

*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

Peter D Smits

Committee on Evolutionary Biology, University of Chicago

May 12, 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?

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.

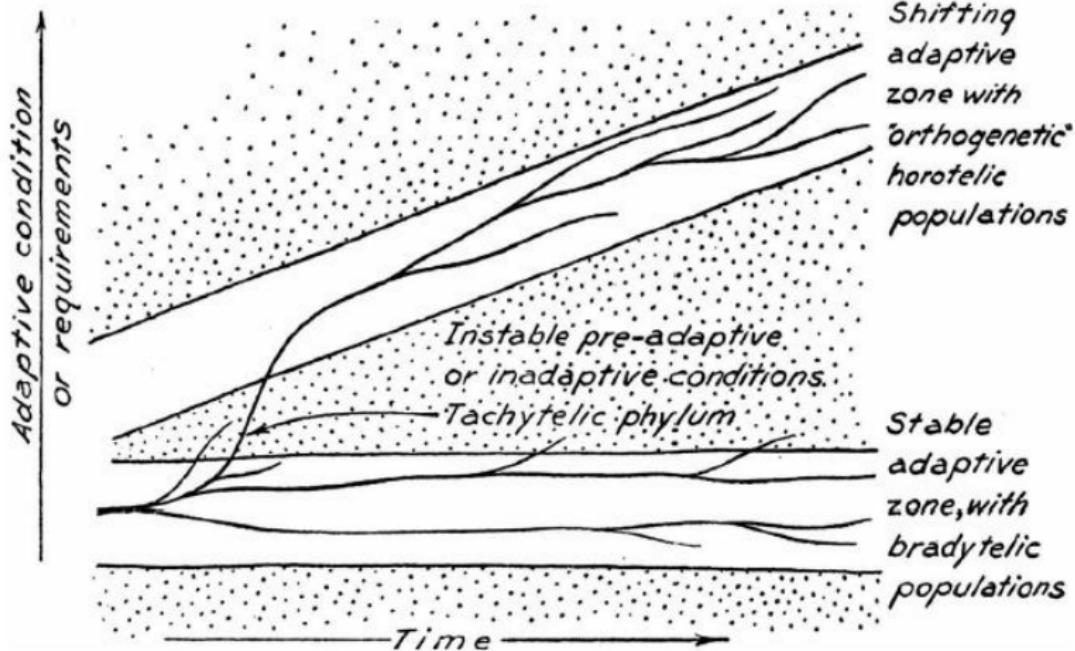
(Kitchell 1985 *Paleobiology*)

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

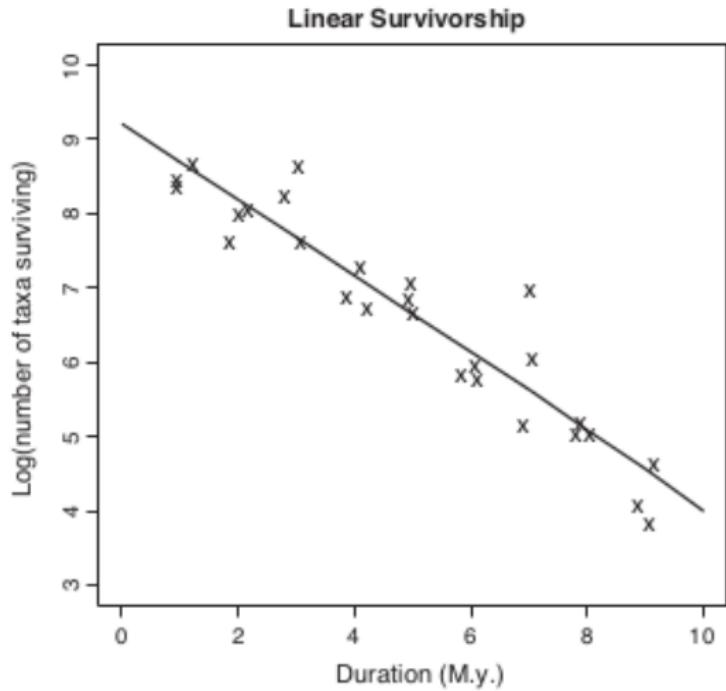
Definition

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

Theory

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Survival

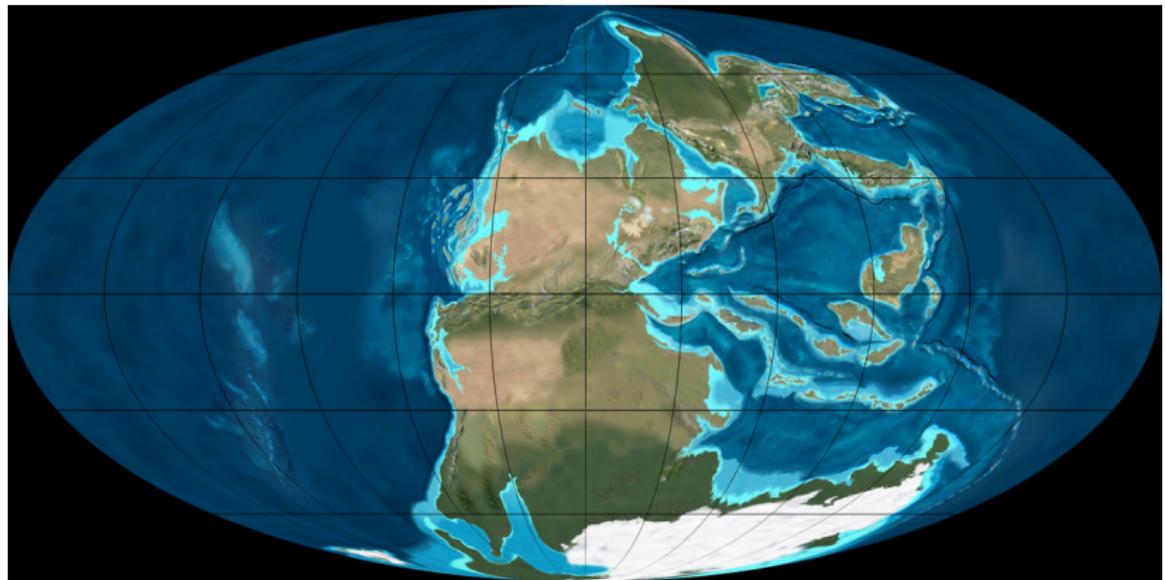
Definition

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

Brachiopods

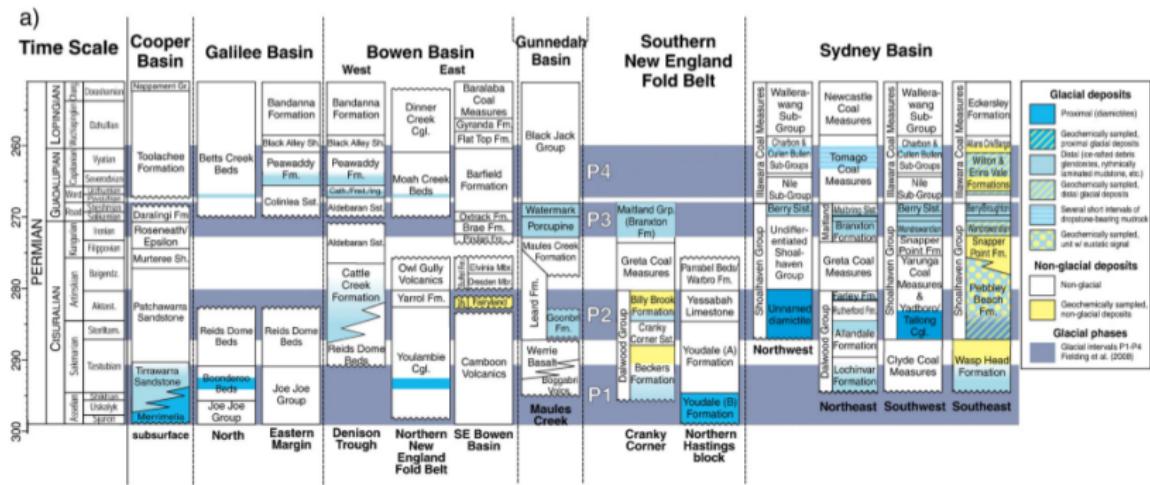


Permian



(Blakey <http://cpgeosystems.com/mollglobe.html>)

Permian of Australia



(Birgenheier et al. 2010 *Paleo*³)

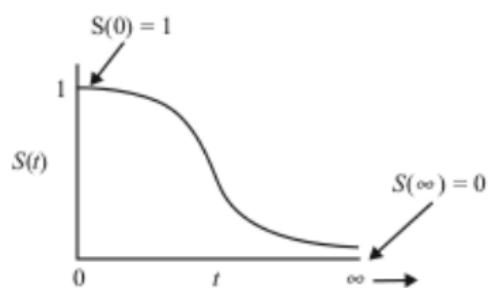
Brachiopods, environmental preference, and extinction

Questions

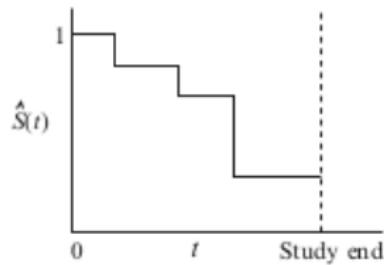
- ▶ Do interactions involved in environmental preference predict differential survival?
 - ▶ Is survival best modeled by a single interactor or multiple interactors?
 - ▶ How do other factors, such as climate, contribute?
- ▶ Is extinction taxon-age independent or dependent?

Probability of survival

Theoretical $S(t)$:

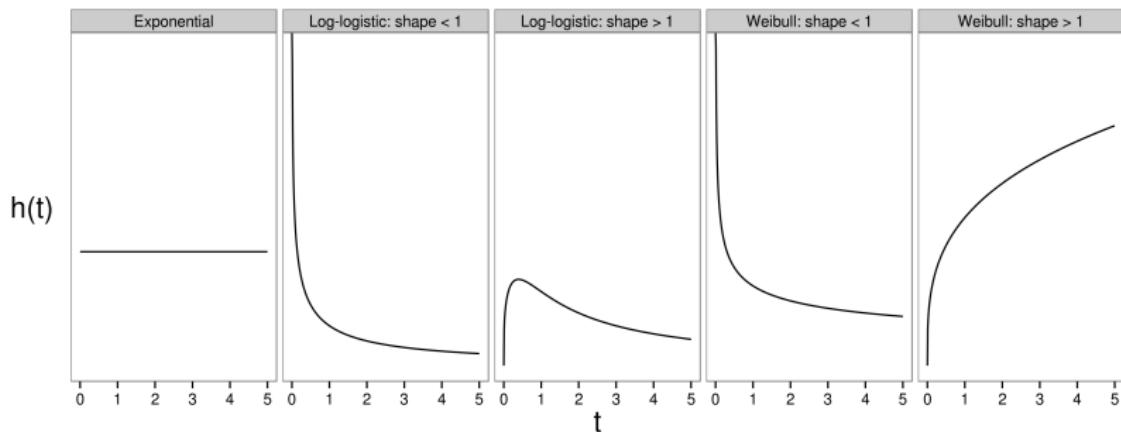


$\hat{S}(t)$ in practice:



(Kleinbaum and Klein 2012)

Extinction function



Formalization of Van Valen

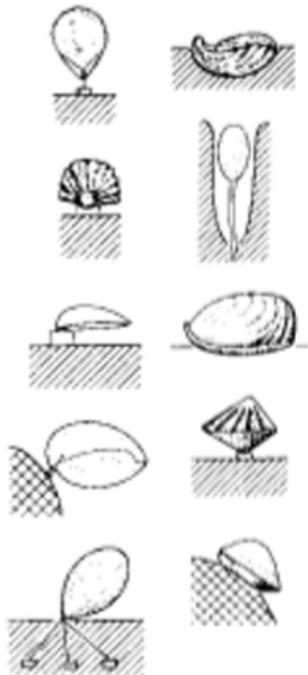
Law of Constant Extinction

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

T : survival time

λ : expected number of extinctions per unit time

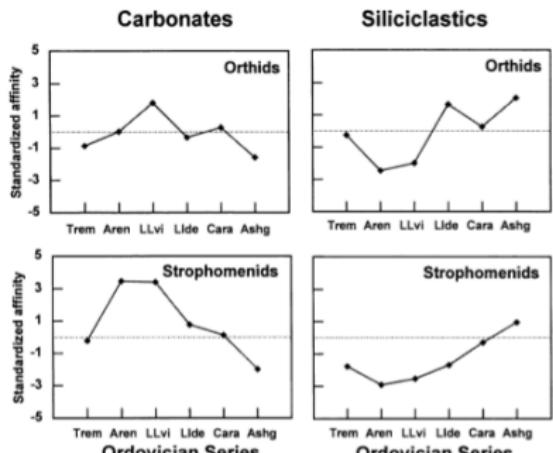
Affixing strategy



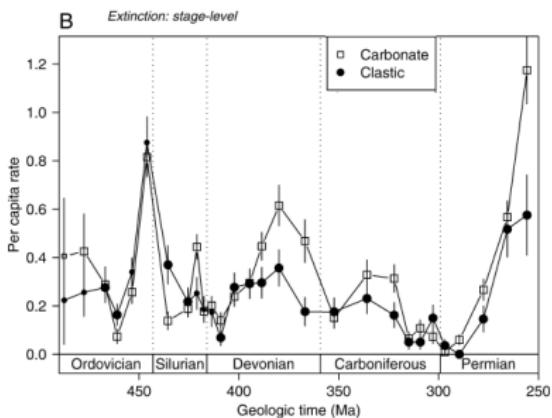
(modified from Johansen 1989 *Paleo*³)

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

Substrate affinity

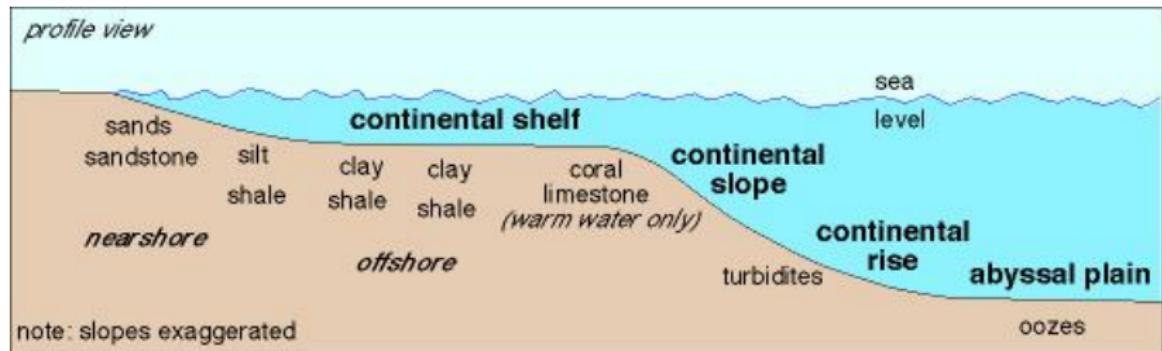


(Miller and Connolly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

Habitat preference



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

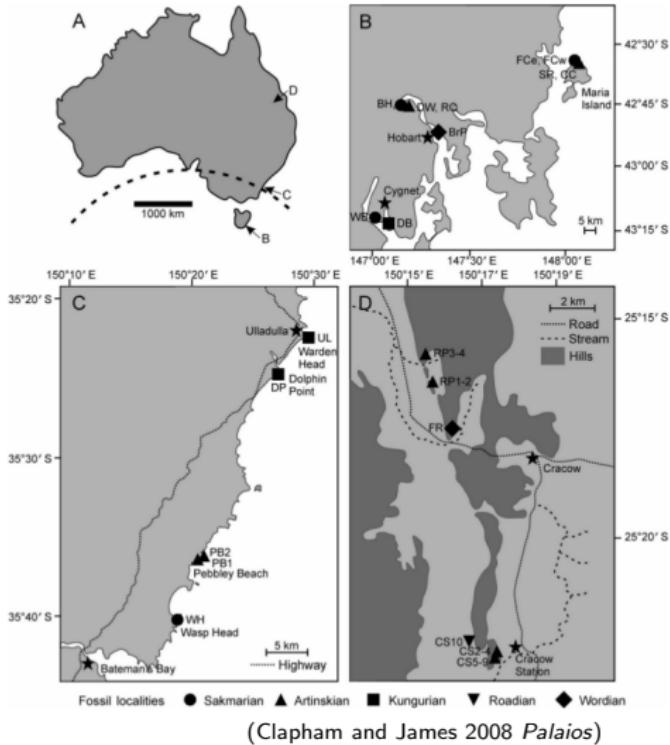
Assigning substrate and habitat

Probability of assignment

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

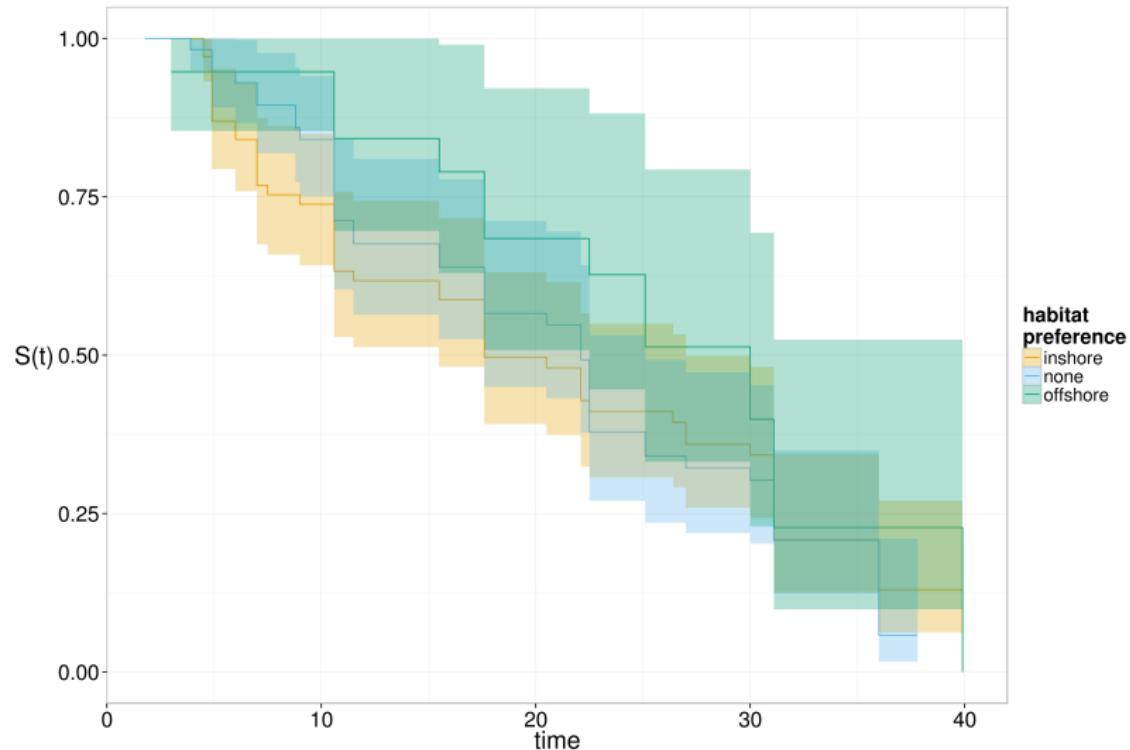
- ▶ p : proportion of all collections (e.g) carbonate
- ▶ n : total # taxon occurrences
- ▶ k : of n , # (e.g.) carbonate occurrences

Analysis

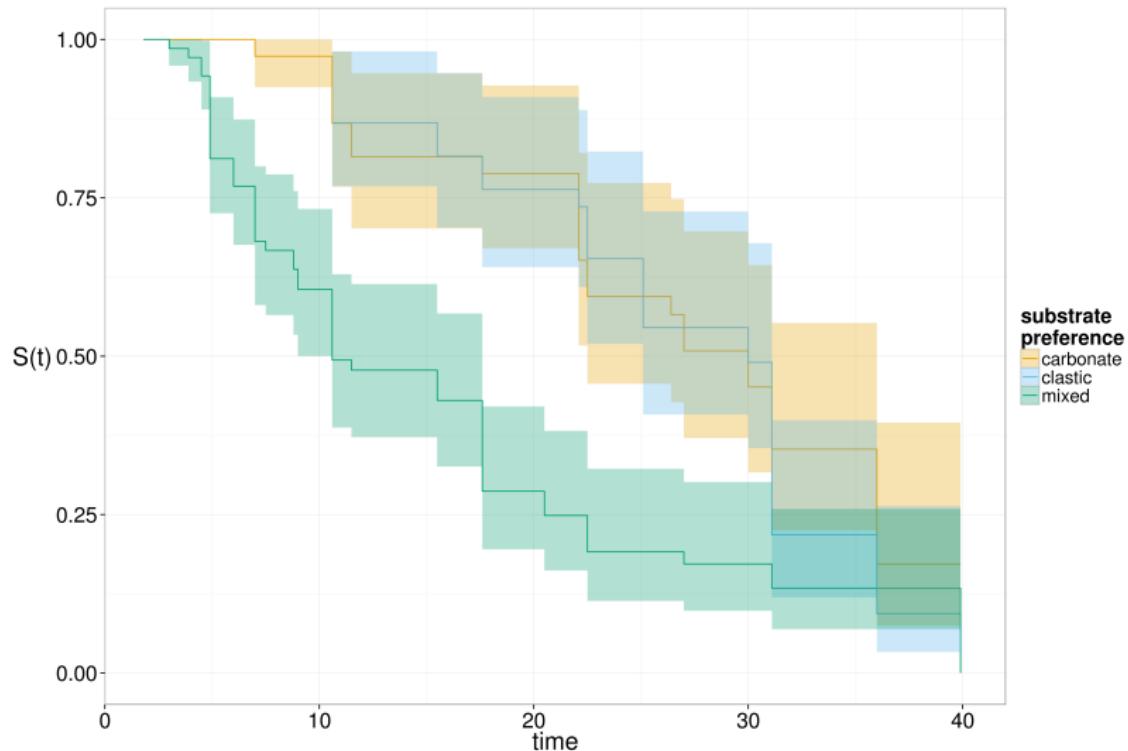


- ▶ age \sim Exponential or Weibull
- ▶ $\lambda \propto$ interactions, k constant
- ▶ range in/out taxa right censored
- ▶ habitat, substrate unedited from PBDB (this analysis)

K-M curve habitat



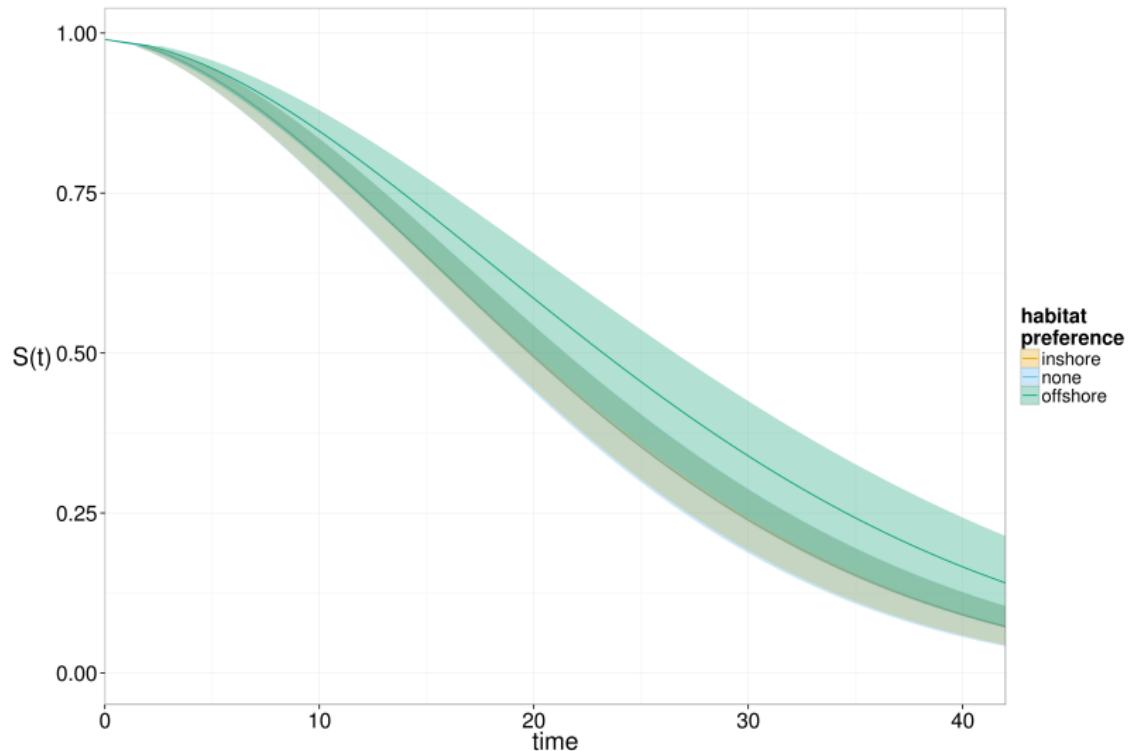
K-M curve substrate



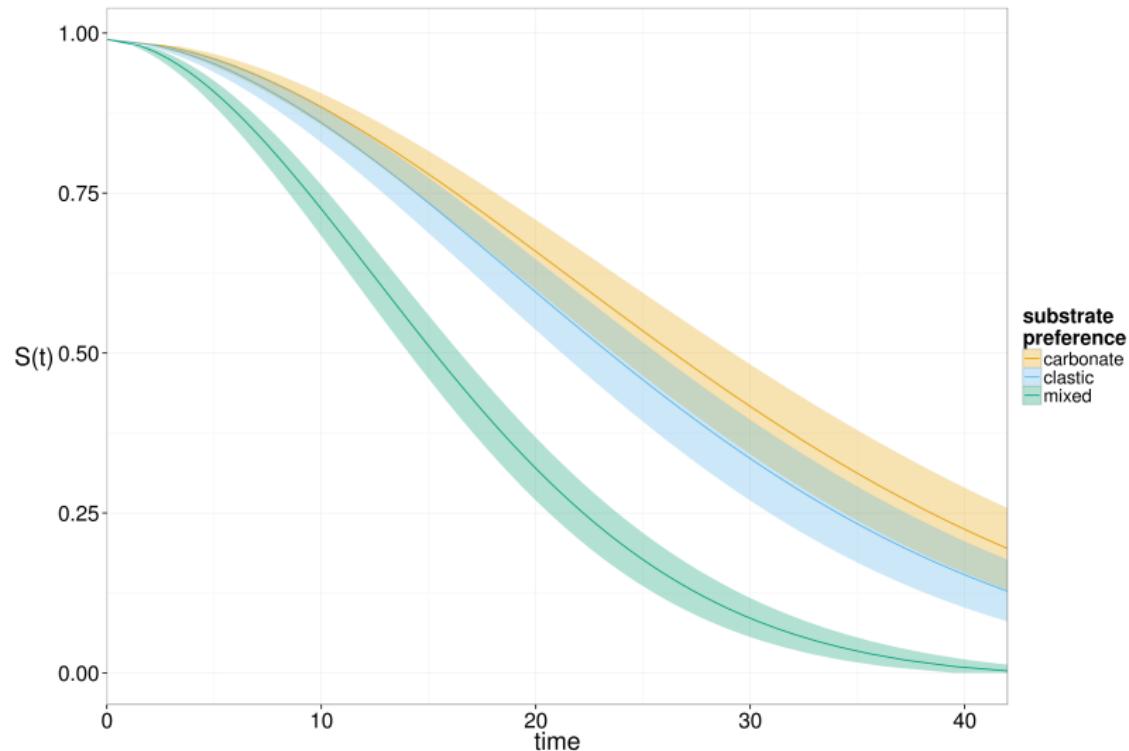
Preliminary results: model comparison

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



Theory

Survival

Communities

Summary

Community connectedness

Definition

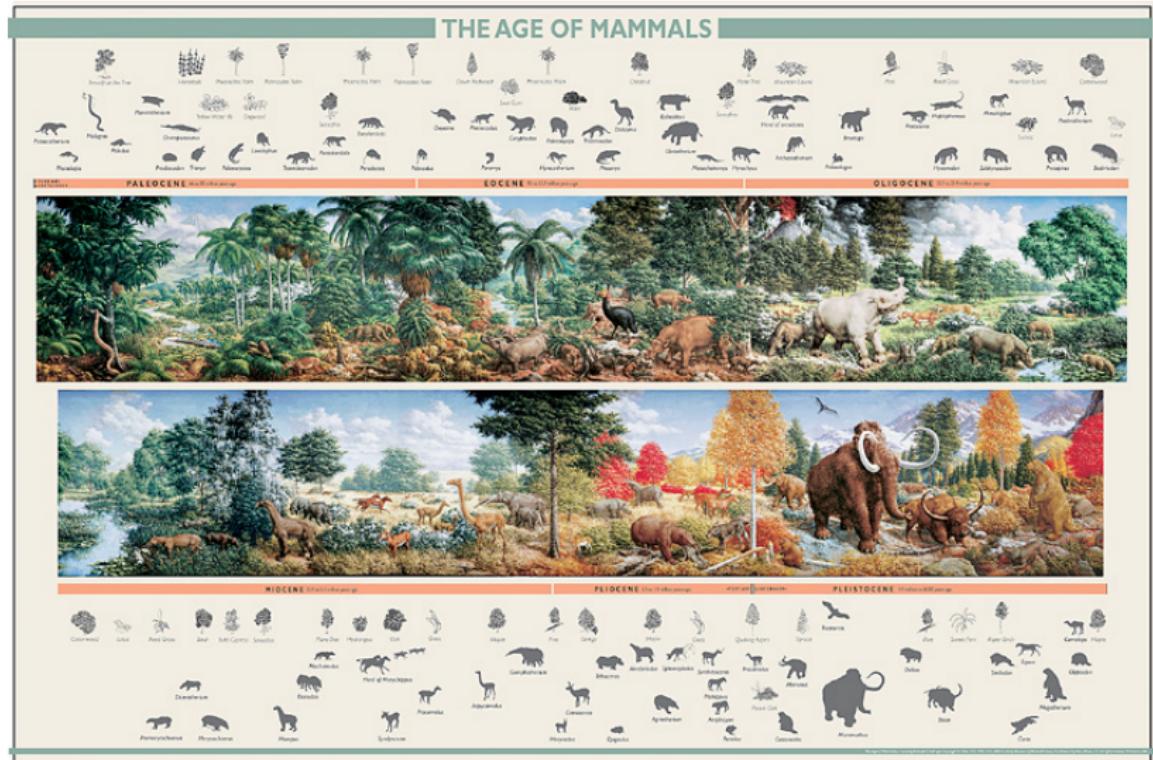
The relationship between α , β diversity and provinciality.

Uniformity and distinctiveness

high α , high distinctiveness, difference in selective pressures

high β , high uniformity, similarity in selective pressures

Mammals



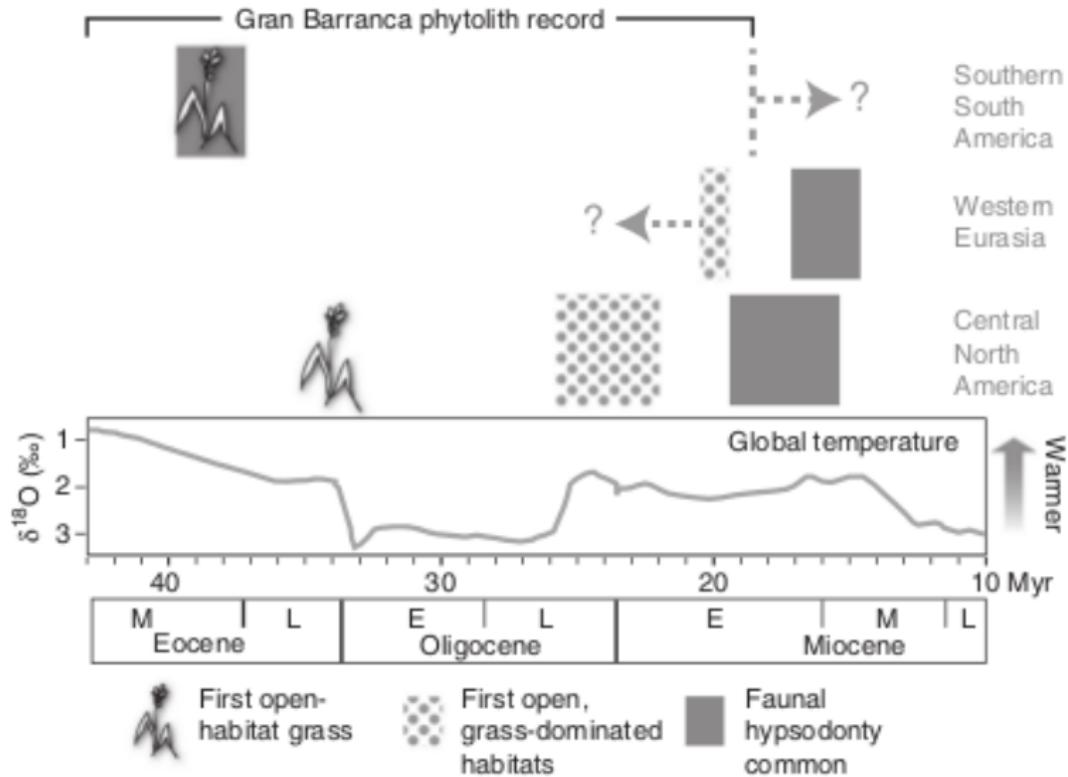
(Yale Peabody Museum)

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?

Environments



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

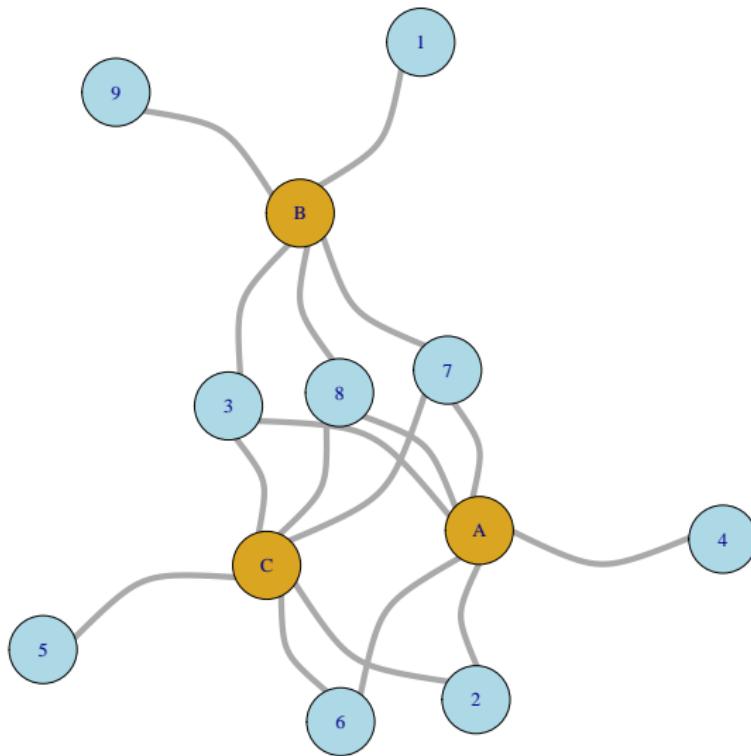
Occurrences

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

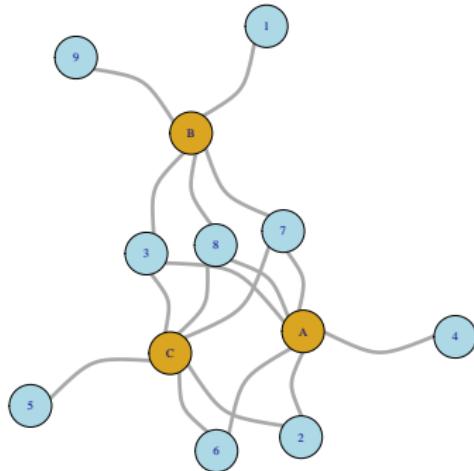
B: 1, 3, 7, 8, 9

C: 3, 5, 6, 7, 8

Biogeographic network



α diversity



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

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

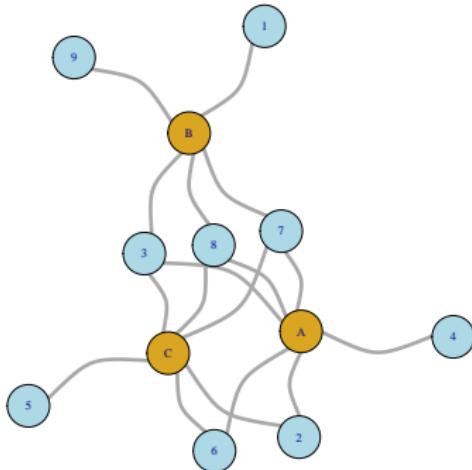
$$L = 3$$

$$E \approx 0.24$$

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

- ▶ 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



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

$$L = 3$$

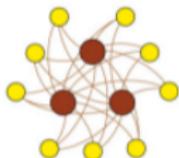
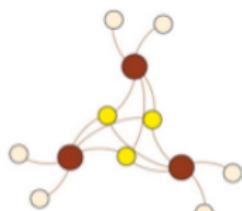
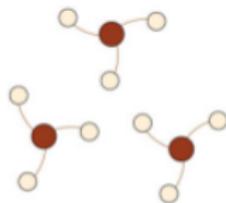
$$N = 9$$

$$Occ \approx 0.63$$

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

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

Uniformity

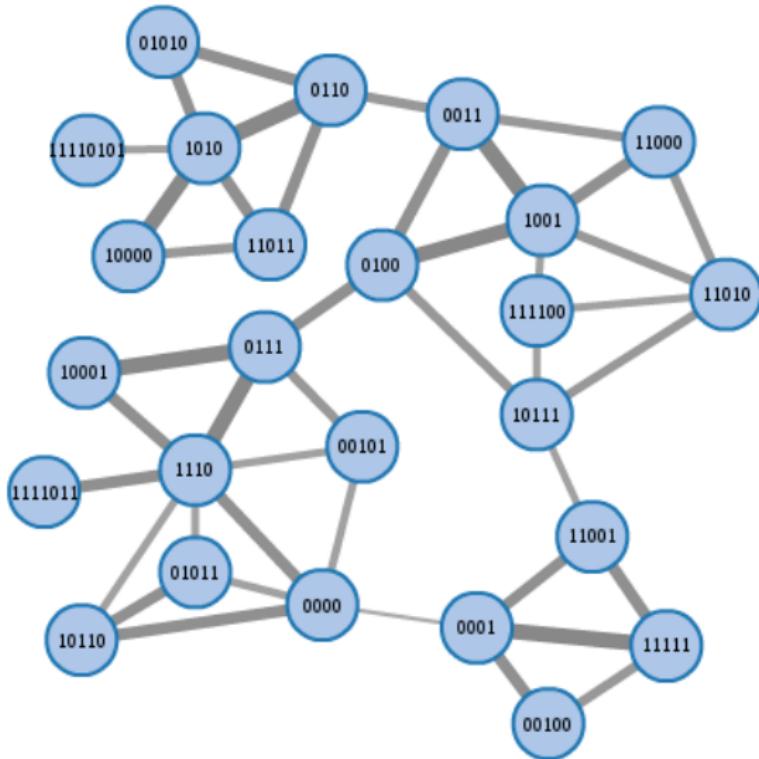


$$BC = \frac{O - N}{LN - N}$$

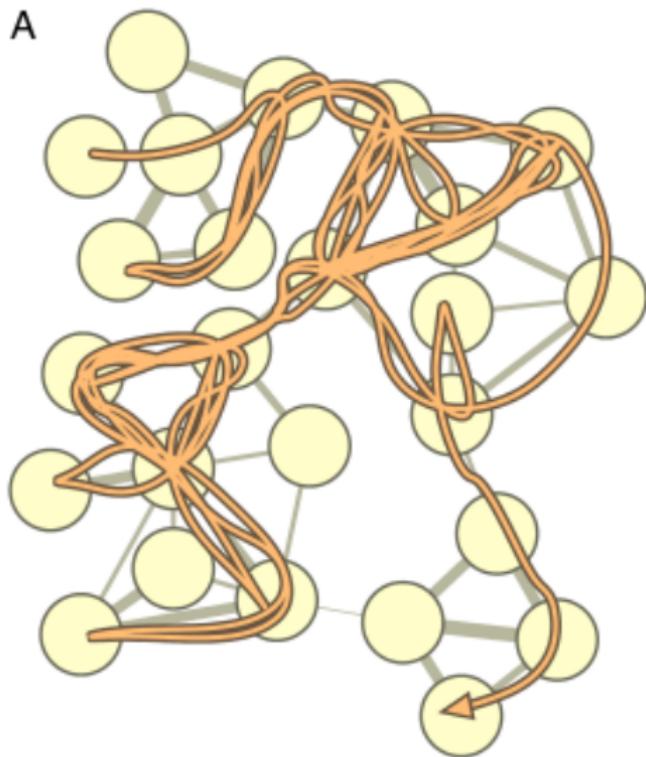
- ▶ O : number of occurrences
- ▶ N : total number of taxa
- ▶ L : number of localities
- ▶ $0 \leq BC \leq 1$

(Sidor et al. 2013 *PNAS*)

Code length

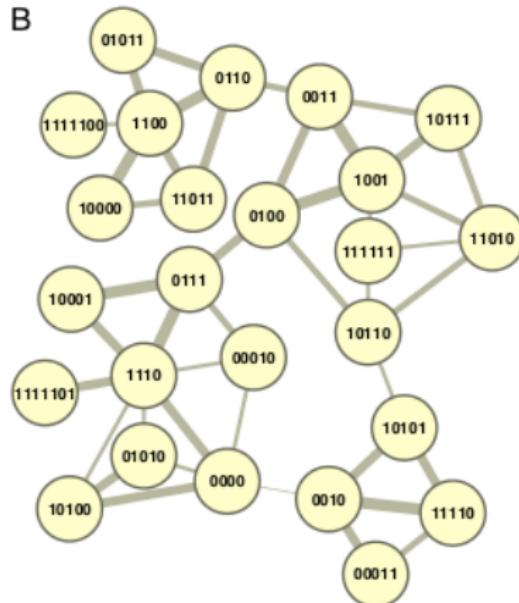


Code length



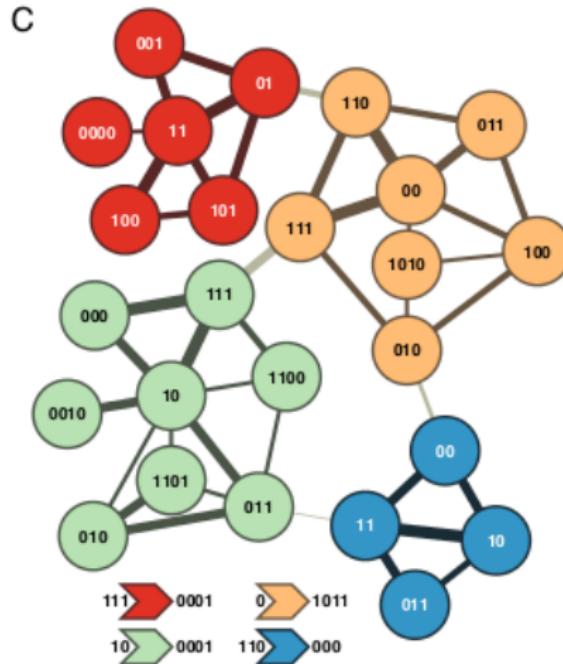
(Rosvall and Bergstrom 2008 *PNAS*)

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
```

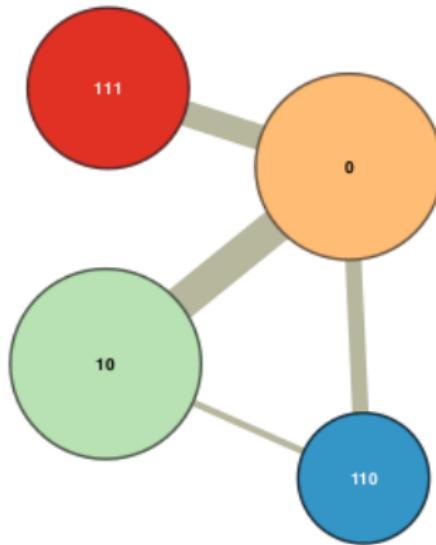
Code length



(Rosvall and Bergstrom 2008 PNAS)

Code length

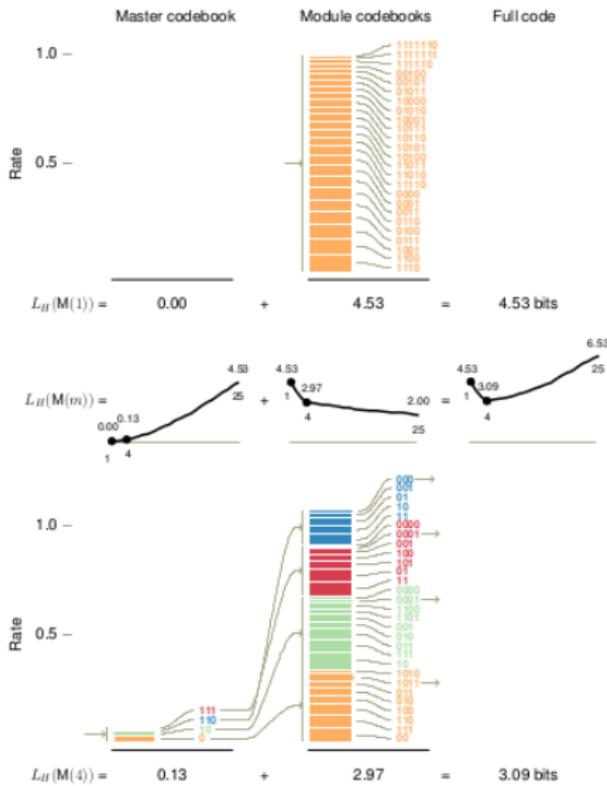
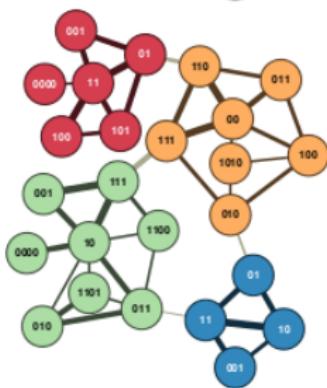
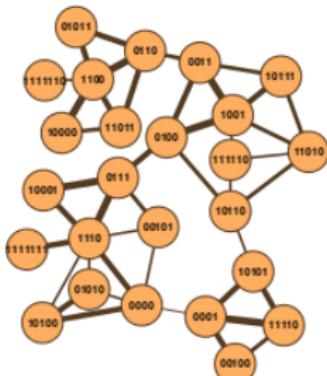
D



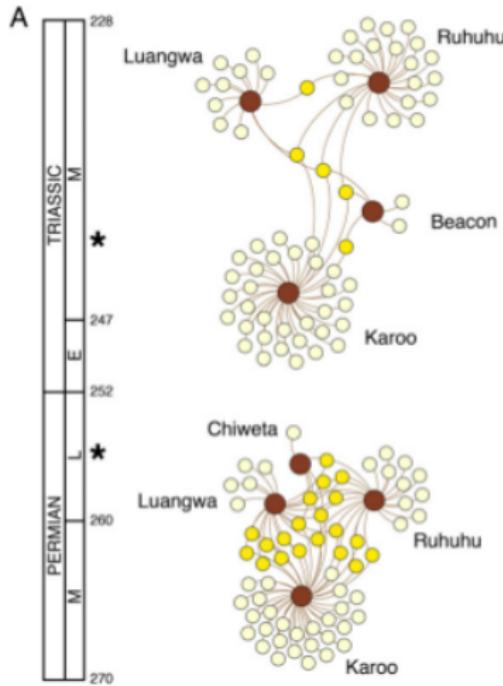
111 0000 11 01 101 100 101 01 0001 0 110 011 00 110 00 111 1011 10
011 000 10 111 000 111 10 011 10 000 111 10 111 10 0010 10 011 010
011 10 000 111 0001 0 111 010 100 011 00 111 00 011 00 111 00 111
110 111 110 1011, 111 01 101 01 0001 0 110 111 00 011 110 111 1011
10 111 000 10 000 111 0001 0 111 010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

(Rosvall and Bergstrom 2008 PNAS)

Two-level compression



Process 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)

Scenario



Locomotor

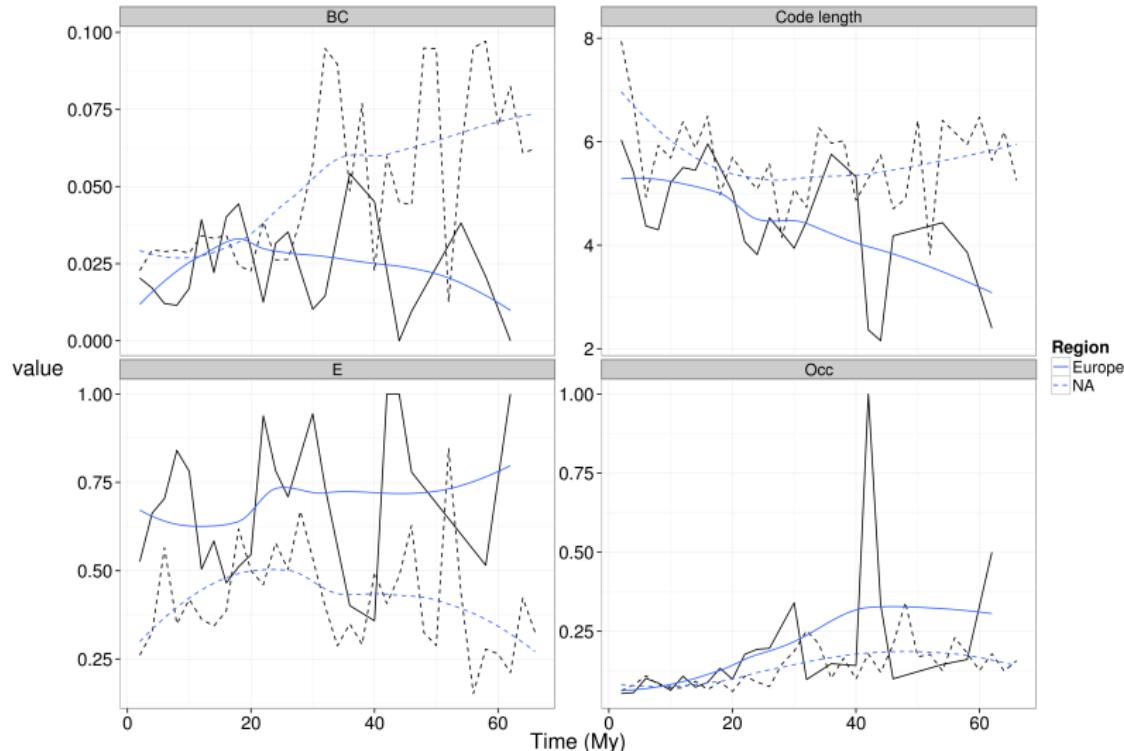
- ▶ ground dwelling,
arboreal, scansorial



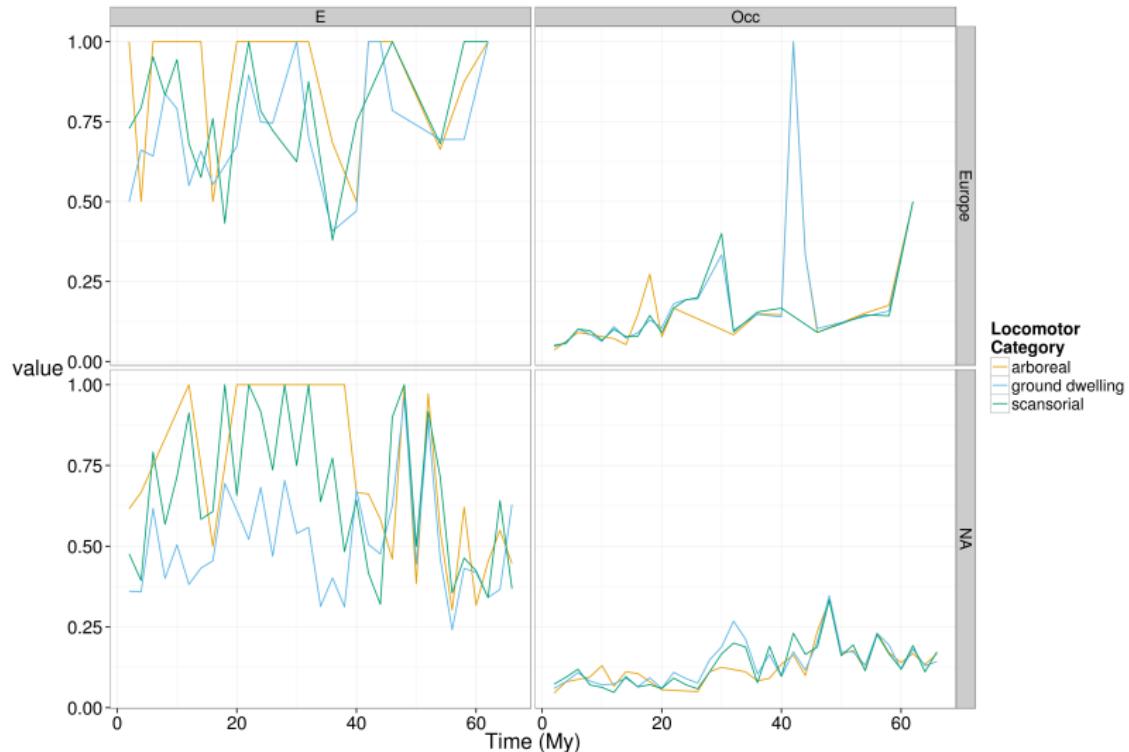
Dietary

- ▶ carnivore, insectivore,
herbivore, omnivore

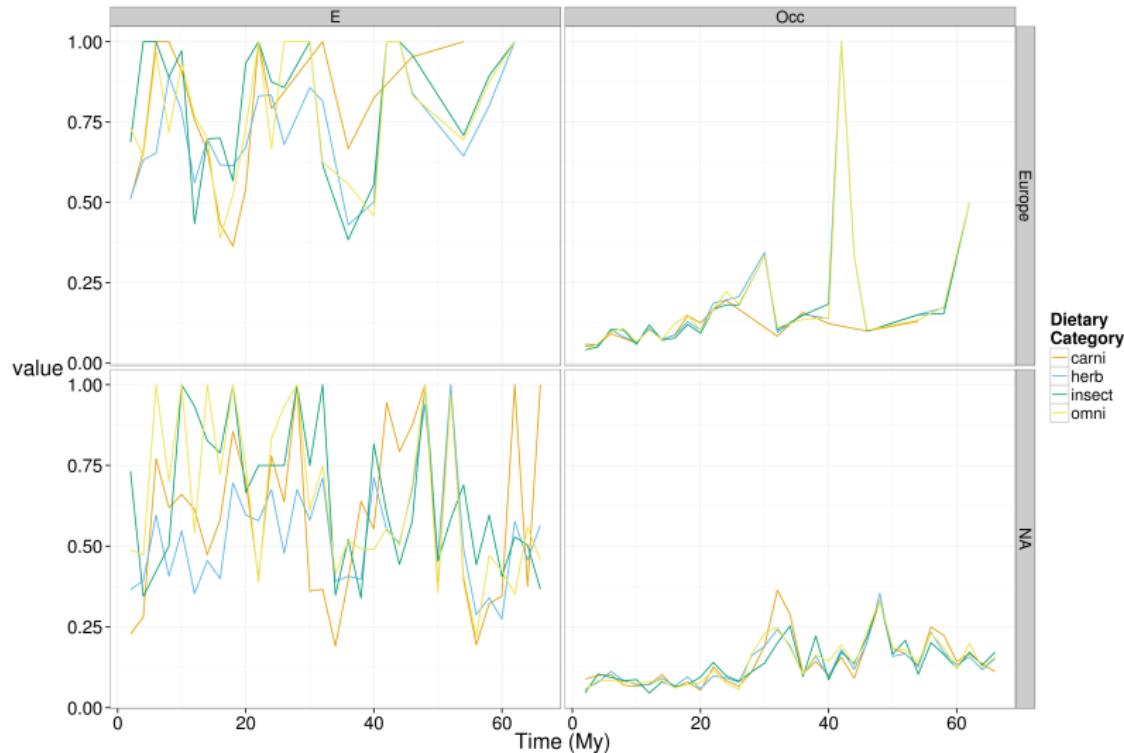
Preliminary results: NA, Eur



Preliminary results: locomotor category



Preliminary results: dietary category



Theory

Survival

Communities

Summary

Fundamental

Question

Why do some taxa go extinct while others do not?

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.

Evolutionary paleoecological rephrasing

Question

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

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



The Field
Museum

Fossilworks



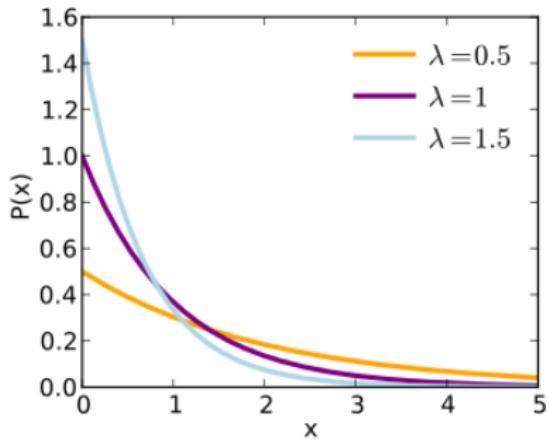
PALEOBIOLOGY
DATABASE



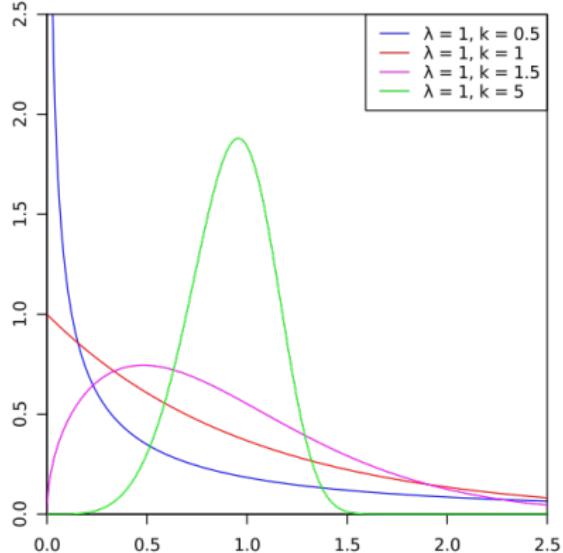
Further concerns

Age distributions

Exponential



Weibull



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

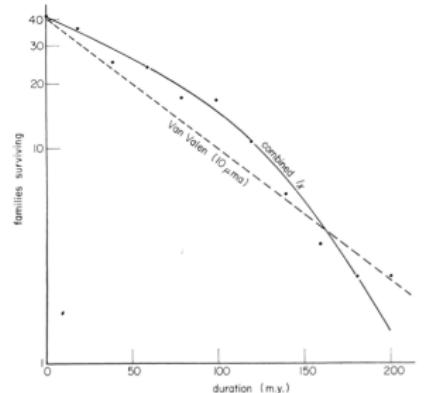
Algebra of age distributions

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

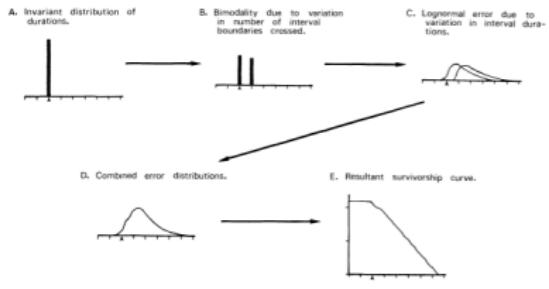
$$f(x; \lambda_{\text{exp}}) = \begin{cases} \lambda \exp^{-\lambda x} & x \geq 0 \\ 0 & x < 0 \end{cases}$$

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

Differential preservation and survival



(Raup 1975 *Paleobio.*)



(Sepkoski 1975 *Paleobio.*)

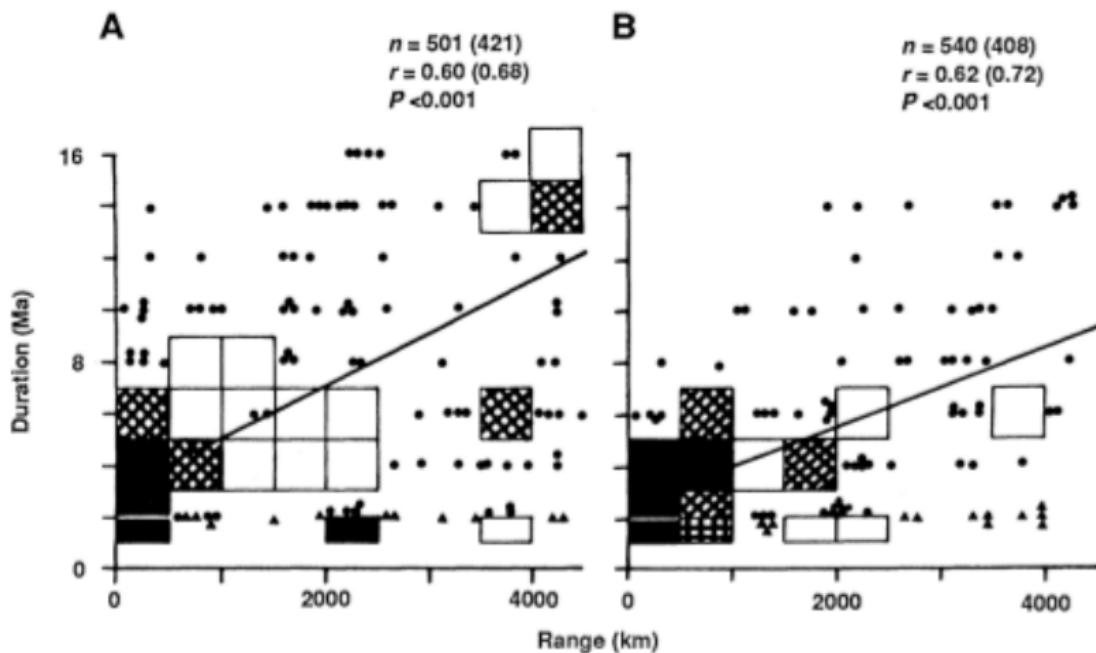
Observe in simulation

Sampling: Poisson process (ϕ)

Diversification: birth-death (λ, μ)

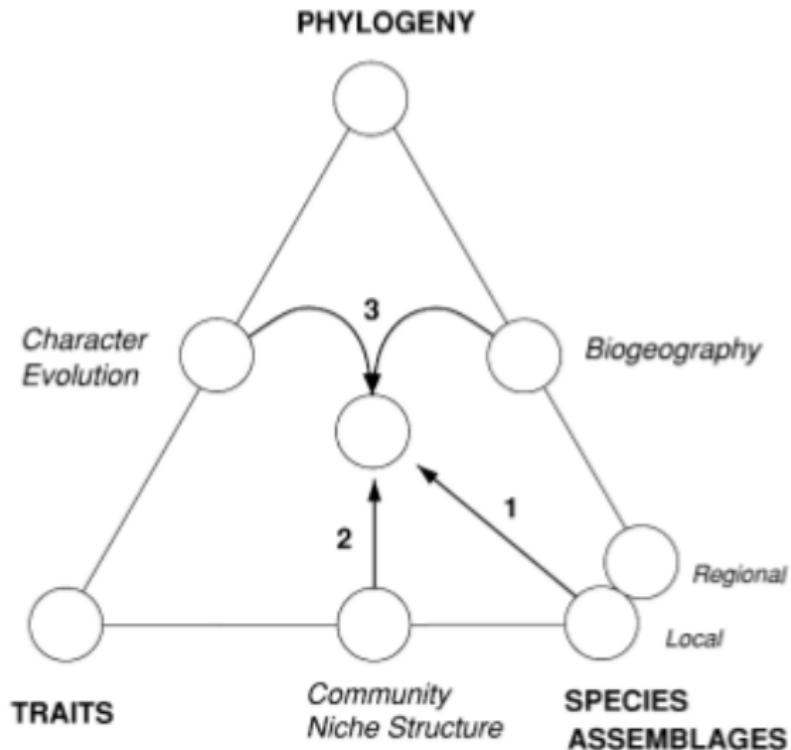
1. = birth, death; =preservation
2. = birth, death; !=preservation
3. != birth, death; = preservation
4. != birth, death; !=preservation

The Elephant in the Range

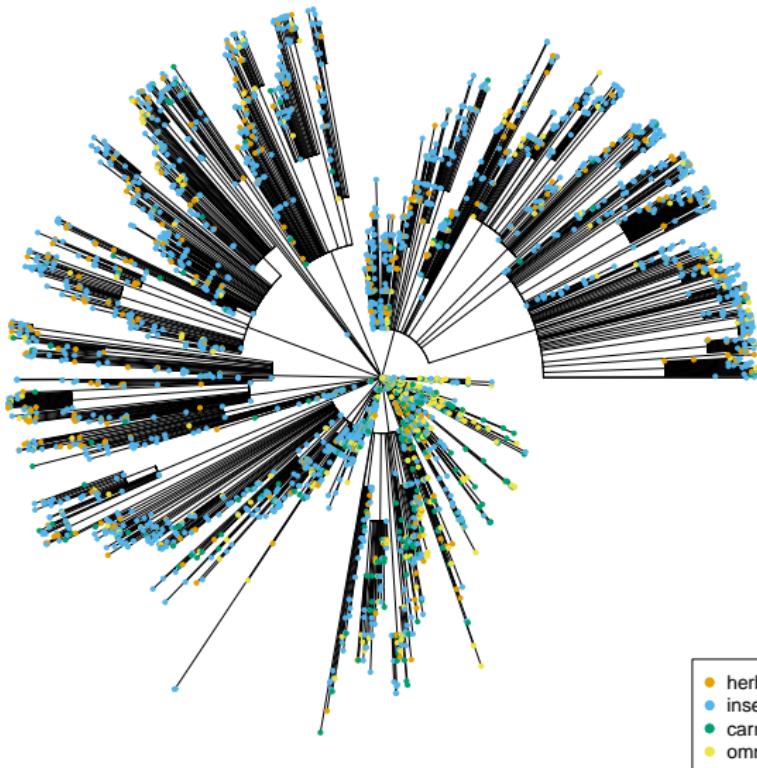


(Jablonski 1987 *Science*)

Phylogeny and communities



(Informal) phylogeny



Compressing a network

Map equation

(Rosvall and Bergstrom 2008 PNAS)

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

- ▶ \mathbf{M} : module partition of n nodes in m partitions
- ▶ $L(\mathbf{M})$: theoretical minimum descriptive length of a single step
- ▶ q_{\curvearrowright} : $P(\text{walk switches modules})$
- ▶ $H(\mathcal{Q})$: entropy of module codewords
- ▶ $H(\mathcal{P}^i)$: entropy within-module movements
- ▶ p_{\circlearrowleft}^i : fraction of within-module use in module i