Evolutionary paleoecology and the biology of extinction

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Theory

Brachiopod survival

Mammal survival

Mammal community connectedness

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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?

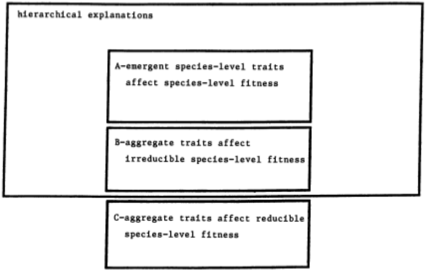
Evolutionary paleoecology

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

(Kitchell 1985 Paleobiology)

adaptive zone $\rightarrow$ speciation
extinction

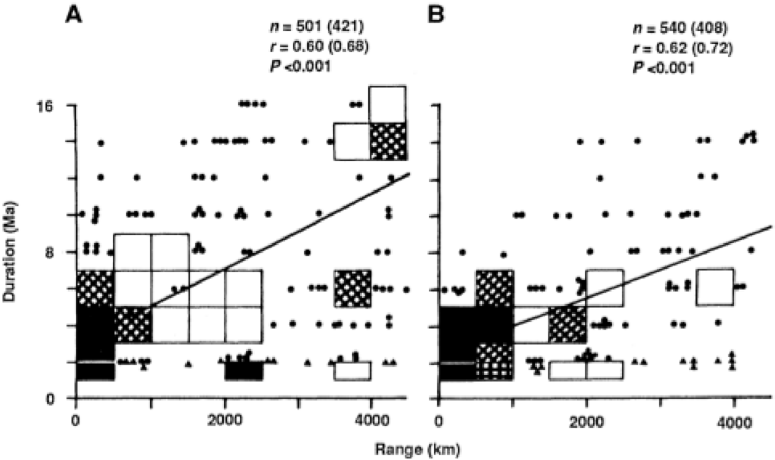
Emergent properties



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

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

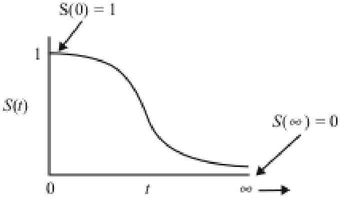
Range size



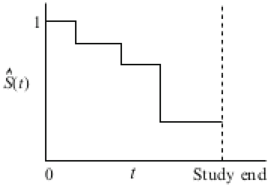
(Jablonski 1987 *Science*)

Probability of survival

Theoretical $S(t)$:



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



(Kleinbaum and Klein 2012)

Survival function

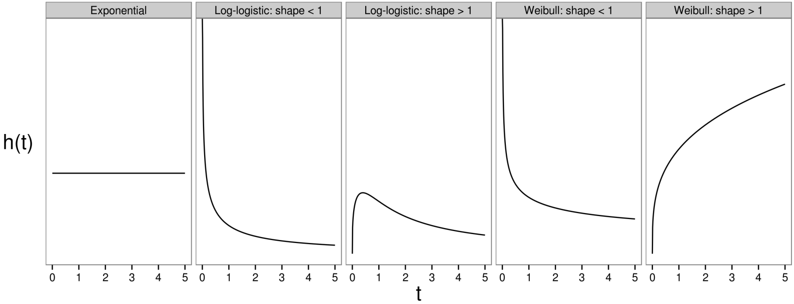
$$S(t) = P(T > t)$$

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

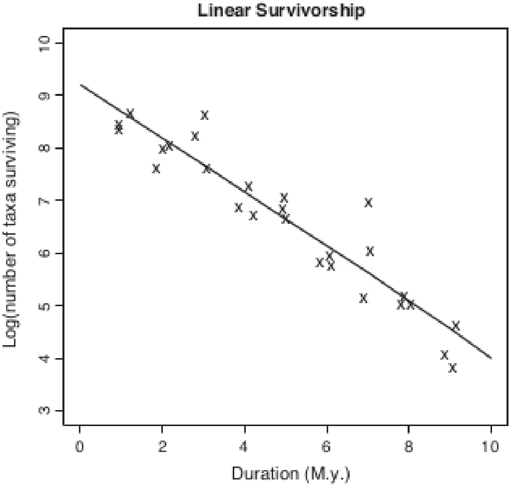
Instantaneous potential of failure (extinction)

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

- 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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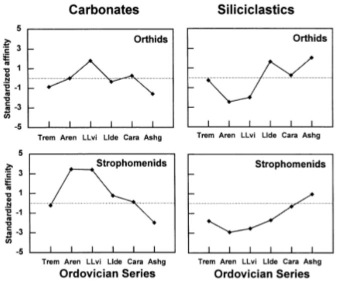
Brachiopods, environmental preference, and extinction

Questions

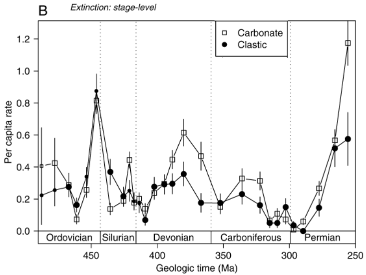
- Are traits related to environmental preference correlated with survival?
- Which trait(s) best model extinction? One or more?
- Is global climate change important to extinction?

Australasian, Permian brachiopods

Substrate affinity



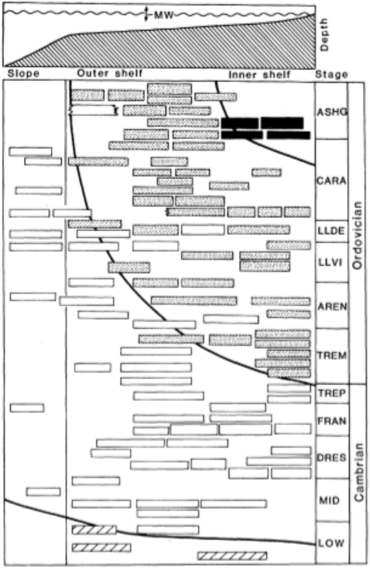
(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

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

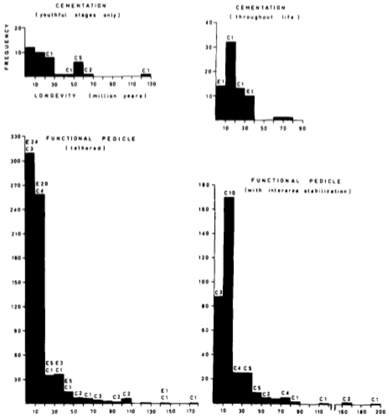
Habitat preference



(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 → 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

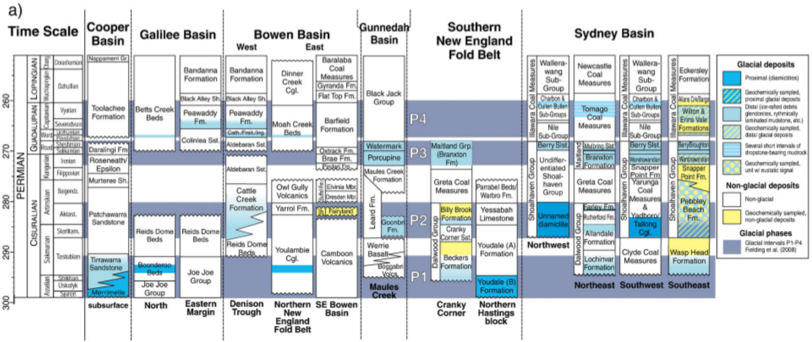
$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

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

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

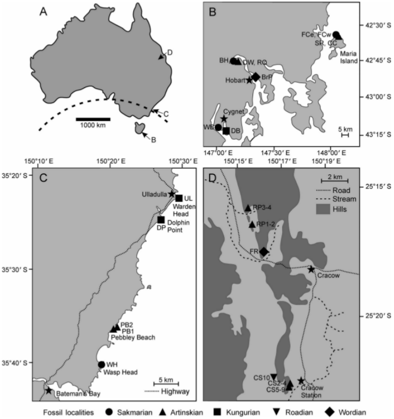
(Simpson and Harnik 2009 *Paleobiology*)

Permian climate



(Birgenheier *et al.* 2010 *Paleo*^{3})

Analysis



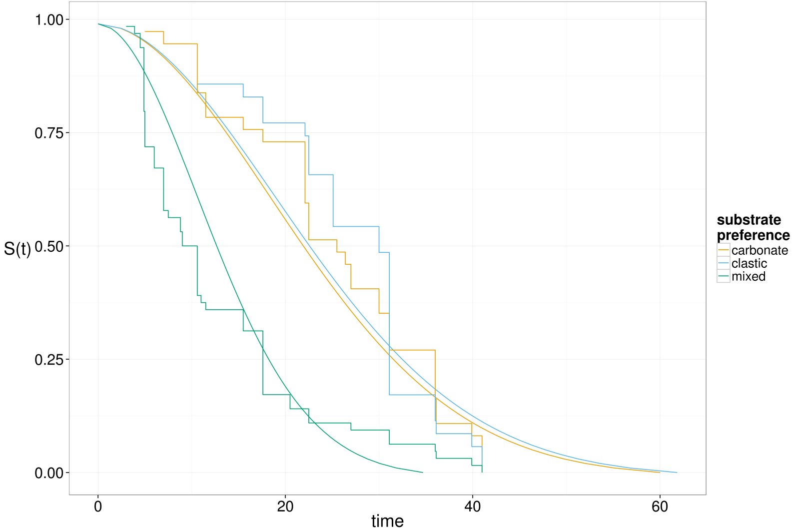
(Clapham and James 2008 *Palaios*)

- 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*(λ, k), *etc.*

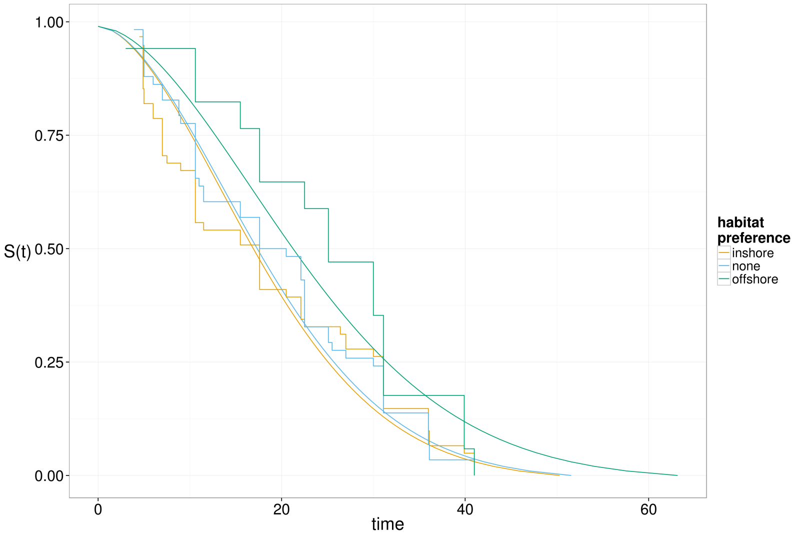
Preliminary results: model comparison

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

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Mammal survival

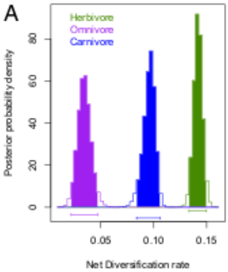
Mammal community connectedness

Ecology and survival in Cenozoic mammals

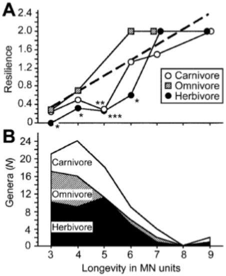
Questions

- How do traits related to range size relate to survival?
- Which trait(s) best model survival? One or more?
- Is climatic change important for modeling survival?

Dietary category



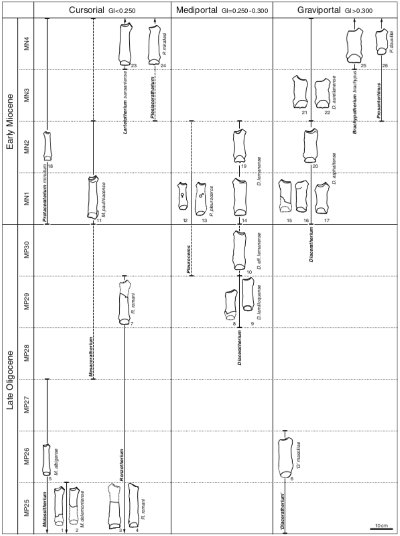
(Price *et al.* 2012 *PNAS*)



(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

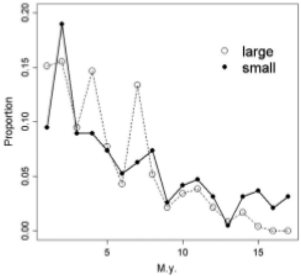
Locomotor category



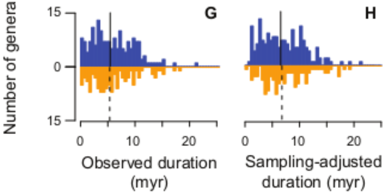
(Scherler *et al.* 2013 *Swiss. J. Geosci.*)

- 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
- **or** $\uparrow$ body size, $\uparrow$ 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: $\exp(\lambda)$, $\mathit{Weibull}(\lambda, k)$, *etc.*

Theory

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Mammal survival

Mammal community connectedness

Community connectedness in Cenozoic mammals

Questions

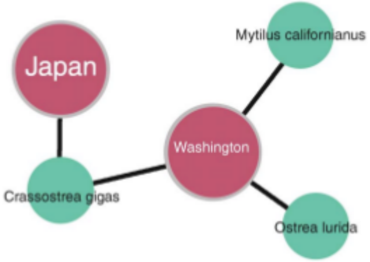
- How does the ratio between endemic and cosmopolitan taxa change over time?
- Is there a single global pattern or does each regions have a different patterns?
- Do these patterns differ between ecological categories?
- Is global climate change an important predictor of these patterns?

Community connectedness

Definition

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

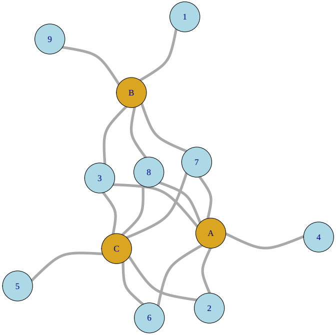
Biogeographic networks



(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

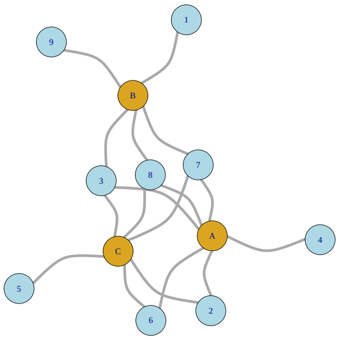


$$u = \{1, 2, 1\}$$
$$n = \{6, 5, 6\}$$
$$L = 3$$
$$E \approx 0.24$$

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

- 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

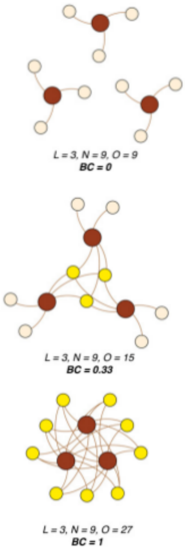


$$Occ = \frac{\sum_{i=1}^{N} \frac{l_i}{L}}{N}$$

- 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

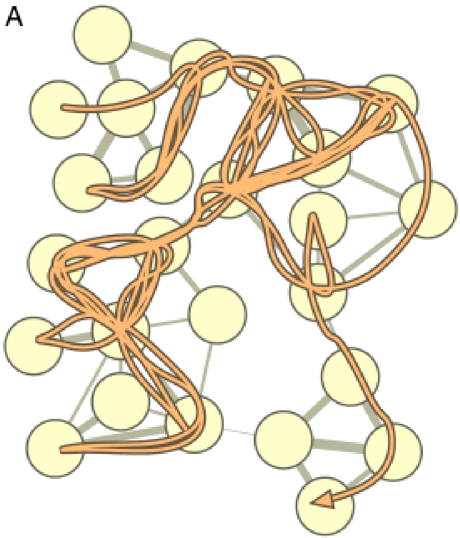


(Sidor et al. 2013 *PNAS*)

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

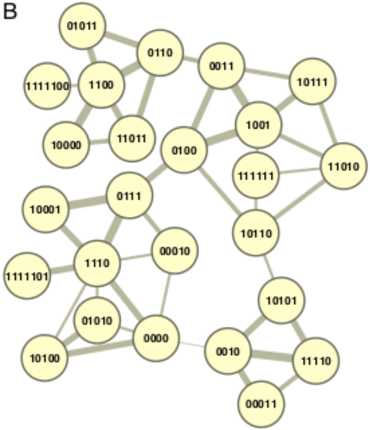
- O: number of occurrences
- N: total number of taxa
- L: number of localities
- $0 \leq BC \leq 1$

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Code length



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1001 0100 0111 10001 1110 0111 10001 0111 1110 0000 1110 10001
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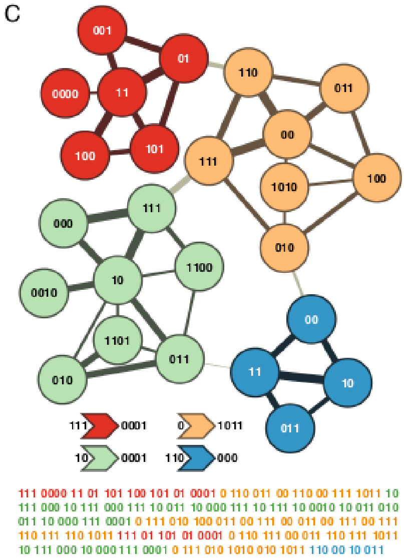
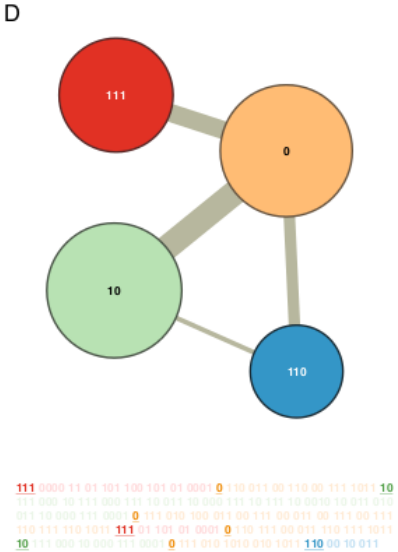
(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

Compressing a network

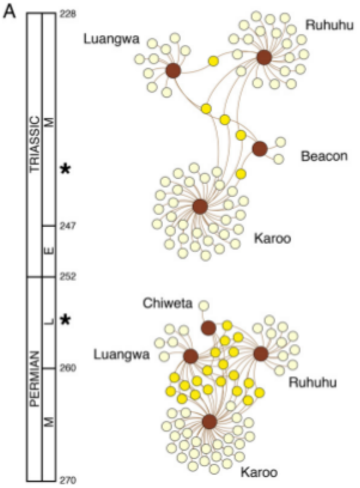
Map equation

(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
- $L(\mathbf{M})$: 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

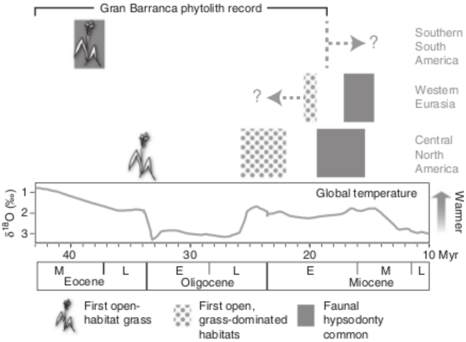
Global versus regional versus local scale



(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

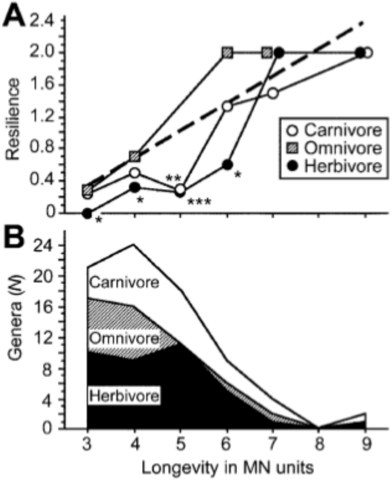
Global expectations: locomotor category



(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



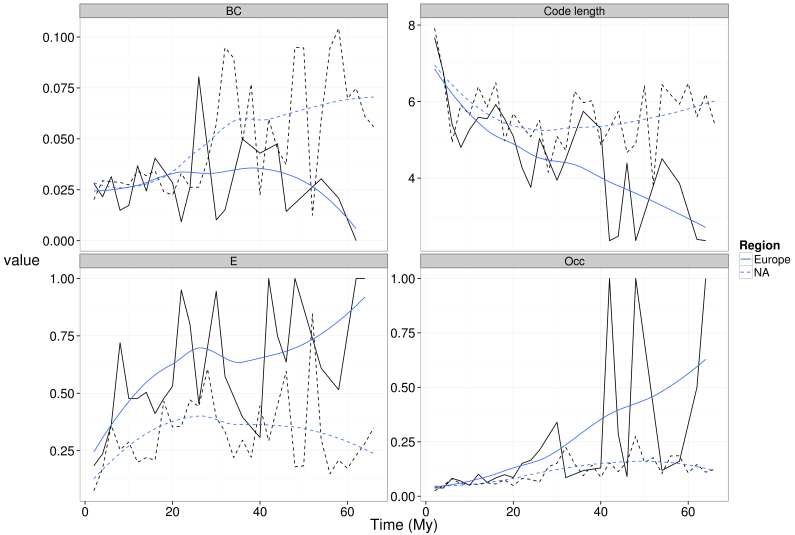
(Jernvall and Fortelius 2004 *Am. Nat.*)

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

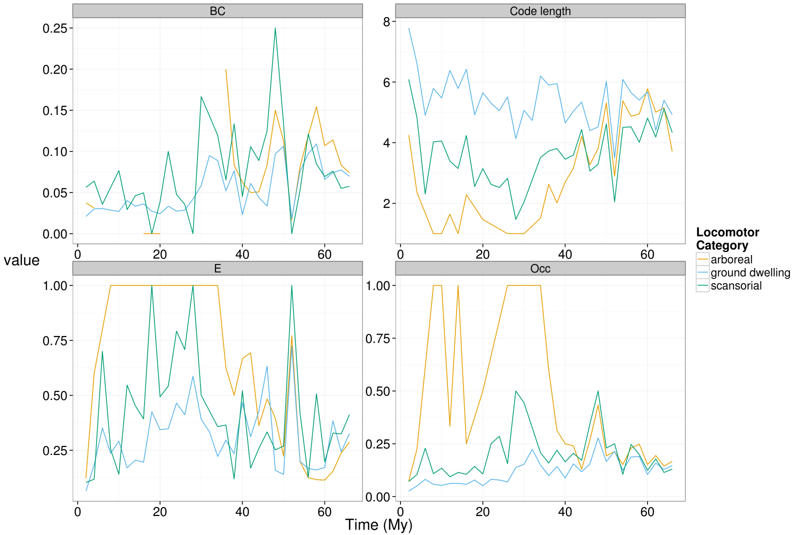
Regional variation

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

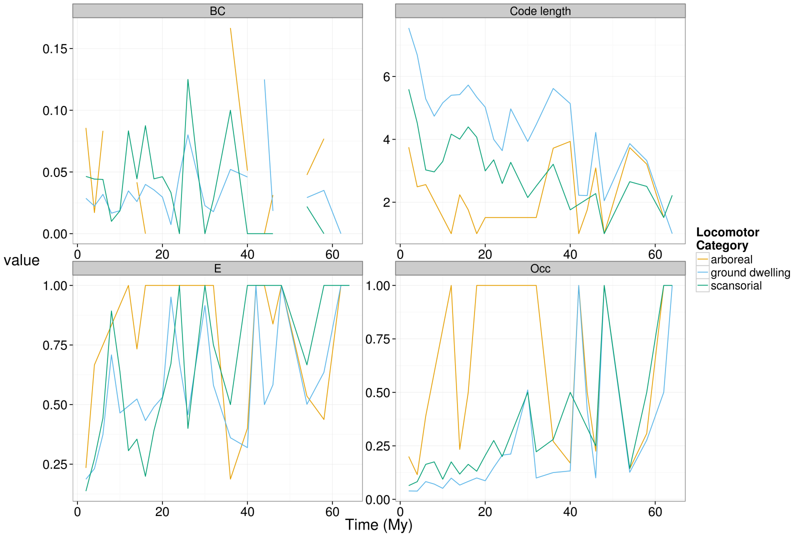
Preliminary results: NA, Eur



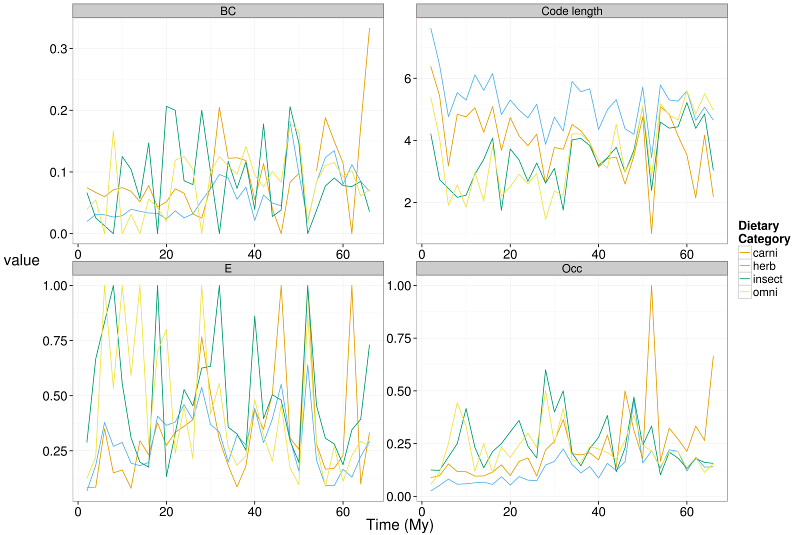
Preliminary results: locomotor category NA



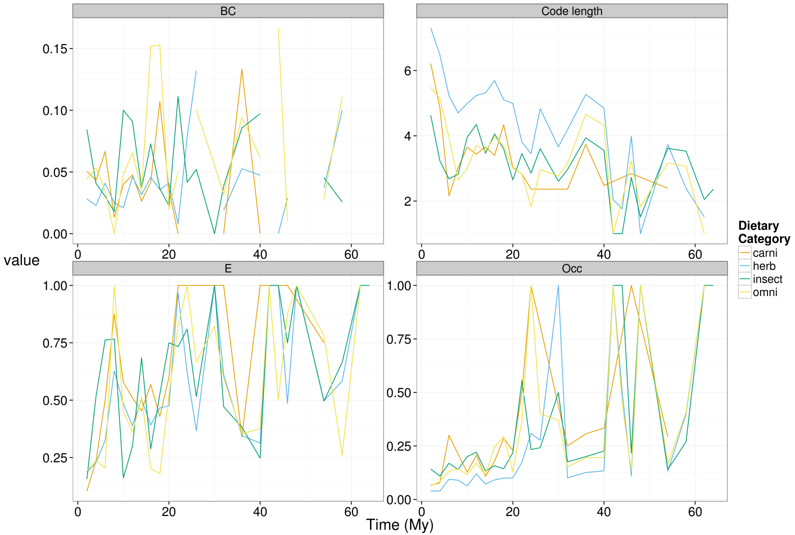
preliminary results: locomotor category Eur



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

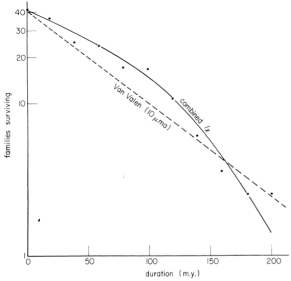
- Permian brachiopod trait based survival
- Cenozoic mammal trait based survival
- Cenozoic mammal community connectedness

Acknowledgements

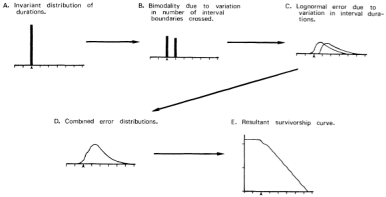
- **Committee**
  - Kenneth D. Angielczyk (co-advisor)
  - Michael J. Foote (co-advisor)
  - P. David Polly
  - Richard H. Ree
- Discussion
  - David Bapst, Megan Boatright, Ben Frable, Colin Kyle, Darcy Ross, Liz Sander
  - John Alroy, Graeme Lloyd, Carl Simpson, Graham Slater

Further concerns

Theseus' ship: simulations and survival



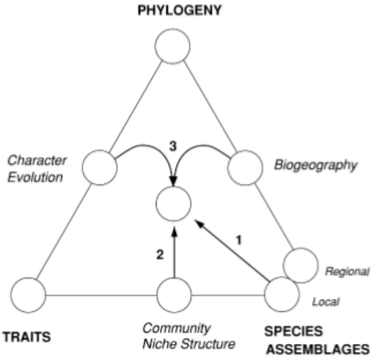
(Raup 1975 *Paleobio.*)



(Sepkoski 1975 *Paleobio.*)

- heterogeneous preservation
  - $P(\phi|A) \neq P(\phi|B)$
- cryptic speciation/anagenesis
  - longer duration than expected
  - proxy generic level?
- time-homogeneous birth-death model
  - constant p, b
  - expected $S(t) = \exp^{-\lambda t}$

Phylogeneic similarity of communities



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

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