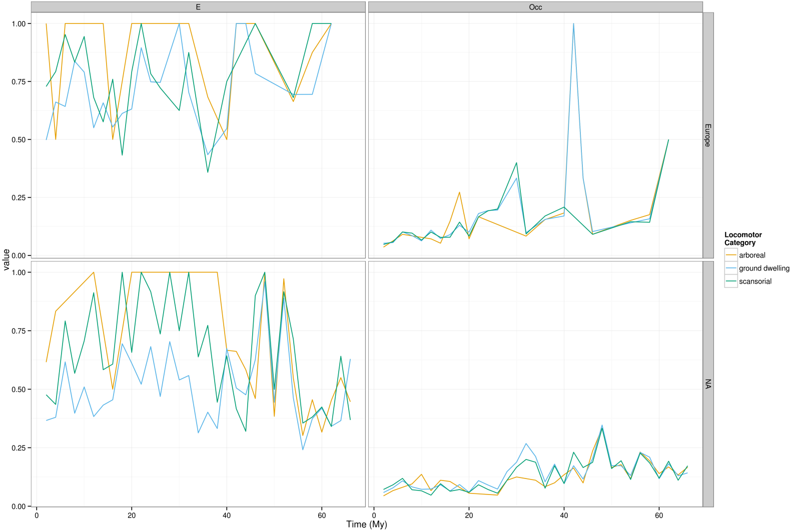
Dietary

- carnivore, insectivore, herbivore, omnivore

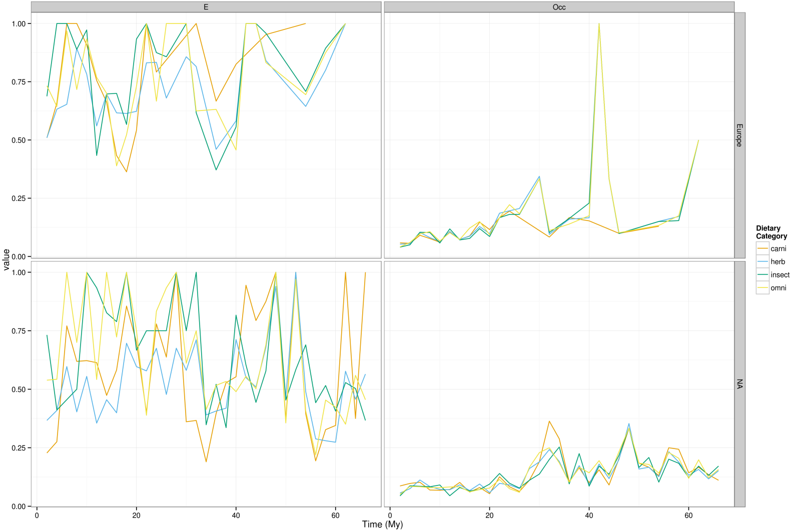
Preliminary results: NA, Eur



Preliminary results: locomotor category



Preliminary results: dietary category



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?

Modes and patterns

Modes of extinction

(Raup 1991 Extinction: Bad Genes or Bad Luck?)

Field of Bullets – Wanton – Fair Game

Law of Constant Extinction

(Van Valen 1973 *Evol. Theory*)

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

Ask the following...

Is there a general pattern of extinction?

What traits matter for extinction and when?

How do traits matter for extinction?

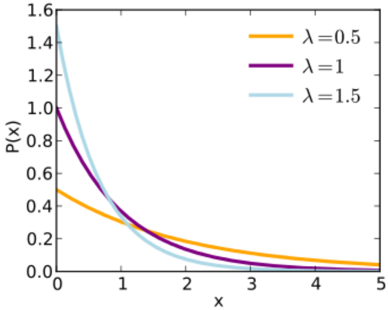
Acknowledgements

- **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, Kathleen Ritterbush, Carl Simpson, Graham Slater

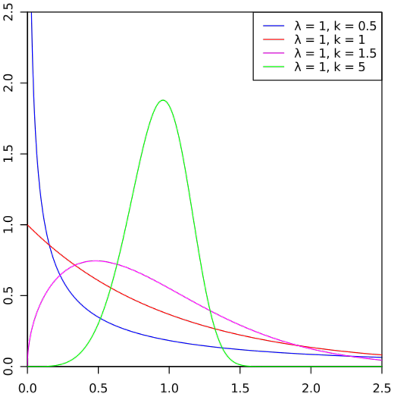
Further concerns

Age distributions

Exponential



Weibull



(http://www.wikimedia.org/)

Algebra of age distributions

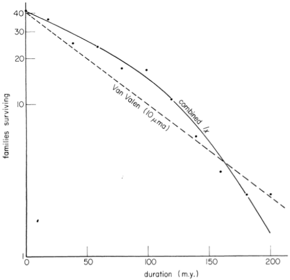
$$f(x; \lambda_{Weibull}, k) = \begin{cases} \frac{k}{\lambda}\frac{x}{\lambda}^{k-1} \exp^{-(x/\lambda)^k} & x \geq 0 \\ 0 & x < 0 \end{cases}$$

$$f(x; \lambda_{\exp}) = \begin{cases} \lambda \exp^{-\lambda x} & x \geq 0 \\ 0 & x < 0 \end{cases}$$

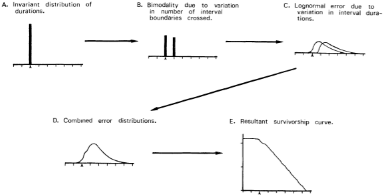
$$\lambda_{Weibull} = \frac{1}{\lambda_{\exp}}$$

$$f(x; \lambda_{Weibull}, k = 1) = f(x; \lambda_{\exp})$$

Differential preservation and survival



(Raup 1975 *Paleobio.*)



(Sepkoski 1975 *Paleobio.*)

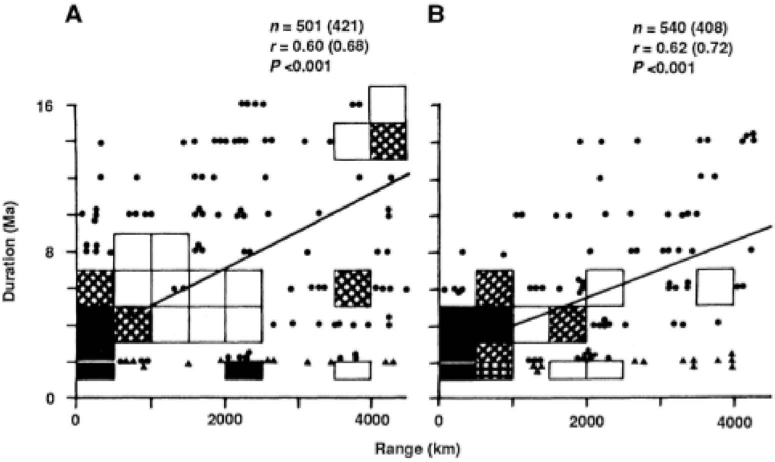
Observe in simulation

Sampling: Poisson process (ϕ)

Diversification: birth-death (λ, μ)

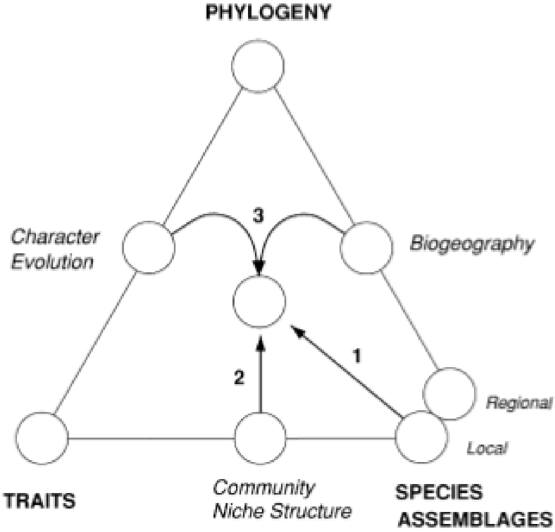
1. $=$ birth, death; $=$preservation
2. $=$ birth, death; ! $=$preservation
3. ! $=$ birth, death; $=$ preservation
4. ! $=$ birth, death; ! $=$preservation

The Elephant in the Range



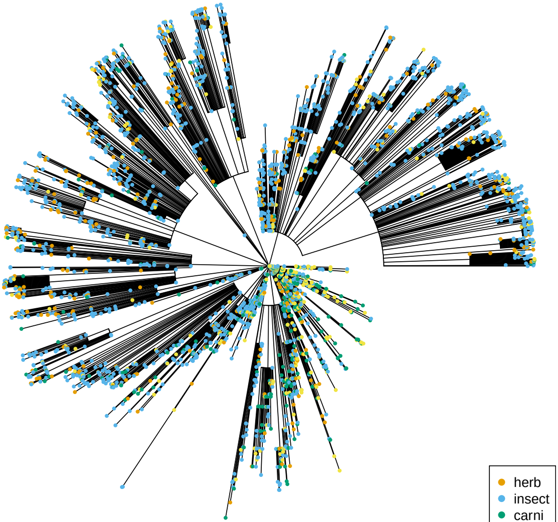
(Jablonski 1987 *Science*)

Phylogeny and communities



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

(Informal) phylogeny



Compressing a network

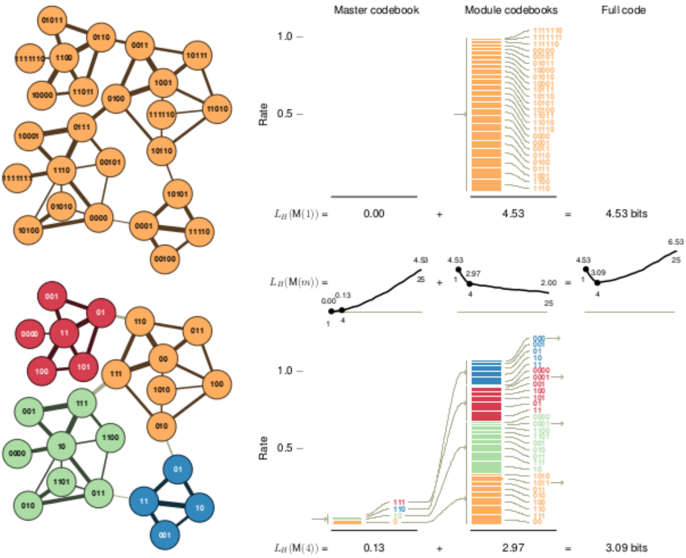
Map equation

(Rosvall and Bergstrom 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
- $L(\mathbf{M})$: theoretical minimum descriptive length of a single step
- $q_{\curvearrowright}$: P(walk switches modules)
- $H(\mathcal{Q})$: entropy of module codewords
- $H(\mathcal{P}^{i})$: entropy within–module movements
- $p_{\circlearrowright}^{i}$: fraction of within–module use in module i

Two-level compression



(Rosvall and Bergstrom 2009 *Euro. Phys. J. Spec. Topics.*)