Diversity Dynamics basics and the divDyn R package

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GeoZentrum Nordbayern

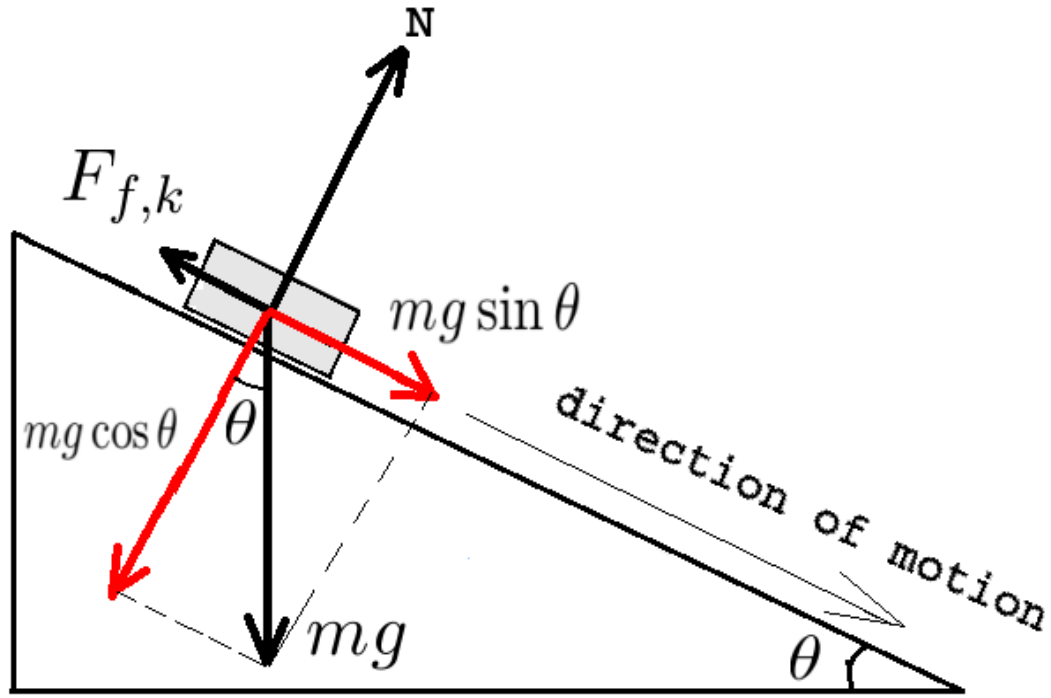
Diversity dynamics (again)

Where, what, why?

Dynamics?

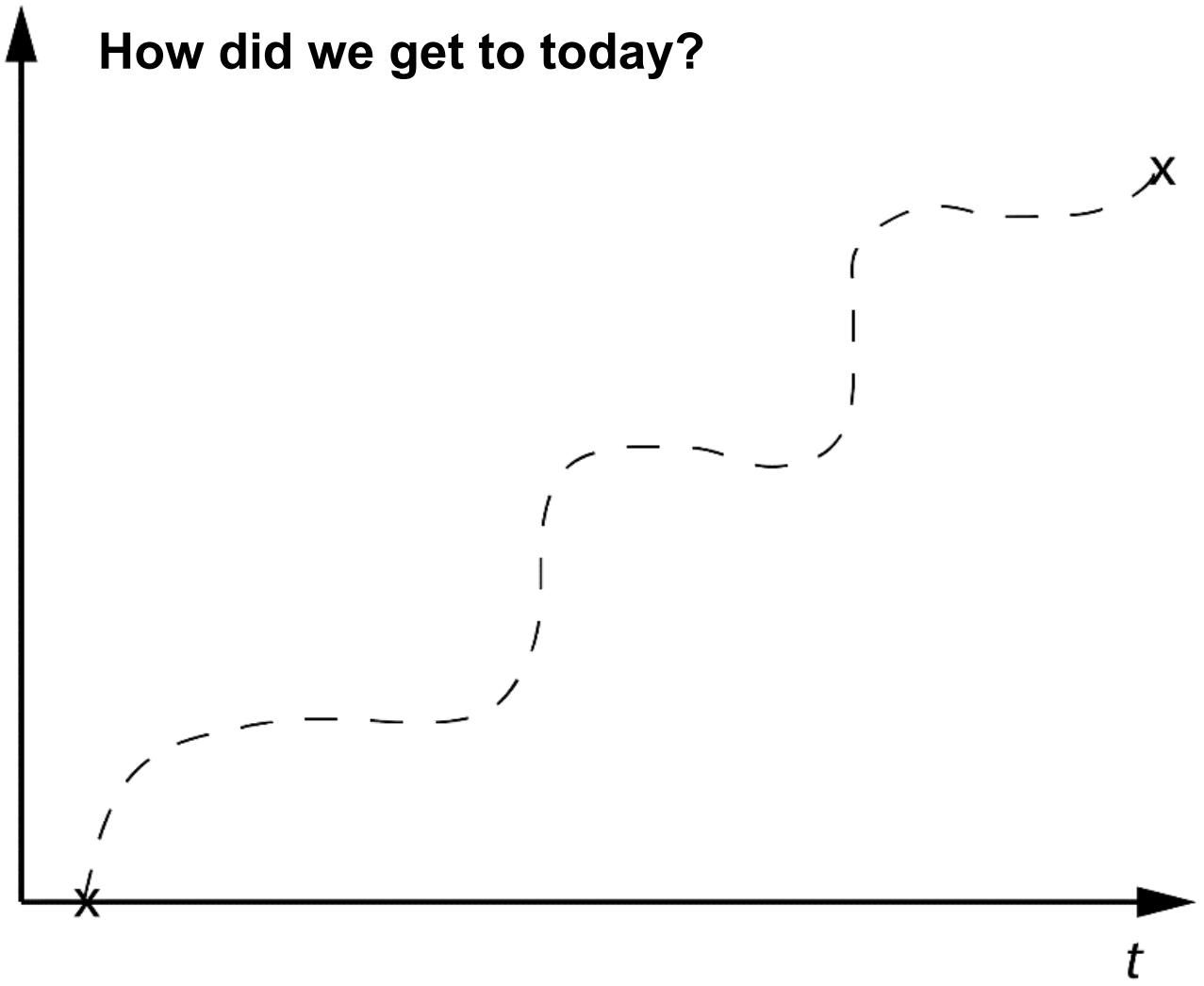
The study of forcing

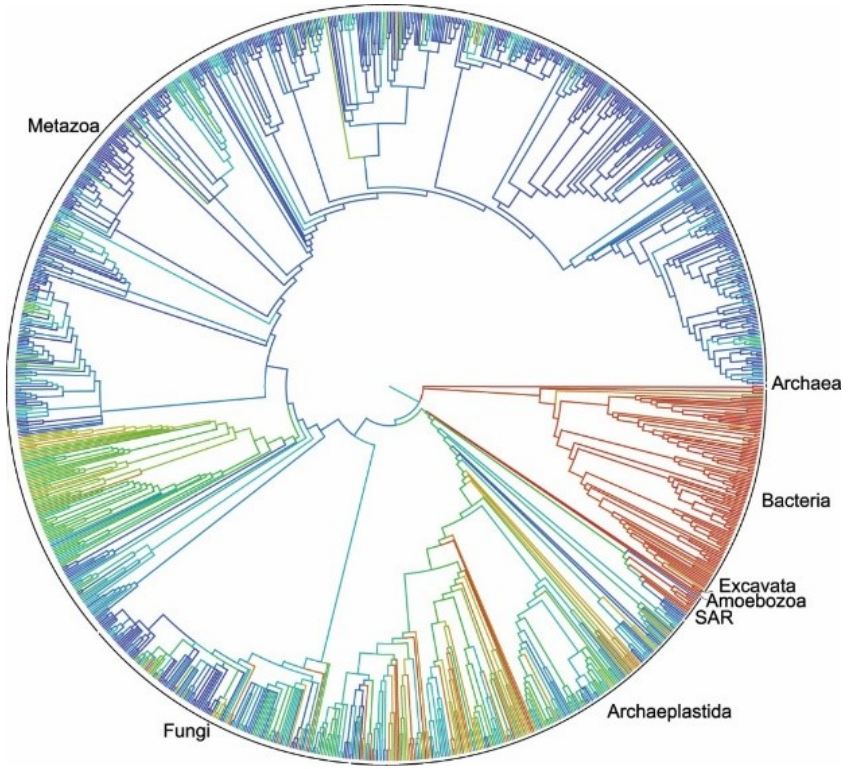
- What is it?
- How does diversity change over time?



What is the story?

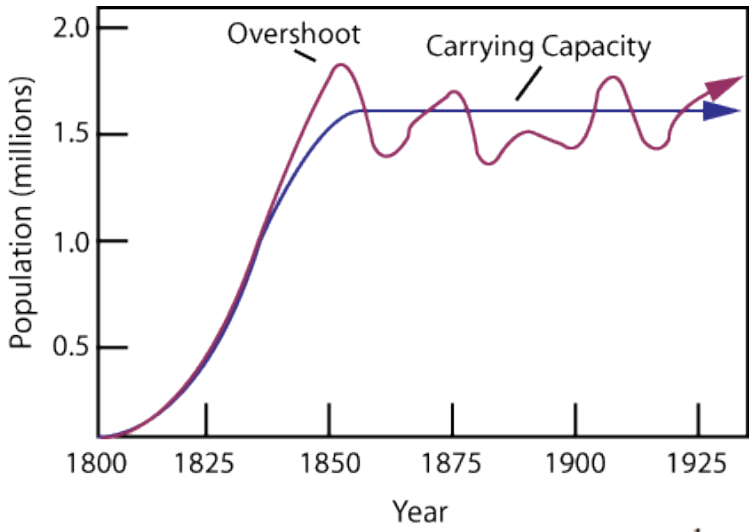
How did we get to today?





Where is the question coming from?

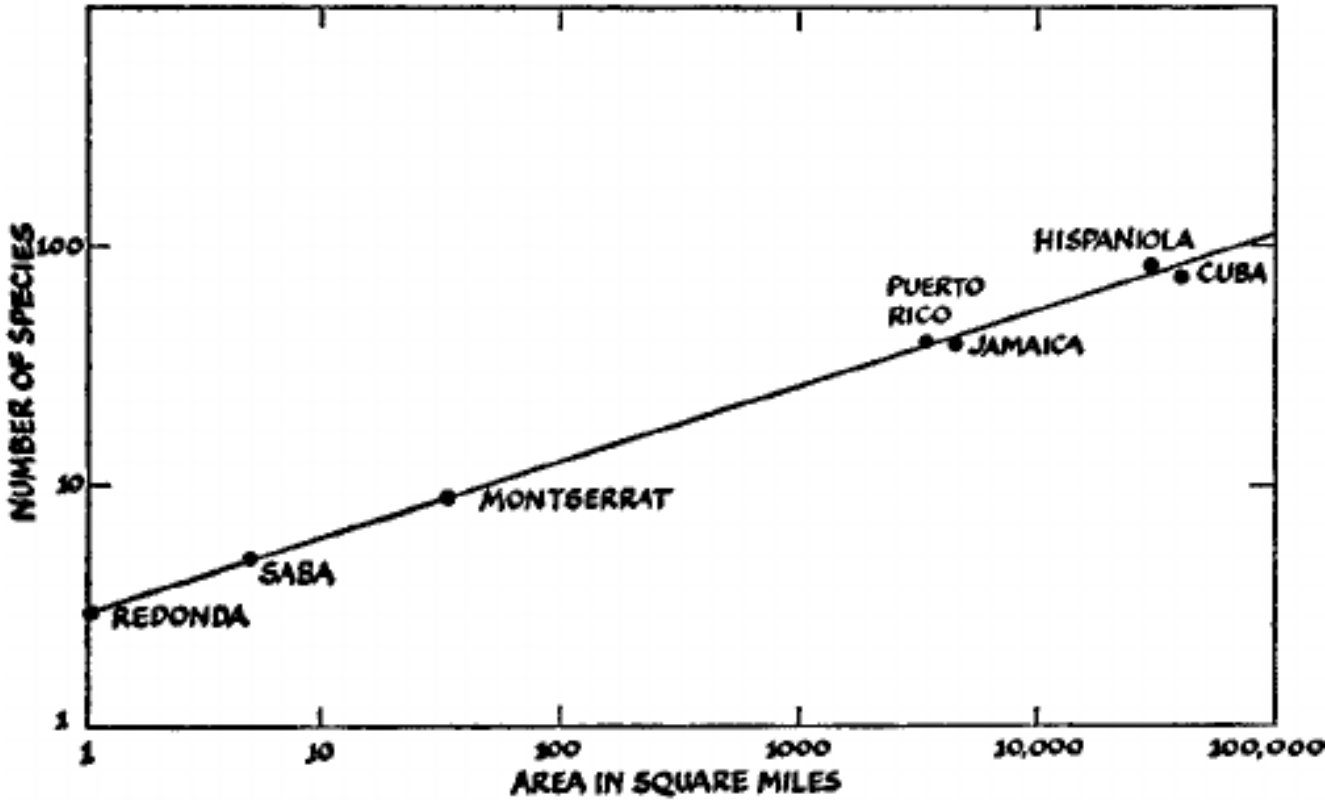
Malthus – population dynamics: logistic models



$$\frac{dN}{dt} = \frac{rN(K-N)}{K},$$

x = N/K

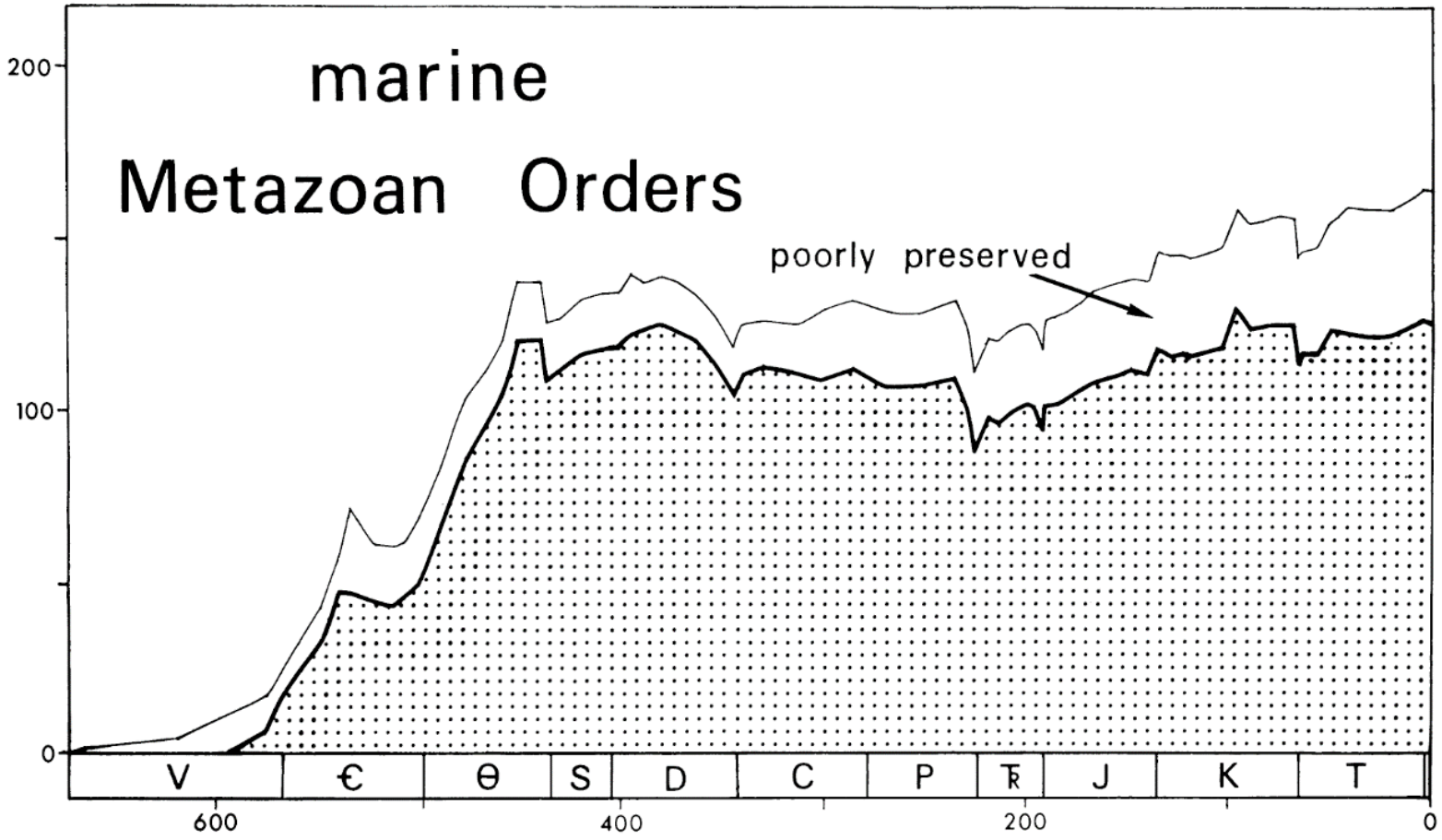
$$x(t) = \frac{1}{1+\left(\frac{1}{x_0}-1\right)e^{-rt}}.$$



McArthur and Wilson (1967) – Island biogeography

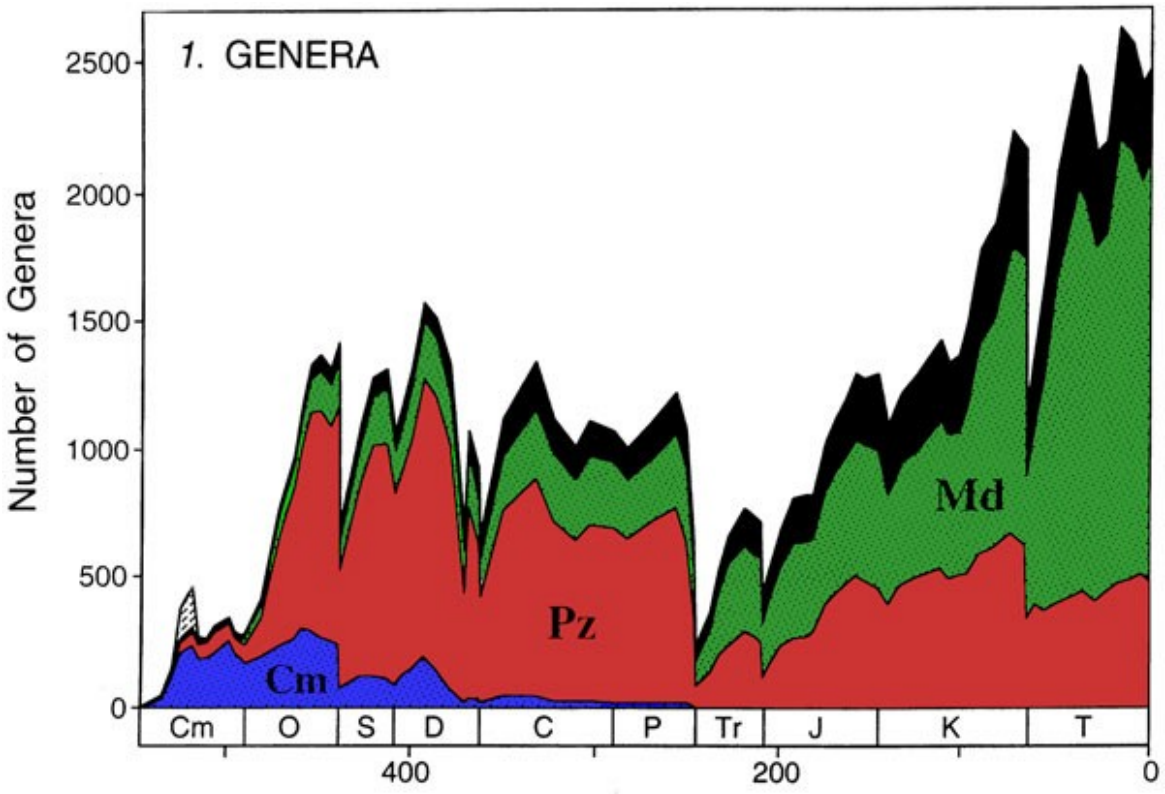
Metazoan orders (Raup and Sepkoski, 1978)

Equilibrium?

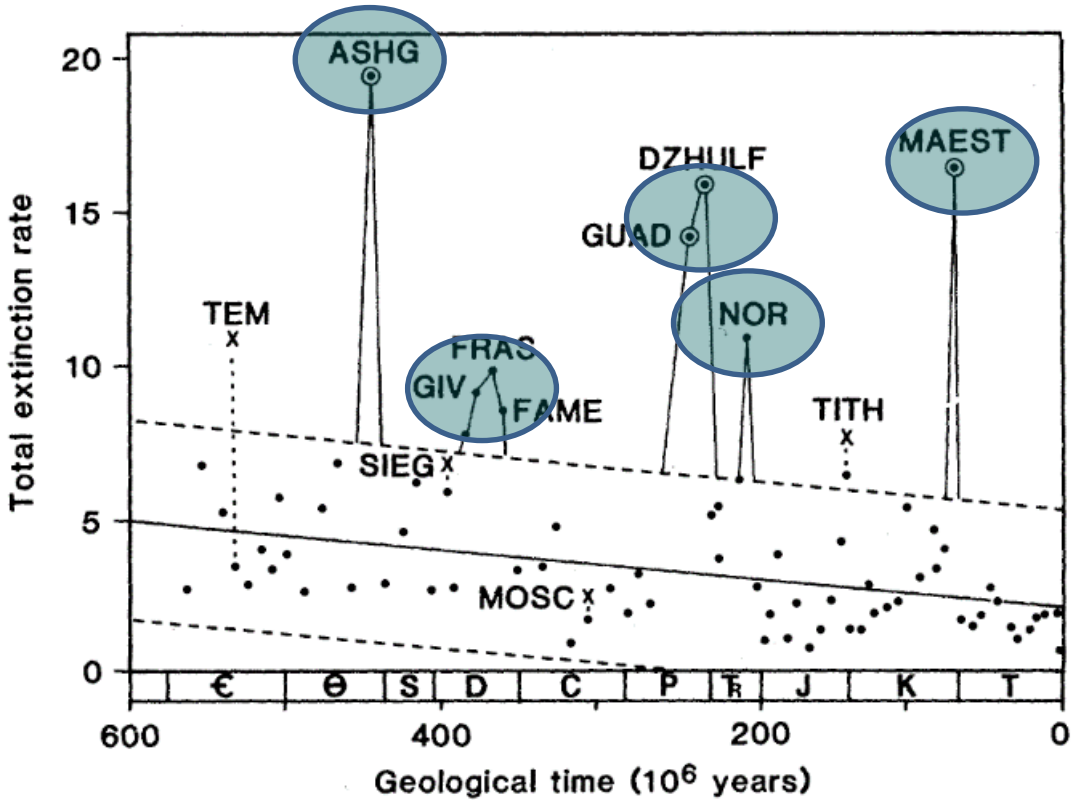


Genera

More complex patterns



Sepkoski (2002 state)

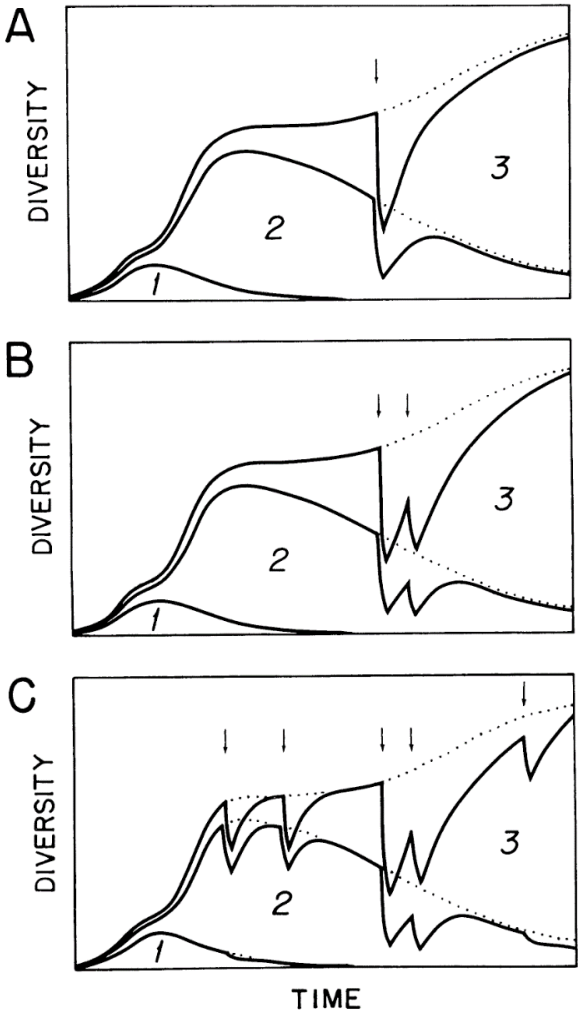


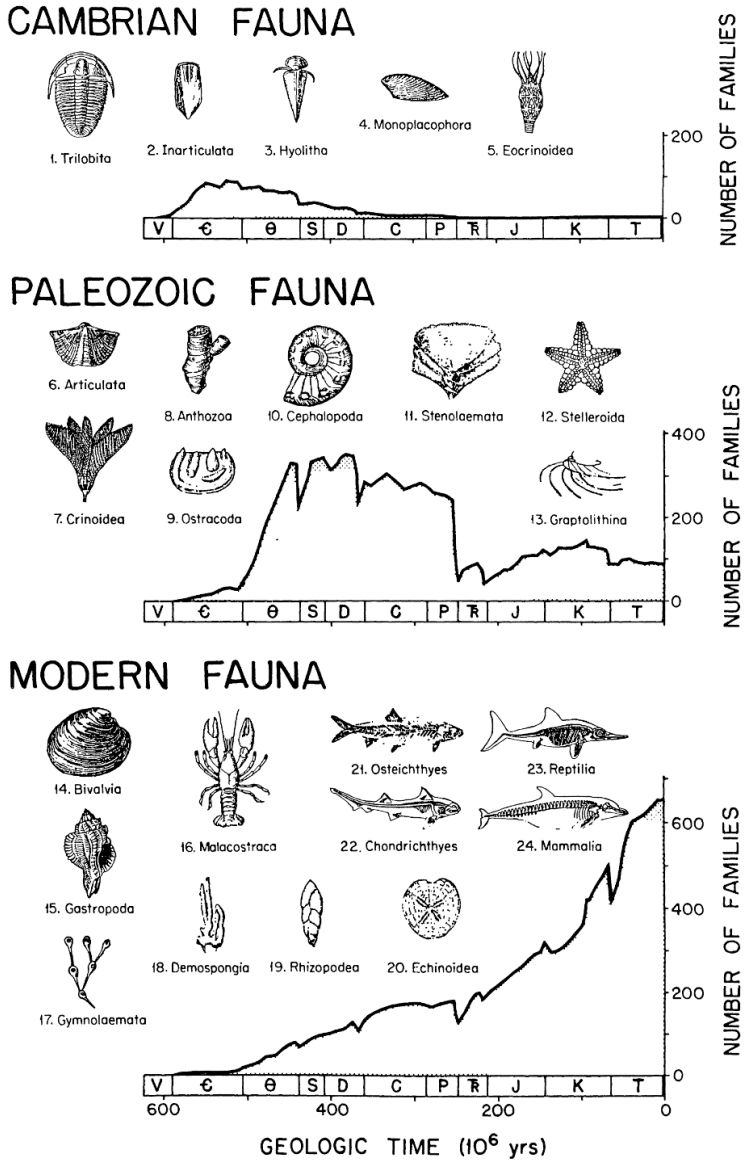
Mass extinctions
(Raup and Sepkoski 1982)

Evolutionary Faunas

Logistic diversification

- Sepkoski 1978, 1982, 1984
- Groups based on factor analysis of diversity
- Simple numeric modelling

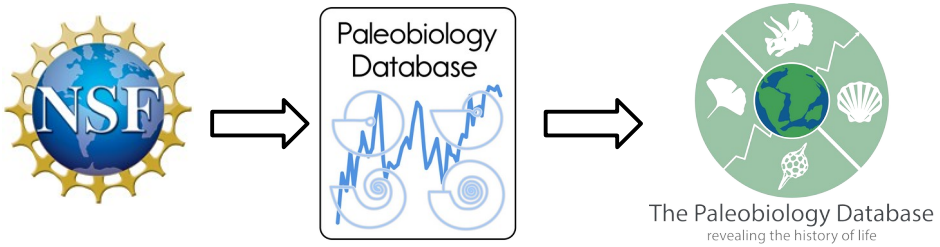


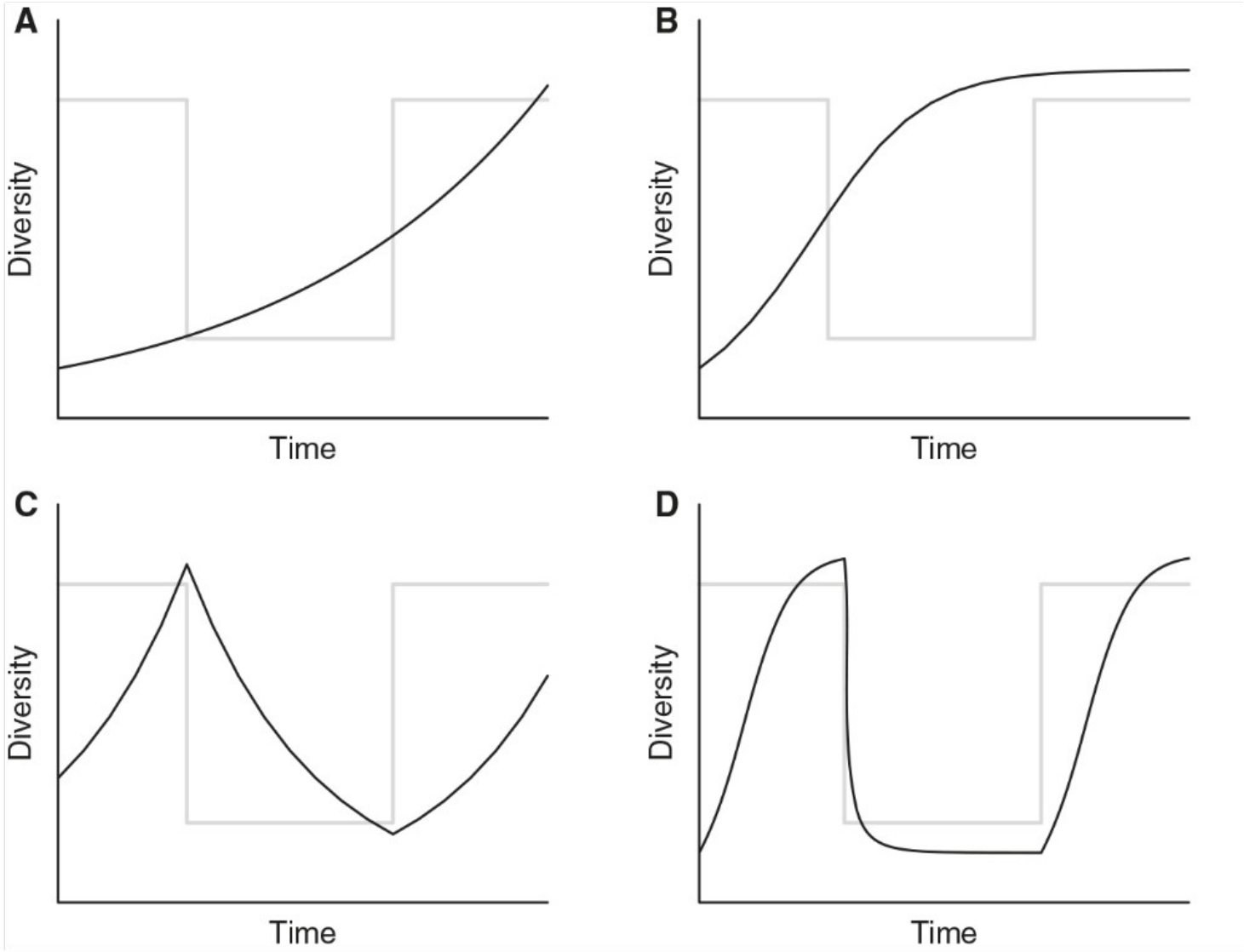


Overall dynamics

Logistic or exponential?

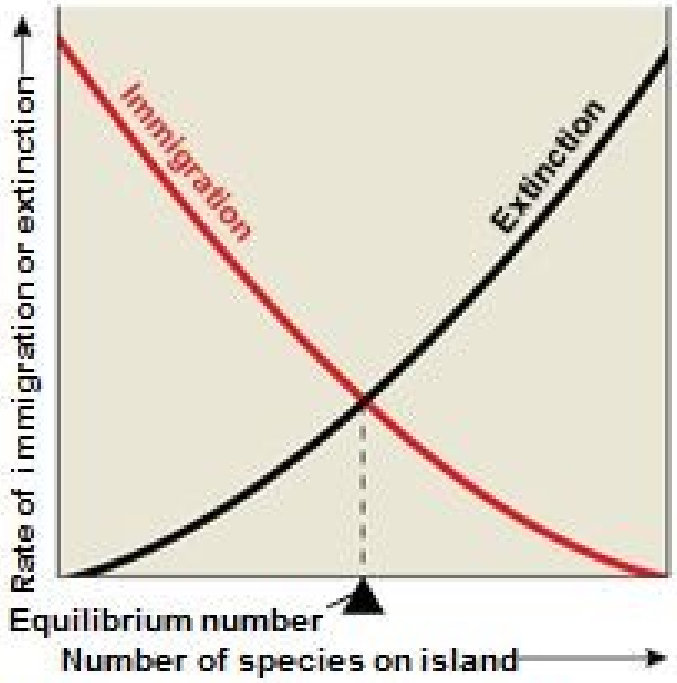
- Biotic vs. abiotic controls of diveristy?
- Marine Paleofaunal database (Alroy and Marshall 1998)



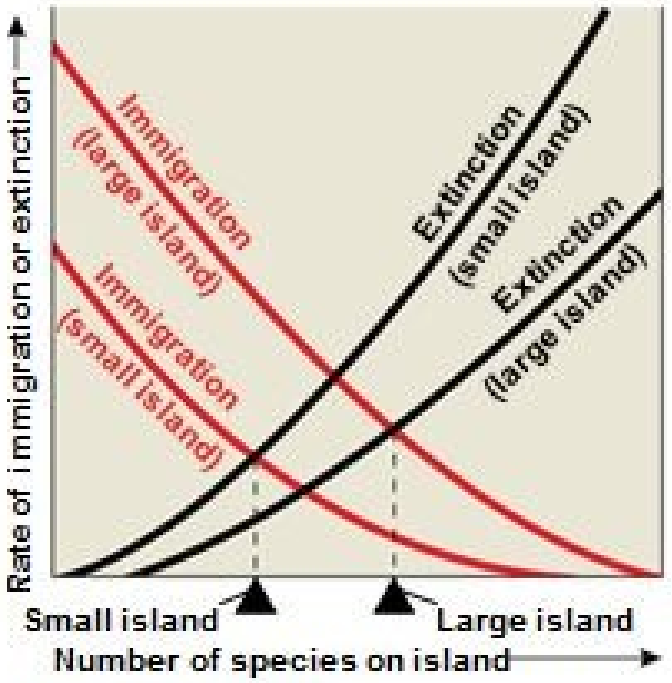


Dynamics in detail: turnover

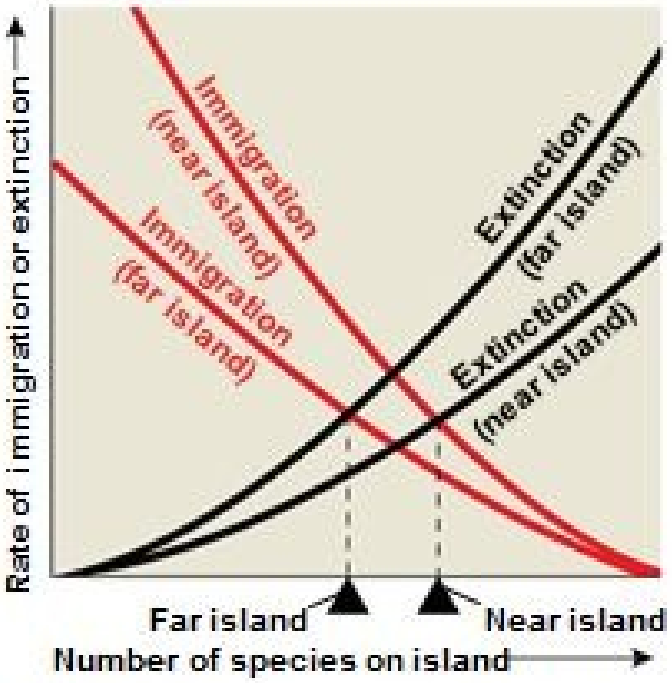
Equilibrium dynamics in island biogeography



(a) Immigration and extinction rates



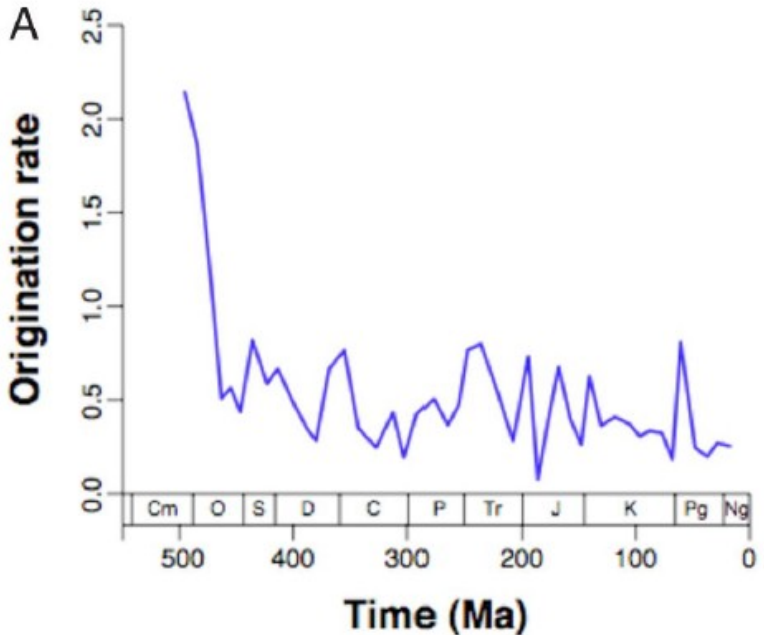
(b) Effect of island size



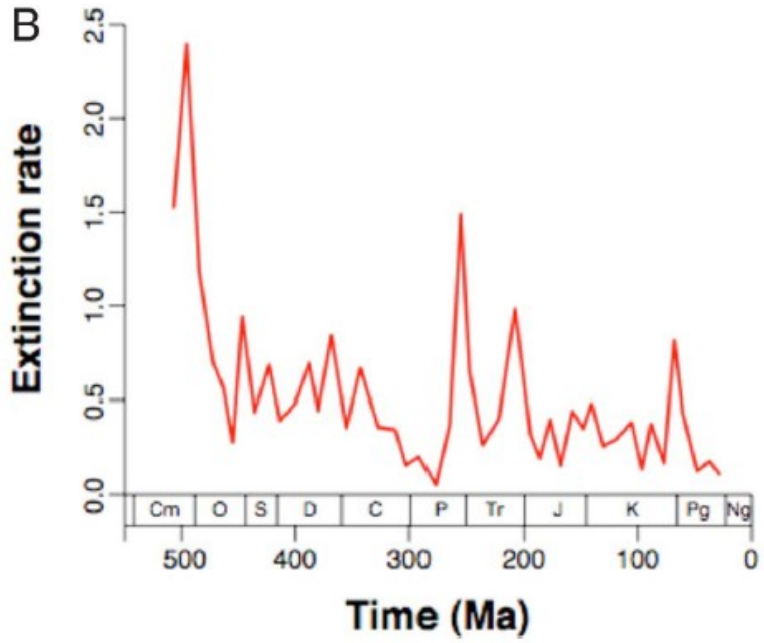
(c) Effect of distance from mainland

Dynamics in detail: turnover

Dynamics over time?



Additions to taxic diversity

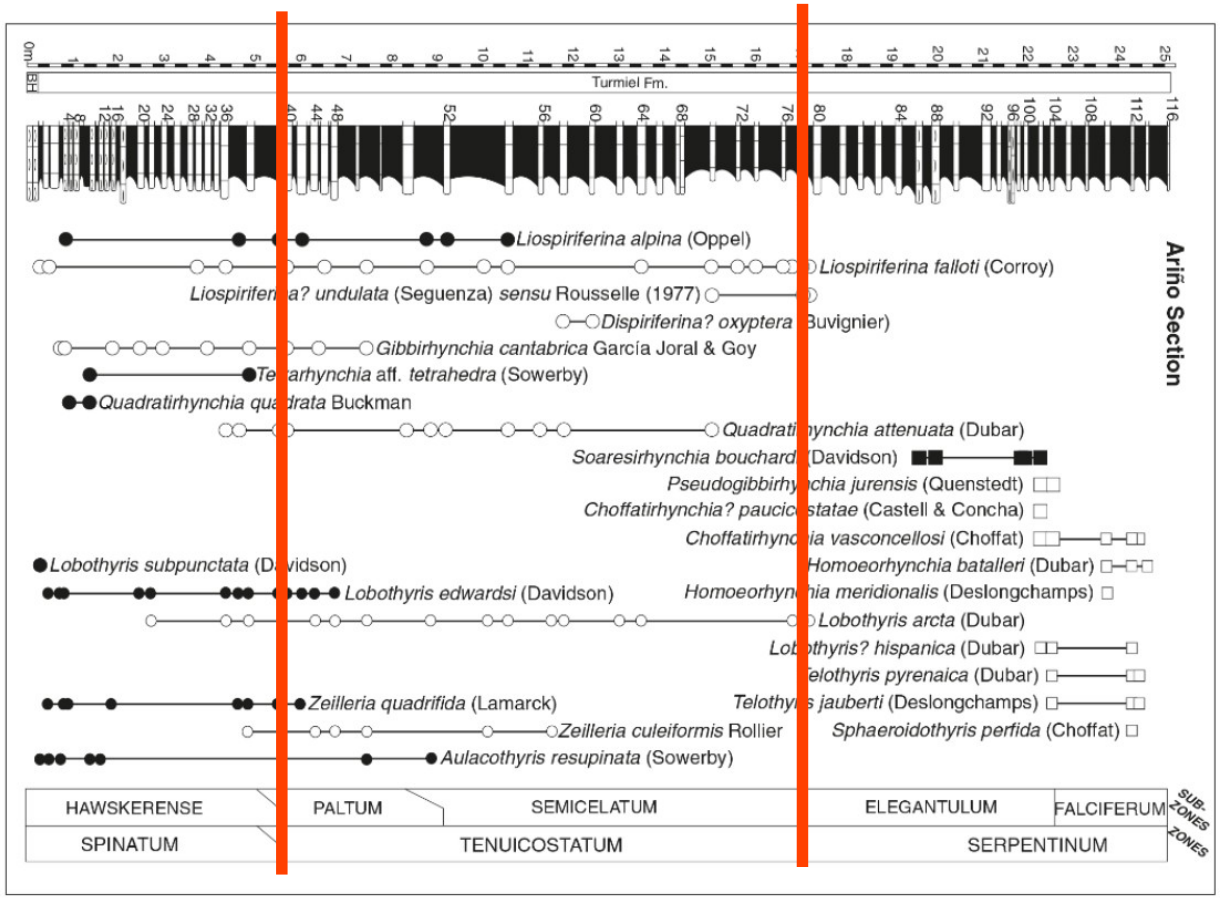


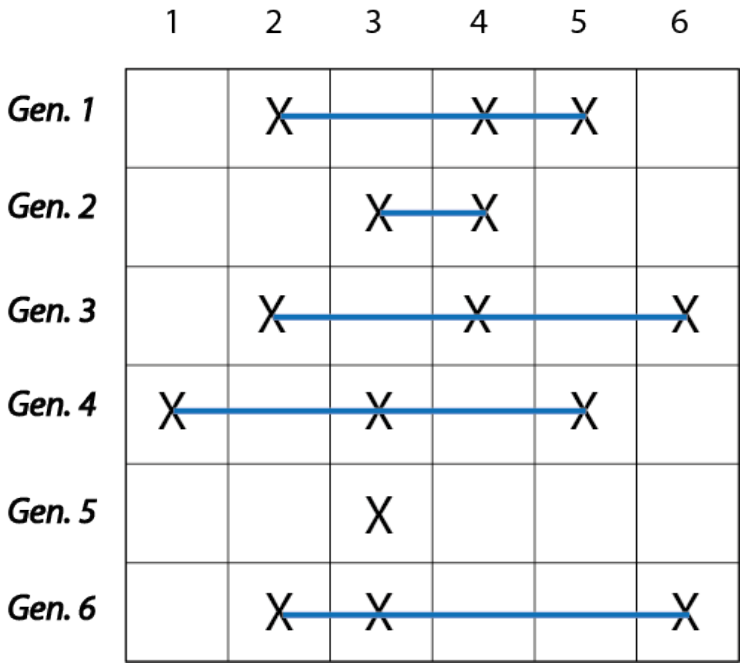
Subtraction from taxic diversity

Metrics of diversity and turnover

Where, what, why?

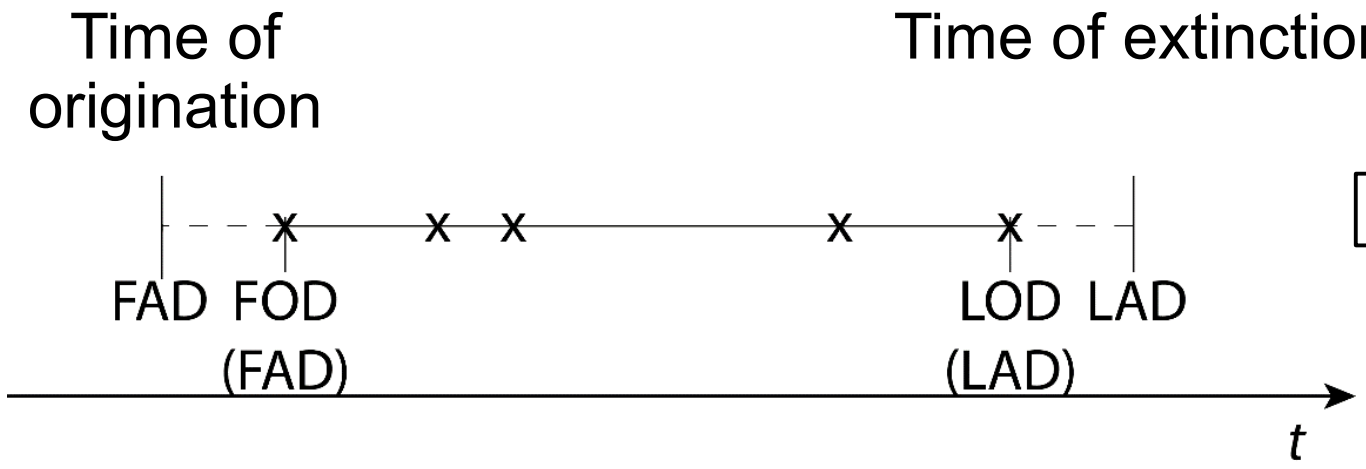
From original data...

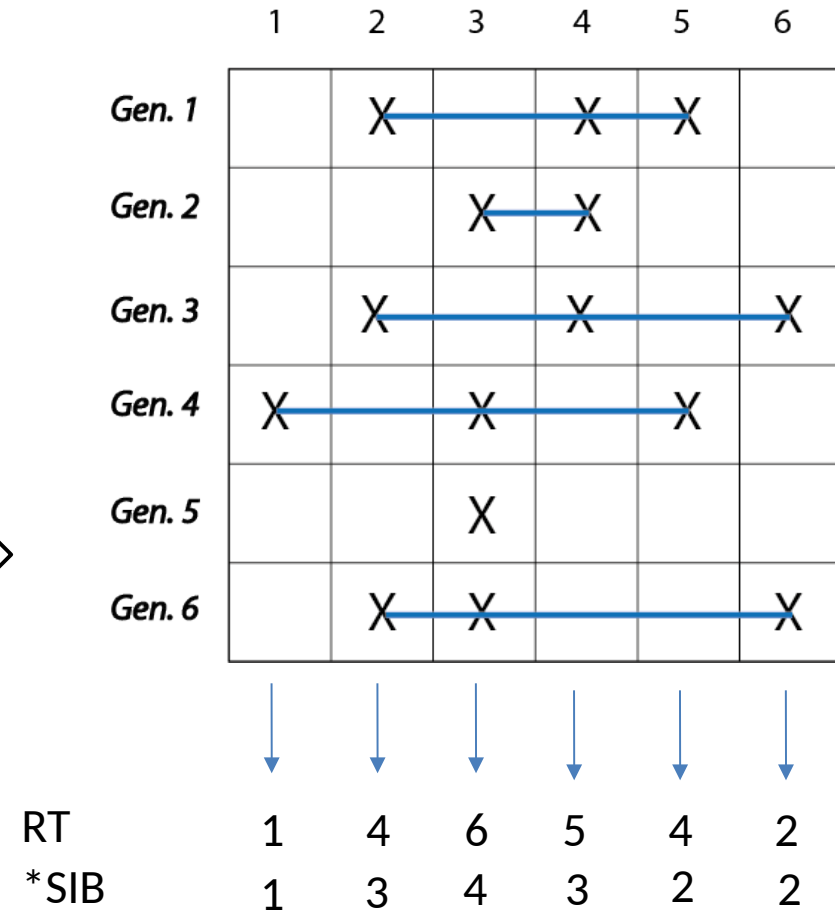




Source data ⇨ Temporal binning ⇨ Summary matrix

… to metrics

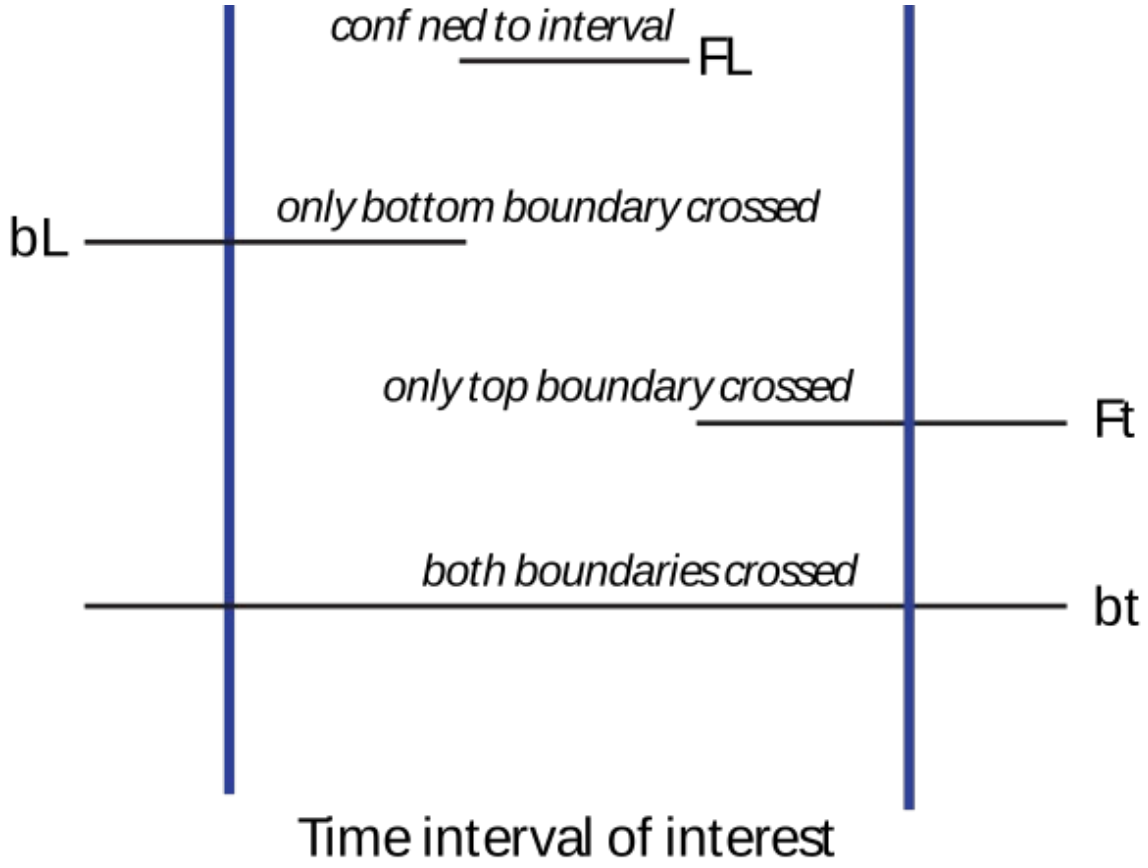




The range-through (RT) assumption

Range-based methods

The per capita rates: categories (Foote, 2000)

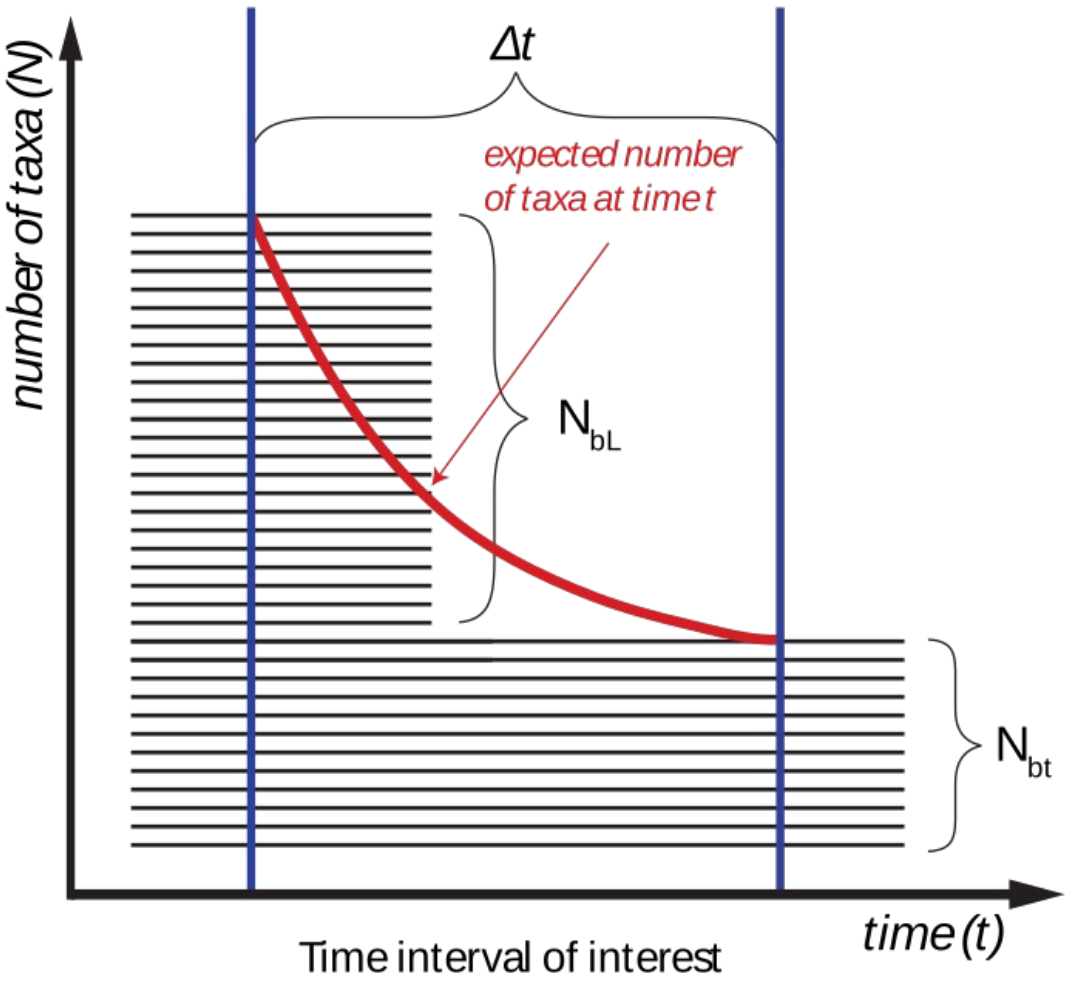


Range-based methods

The per capita rates: idea (extinction)

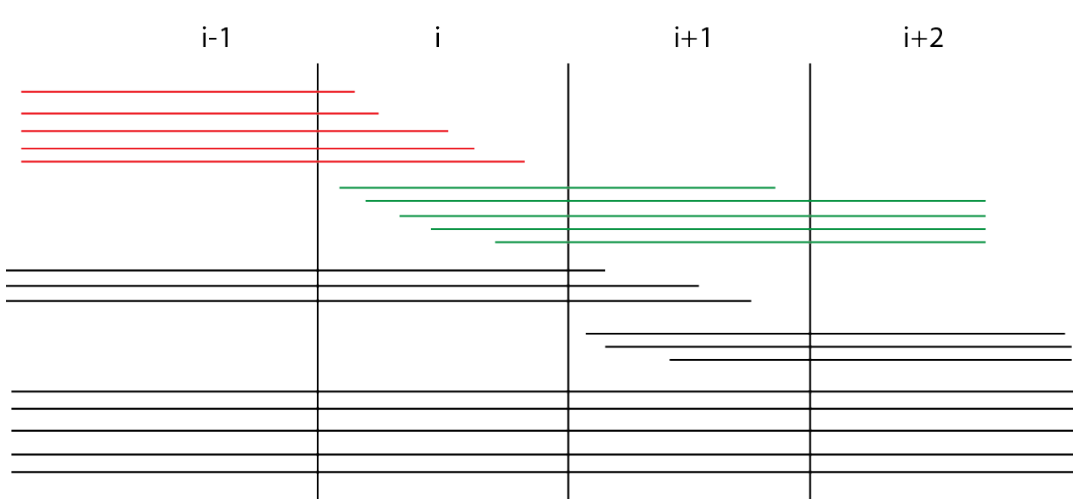
- We do not know the precise date of extinction
- We assume a constant chance for species to go extinct in the bin
- The extinction rate becomes

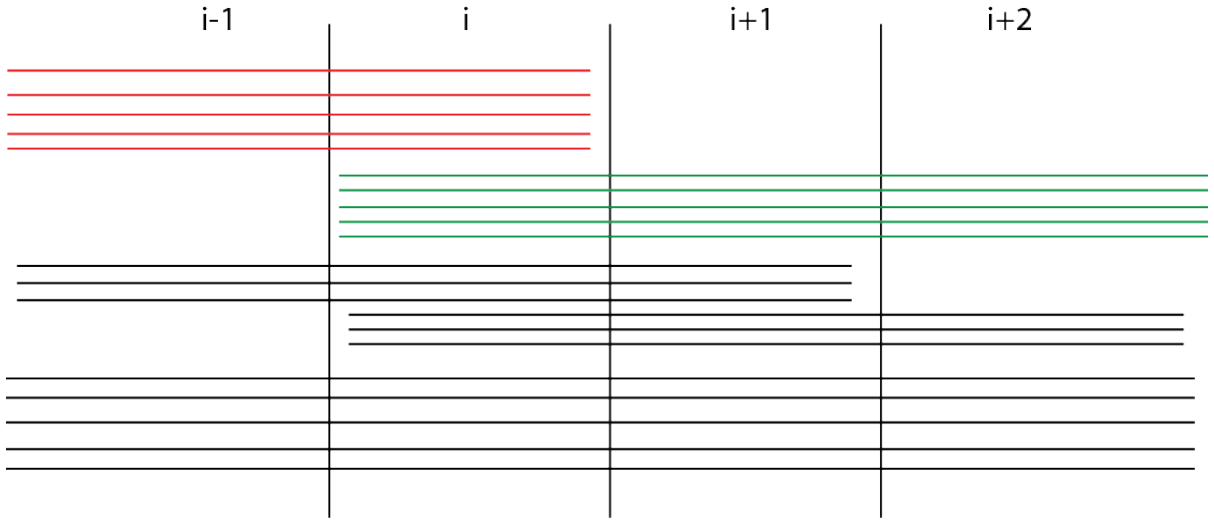
$$- \log(N_{bL} / N_{bt} + N_{bL}) / \Delta t$$



Time bins

Distribution of turnover





Continuous turnover

$- \log(N_{bL} / N_{bt} + N_{bL}) / \Delta t$

Pulsed turnover

$- \log(N_{bL} / N_{bt} + N_{bL})$

Based on (Foote 2005)

Time bins

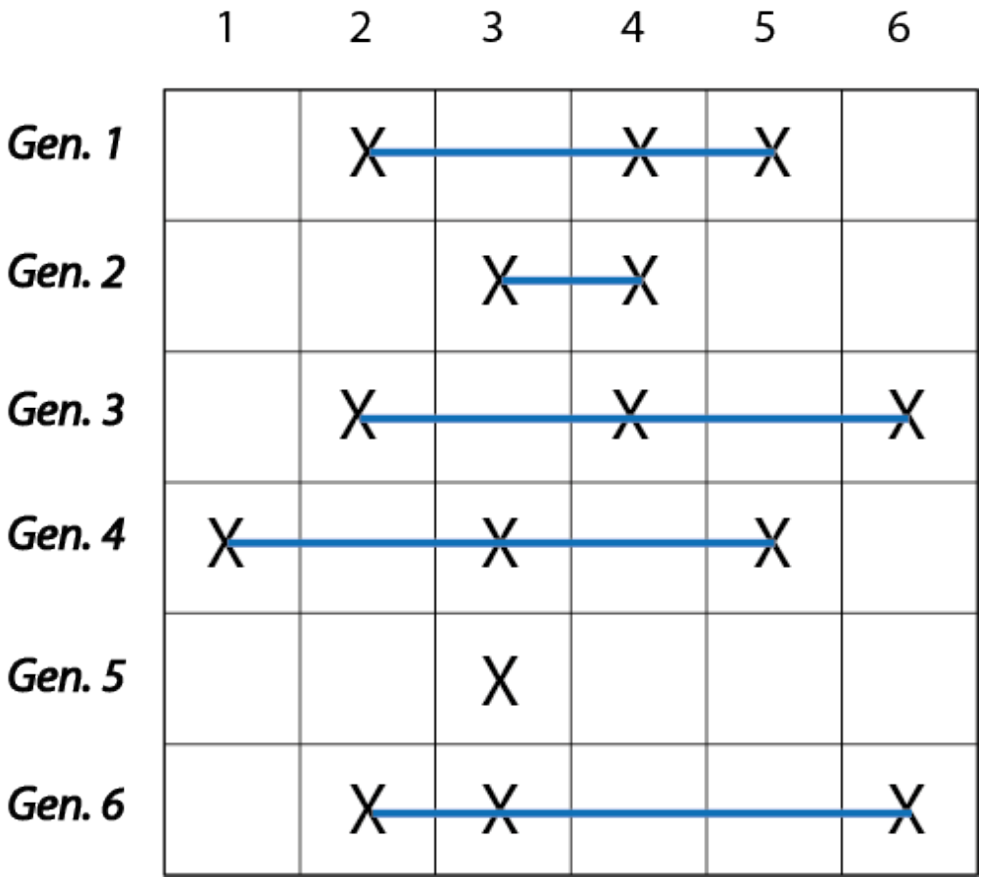
Distribution of turnover

- Stages vary quite much (95-bin time scale)
- The 10/11My time scale of the PBDB (49-bin time scale)
- Coarser, weaker filter on stratigraphy

row.names	X10	bottom	mid	top	dur	ten
30	Jurassic 1	199.60	194.60	189.60	10.00	30
31	Jurassic 2	189.60	186.30	183.00	6.60	31
32	Jurassic 3	183.00	177.30	171.60	11.40	32
33	Jurassic 4	171.60	168.15	164.70	6.90	33
34	Jurassic 5	164.70	157.75	150.80	13.90	34
35	Jurassic 6	150.80	148.15	145.50	5.30	35
36	Cretaceous 1	145.50	140.95	136.40	9.10	36
37	Cretaceous 2	136.40	130.70	125.00	11.40	37
38	Cretaceous 3	125.00	118.50	112.00	13.00	38
39	Cretaceous 4	112.00	105.80	99.60	12.40	39
40	Cretaceous 5	99.60	96.55	93.50	6.10	40
41	Cretaceous 6	93.50	88.50	83.50	10.00	41
42	Cretaceous 7	83.50	77.05	70.60	12.90	42
43	Cretaceous 8	70.60	68.05	65.50	5.10	43
44	Cenozoic 1	65.50	60.65	55.80	9.70	44
45	Cenozoic 2	55.80	48.10	40.40	15.40	45
46	Cenozoic 3	40.40	37.15	33.90	6.50	46
47	Cenozoic 4	33.90	28.45	23.00	10.90	47
48	Cenozoic 5	23.00	17.30	11.60	11.40	48
49	Cenozoic 6	11.60	5.81	0.01	11.59	49

Range-based methods

The record is gappy!

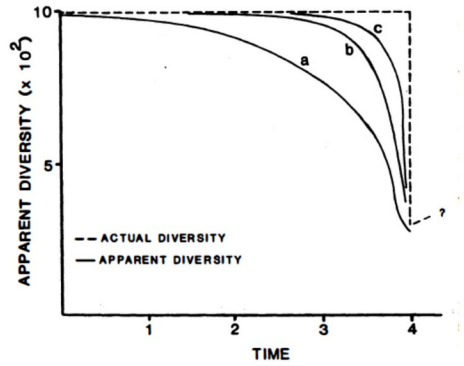


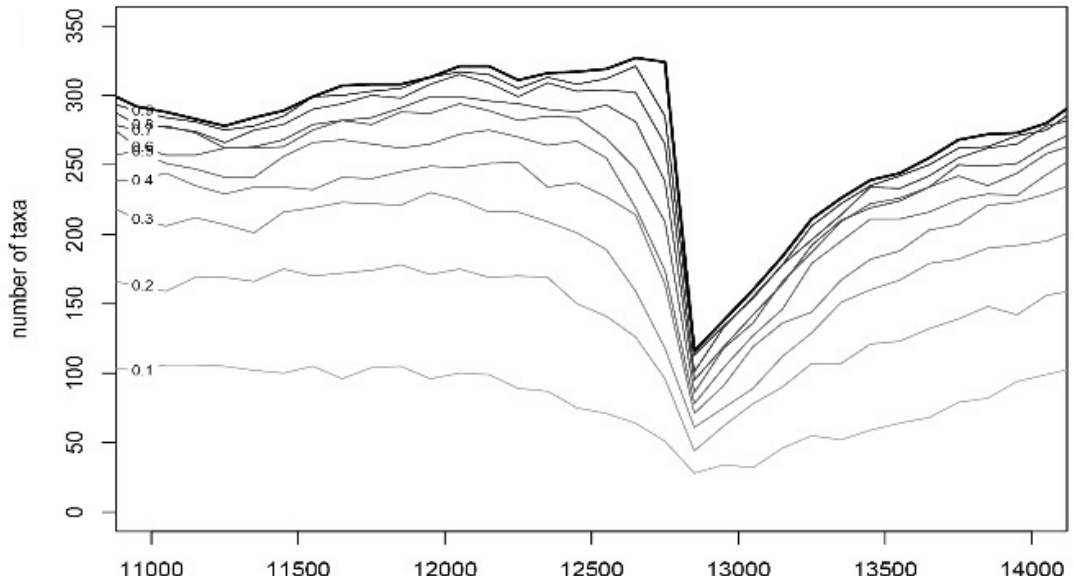
Overall gappiness (Paul 1982):

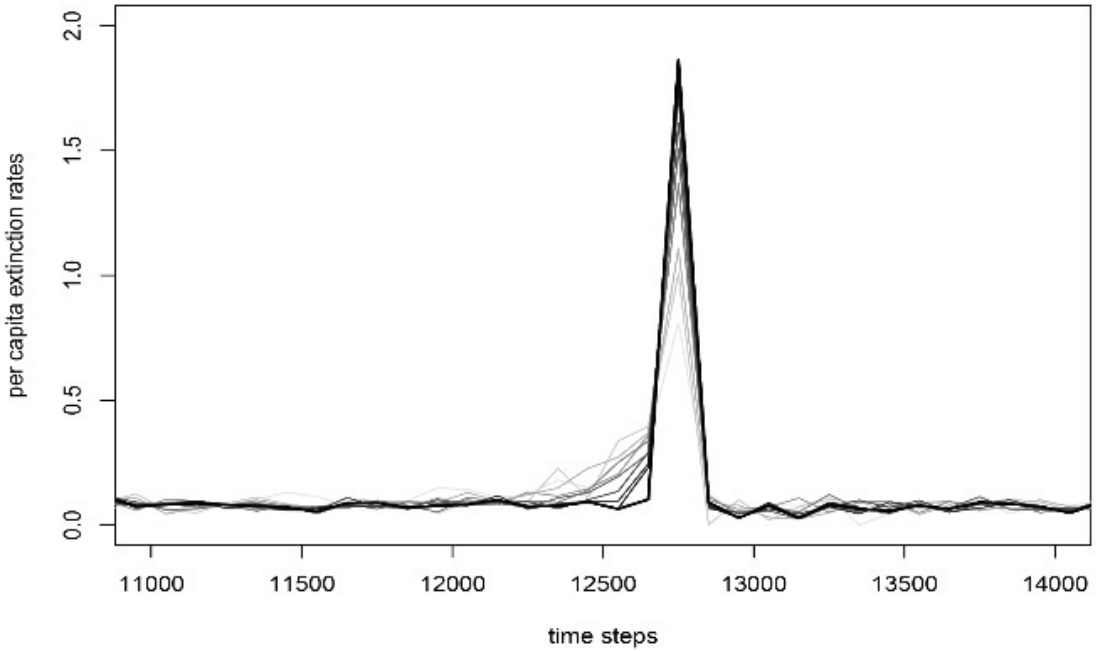
sampling events vs. opportunities

Range-based methods

Issues: The Signor-Lipps effect (1982)







Number of taxa

Extinctions

Range-based methods

Issues: Edge effects (Foote 2000)

- Extinction increases towards the end
- Origination increases towards the beginning
- + The Pull of the Recent (*abnormally good preservation at the end increases diversity and dampens extinction in recent organisms included*)

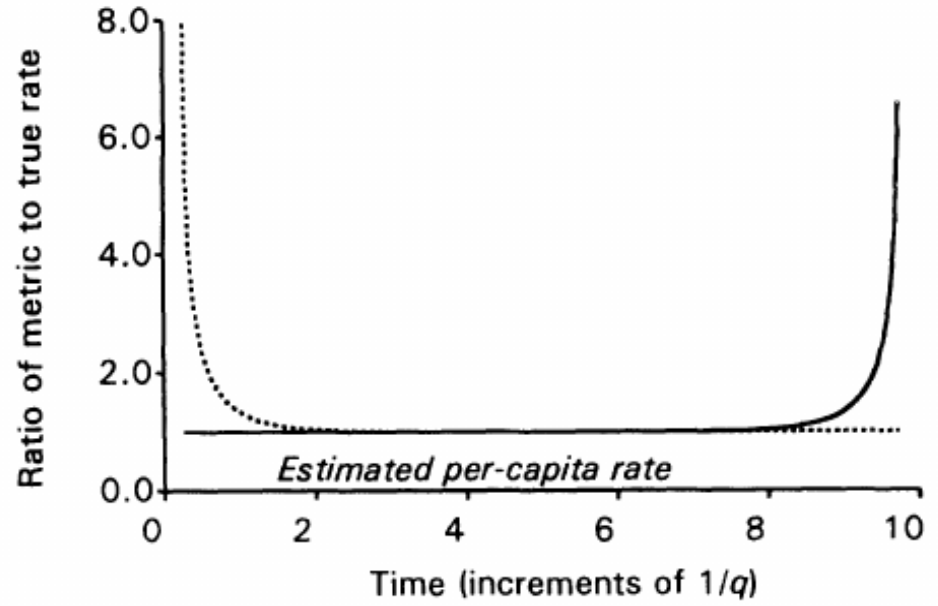
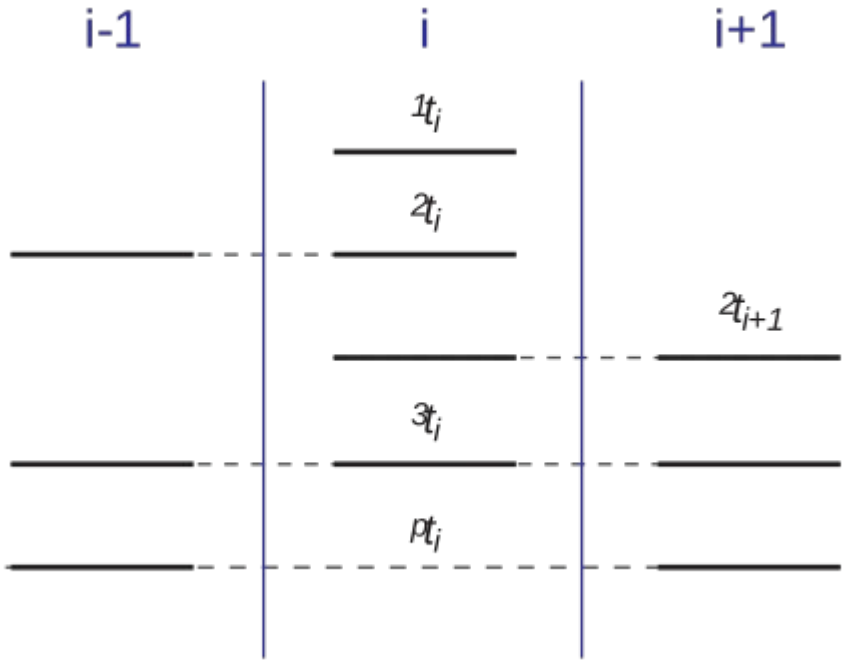


FIGURE 7. Edge effects on taxonomic rate metrics. In all cases $p = q$, $r = q$, and interval length is equal to $0.5/q$. Solid line, extinction metric; dotted line, origination metric. All rate metrics except estimated per-capita rate are affected at both edges.

Incidence-based methods

John Alroy's idea: use a moving window



$^{1}t_i$: single interval pattern

$^{2}t_i$:lower two-timer pattern

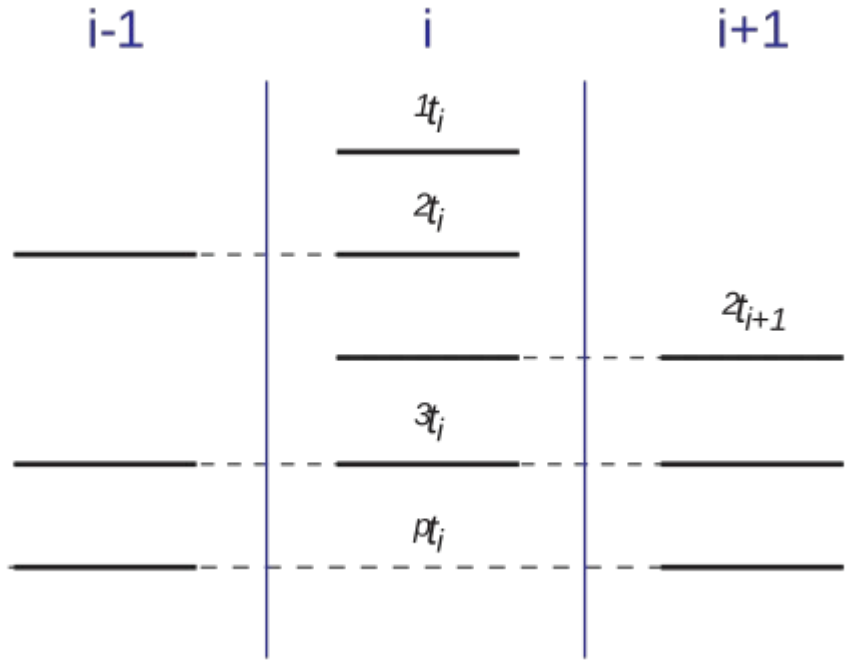
$^{2}t_{i+1}$: upper two-timer pattern

$^{3}t_i$: three-timer pattern

$^{p}t_i$: part-timer pattern

Incidence-based methods

John Alroy's idea: use a moving window



$\log({}^{2}t_i/{}^{3}t_i)$: extinction rate

$\log({}^{2}t_{i+i}/{}^{3}t_i)$: origination rate

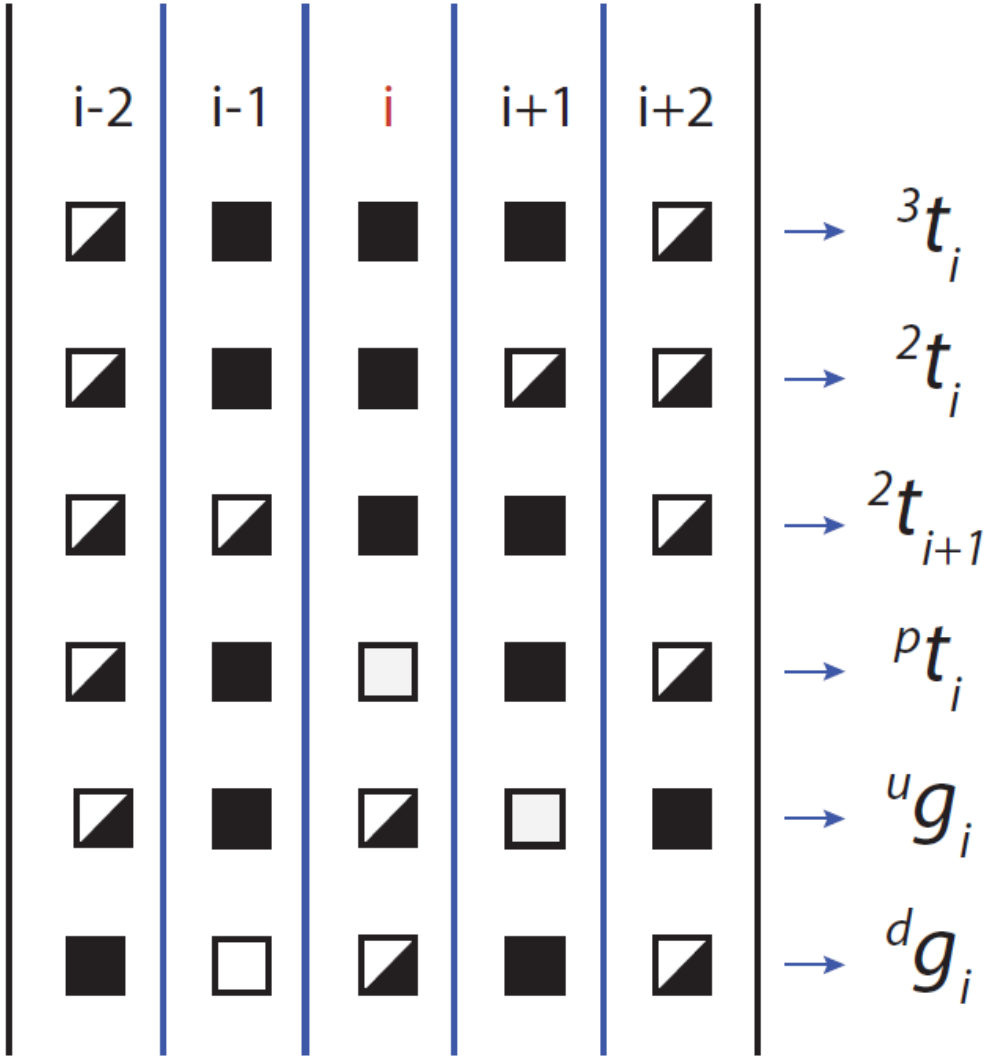
${}^{3}t_i/({}^{3}t_i + {}^{p}t_i)$: three-timer sampling completeness

Corrected SIB: SIB / ${}^{3}t_i/({}^{3}t_i + {}^{p}t_i)$

Incidence-based methods

John Alroy's idea: use a moving window

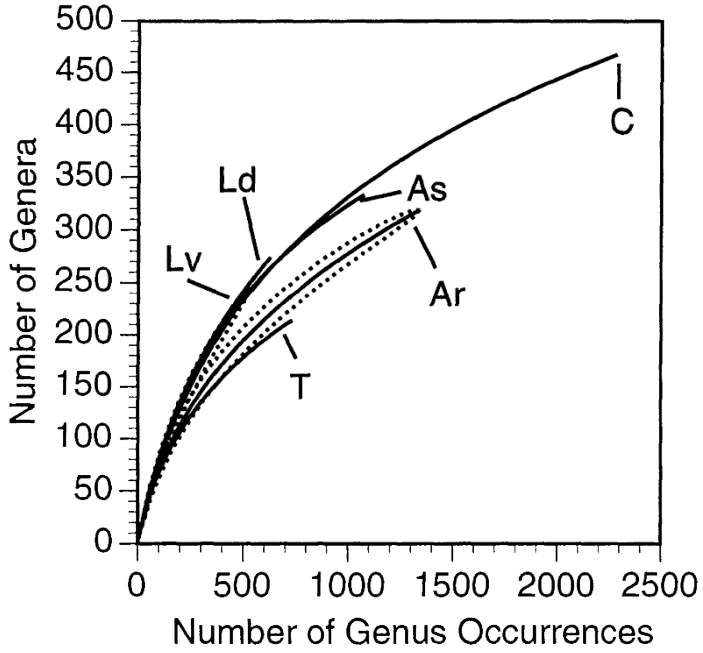
- 3 Major updates
  - Corrected three-timer rates (Alroy 2008)
  - Gap-filler rates (Alroy 2014)
  - 2nd-for 3rd substitution rates Alroy (2015)

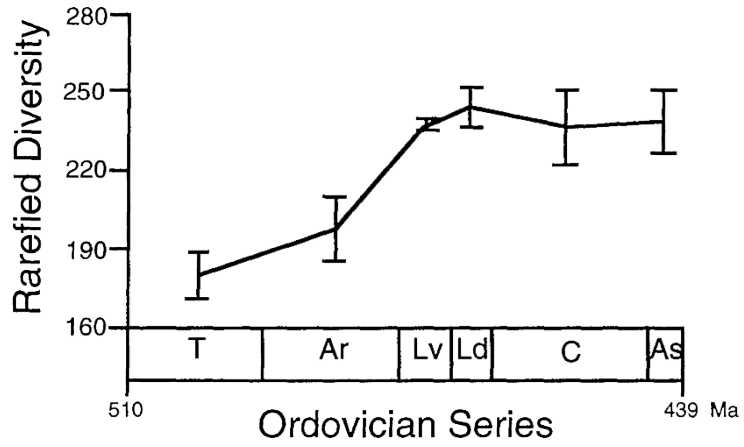


Subsampling

The metrics account for issues due to *random* sampling

- Sampling change from one bin to bin
- How do the patterns look like, when the sampling intensity is equal?
- Use it as a sensitivity analysis tool! Does it affect your hypothesis?



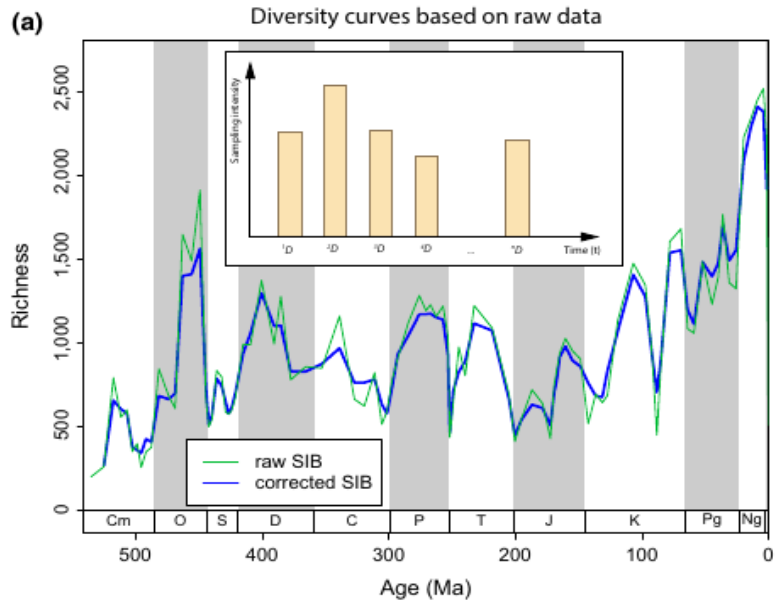


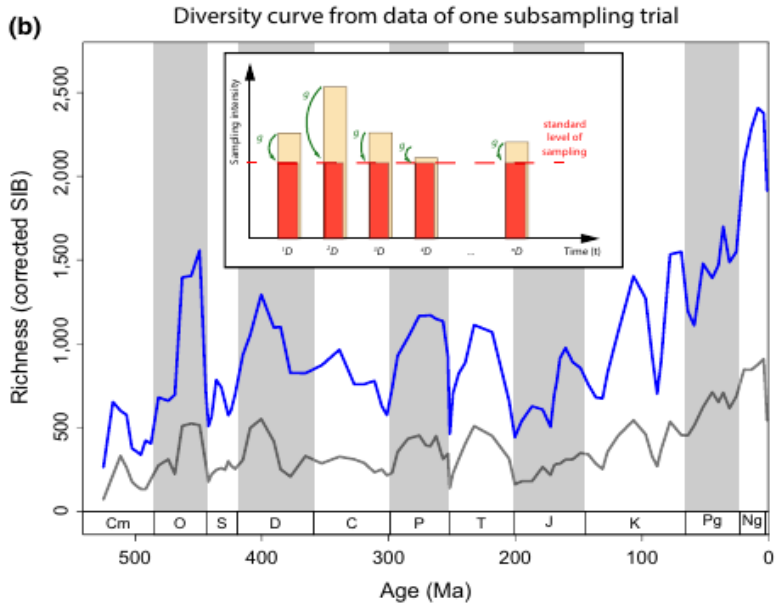
Miller and Foote (1996)

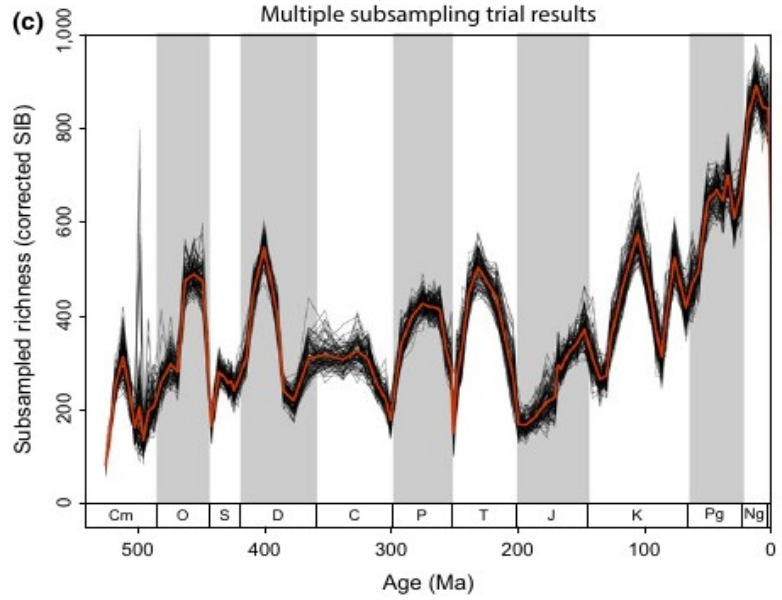
Subsampling: example

Calculating diversity

- The methods depend on the entire dataset!
- One replicate is based on combination of data from multiple bins







Adam’s impressions

John Alroy’s idea: use a moving window to get rid smearing

- The methods converge with perfect sampling!
- Use per-capita rates for initial analysis, they conserve the most information
- The Three-time approach is designed to be less affected by smearing effects, use the most up-to-date (e.g. for extinction assessment)

This is not all… why?

There are multiple approaches to getting to these dimensions

- Comparability with previous results
- **Computationally very efficient (simple)**
- Might not be the best...
  - **Capture-Mark-Recapture**: estimates sampling the same time as the rest
  - **Phylogenetic Approaches:** more explicit assumptions on the process creating lineages

About divDyn

A very short story and basics

Why

In Erlangen and Sydney? (2014)

- Workflow from Wolfgang Kiessling
- Based on discrete temporal bins
- Motivation: reproducibility!
- Based on interactions in Erlangen and Sydney (2014)
- Published in 2019 – Kocsis et al.

GitHub https://divdyn.github.io/r-package/

What?

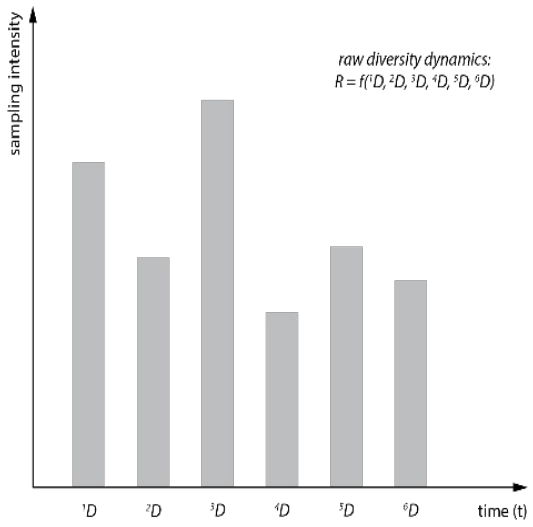
Basic turnover and diversity metrics

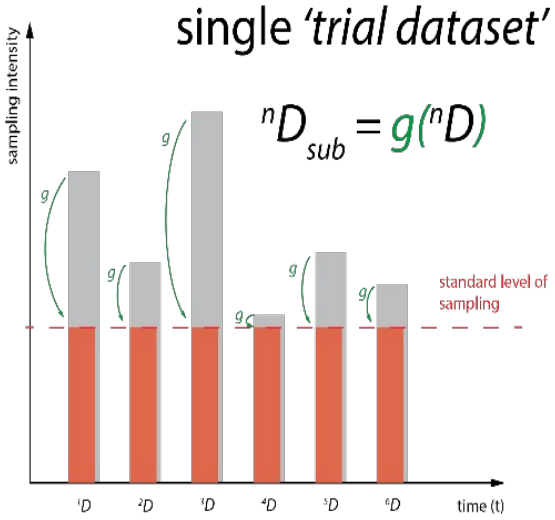
- Traditional/counting approaches
- Subsampling wrappers

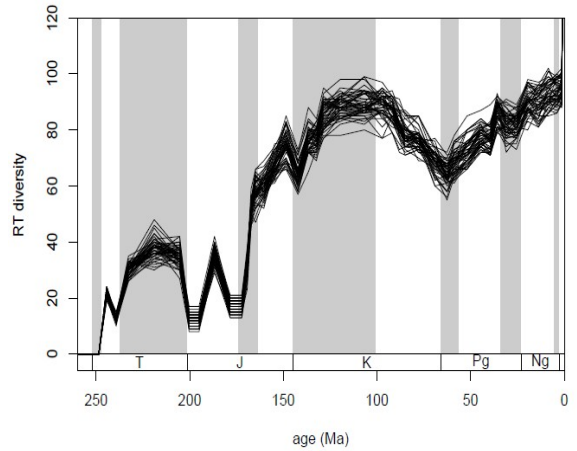
Variable name	Metric name	Type	Reference
`tSing, tOri, tExt, tThrough`	Range-based taxon patterns	Counts	Foote (1999)
`t2d, t2u, t3, tPart, tGFu, tGFd`	Occurrence-based taxon patterns	Counts	Alroy (2008, 2014)
`extProp, oriProp`	Proportional extinctions and originations	Turnover	Newell (1952)
`extPC, oriPC`	Per capita extinction and origination rates	Turnover	Foote (1999); Alroy (1996)
`ext3t, ori3t`	Three-timer extinction and origination rates	Turnover	Alroy (2008)
`extC3t, oriC3t`	Corrected three-timer extinction and origination rates	Turnover	Alroy (2008)
`extGF, oriGF`	Gap-filler extinction and origination rates	Turnover	Alroy (2014)
`ext2f3, ori2f3`	Second-for-third substitution extinction and origination rates	Turnover	Alroy (2015)
`divSIB`	Sampled-in-bin diversity (SIB)	Richness	Miller and Foote (1996)
`divRT`	Range-through diversity (RT)	Richness	Newell (1952)
`divBC`	Boundary-crosser diversity (BC)	Richness	Carr and Kitchell (1980)
`divCSIB`	Corrected sampled-in-bin diversity	Richness	Alroy et al. (2008)
`samp3t`	Three-timer sampling completeness	Sampling completeness	Alroy (2008)
`sampRange`	Range-based sampling completeness	Sampling completeness	Foote and Miller (2007)

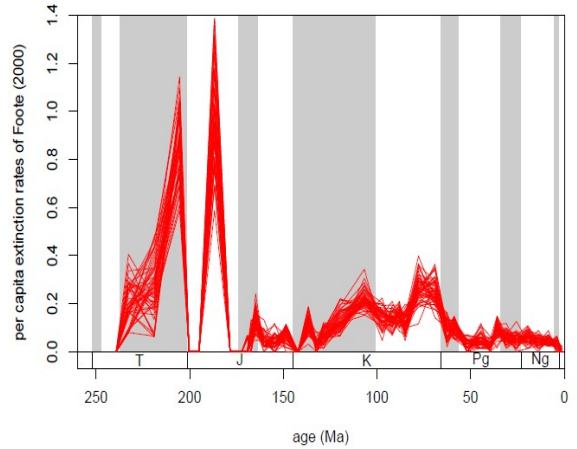
What it does

Subsampling









$R_{raw} = f(^1D, ^2D, ^3D, ^4D, ^5D, ^6D)$

f:= applied function
(e.g. `divDyn()`)

${}_1R_{sub} = f(g(^1D), g(^2D), \ldots g(^6D))$

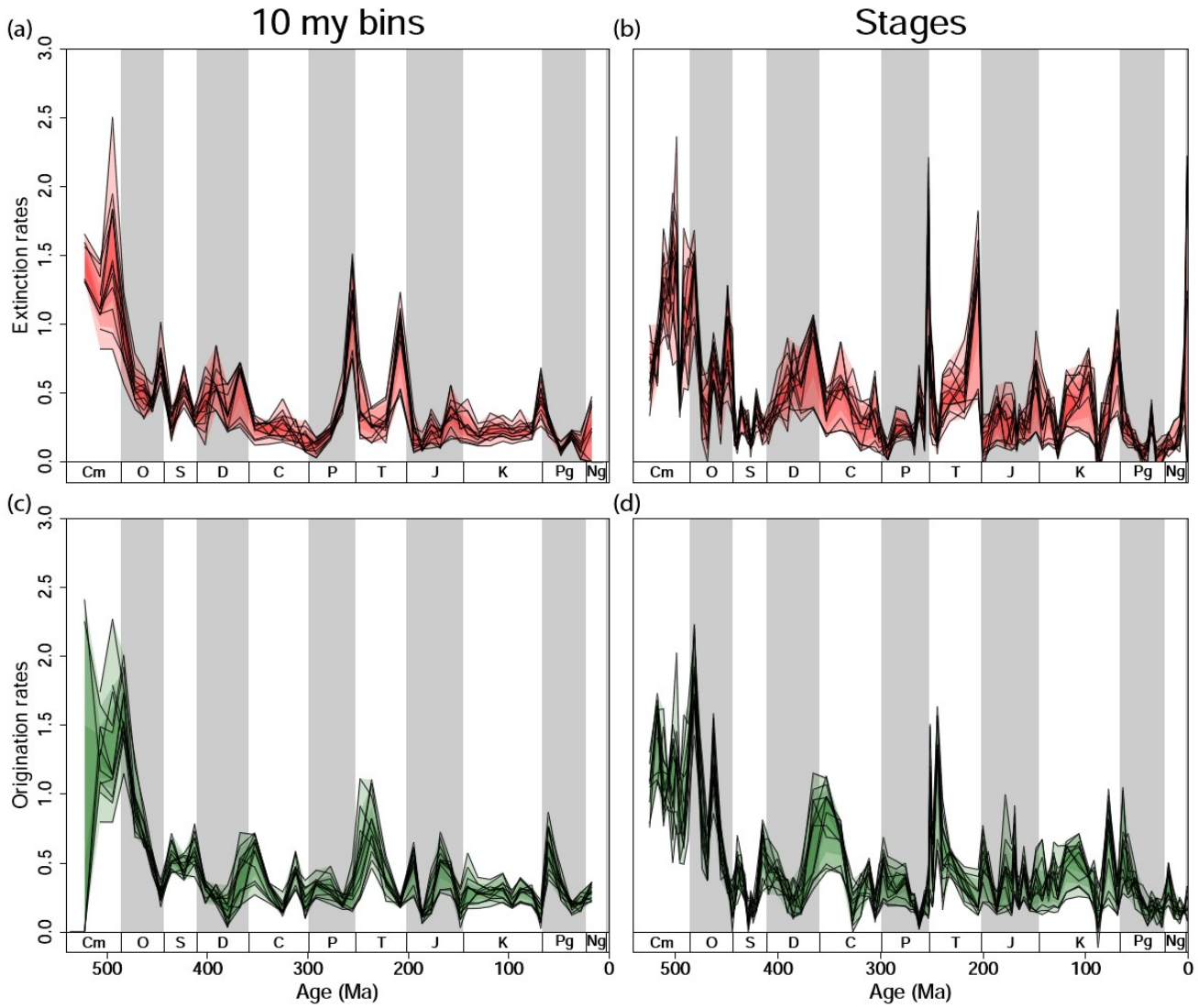
g:= subsampler function

Repeated, variation of
R_{sub}

Examples

Phanerozoic diversity and turnover

- Desperate attempt at reproducibility
- Taxonomic environmental scope similar to Sepkoski's compendium



Examples

The Corals example

Zooxanthellate (Z)

Azooxanthellate (AZ + AP)

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DOI: 10.1017/pab.2015.6

Biodiversity dynamics and environmental occupancy of fossil azooxanthellate and zooxanthellate scleractinian corals

Wolfgang Kiessling and Ádám T. Kocsis

Abstract.—Scleractinian corals have two fundamentally different life strategies, which can be inferred from morphological criteria in fossil material. In the non-photosymbiotic group nutrition comes exclusively from heterotrophic feeding, whereas the photosymbiotic group achieves a good part of its nutrition from algae hosted in the coral's tissue. These ecologic differences arose early in the evolutionary history of corals but with repeated evolutionary losses and presumably also gains of symbiosis since then. We assessed the biodiversity dynamics and environmental occupancy of both ecologic groups to identify times when the evolutionary losses of symbiosis as inferred from molecular analyses might have occurred and if these can be linked to environmental change. Two episodes are likely: The first was in the mid-Cretaceous when non-symbiotic corals experienced an origination pulse and started to become more common in deeper, non-reef habitats and on siliciclastic substrates initiating a long-term offshore trend in occupancy. The second was around the Cretaceous/Paleogene boundary with another origination pulse and increased occupancy of deep-water settings in the non-symbiotic group. Environmental factors such as rapid global warming associated with mid-Cretaceous anoxic events and increased nutrient concentrations in Late Cretaceous–Cenozoic deeper waters are plausible mechanisms for the shift. Turnover rates and durations are not significantly different between the two ecologic groups when compared over the entire history of scleractinians. However, the deep-water shift of non-symbiotic corals was accompanied by reduced extinction rates, supporting the view that environmental occupancy is a prominent driver of evolutionary rates.

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Future… divDyn 2.0

- Going fully spatial (loc =)
- Customizable subsampling (including spatial)
- Move more code to C++ - separate library