Evolutionary paleoecology and the biology of extinction

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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?

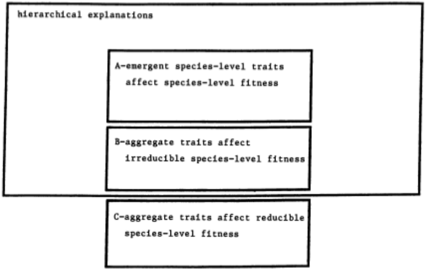
Evolutionary paleoecology

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

(Kitchell 1985 Paleobiology)

environmental interactions $\rightarrow$ macroevolution

Emergent properties



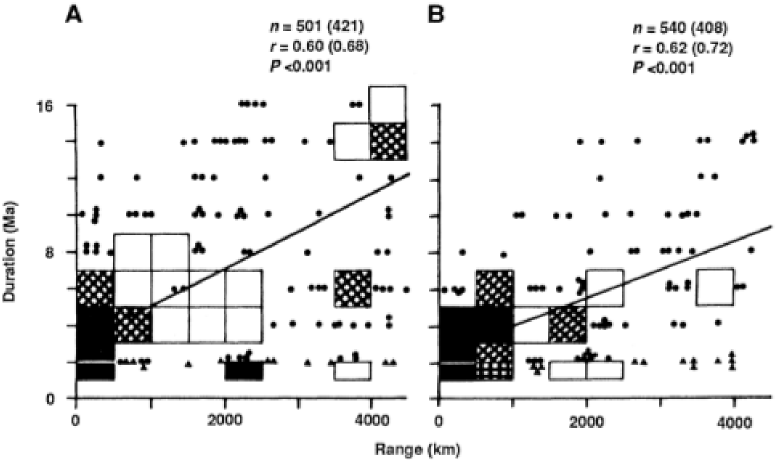
(Grantham 1995 *Ann. Rev. Ecol. Syst.*)

Species level

Trait that cannot be reduced to organismal level

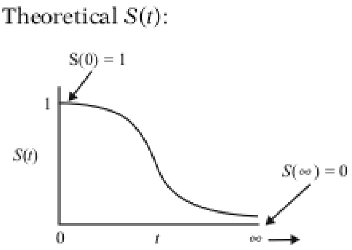
Product of one or more traits/factors

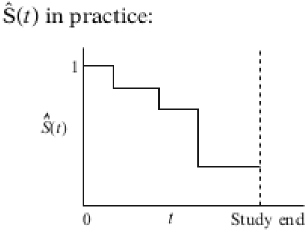
Range size



(Jablonski 1987 *Science*)

Probability of survival





(Kleinbaum and Klein 2012)

Survival function

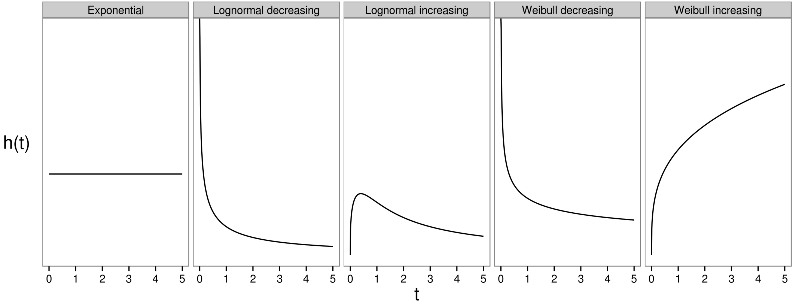
$$S(t) = P(T > t)$$

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

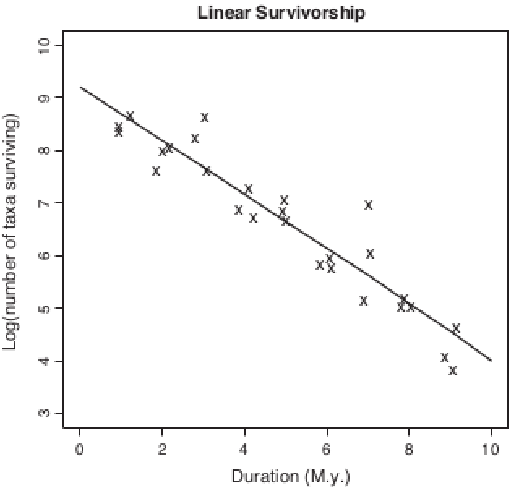
Instantaneous potential of failure (extinction)

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 of survival



(Liow et al. 2011 *TREE*)

Law of Constant Extinction

Definition

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

(Van Valen 1973 *Evol. Theory*)

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

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

Brachiopods and mammals: a comparison

brachiopods

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

mammals

- terrestrial
- motile
- Cenozoic ($\sim$ 65 My)
- North America, Europe, South America
- global cooling

Series of related questions

- generic level survival in brachiopods
  - ecological traits re. environmental pref. (emergence)
  - survival distribution
- specific level survival in mammals
  - ecological traits re. range size (emergence)
  - generic versus specific survival
  - anagenesis/species:genus simulation
  - survival distribution
- community connectedness in mammals
  - global versus regional versus local scale processes
  - ecological traits (trophic/locomotion)

Introduction and theory

Brachiopods, environmental preference, and extinction

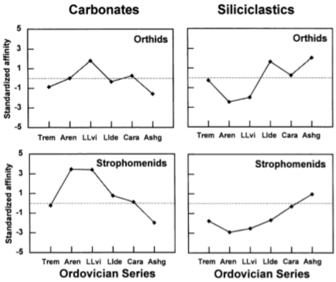
Ecology and survival in Cenozoic mammals

Community connectedness in Cenozoic mammals

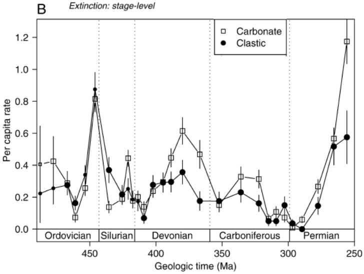
Traits relating to environment and range size

- substrate affinity
  - physical, chemical
  - availability
- habitat preference
  - energetics
  - availability
- affixing strategy
  - energetics
  - optimality

Substrate affinity



(Miller and Connoly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

- carbonates, clastics, mixed
- lithology/deposition environment
- Pharenozoic decrease in carbonates:clastics

Habitat preference

- on-shore, off-shore, none
- sea-level and energetics
- Pharenozoic decrease in on-shore:off-shore

Affixing strategy

- pedunculate, reclining, cementing
- pedunculate:on-shore, reclining:off-shore
- environmental energetics

Assigning substrate and habitat

Probability of assignment

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

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

- n: total # of occ
- k: # (e.g.) carbonate occ

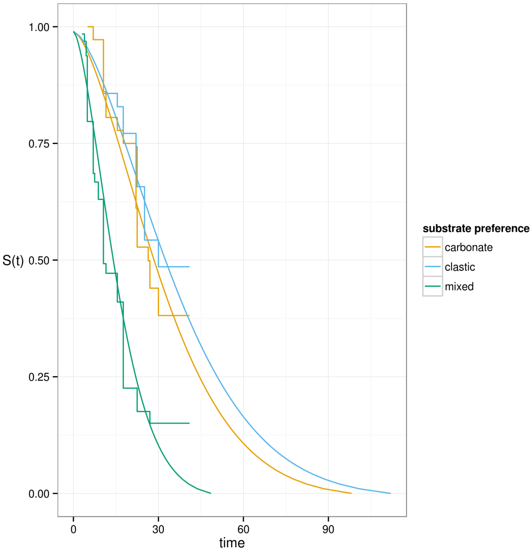
(Simpson and Harnik 2009 *Paleobiology*)

Models

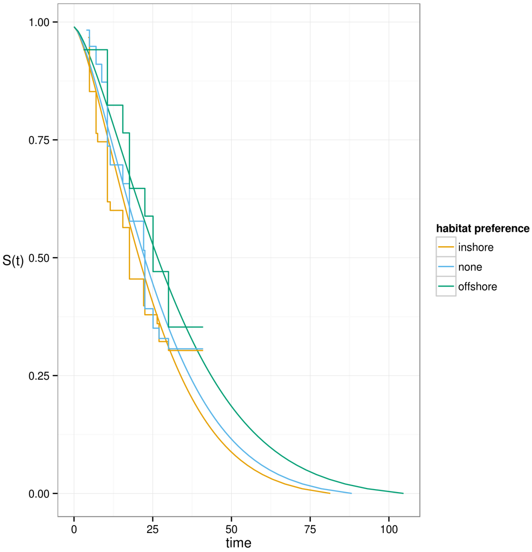
Preliminary results: model comparison

formula	distribution	shape	df	logLik	AICc
˜ aff	weibull	1.91	4	-497.5745	1003.4543
˜ aff + hab	weibull	1.92	6	-496.8553	1006.3618
˜ aff * hab	weibull	1.94	10	-495.7702	1013.3003
˜ aff:hab	weibull	1.94	11	-495.7702	1015.6693
˜ 1	weibull	1.76	2	-515.1666	1034.4234
˜ hab	weibull	1.76	4	-513.9591	1036.2236
˜ aff	exponential		3	-532.8690	1071.9199
˜ aff + hab	exponential		5	-532.5798	1075.6211
˜ 1	exponential		1	-540.9218	1083.8734
˜ aff * hab	exponential		9	-532.3099	1084.0485
˜ aff:hab	exponential		10	-532.3099	1086.3799
˜ hab	exponential		3	-540.2811	1086.7439

Preliminary results: best substrate



Preliminary results: best habitat



Introduction and theory

Brachiopods, environmental preference, and extinction

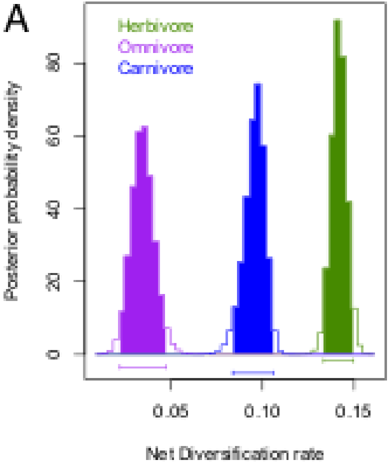
Ecology and survival in Cenozoic mammals

Community connectedness in Cenozoic mammals

Ecological traits

- dietary category
  - energetics
  - availability
- locomotor category
  - availability
  - dispersal
- body size
  - energetics
  - home range size

Predictions: dietary category



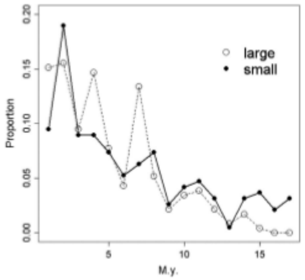
(Price *et al.* 2012 *PNAS*)

- 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

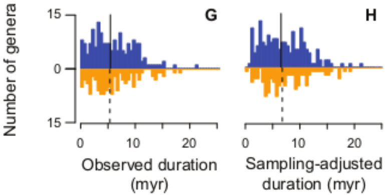
Predictions: locomotor category

- Paleogene $\rightarrow$ Neogene
  - open $\rightarrow$ closed environment

Predictions: 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

Methodology

Biases to survival: a simulation study

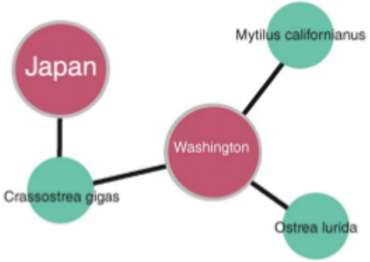
- bias away from $h(t) = \lambda$
  - species:genus
  - anagenesis/cryptic speciation
- time-homogeneous birth-death model
  - common phylogenetic model
  - constant p, b
  - expected $S(t) = \exp^{-\lambda t}$
  - vary (cryptic) anagenesis

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

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

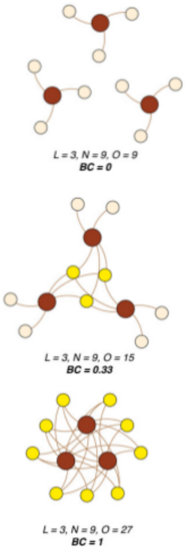
- L: number of localities
- u: number of taxa unique to a locality
- n: number of taxa at a locality
- $0 \leq E \leq 1$

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
- $0 \leq Occ \leq 1$

Biogeographic connectedness

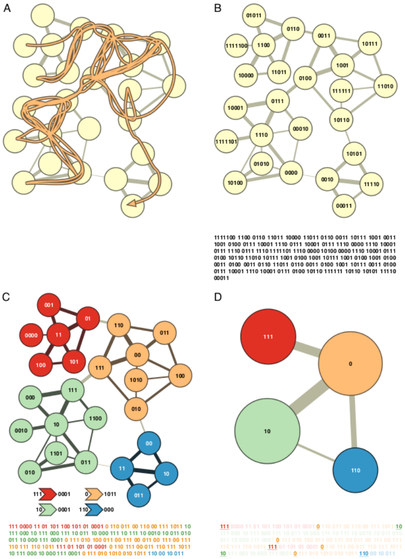


(Sidor et al. 2013 *PNAS*)

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

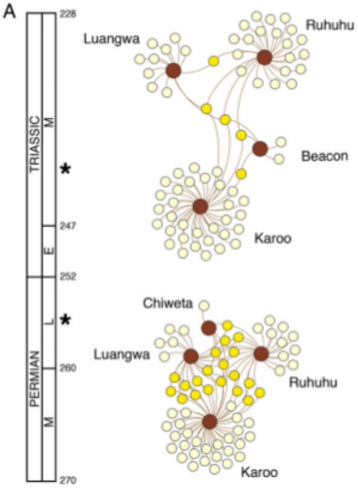
- O: number of occurrences
- N: total number of taxa
- L: number of localities
- $0 \leq BC \leq 1$

Code length



(Rosvall and Bergstrom 2008 *PNAS*)

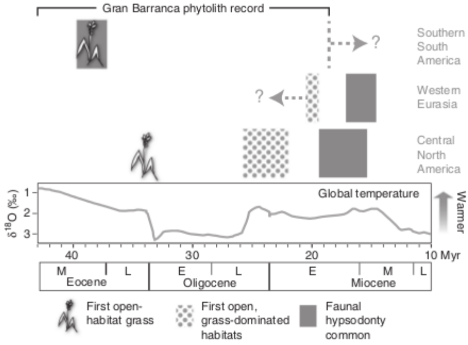
Global versus regional versus local scale processes



(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

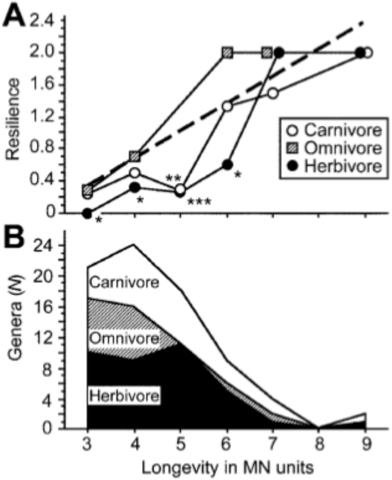
Expectations: locomotor category



(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

Expectations: dietary category



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

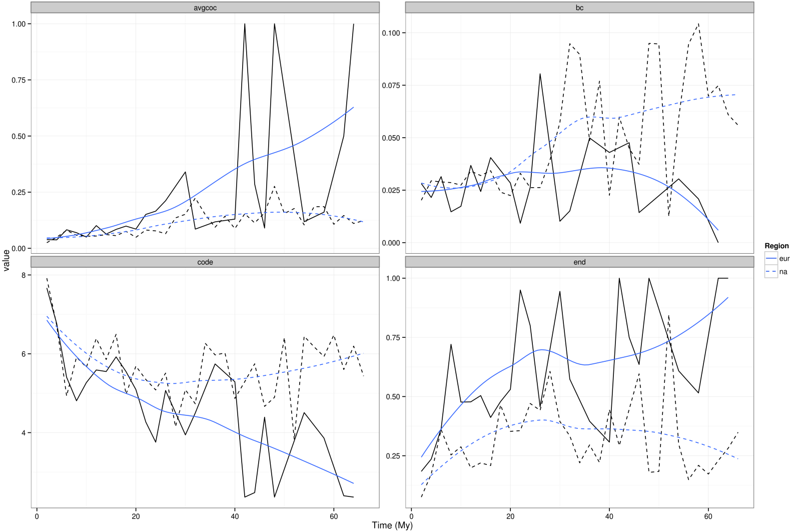
- herbivore
  - most like all taxa
- carnivore
  - constant $\vee$ corr w/ herbivores
- omnivore
  - constant $\vee$ random

Community connectedness of North America

Community connectedness of Europe

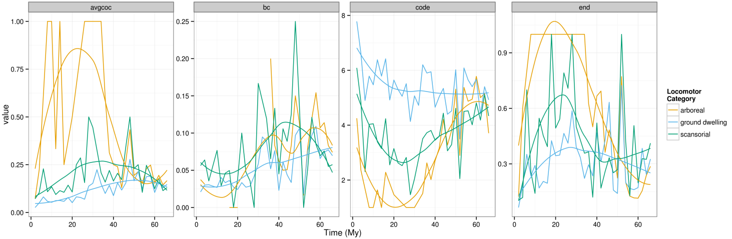
Community connectedness of South America

Preliminary results: NA, Eur

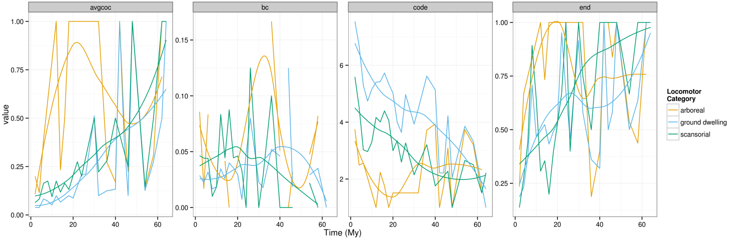


Preliminary results: locomotor category

North America

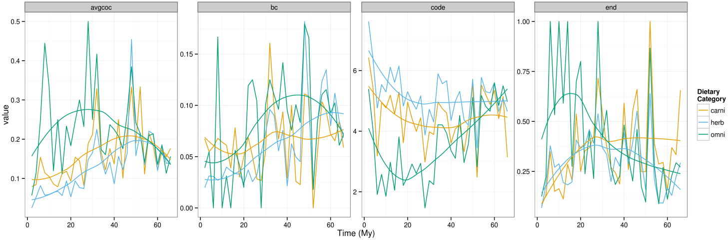


Europe

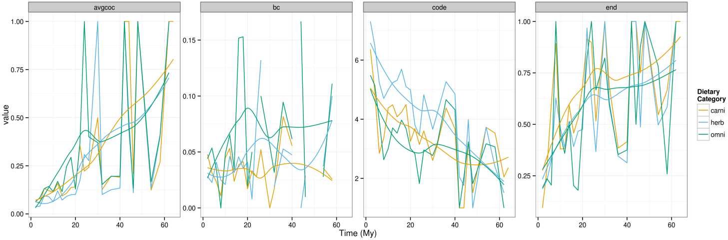


Preliminary results: dietary category

North America



Europe



Questions

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- 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?

Summary of proposed research

Studies

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

Acknowledgements

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