

# Evolutionary paleoecology and the biology of extinction

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Introduction and theory

Brachiopods, environmental preference, and extinction

Ecology and survival in Cenozoic mammals

Community connectedness in Cenozoic mammals

## Introduction and theory

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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?

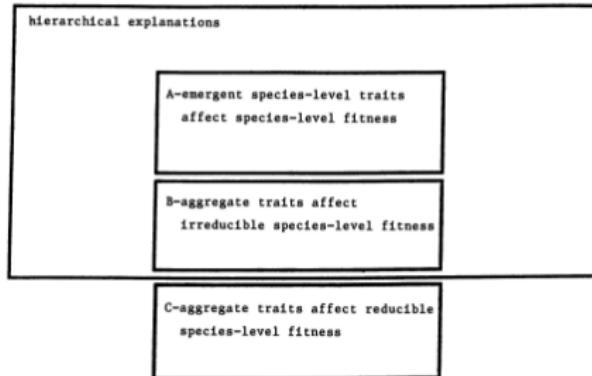
# Evolutionary paleoecology

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

*(Kitchell 1985 Paleobiology)*

environmental interactions → macroevolution

# Emergent properties



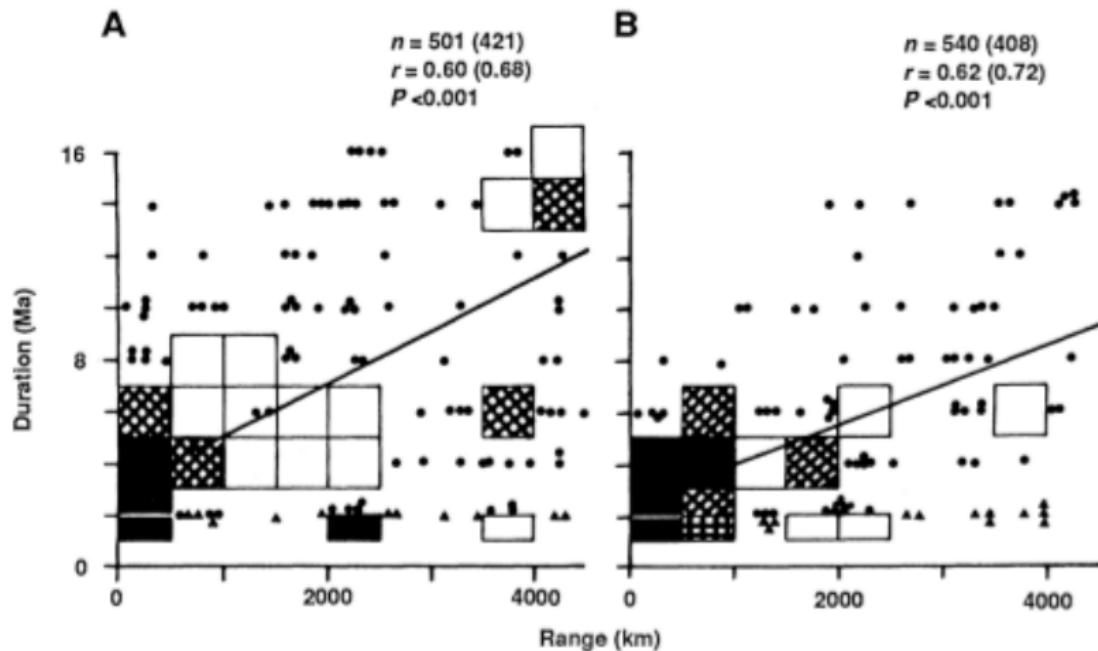
(Grantham 1995 *Ann. Rev. Ecol. Syst.*)

## Species level

Trait that cannot be reduced to organismal level

Product of one or more traits/factors

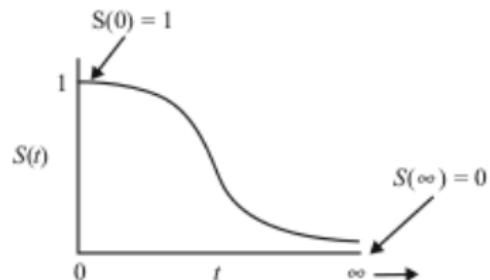
# Range size



(Jablonski 1987 *Science*)

# Probability of survival

Theoretical  $S(t)$ :

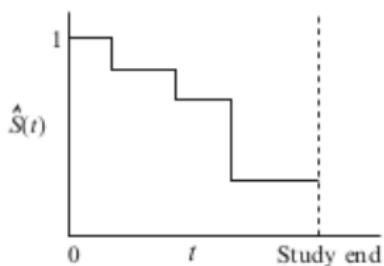


## Survival function

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

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

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

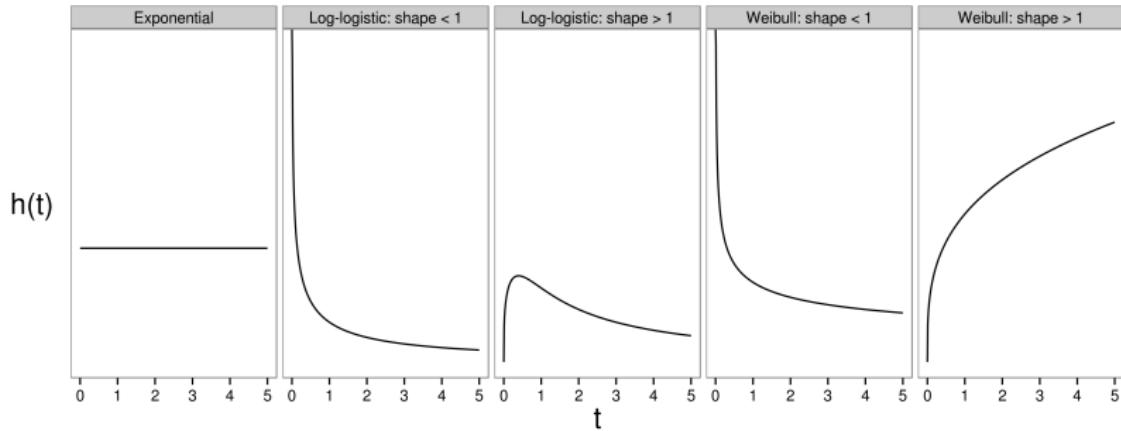


(Kleinbaum and Klein 2012)

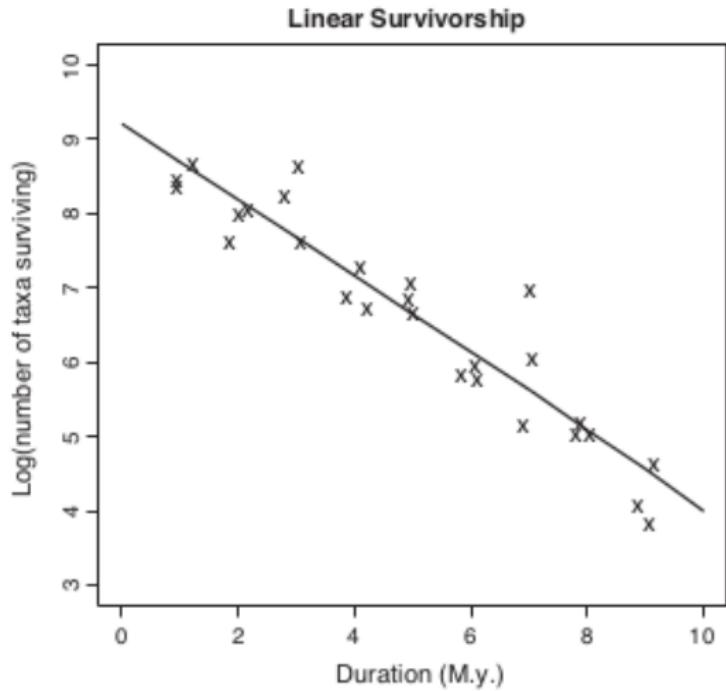
# Instantaneous potential of failure (extinction)

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 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)

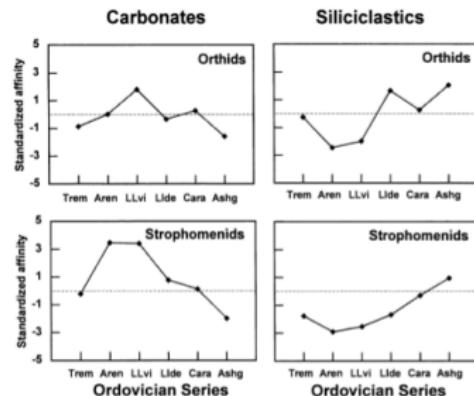
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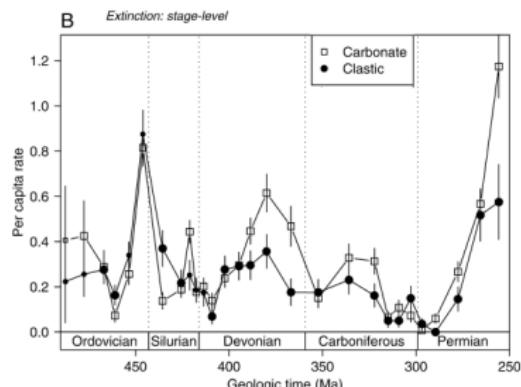
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# Substrate affinity



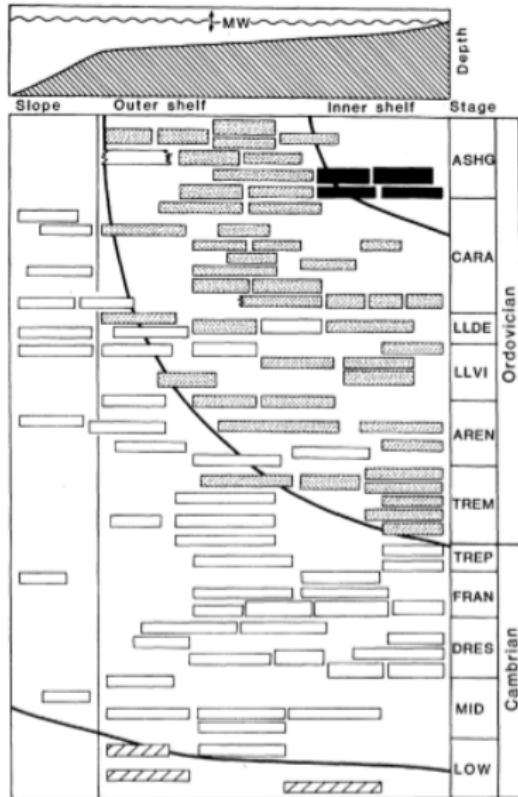
(Miller and Connolly 2001 *Paleobio.*)



(Foote 2006 *Paleobio.*)

- ▶ carbonates, clastics, mixed
- ▶ lithology/deposition environment
- ▶ Phanerozoic decrease in carbonates:clastics predictions
  - ▶ clastics > carbonates

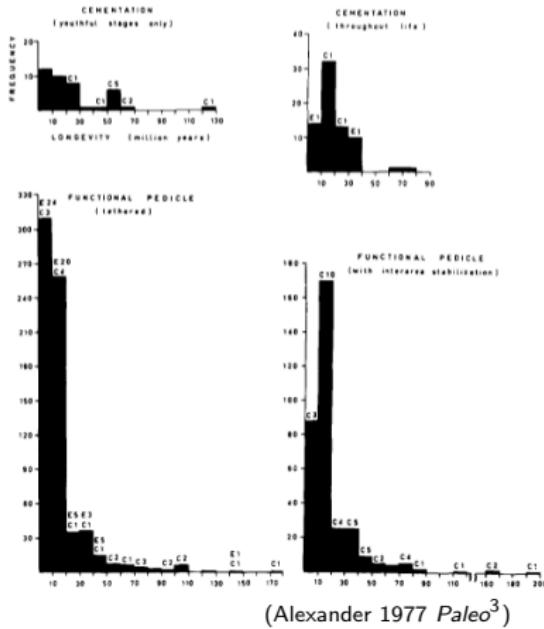
# Habitat preference



(Jablonski *et al.* 1983 *Science*)

- ▶ classically invoked re. diversification of higher taxa
  - ▶ onshore → offshore
- ▶ on-shore, off-shore, none
  - ▶ above/below storm wave base

# Affixing strategy



- ▶ 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

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

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

(Simpson and Harnik 2009 *Paleobiology*)

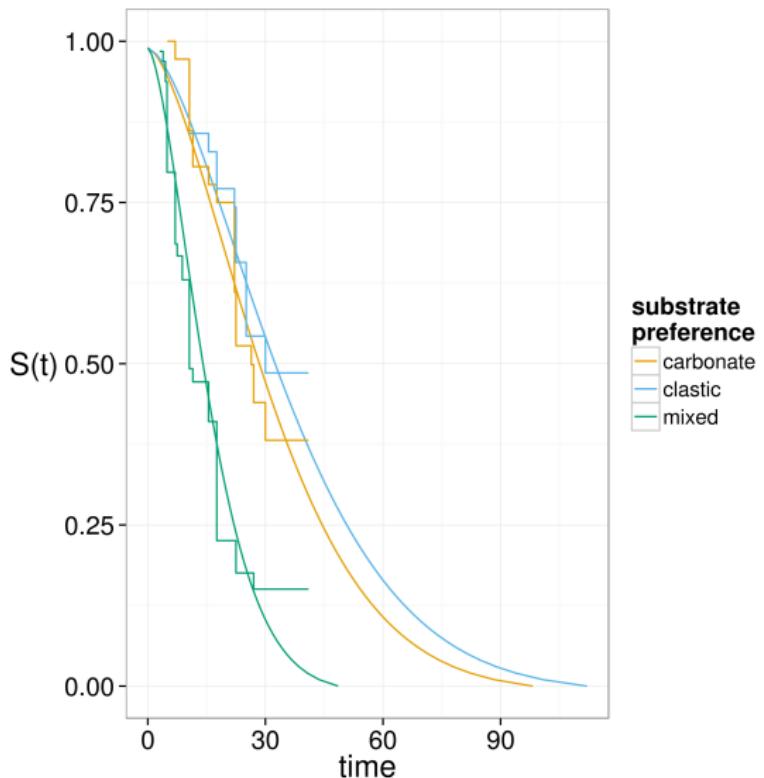
# Analysis

- ▶ data: genus FAD–LAD
  - ▶ Australasia
  - ▶ all taxa occurring in and ranging into/out of Permian
  - ▶ PBDB (h/t Clapham)
- ▶ traits: time-indep. covariate
  - ▶ substrate following Foote 2006 *Paleobio.*
  - ▶ habitat following Kiessling *et al.* 2007 *Paleo*<sup>3</sup>
- ▶ climate: time-dep. covariate
  - ▶ continuous or Heaviside step function
- ▶ distributions of survival:  $\exp(\lambda)$ , *Weibull*( $\lambda, k$ ), etc.

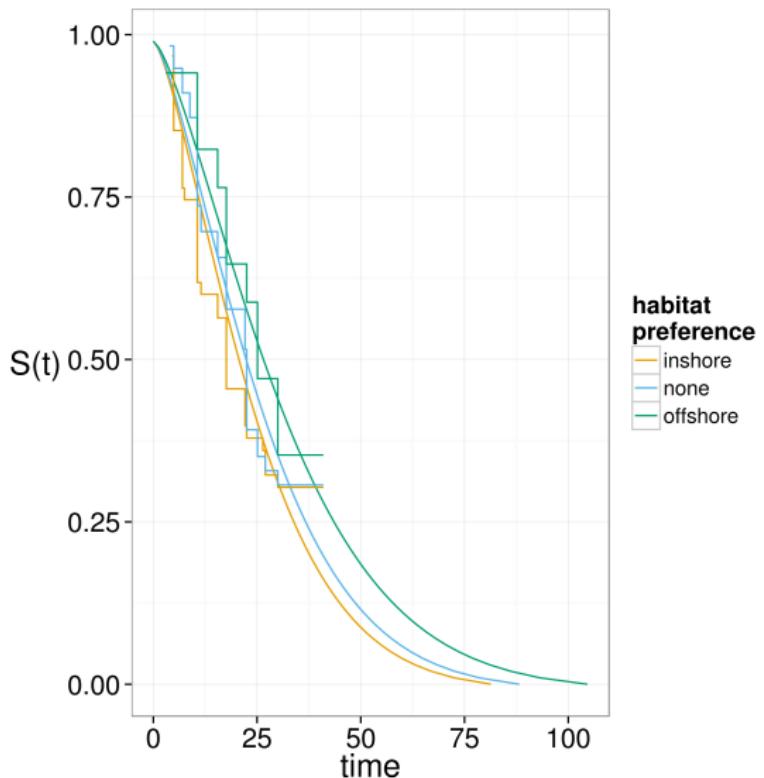
## Preliminary results: model comparison

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



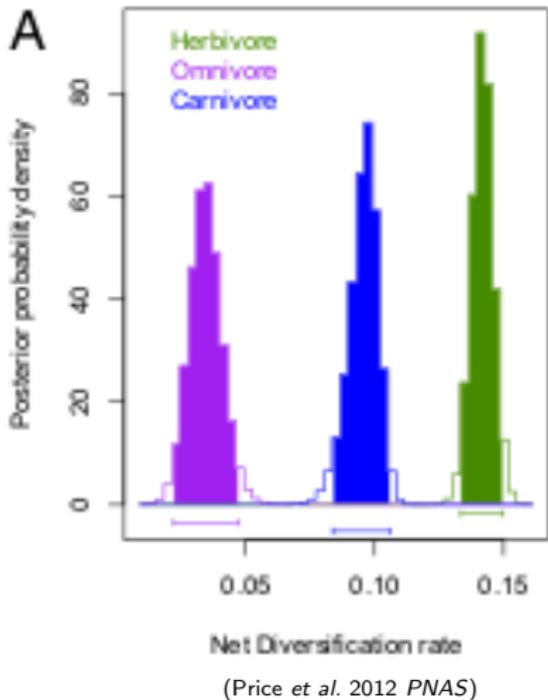
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Community connectedness in Cenozoic mammals

# Predictions: dietary category

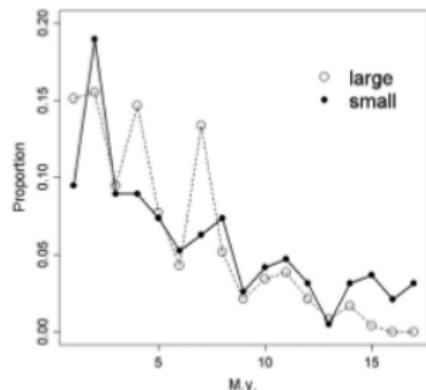


- ▶ trophic hierarchy (stability → duration)
  - ▶ herb: most stable, longest duration
  - ▶ carni: least stable, shortest duration
  - ▶ omni: avg. stability, avg. duration
- ▶ ↑ diversification
  - ▶ ↑ origination;  $\simeq$  extinction
  - ▶  $\simeq$  origination; ↓ extinction

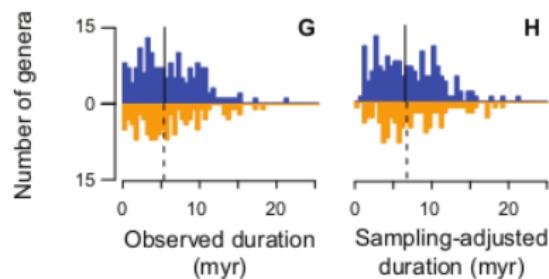
## Predictions: locomotor category

- ▶ Paleogene → Neogene
  - ▶ open → closed environment
  - ▶ arboreal:  
Paleogene > Neogene
  - ▶ ground dwelling:  
Paleogene < Neogene
  - ▶ scansorial:  
Paleogene ≈ Neogene

# Predictions: body size



(Liow et al. 2008 PNAS)



(Tomiya 2013 Am. Nat.)

- ▶ ↑ body size, ↑ energy req,  
↑ range size, ↓ extinction
- ▶ Europe
  - ▶ lrg body size genera:  
↑ extinction
- ▶ North America
  - ▶ generic body size:  
 $\simeq$  extinction

# Analysis

- ▶ data: genus and 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
- ▶ distributions of survival:  $\exp(\lambda)$ , *Weibull*( $\lambda, k$ ), etc.

# 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

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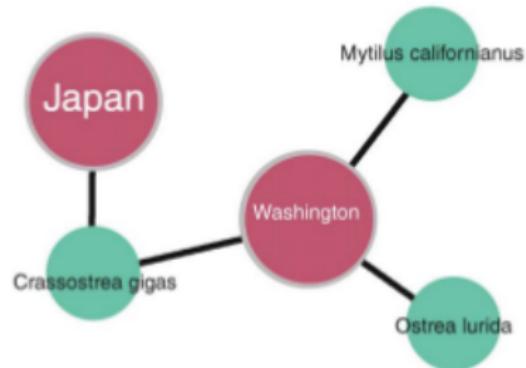
Community connectedness in Cenozoic mammals

# 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

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

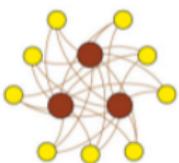
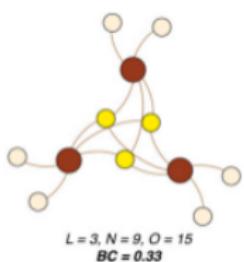
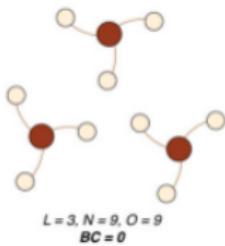
- ▶  $L$ : number of localities
- ▶  $u$ : number of taxa unique to a locality
- ▶  $n$ : number of taxa at a locality
- ▶  $0 \leq E \leq 1$

## Average relative occupancy per taxon

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

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

# Biogeographic connectedness

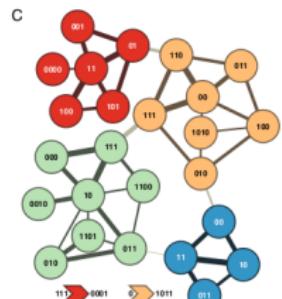
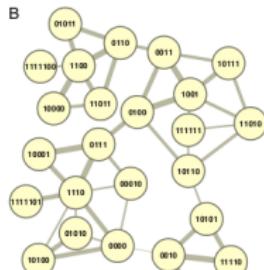
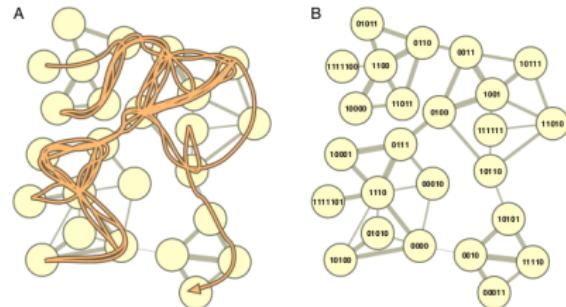


$$BC = \frac{O - N}{LN - N}$$

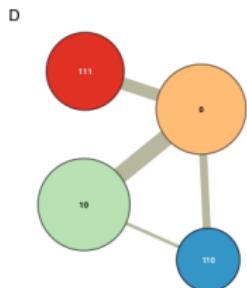
- ▶  $O$ : number of occurrences
- ▶  $N$ : total number of taxa
- ▶  $L$ : number of localities
- ▶  $0 \leq BC \leq 1$

(Sidor et al. 2013 PNAS)

# Code length



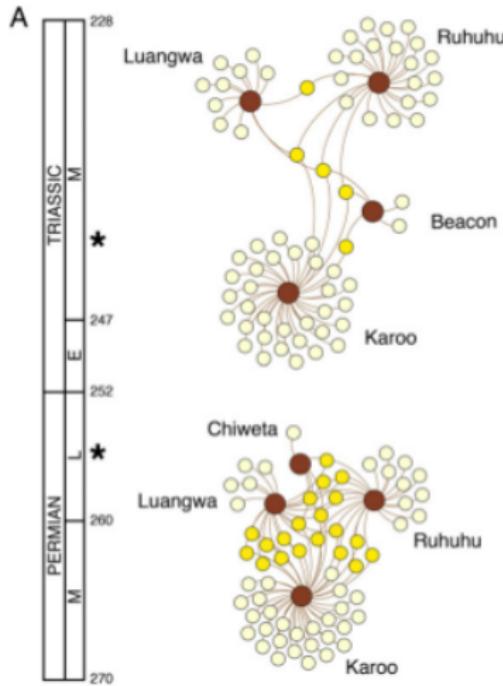
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(Rosvall and Bergstrom 2008 PNAS)

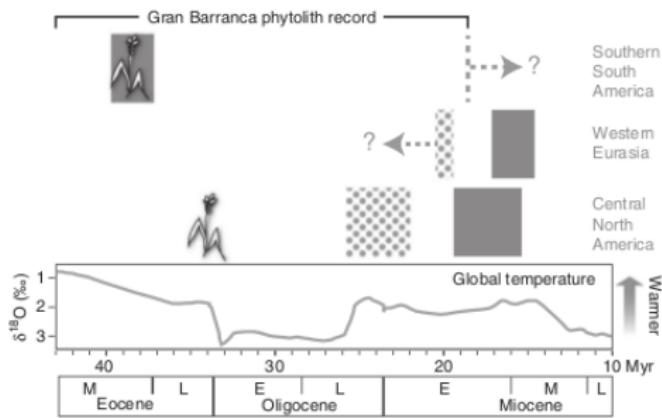
# Global versus regional versus local scale processes



- ▶ 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)

# Expectations: locomotor category



(Strömberg et al. 2013 *Nature Com.*)

## ► arboreal

- ▶ ↑  $E$ , ↑ code
- ▶ ↓  $BC$ , ↓  $Occ$

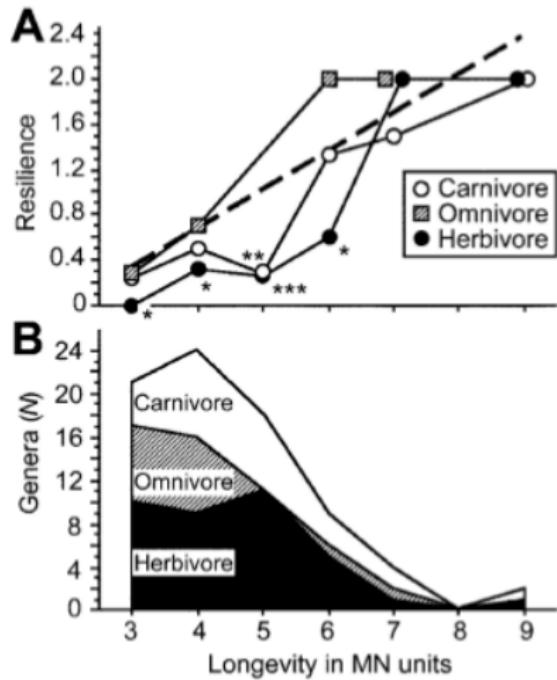
## ► ground dwelling

- ▶ ↓  $E$ , ↓ code
- ▶ ↑  $BC$ , ↑  $Occ$

## ► scansorial

- ▶ constant ∨ random

# Expectations: dietary category



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

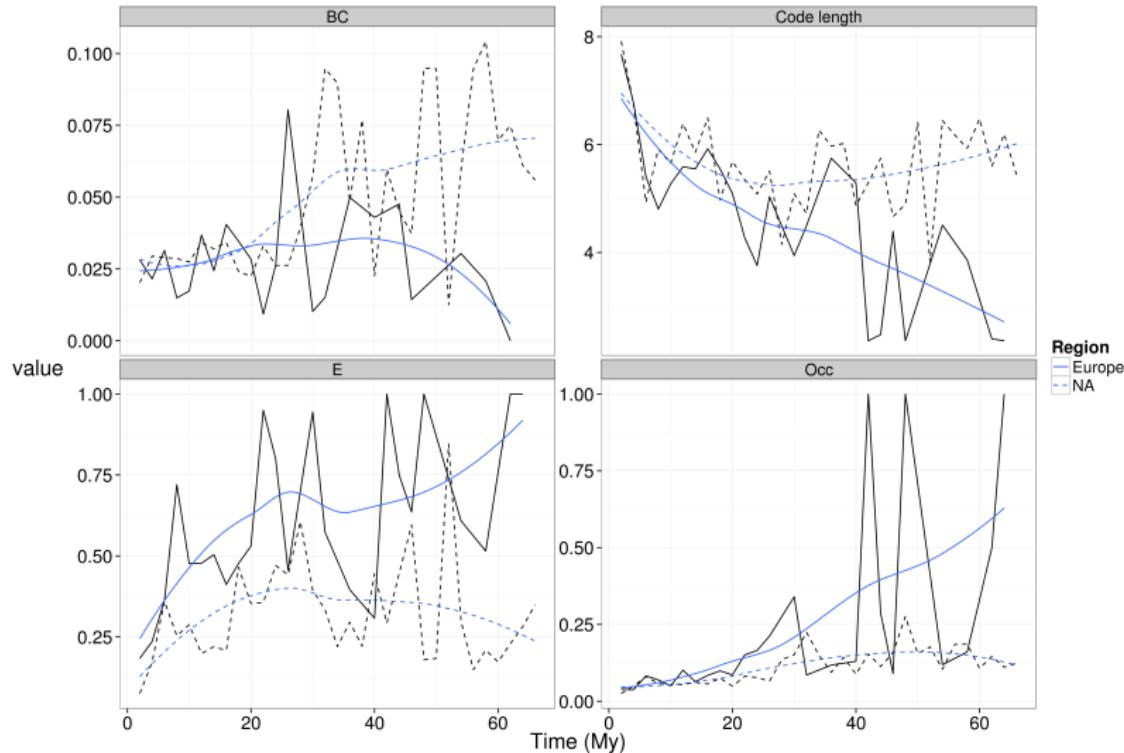
(Jernvall and Fortelius 2004 *Am. Nat.*)

# Community connectedness of North America

# Community connectedness of Europe

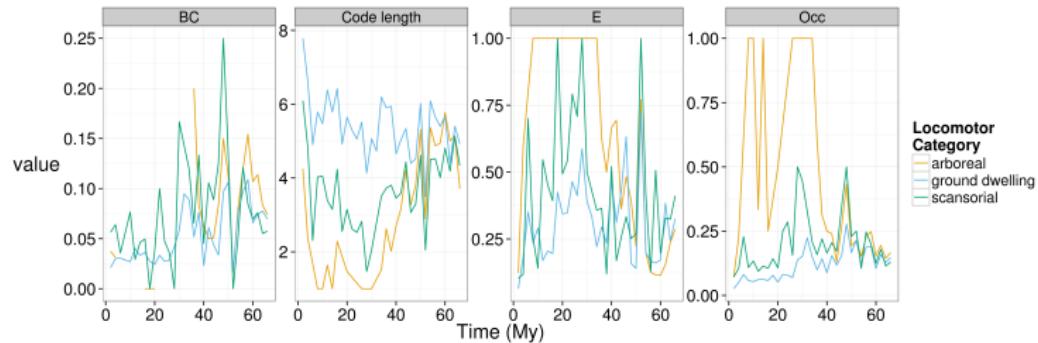
# Community connectedness of South America

# Preliminary results: NA, Eur

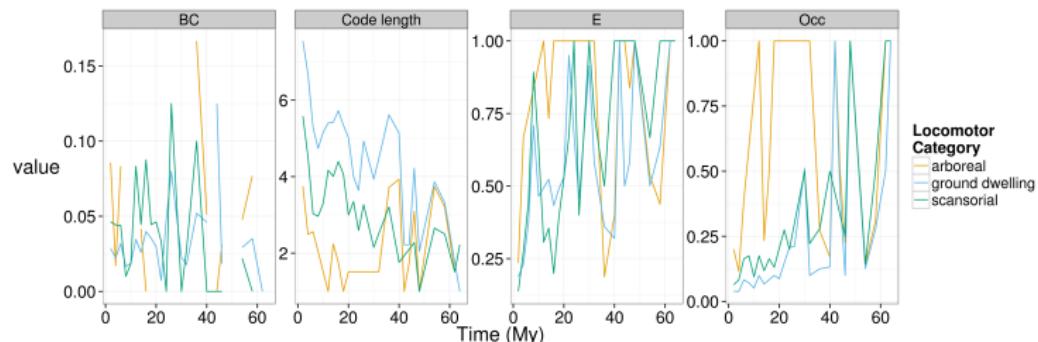


# Preliminary results: locomotor category

North America

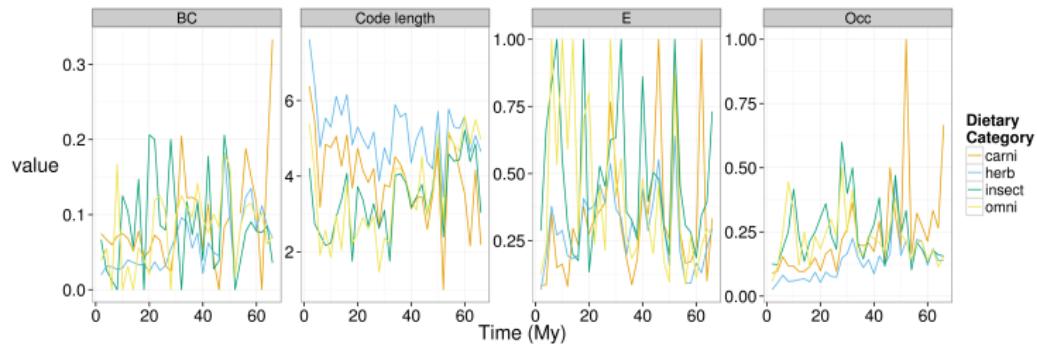


Europe

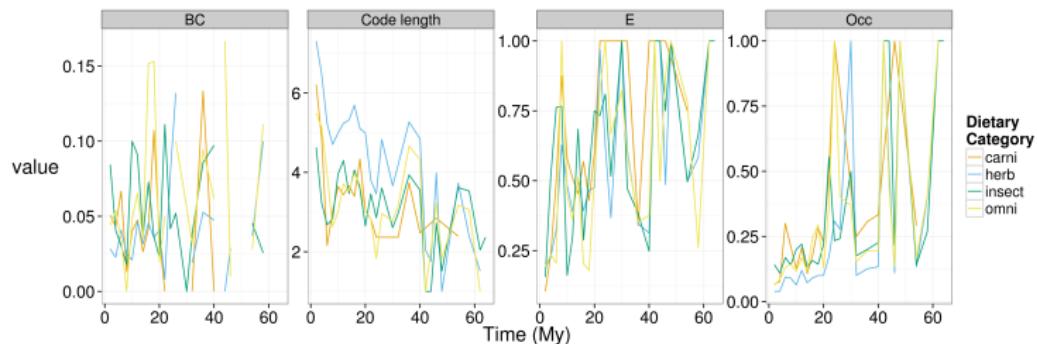


# Preliminary results: dietary category

North America



Europe



# Questions

## 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?

# 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

