

# Evolutionary paleoecology and the biology of extinction

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Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

## Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

# Framework

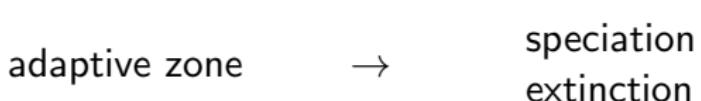
## Questions

- ▶ Why do certain taxa go extinct while others do not?
  - ▶ Is extinction risk taxon–age independent?
- ▶ How is emergence “formed?” When should it be invoked?
- ▶ When should global, regional, or local processes expected to dominate?

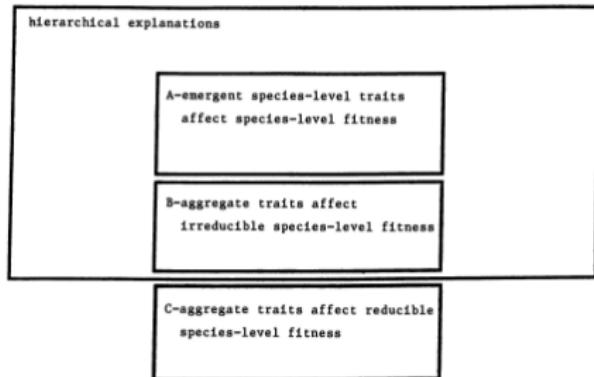
# Evolutionary paleoecology

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

(Kitchell 1985 *Paleobiology*)



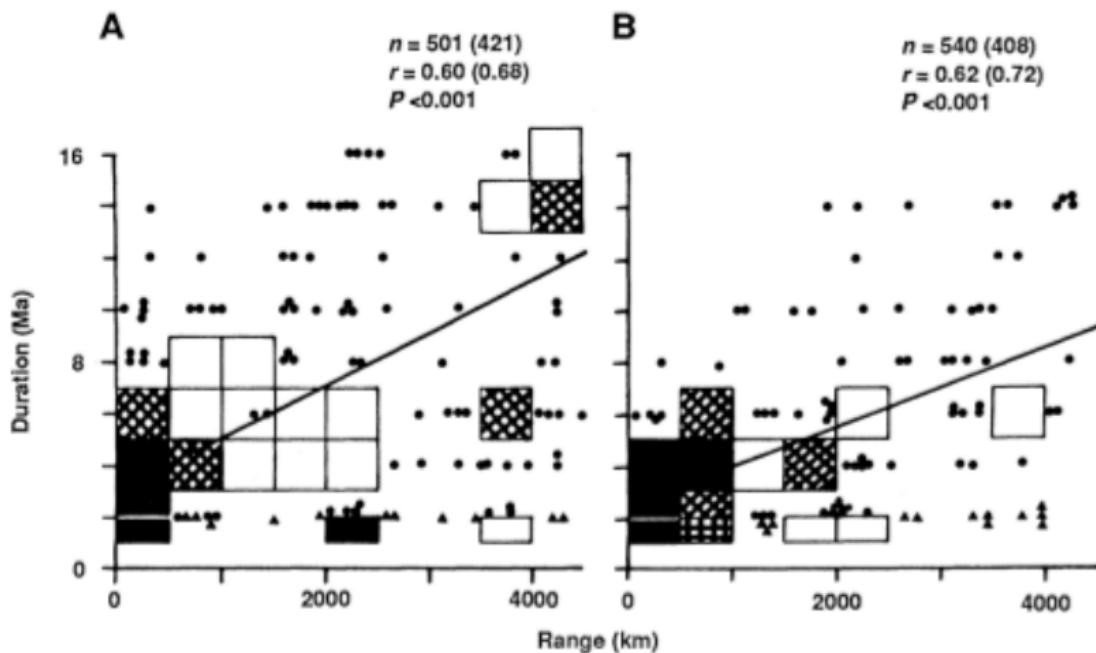
# Emergent properties



(Grantham 1995 *Ann. Rev. Ecol. Syst.*)

**Criteria:** cannot be reduced to lower level (e.g. organismal)

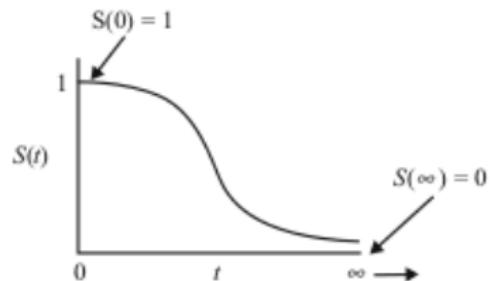
# Range size



(Jablonski 1987 *Science*)

# Probability of survival

Theoretical  $S(t)$ :

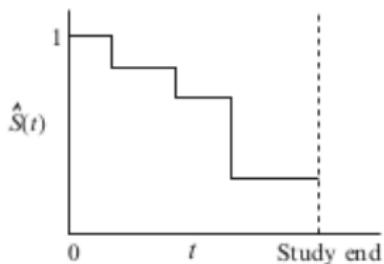


## Survival function

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

- ▶  $T$ : survival time ( $\geq 0$ )
- ▶  $t$ : specified time

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

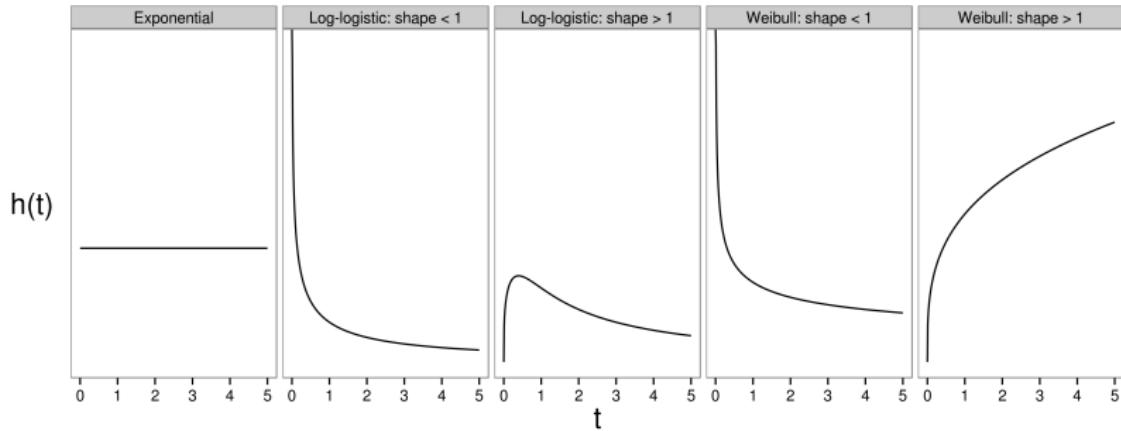


(Kleinbaum and Klein 2012)

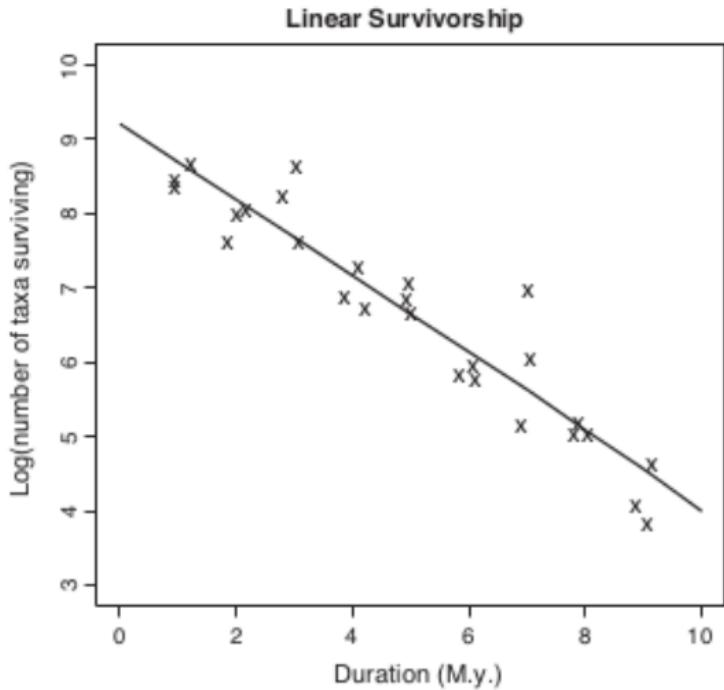
# Instantaneous potential of failure (extinction)

Hazard function  $\equiv$  conditional failure rate

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



# 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*)

translation: hazard is constant with respect to time  
(exponential survival)

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

# Study systems

## brachiopods

- ▶ marine
- ▶ sessile
- ▶ Permian ( $\sim 47$  My)
- ▶ global warming
- ▶ Australasia



## mammals

- ▶ terrestrial
- ▶ motile
- ▶ Cenozoic ( $\sim 65$  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?

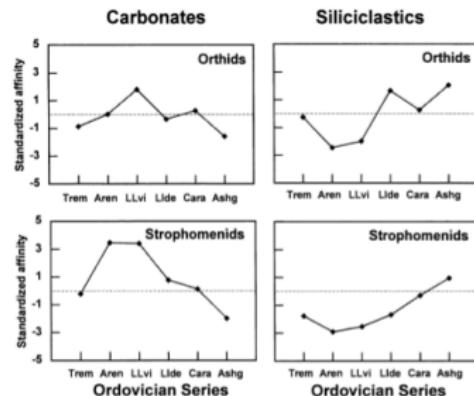
Theory

Brachiopod survival

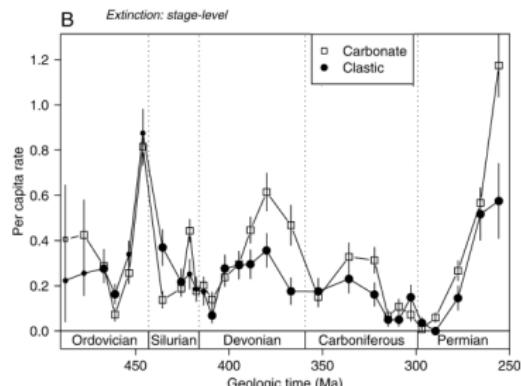
Mammal survival

Mammal community connectedness

# Substrate affinity



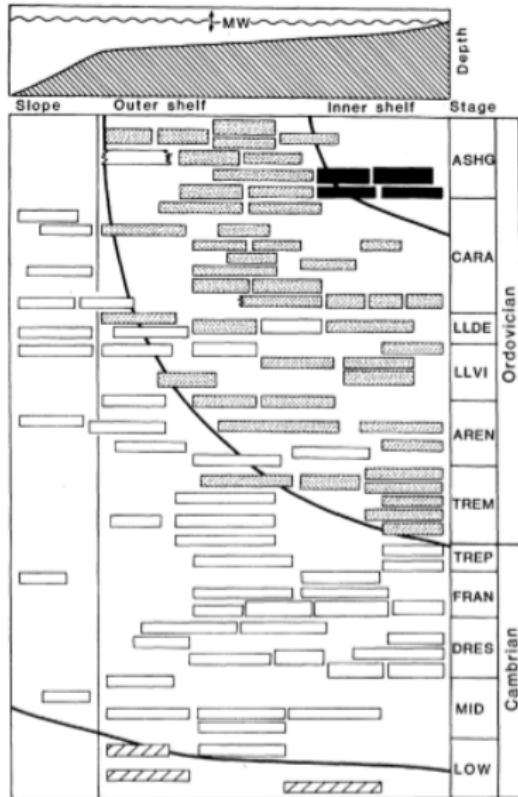
(Miller and Connolly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

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

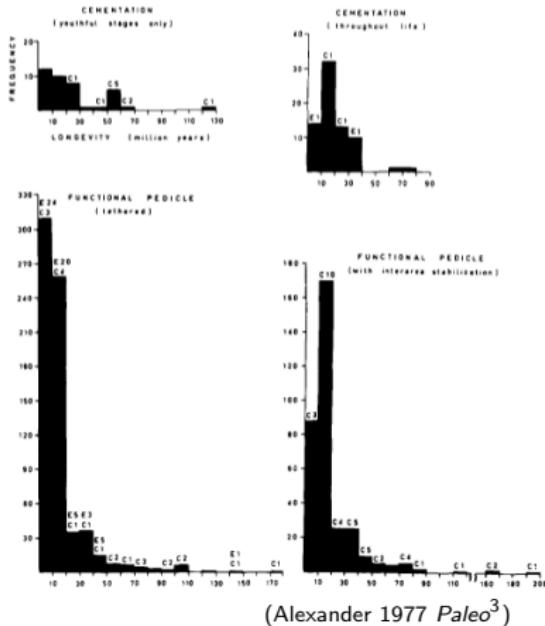
# Habitat preference



(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

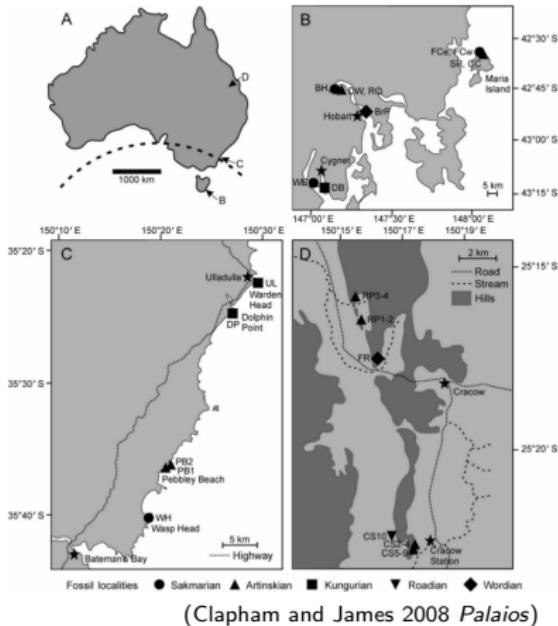
## Probability of assignment

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

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

(Simpson and Harnik 2009 *Paleobiology*)

# Analysis

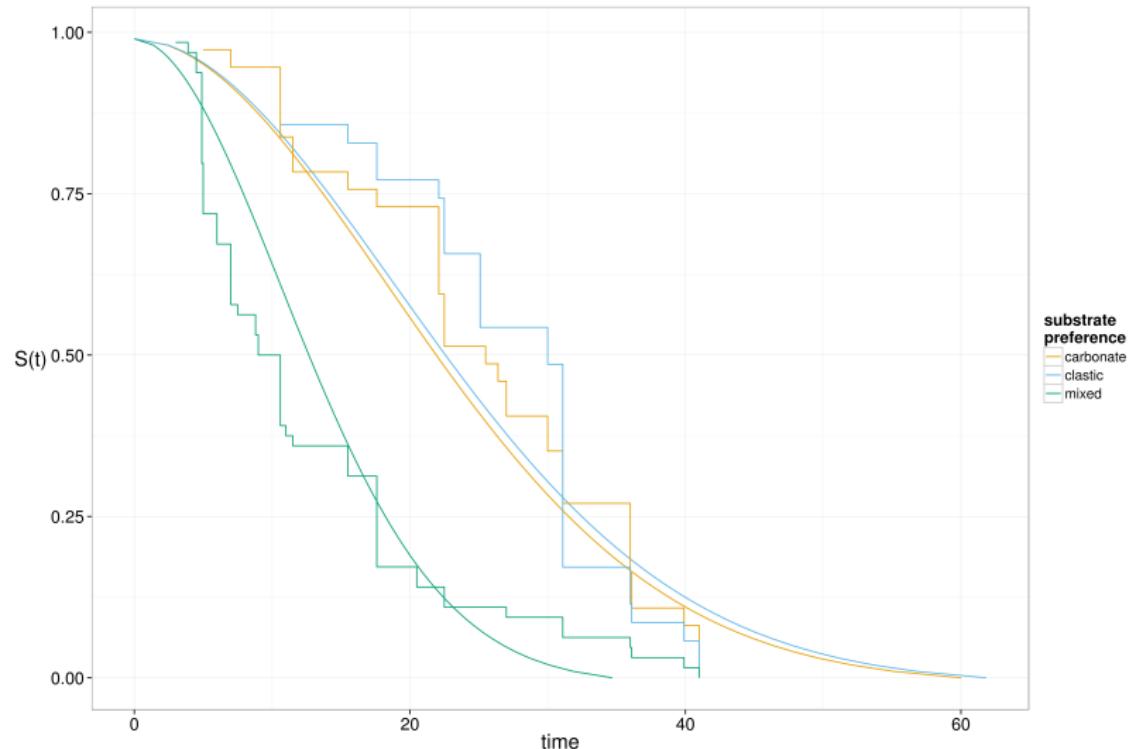


- ▶ genus FAD–LAD
  - ▶ occurring in, ranging into/out of Permian
  - ▶ interval censoring
- ▶ time-independent traits
  - ▶ substrate following Foote 2006 *Paleobio.*
  - ▶ habitat following Kiessling *et al.* 2007 *Paleo*<sup>3</sup>
- ▶ time-dependent climate
- ▶ survival distributions:  $\exp(\lambda)$ ,  $Weibull(\lambda, k)$ , etc.

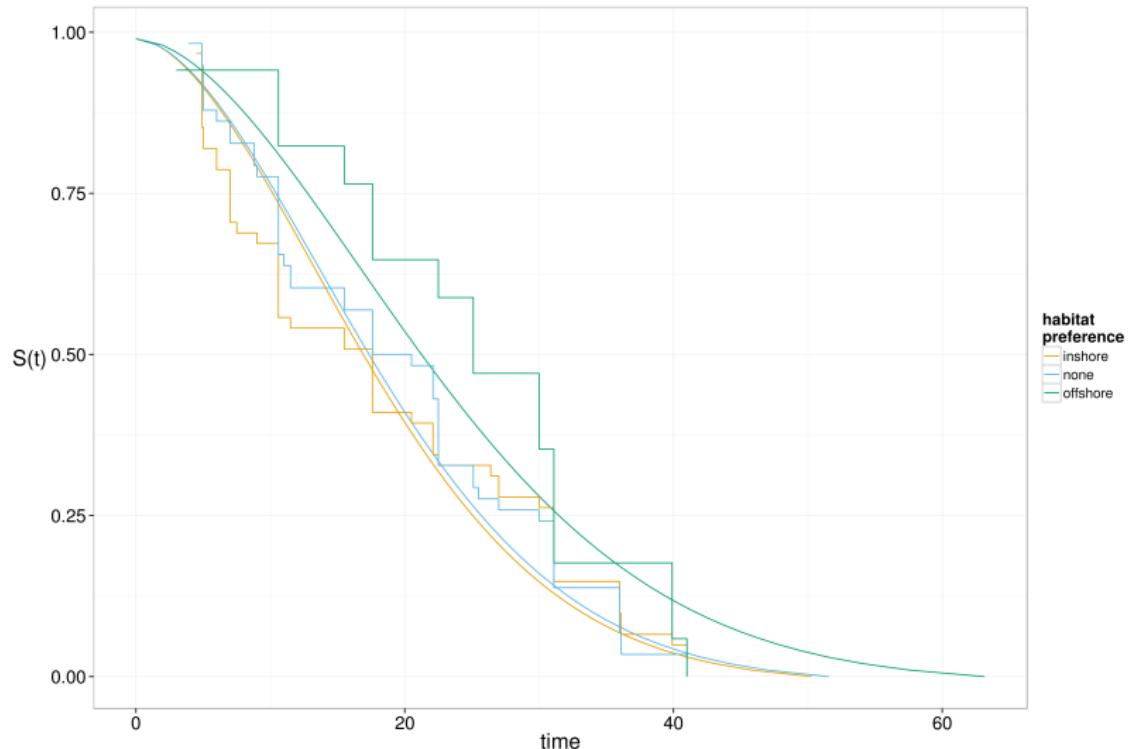
## Preliminary results: model comparison

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



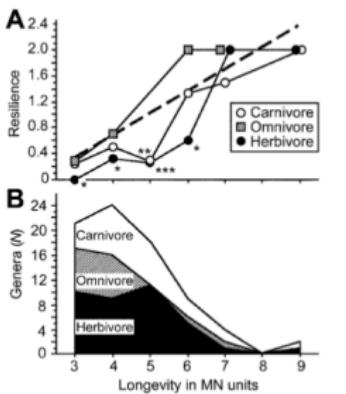
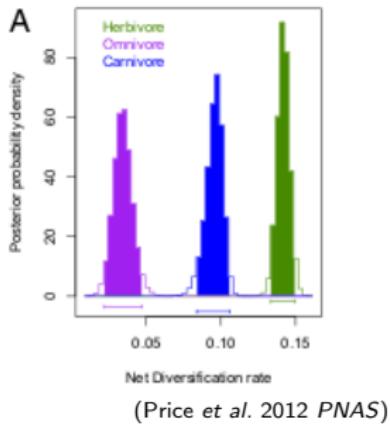
Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

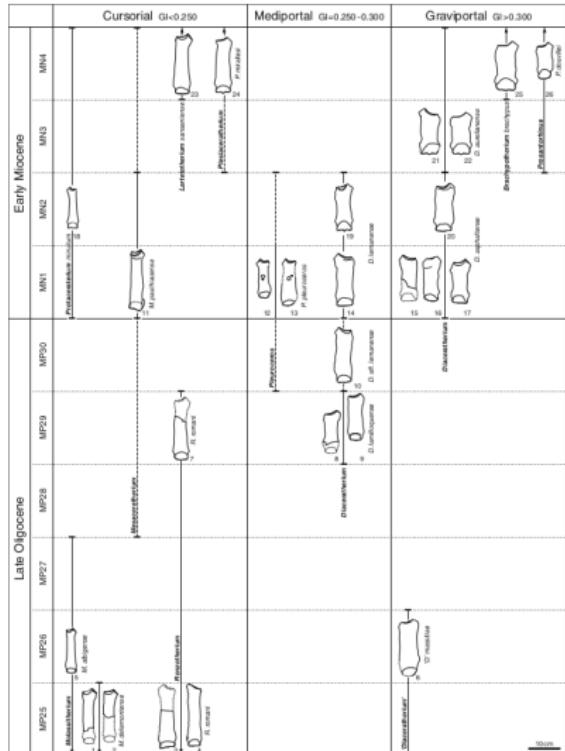
# Dietary category



(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

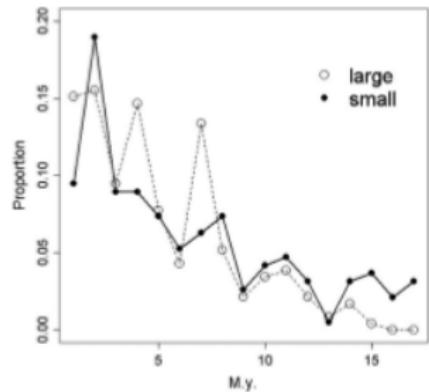
# Locomotor category



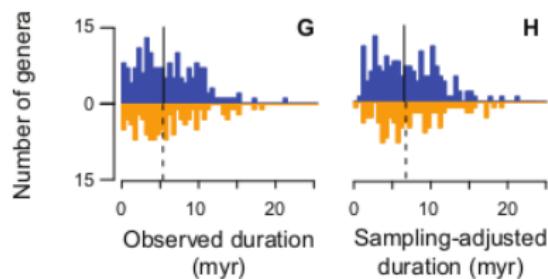
(Scherler et al. 2013 Swiss. J. Geosci.)

- ▶ 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  $\delta O^{18}$  isotope (Zachos *et al.* 2008 *Nature*)
- ▶ Paleogene versus Neogene
- ▶ survival distributions:  $\exp(\lambda)$ ,  $Weibull(\lambda, k)$ , etc.

Theory

Brachiopod survival

Mammal survival

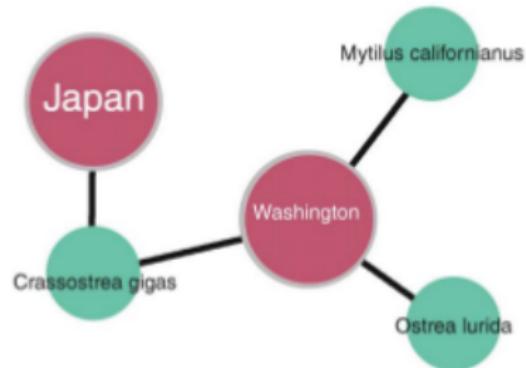
Mammal community connectedness

# Community connectedness

## Definition

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

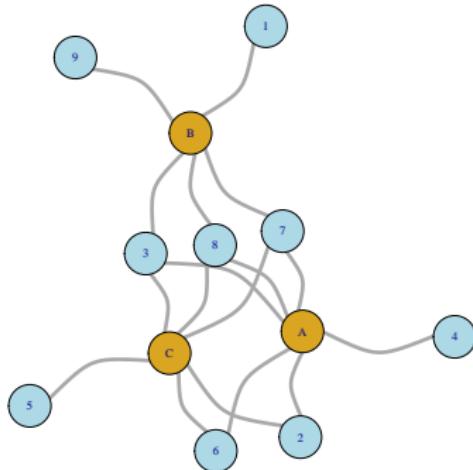
# Biogeographic networks



(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



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

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

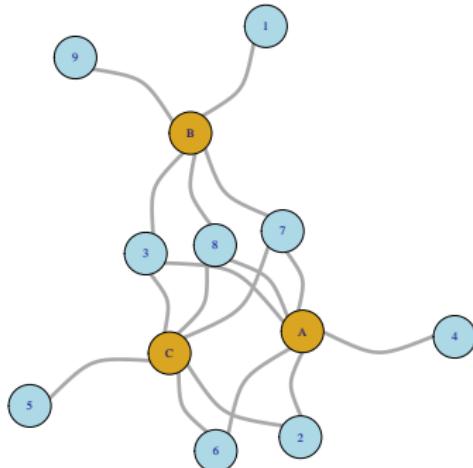
$$L = 3$$

$$E \approx 0.24$$

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

- ▶  $L$ : 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



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

$$L = 3$$

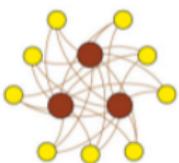
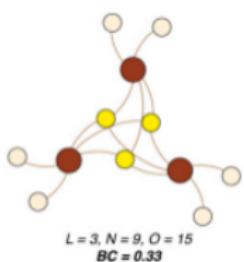
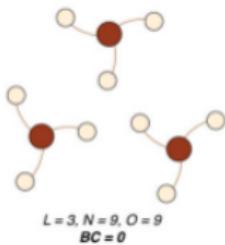
$$N = 9$$

$$Occ \approx 0.63$$

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

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

# Biogeographic connectedness

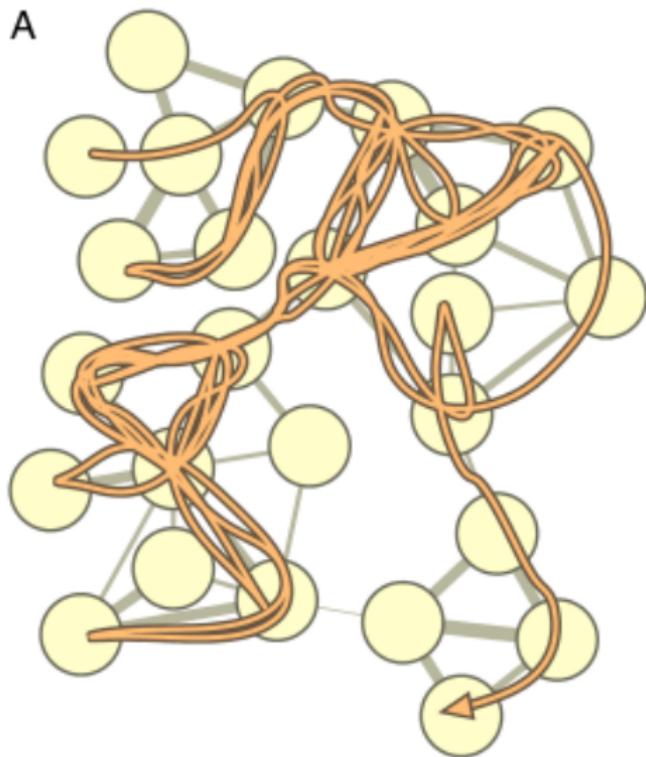


$$BC = \frac{O - N}{LN - N}$$

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

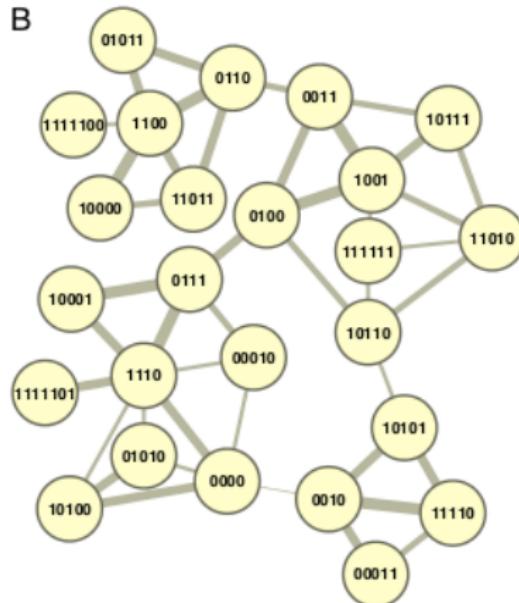
(Sidor et al. 2013 PNAS)

# Code length



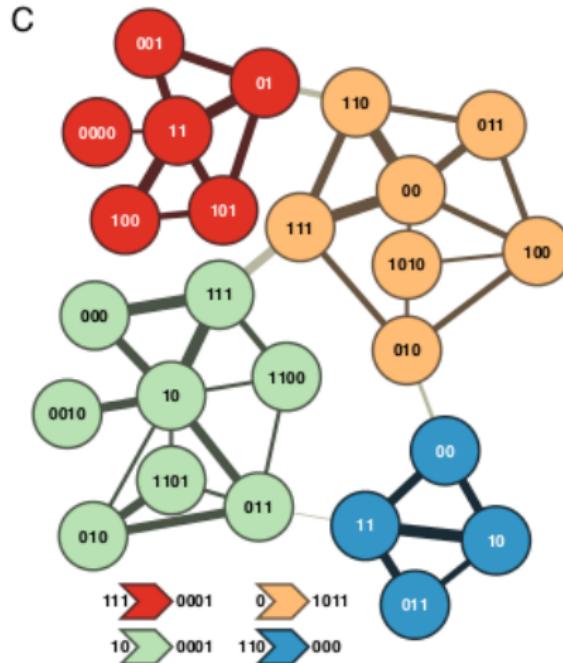
(Rosvall and Bergstrom 2008 PNAS)

# 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
```

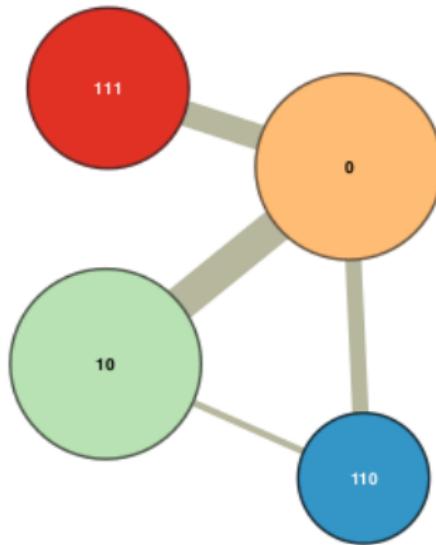
# Code length



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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



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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

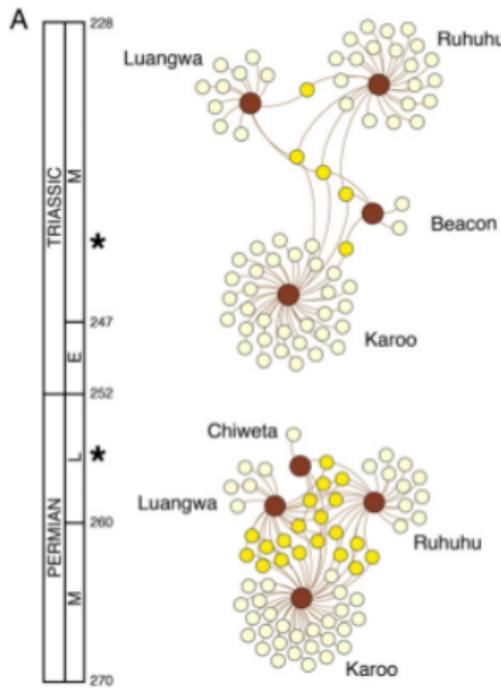
## Map equation

(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

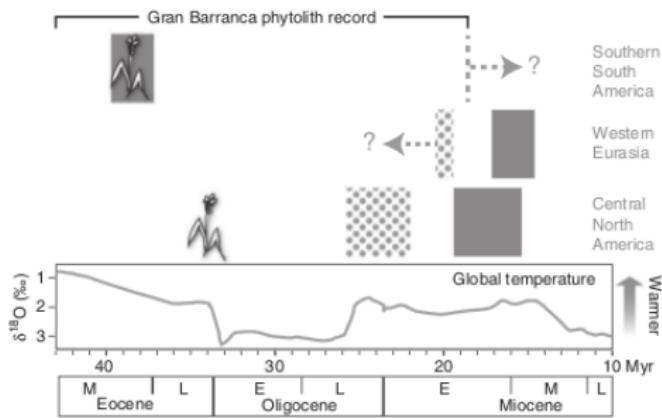
# Global versus regional versus local scale



- ▶ 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)

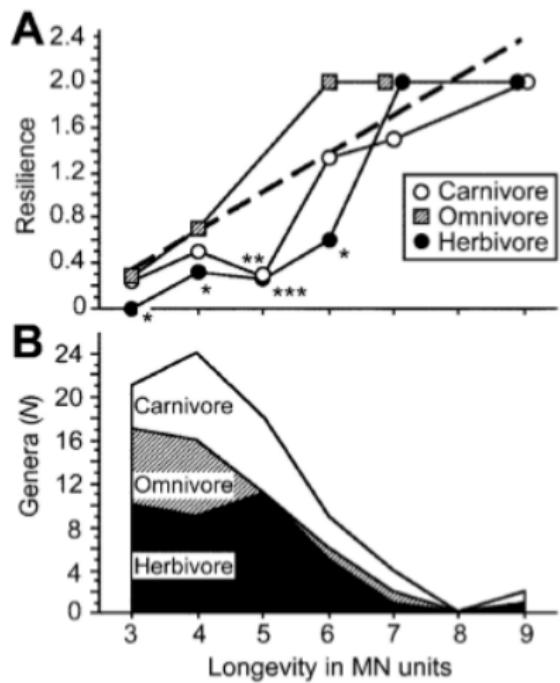
# Global expectations: locomotor category



(Strömberg et al. 2013 *Nature Com.*)

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

# Global expectations: dietary category



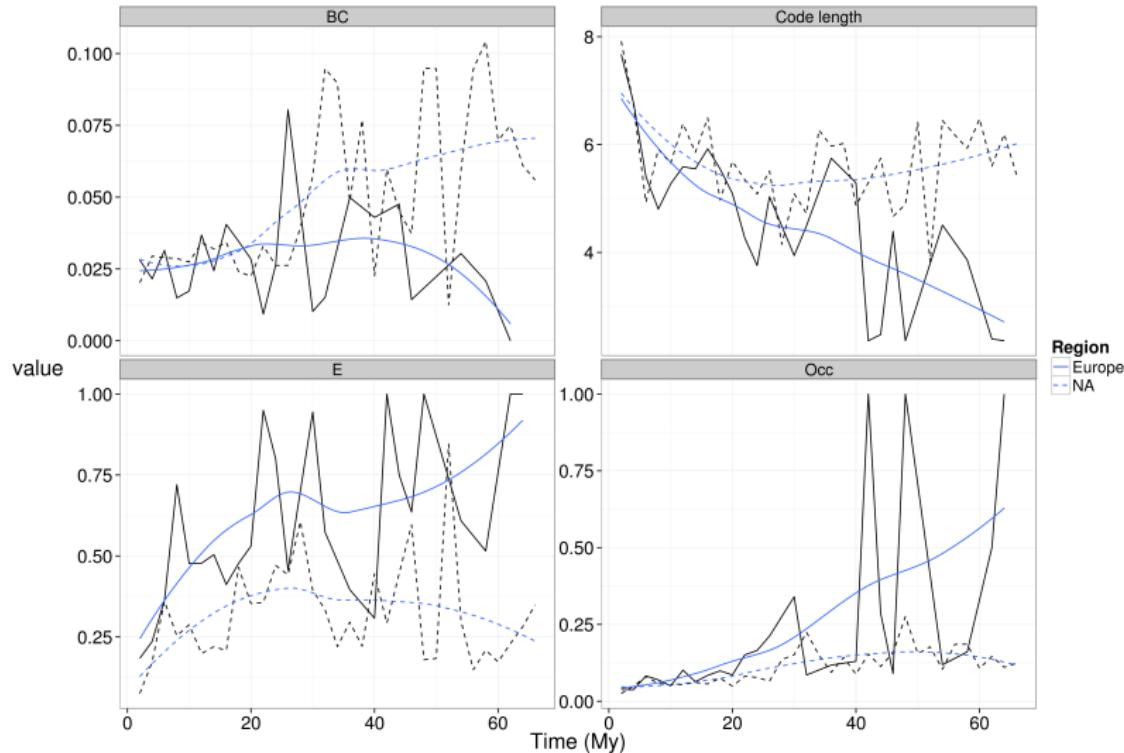
- ▶ herbivore
  - ▶ most like all taxa
- ▶ carnivore
  - ▶ constant √ corr w/ herbivores
- ▶ omnivore
  - ▶ constant √ random

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

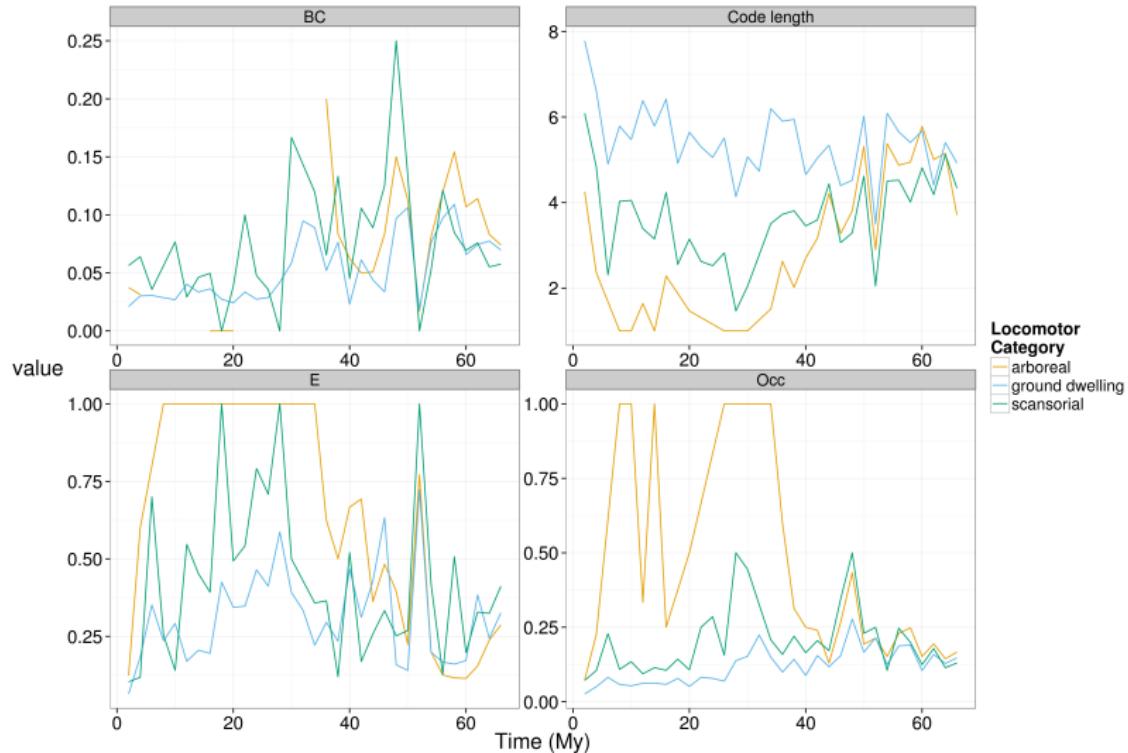
# Regional variation

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

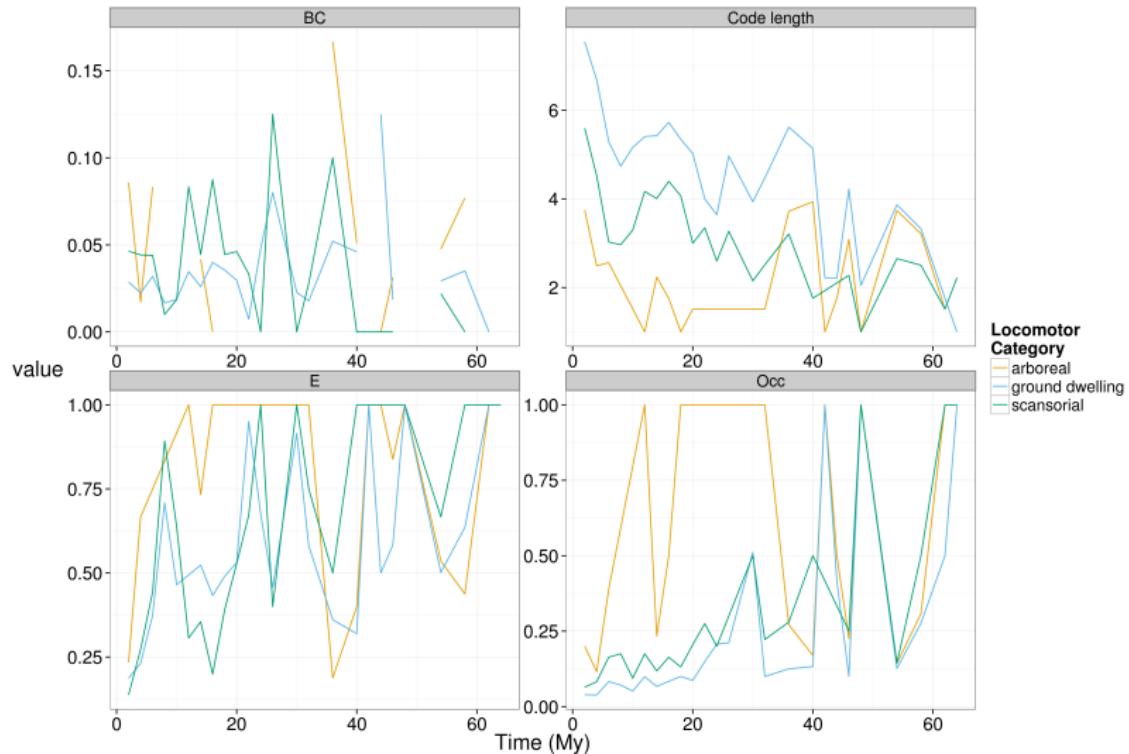
# Preliminary results: NA, Eur



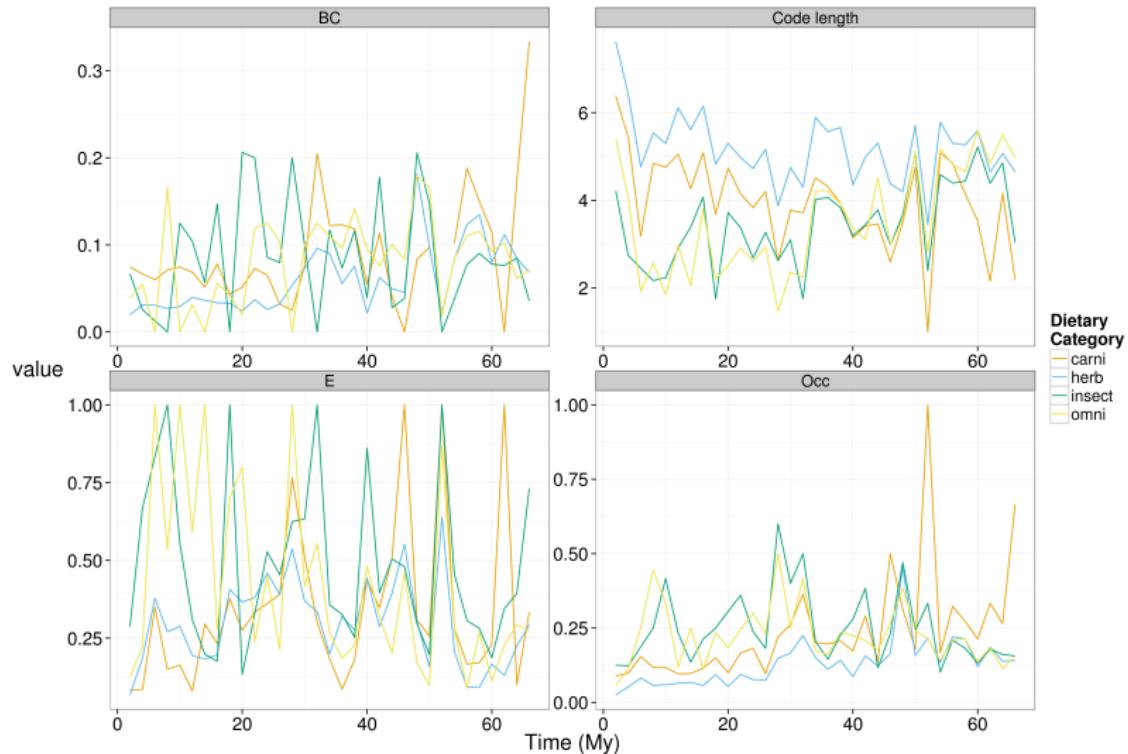
# Preliminary results: locomotor category NA



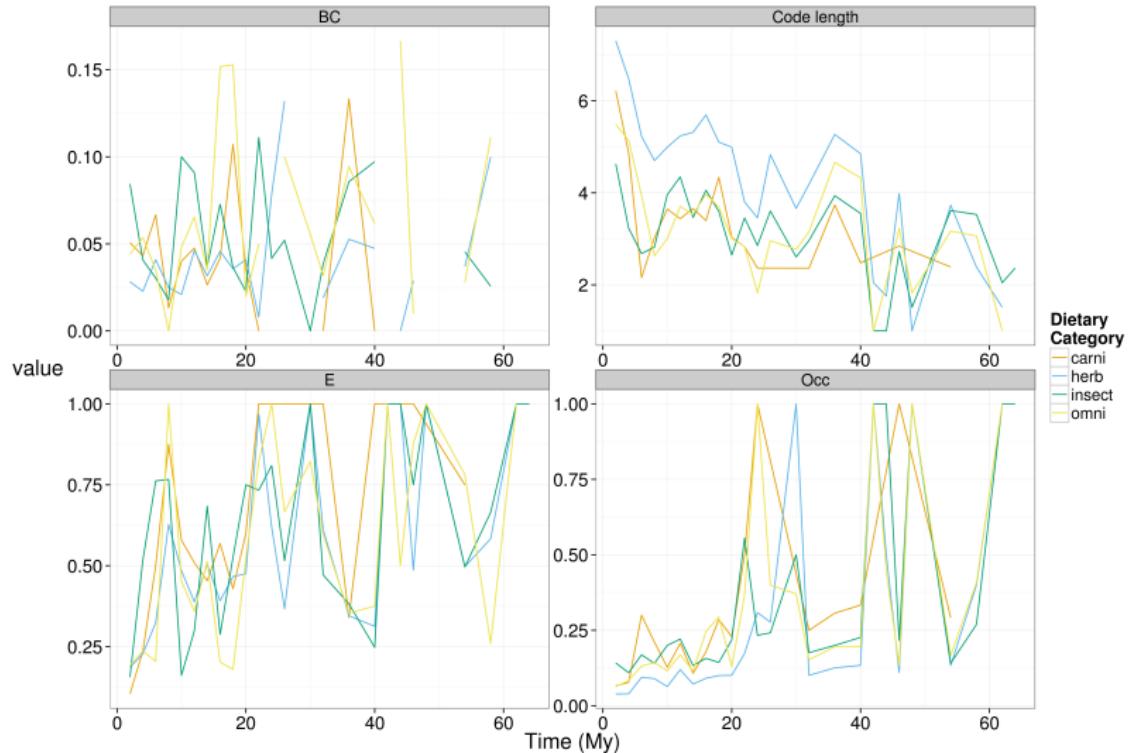
# preliminary results: locomotor category Eur



# Preliminary results: dietary category NA



# Preliminary results: dietary category Eur



# Questions

## Questions

- ▶ Why do certain taxa go extinct while others do not?
  - ▶ Is extinction rate taxon–age independent?
- ▶ How is emergence “formed?” When should it be invoked?
- ▶ When should global, regional, or local processes expected to dominate?

# Summary of proposed research

## Studies

- ▶ Permian brachiopod trait based survival
- ▶ Cenozoic mammal trait based survival
- ▶ Cenozoic mammal community connectedness

# Acknowledgements

## ► Committee

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

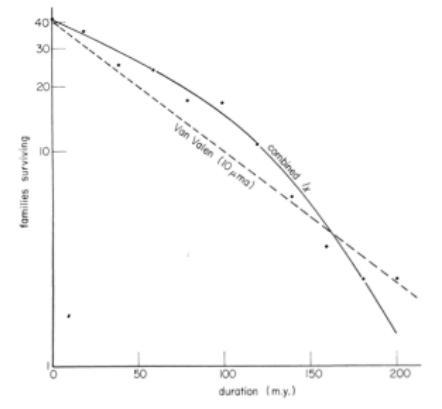
## ► Discussion

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

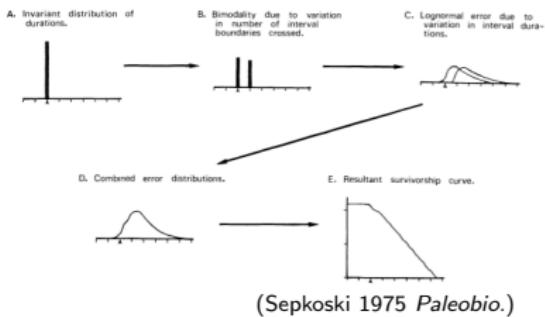


## Further concerns

# Theseus' ship: biases to analyzing survival



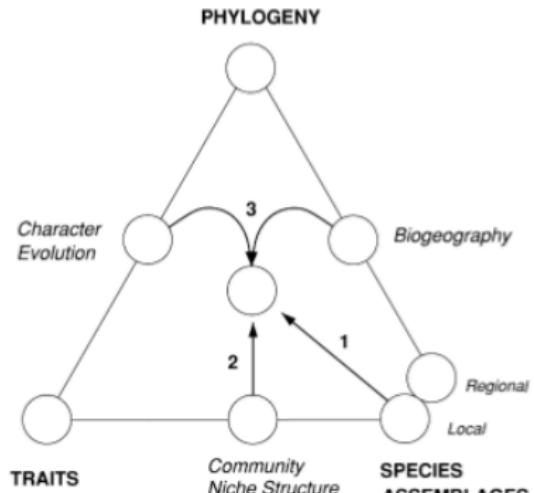
(Raup 1975 *Paleobio.*)



(Sepkoski 1975 *Paleobio.*)

- ▶ bias away from  $h(t) = \lambda$ ?
  - ▶ censoring
  - ▶ sampling/stratigraphy
  - ▶ species vs genus
  - ▶ anagenesis/cryptic speciation
- ▶ use time-homogeneous birth-death model
  - ▶ constant  $p, b$
  - ▶ expected  $S(t) = \exp^{-\lambda t}$
  - ▶ vary anagenesis/sampling

# Phylogenetic similarity of communities



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

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