Evolutionary paleoecology and the biology of extinction

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Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

Framework

Questions

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

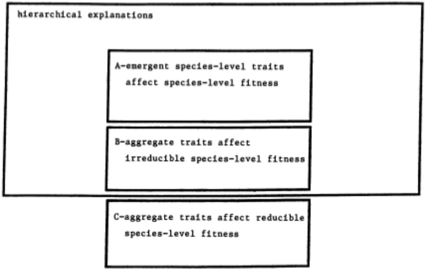
Evolutionary paleoecology

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

(Kitchell 1985 Paleobiology)

environmental interactions	$\rightarrow$	speciation extinction

Emergent properties

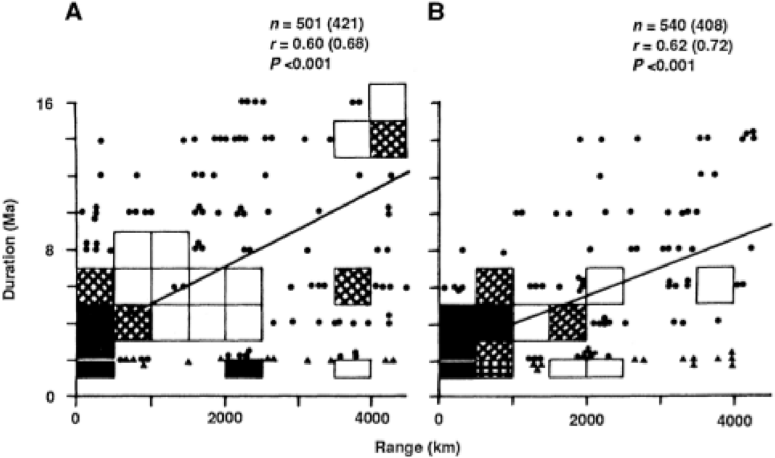


(Grantham 1995 *Ann. Rev. Ecol. Syst.*)

Criteria

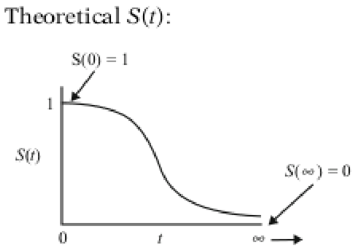
Cannot be reduced to lower level (e.g. organismal)

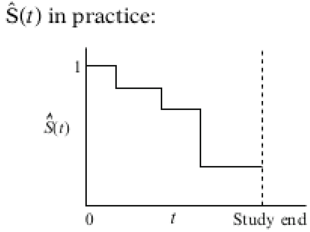
Range size



(Jablonski 1987 *Science*)

Probability of survival





(Kleinbaum and Klein 2012)

Survival function

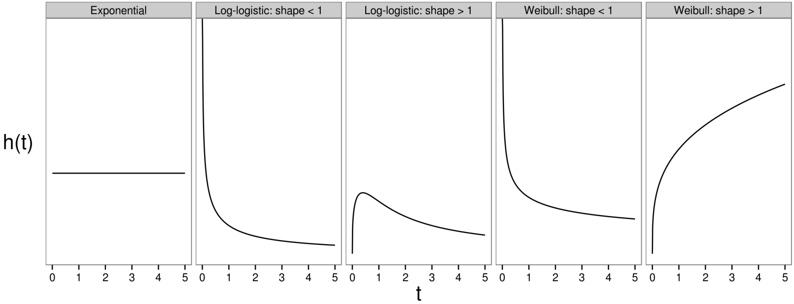
$$S(t) = P(T > t)$$

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

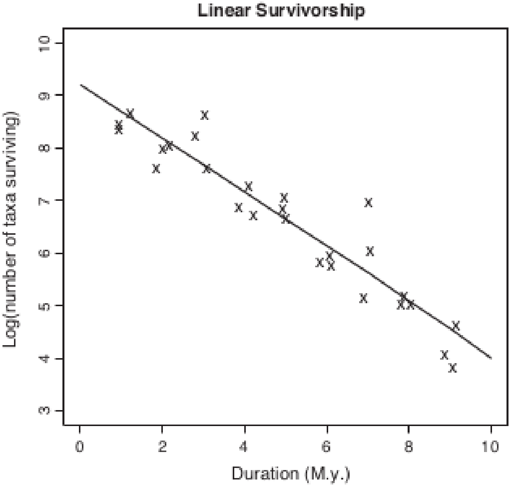
Instantaneous potential of failure (extinction)

Hazard function $\equiv$ conditional failure rate

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



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

Chapters

- 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

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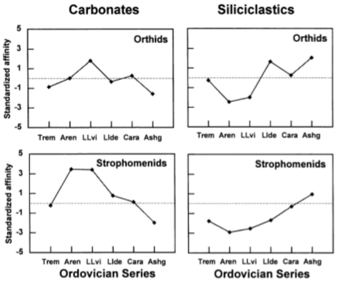
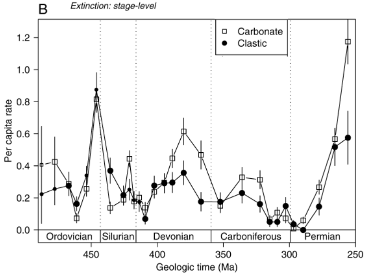
Substrate affinity



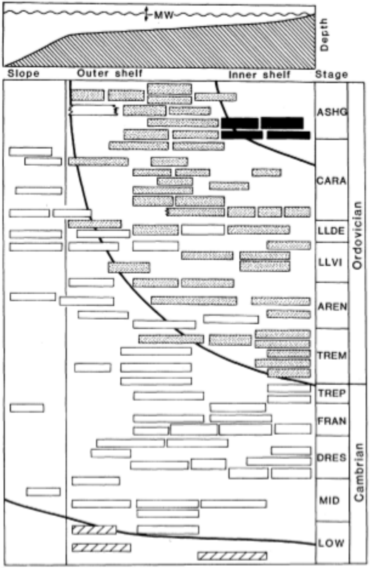
(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

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

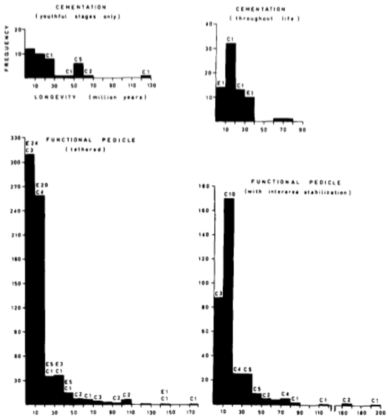
Habitat preference



(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 $\rightarrow$ offshore

Affixing strategy



(Alexander 1977 *Paleo*[3])

- 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

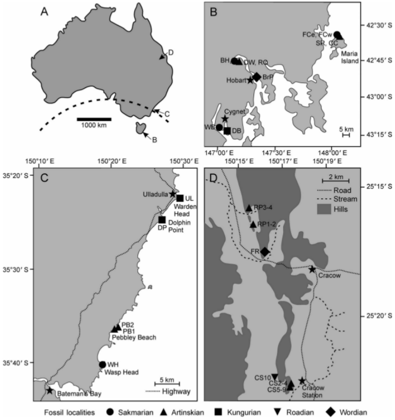
$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

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

- 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



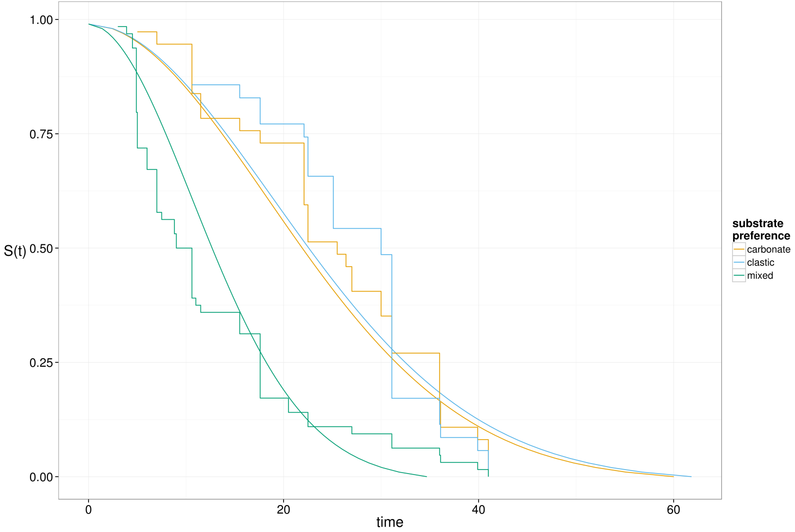
(Clapham and James 2008 *Palaios*)

- 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*[3]
- time-dependent climate
- survival distributions: $\exp(\lambda)$, $Weibull(\lambda, k)$, *etc.*

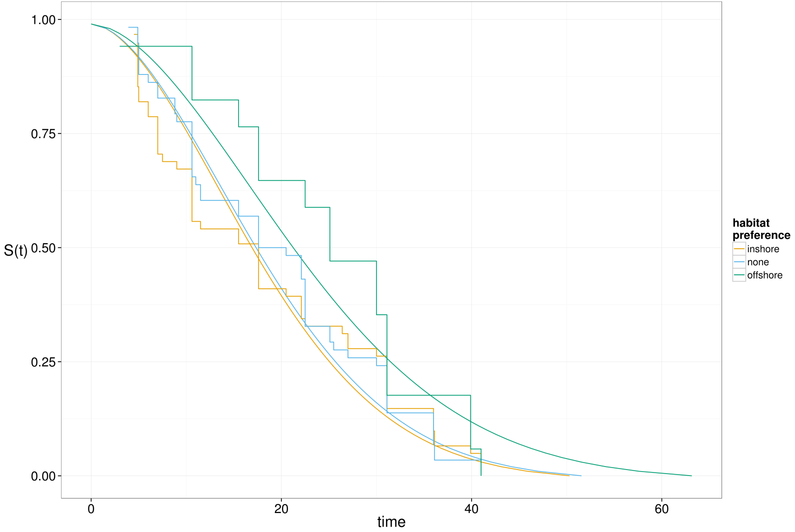
Preliminary results: model comparison

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



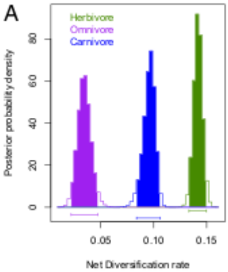
Theory

Brachiopod survival

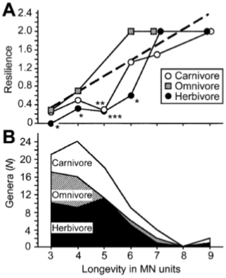
Mammal survival

Mammal community connectedness

Dietary category



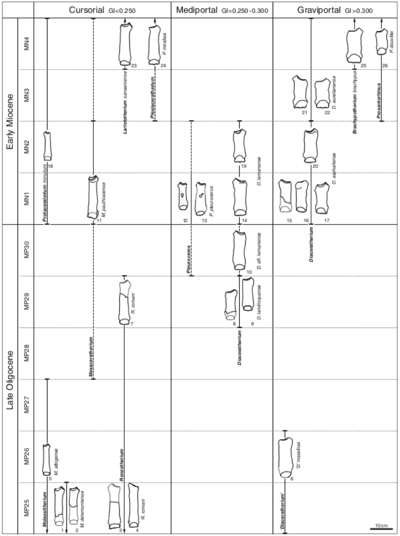
(Price *et al.* 2012 *PNAS*)



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

- trophic hierarchy (stability $\rightarrow$ duration)
  - herb: most stable, longest duration
  - carni: least stable, shortest duration
  - omni: avg. stability, avg. duration
- $\uparrow$ diversification
  - $\uparrow$ origination; $\simeq$ extinction
  - $\simeq$ origination; $\downarrow$ extinction

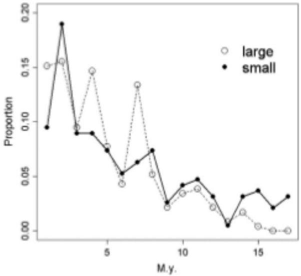
Locomotor category



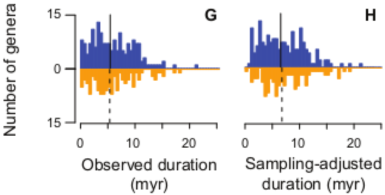
(Scherler *et al.* 2013 *Swiss. J. Geosci.*)

- Paleogene $\rightarrow$ Neogene
  - open $\rightarrow$ closed environment
- predictions
  - arboreal: Paleogene $>$ Neogene
  - ground dwelling: Paleogene $<$ Neogene
  - scansorial: Paleogene $\approx$ Neogene

Body size



(Liow *et al.* 2008 *PNAS*)



(Tomiya 2013 *Am. Nat.*)

- $\uparrow$ body size, $\uparrow$ energy req, $\uparrow$ range size, $\downarrow$ extinction
- Europe
  - lrg body size genera: $\uparrow$ 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 δO^{18} isotope (Zachos *et al.* 2008 *Nature*)
- Paleogene versus Neogene
- survival distributions: $\exp(\lambda)$, $Weibull(\lambda, k)$, *etc.*

Theory

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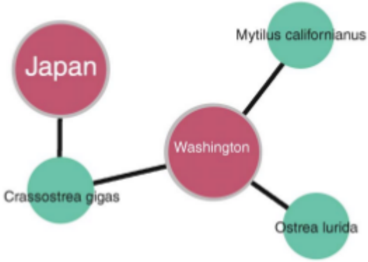
Mammal community connectedness

Community connectedness

Definition

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

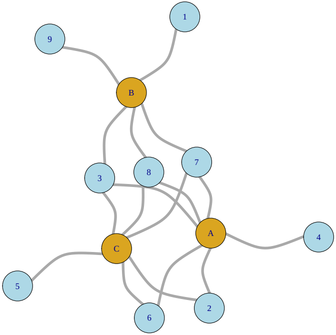
Biogeographic networks



(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

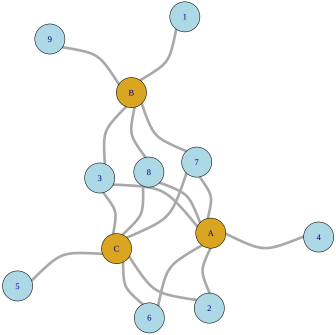


$$u = \{1, 2, 1\}$$
$$n = \{6, 5, 6\}$$
$$L = 3$$
$$E \approx 0.24$$

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

- 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

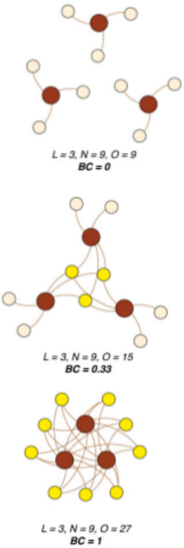


$$Occ = \frac{\sum_{i=1}^{N} \frac{l_i}{L}}{N}$$

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

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

Biogeographic connectedness

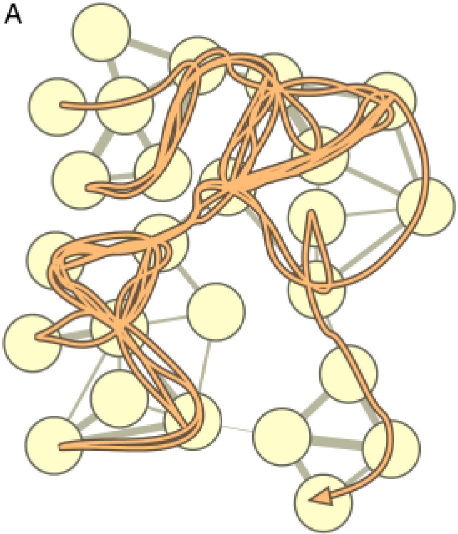


(Sidor et al. 2013 *PNAS*)

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

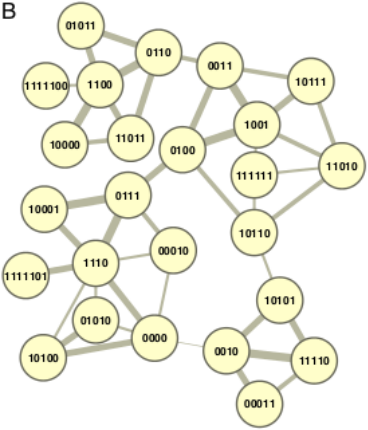
- O: number of occurrences
- N: total number of taxa
- L: number of localities
- $0 \leq BC \leq 1$

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Code length



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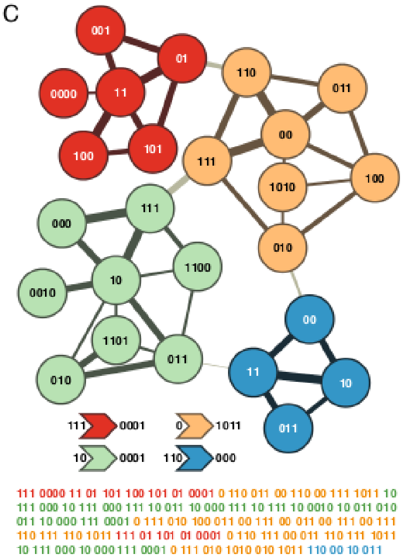
00011

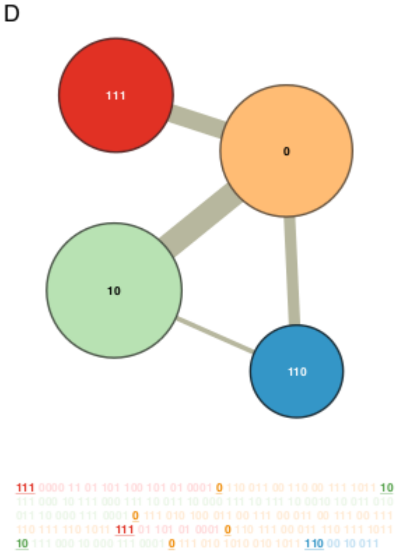
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

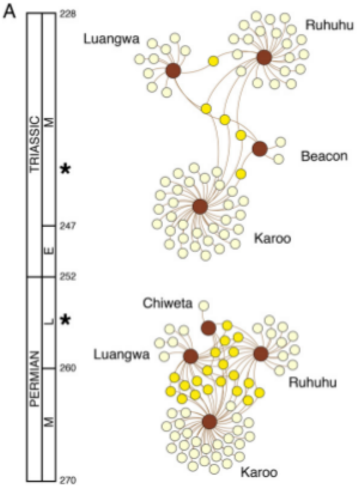
Compressing a network

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
- $L(\mathbf{M})$: code length of network
- $q_{\curvearrowright}$: P(random walk switches modules)
- $H(\mathcal{Q})$: entropy module codewords
- $H(\mathcal{P}^{i})$: entropy within–module
- $p_{\circlearrowright}^{i}$: rate of within–module use

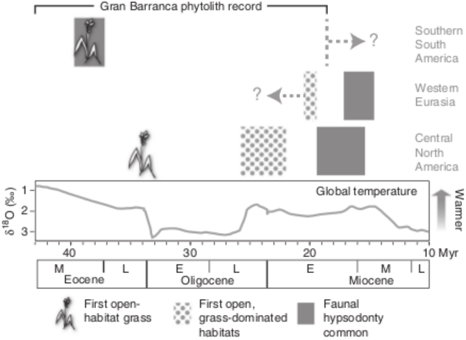
Global versus regional versus local scale



(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

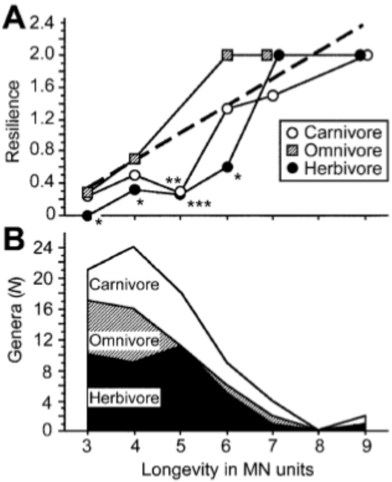
Global expectations: locomotor category



(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 $\vee$ random

Global expectations: dietary category



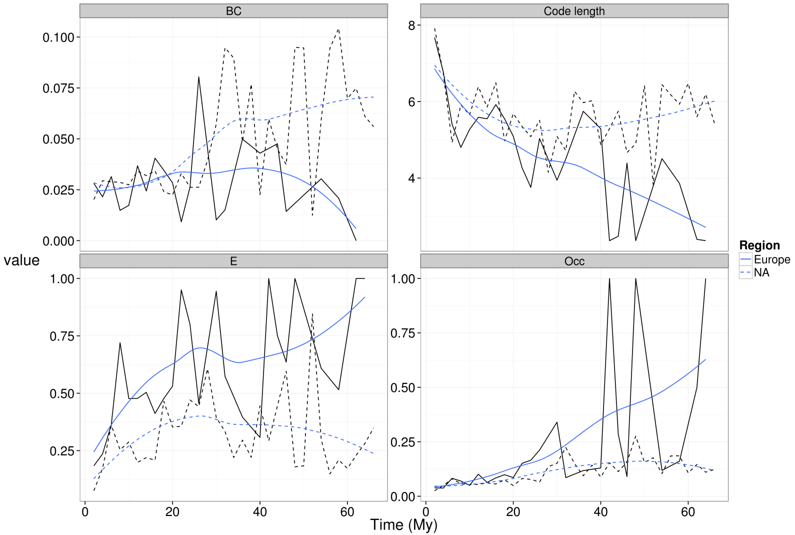
(Jernvall and Fortelius 2004 *Am. Nat.*)

- herbivore
  - most like all taxa
- carnivore
  - constant $\vee$ corr w/ herbivores
- omnivore
  - constant $\vee$ random

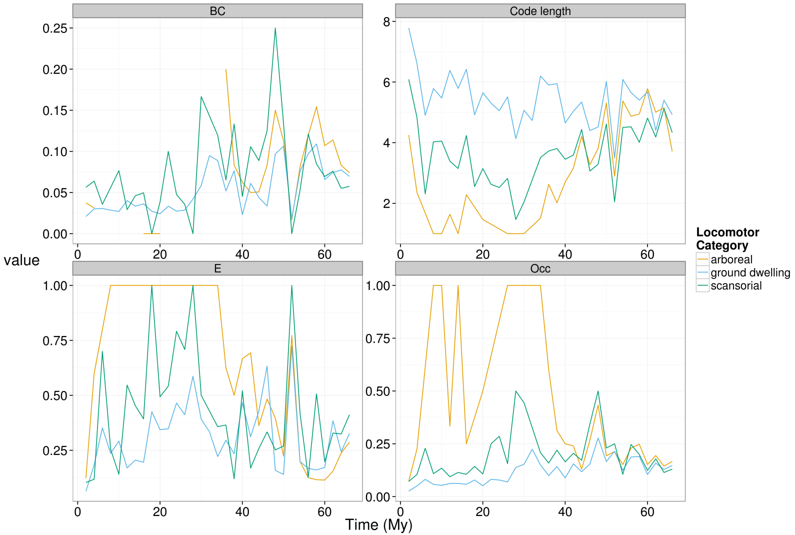
Regional variation

- North America
  - similar to global predictions
  - major lit. questions re. effects climate change
- Europe
  - stable trophic diversity
  - abundant herbivores drive patterns
- South America
  - high provincialism
  - early expansion of ground dwelling taxa

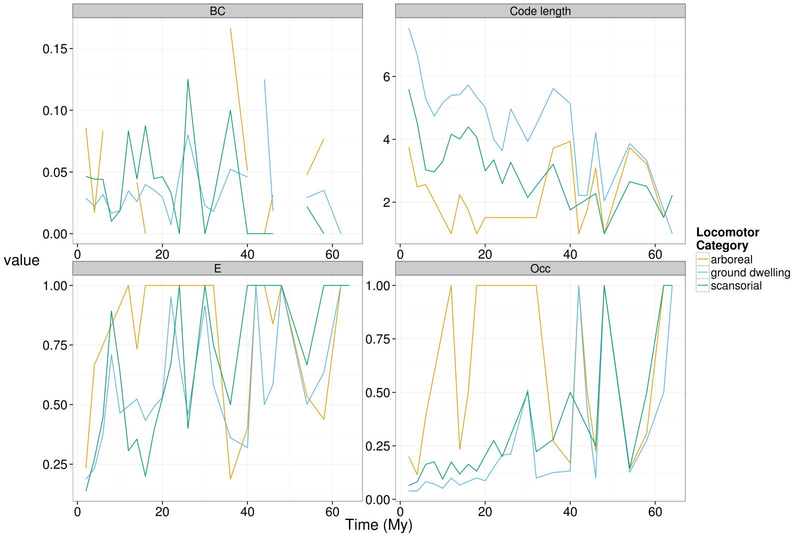
Preliminary results: NA, Eur



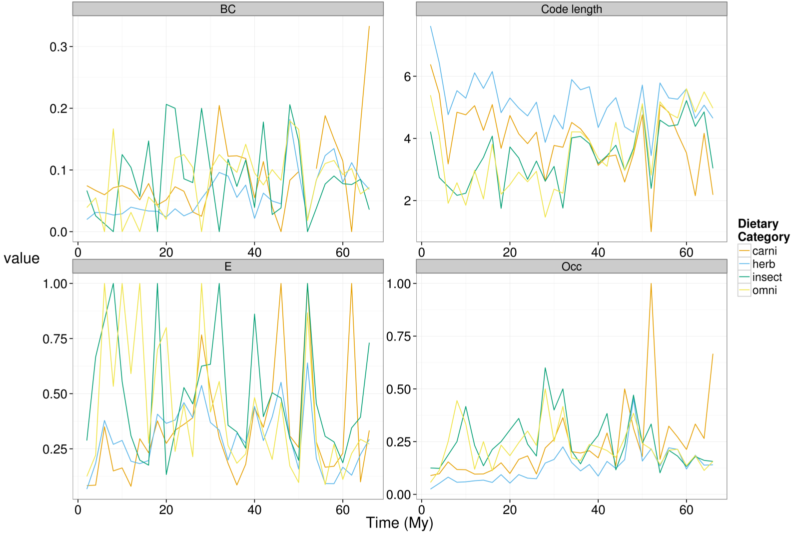
Preliminary results: locomotor category NA



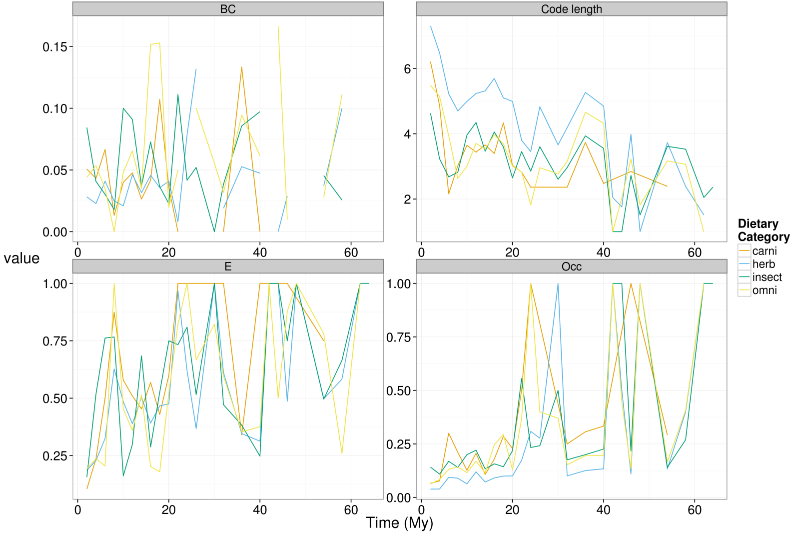
preliminary results: locomotor category Eur



Preliminary results: dietary category NA



Preliminary results: dietary category Eur



Questions

Questions

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

Summary of proposed research

Studies

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

Acknowledgements

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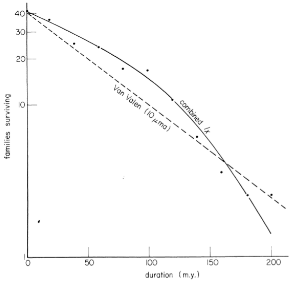
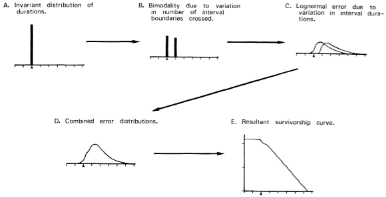
  - Kenneth D. Angielczyk (co-advisor)
  - Michael J. Foote (co-advisor)
  - P. David Polly
  - Richard H. Ree
- Discussion
  - David Bapst, Megan Boatright, Ben Frable, Colin Kyle, Darcy Ross, Liz Sander
  - John Alroy, Graeme Lloyd, Carl Simpson, Graham Slater

Further concerns

Theseus' ship: biases to analyzing survival



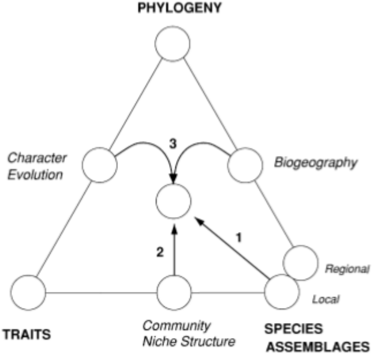
(Raup 1975 *Paleobio.*)



(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

Phylogeneic 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*)