*O species, stunned by your terror of chill death, why fear the Styx, why fear the ghosts and empty names, the stuff of poets, the spectres of a phantom world?*

*(Ovid, Metamorphoses, book XV: 143-175, A. S. Kline trans.)*

# Evolutionary paleoecology and the biology of extinction

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April 29, 2014

Theory

Survival

Communities

Summary

# Extinction

*All species that have ever lived are, to a first approximation, dead.*

*(Raup 1986 The Nemesis Affair)*

# Foundation

**Question**

Why do certain taxa go extinct while others do not?

# Modes of extinction

Field of Bullets : Wanton : Fair Game

(Raup 1991 Extinction: Bad Genes or Bad Luck?)

# Evolutionary paleoecology

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

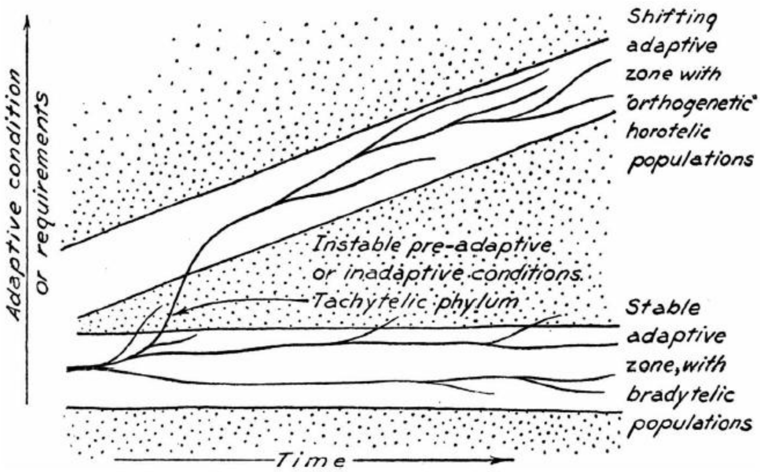
*(Kitchell 1985 Paleobiology)*

# In context of this study

**Rephrased**

How does a taxon's adaptive zone affect its extinction risk?

# Adaptive zones




(Simpson 1944 Tempo and Mode)

# Simpson's terms

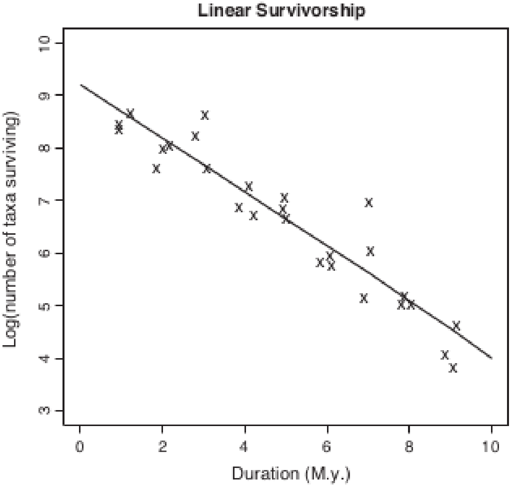
## Definition

**Environment:** The set of all possible interactions, both biotic and abiotic.

**Adaptive zone:** The set of all interactions, biotic and abiotic, that a individual/taxon is adapted to or experiences in a given environment.

(Simpson 1944 Tempo and Mode, Simpson 1953 Major Features)

# Van Valen's observation




(Liow et al. 2011 *TREE*)

# Theory

**Law of Constant Extinction**

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

(Van Valen 1973 *Evol. Theory*)

# Approach

### Concerns

Model extinction in context of adaptive zone (selective pressure).

Survival

- traits, factors duration
- extinction mode

Communities

- $\alpha, \beta$ diversity
- biome distinctiveness

# Systems

**Brachiopods**

**Mammals**

# Proposed studies

Australian Permian brachiopods

- survival patterns
- community connectedness (not shown)
- substrate, habitat, affixing strategy

Cenozoic mammals

- survival patterns (not shown; come to Evolution2014)
- community connectedness
- dietary and locomotor categories, body size

Theory

Survival

Communities

Summary

# Survival

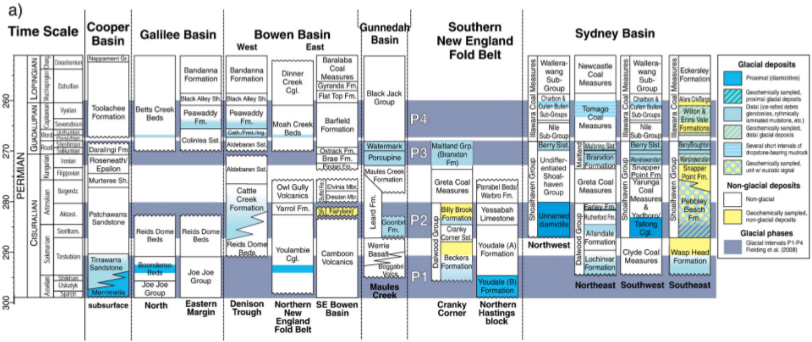
**Definition**

Time from origination to extintion of a taxon (age).

# Brachiopods

(http://earthphysicsteaching.homestead.com)

# Permian of Australia




(Birgenheier *et al.* 2010 *Paleo*$^3$)

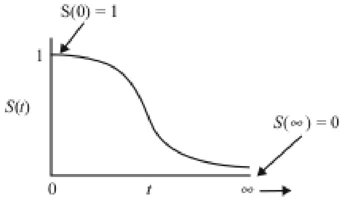
# Brachiopods, environmental preference, and extinction

## Questions

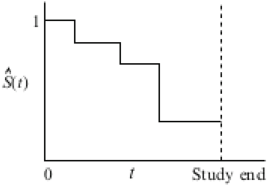
- Do traits related to environmental preference have different distributions of taxonomic duration?
  - Is survival best modeled by a single trait or multiple?
  - How do other factors, such as climate, affect these patterns?
- Is extinction taxon-age independent or dependent?

# Probability of survival

Theoretical $S(t)$:

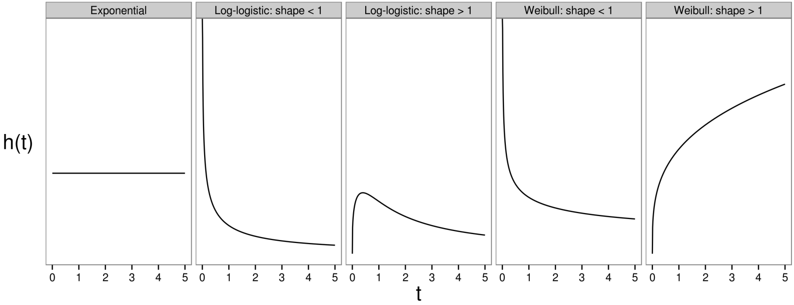



$\hat{S}(t)$ in practice:




(Kleinbaum and Klein 2012)

# Extinction function



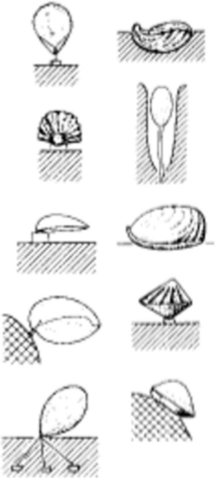
# Formalization of Van Valen

## Law of Constant Extinction

$$T \sim Exp(\lambda)$$

$T$: survival time
$\lambda$: extinction rate

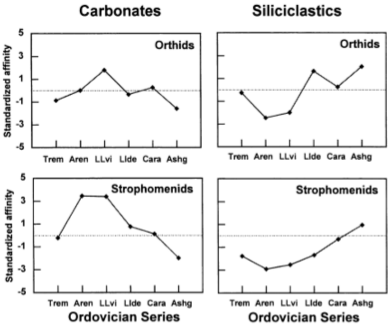
# Affixing strategy



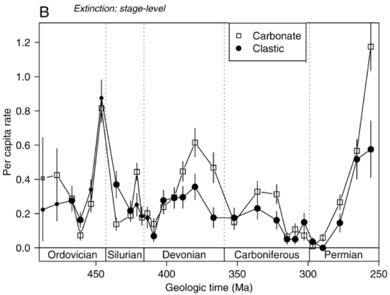
(modified from Johansen 1989 *Paleo*[3])

- Alexander 1977 *Paleo*[3]
  - endemic:
    reclining > others
  - cosmopolitan:
    ped./cement > others
- Clapham and Bottjer 2007 *Paleo*[3]
  - penduculate: on-shore
  - reclining: off-shore

# Substrate affinity

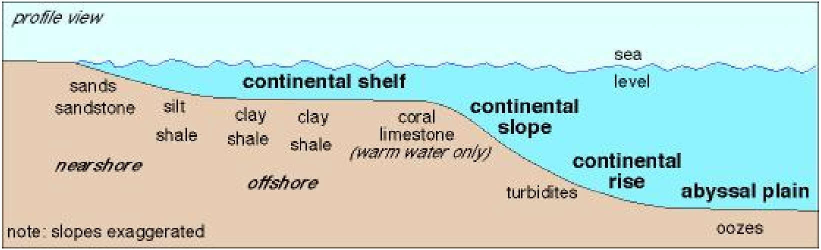



(Miller and Connoly 2001 *Paleobio.*)




(Foote 2006 *Paleobio.*)

# Habitat preference




(http://www.columbia.edu/)

# Assigning substrate and habitat

## Probability of assignment

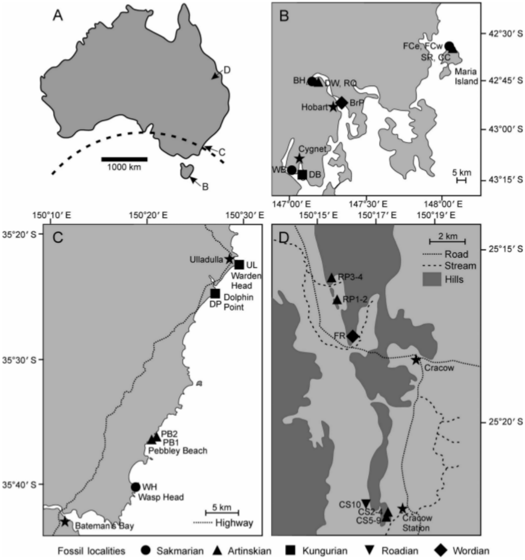
$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)}$$

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

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

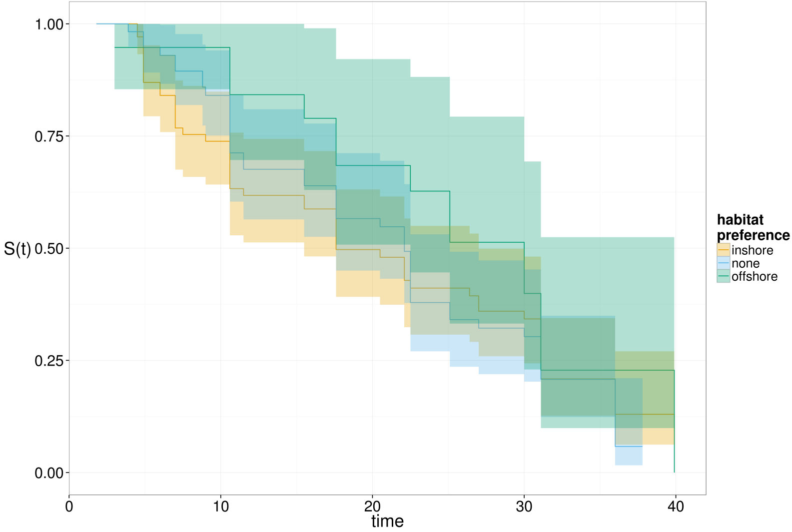
(Simpson and Harnik 2009 *Paleobiology*)

# Analysis

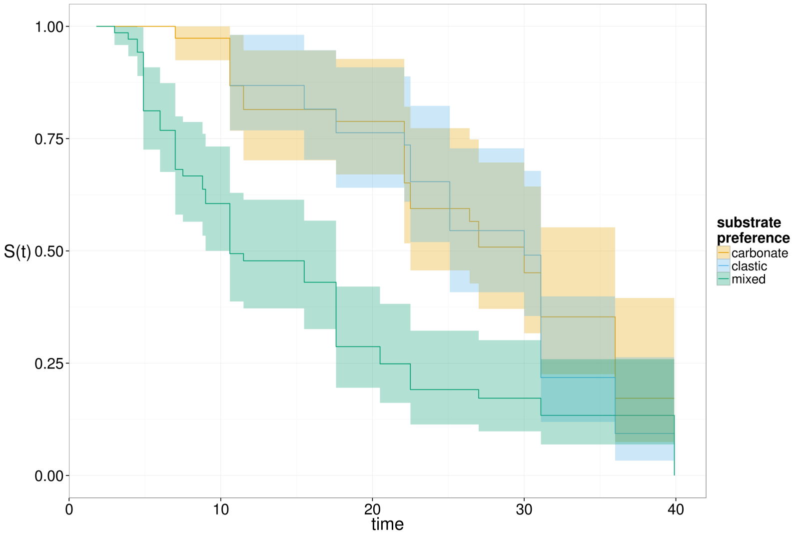



(Clapham and James 2008 *Palaios*)

# K-M curve habitat



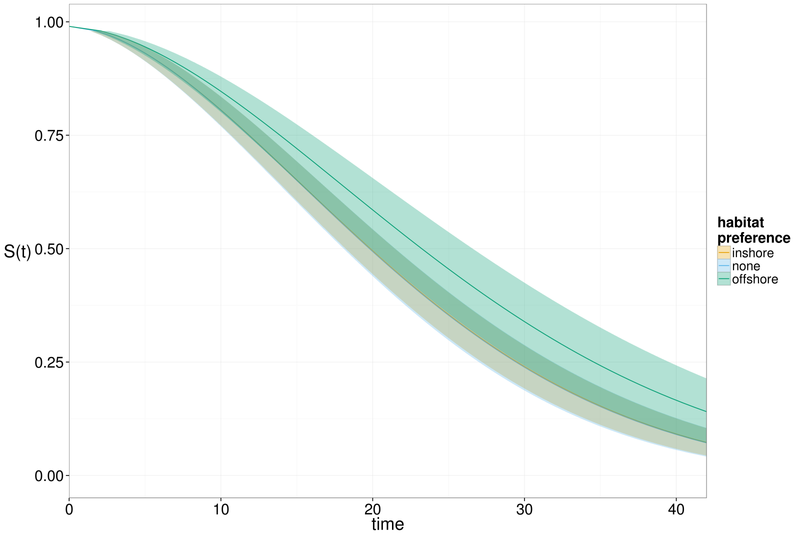
# K-M curve substrate



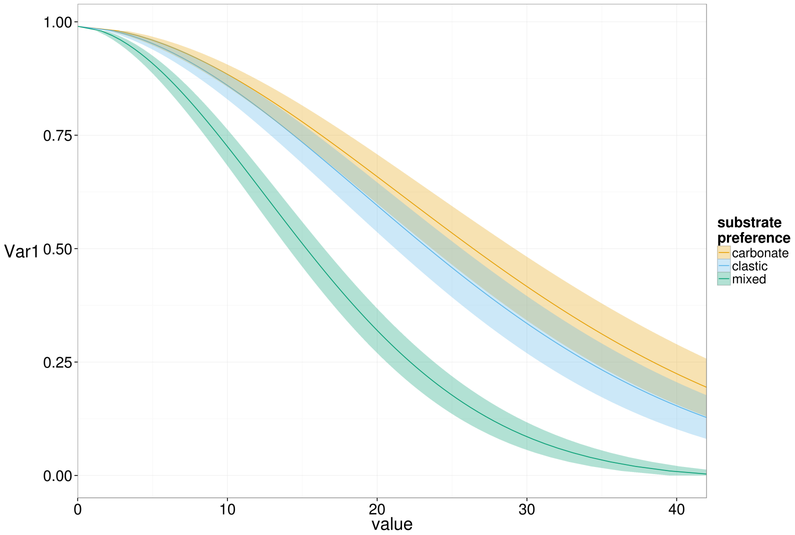
# Preliminary results: model comparison

| formula | distribution | shape | df | AICc | weight |
|---|---|---|---|---|---|
| ~ aff | weibull | 1.85 | 4 | 941.6757 | 0.65 |
| ~ aff + hab | weibull | 1.87 | 6 | 942.9977 | 0.34 |
| ~ aff * hab | weibull | 1.89 | 10 | 949.0816 | 0.02 |
| ~ 1 | weibull | 1.74 | 2 | 960.2550 | 0.00 |
| ~ hab | weibull | 1.75 | 4 | 963.3091 | 0.00 |
| ~ aff | exponential | | 3 | 993.1724 | 0.00 |
| ~ aff + hab | exponential | | 5 | 996.4089 | 0.00 |
| ~ 1 | exponential | | 1 | 1000.2592 | 0.00 |
| ~ aff * hab | exponential | | 9 | 1003.7639 | 0.00 |
| ~ hab | exponential | | 3 | 1003.9227 | 0.00 |

# Estimated survival curve habitat



# Estimated survival curve substrate

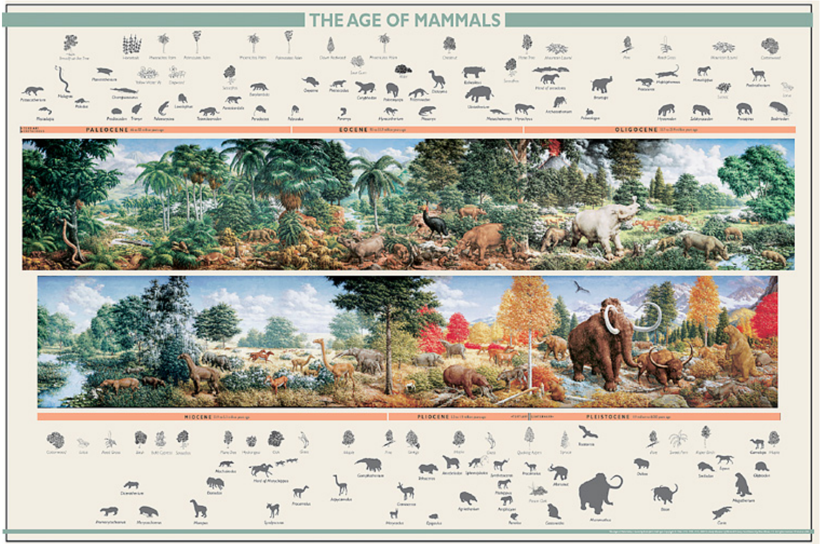


# Community connectedness

**Definition**

The relationship between $\alpha$, $\beta$ diversity and provinciality.

# Mammals




(Yale Peabody Museum)

# Community connectedness in Cenozoic mammals

## Questions

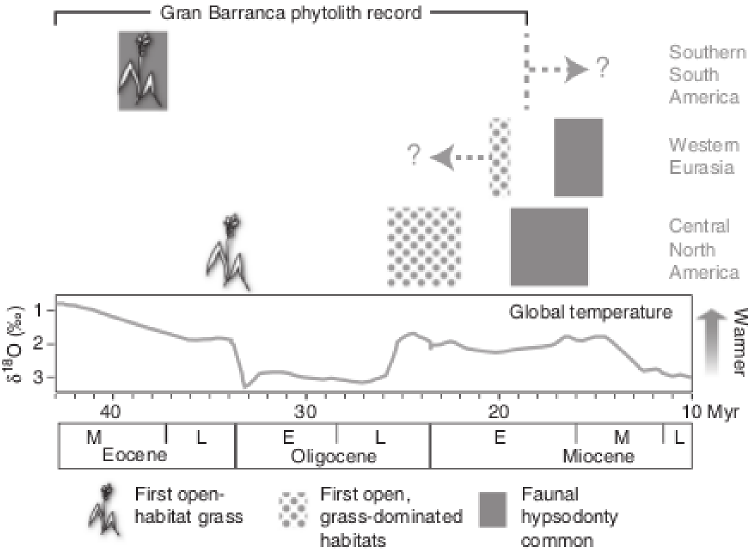
- How does the ratio of cosmopolitan to endemic taxa, per locality, change over time?
  - Is this pattern different between taxa exhibiting different traits?
  - How does this pattern vary in relation to phylogenetic similarity?
- When would we expect global, regional, and/or local processes to most strongly shape taxonomic patterns?

# Uniformity and distinctiveness

high $\alpha$, high distinctiveness, difference in selective pressures

high $\beta$, high uniformity, similarity in selective pressures

# Environments




(Strömberg *et al.* 2013 *Nature Com.*)

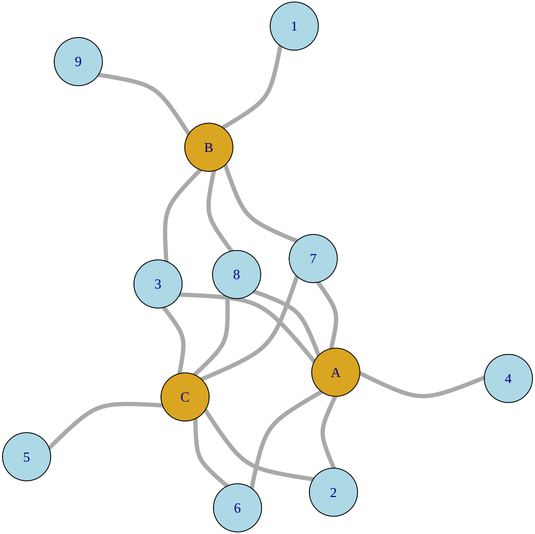
# Occurrences

**A**: 2, 3, 4, 6, 7, 8

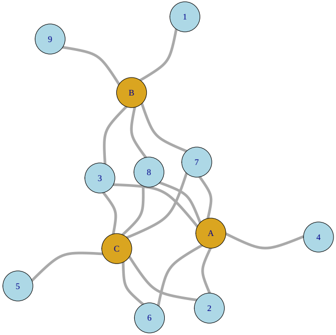
**B**: 1, 3, 7, 8, 9

**C**: 3, 5, 6, 7, 8

# Biogeographic network



# $\alpha$ diversity

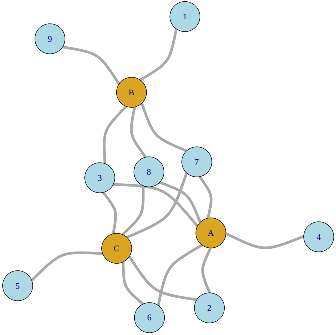



$$u = \{1, 2, 1\}$$
$$n = \{6, 5, 6\}$$
$$L = 3$$
$$E \approx 0.24$$

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

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

# $\beta$ diversity contribution

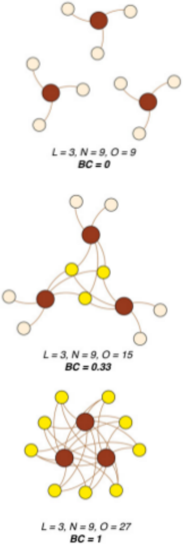



$$I = \{1, 2, 3, 1, 1, 2, 3, 3, 1\}$$
$$L = 3$$
$$N = 9$$
$$Occ \approx 0.63$$

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

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

# Uniformity

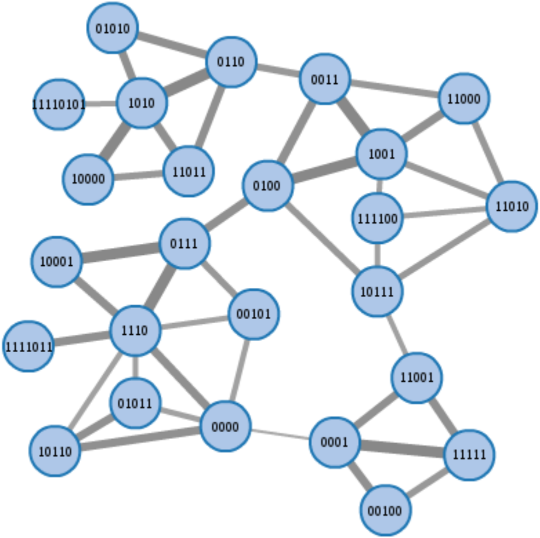



(Sidor et al. 2013 *PNAS*)

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

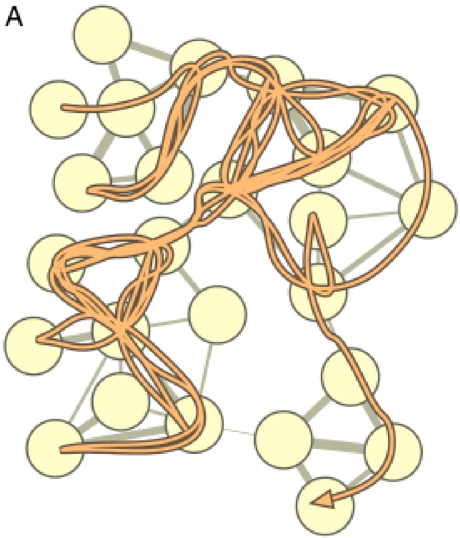
- $O$: number of occurrences
- $N$: total number of taxa
- $L$: number of localities
- $0 \leq BC \leq 1$

# Code length



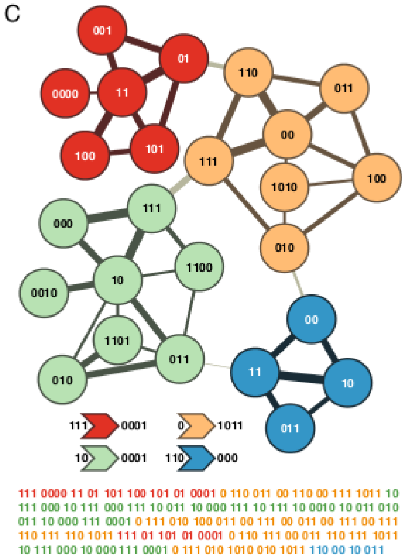

(mapequation.org)

# Code length



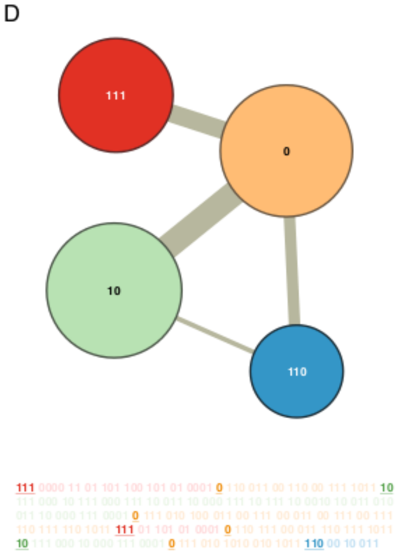

(Rosvall and Bergstrom 2008 *PNAS*)

# Code length



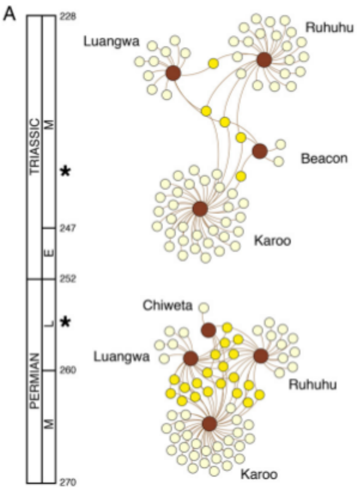

(Rosvall and Bergstrom 2008 *PNAS*)

# Code length




(Rosvall and Bergstrom 2008 *PNAS*)

# Process 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

# Scenario

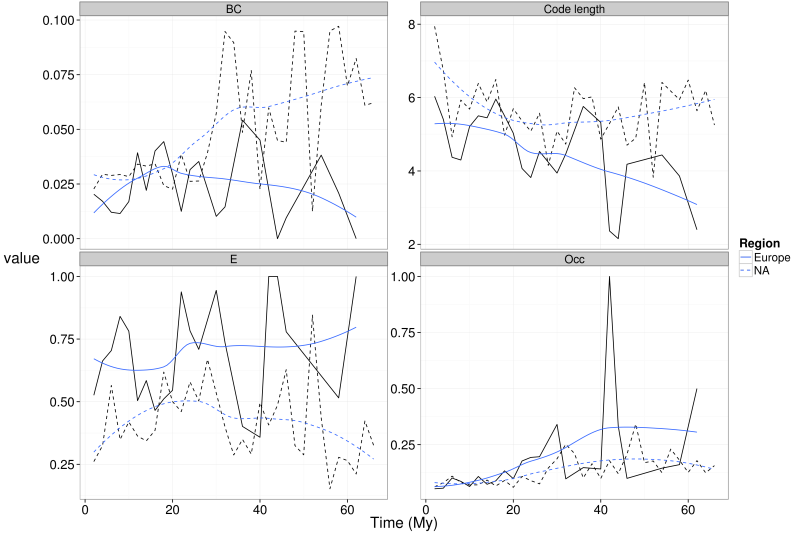
Locomotor

- ground dwelling, arboreal, scansorial

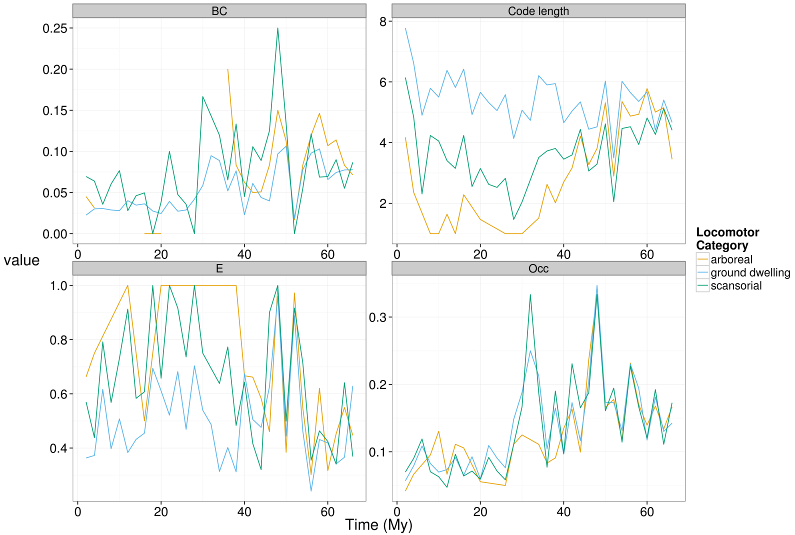
Dietary

- carnivore, insectivore, herbivore, omnivore

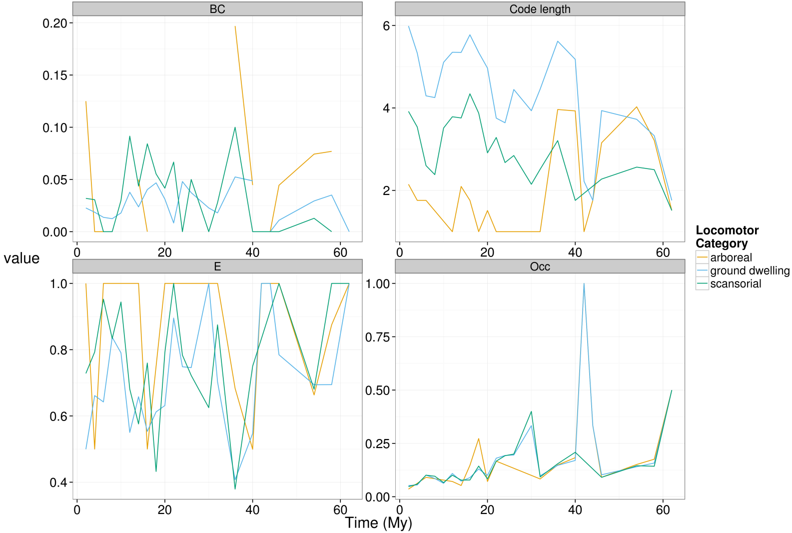
# Preliminary results: NA, Eur



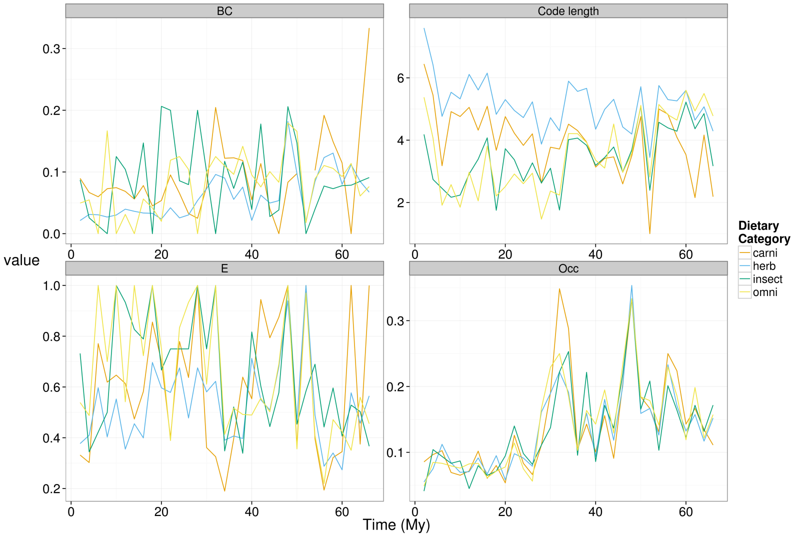
# Preliminary results: locomotor category NA



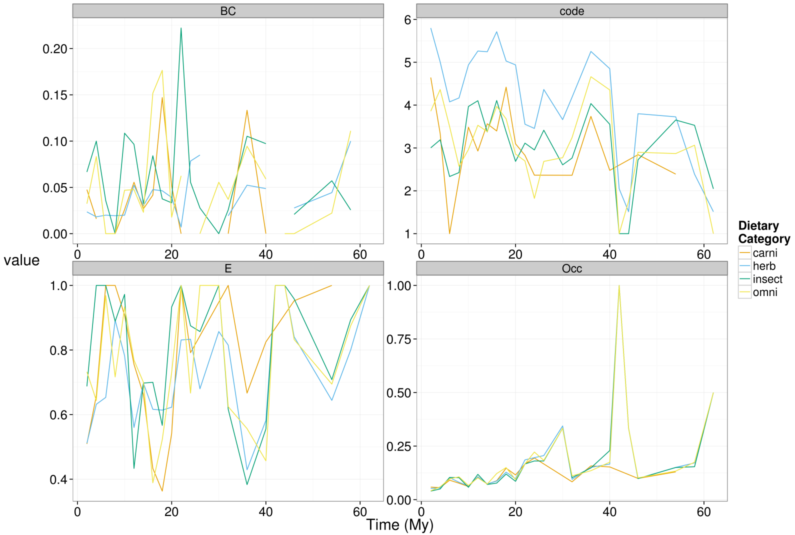
# preliminary results: locomotor category Eur



# Preliminary results: dietary category NA



# Preliminary results: dietary category Eur



# Fundamental

**Question**

Why do some taxa go extinct while others do not?

# Evolutionary paleoecological rephrasing

**Question**

How does a taxon's adaptive zone affect extinction risk?

# "Testing" the Law of Constant Extinction

**Law of Constant Extinction** (Liow et al. 2011 *TREE*)

Only applies during periods of relatively constant environment.

measure, analyze, model

# Ask the following. . .

Is there a general pattern of extinction?

What traits matter for extinction and when?

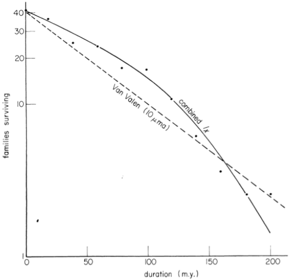
How do traits matter for extinction?

Acknowledgements

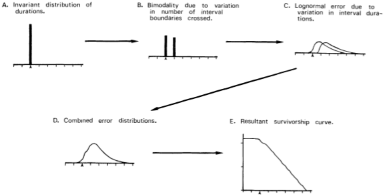
- **Committee**
  - Kenneth D. Angielczyk (co-advisor)
  - Michael J. Foote (co-advisor)
  - P. David Polly
  - Richard H. Ree
- Discussion
  - David Bapst, Megan Boatright, Ben Frable, Colin Kyle, Darcy Ross, Liz Sander
  - John Alroy, Graeme Lloyd, Kathleen Ritterbush, Carl Simpson, Graham Slater

# Further concerns

# Differential preservation and survival




(Raup 1975 *Paleobio.*)




(Sepkoski 1975 *Paleobio.*)

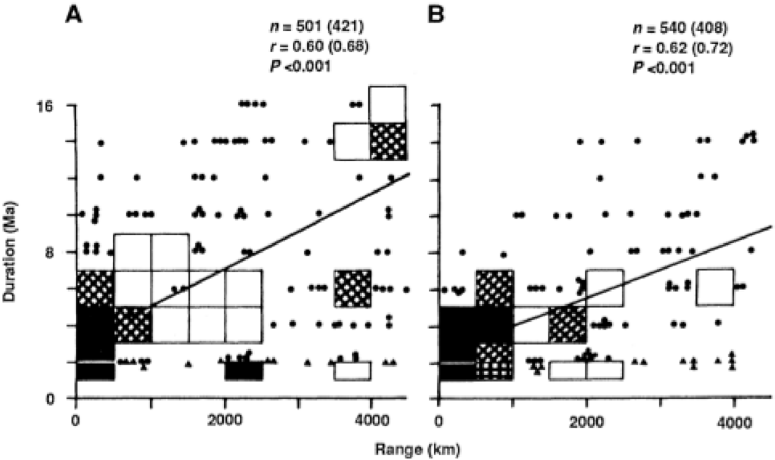
# Observe in simulation

Sampling: Poisson process ($\phi$)

Diversification: birth-death ($\lambda, \mu$)

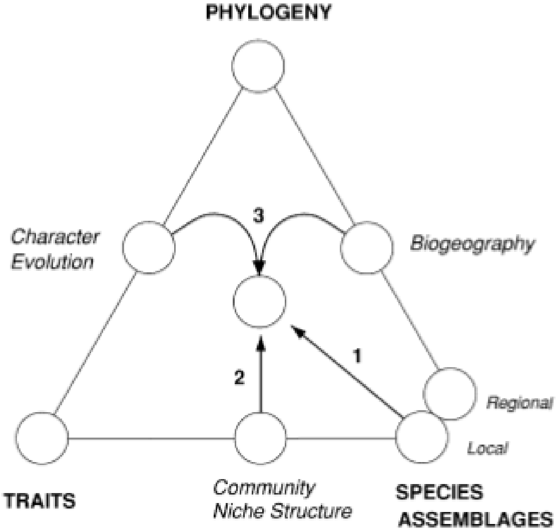
1. $=$ birth, death; $=$preservation
2. $=$ birth, death; ! $=$preservation
3. ! $=$ birth, death; $=$ preservation
4. ! $=$ birth, death; ! $=$preservation

# The Elephant in the Range



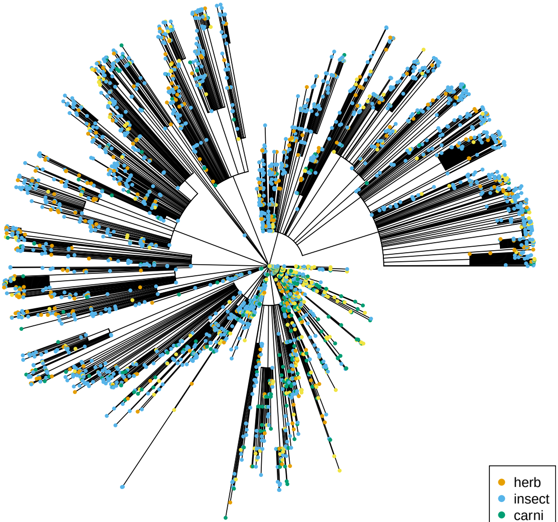

(Jablonski 1987 *Science*)

# Phylogeny and communities




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

# (Informal) phylogeny



# Compressing a network

## Map equation

(Rosvall and Bargstrom 2008 *PNAS*)

$$L(\mathbf{M}) = q_{\curvearrowright} H(\mathcal{Q}) + \sum_{i=1}^{m} p_{\circlearrowright}^{i} H(\mathcal{P}^{i})$$

- **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