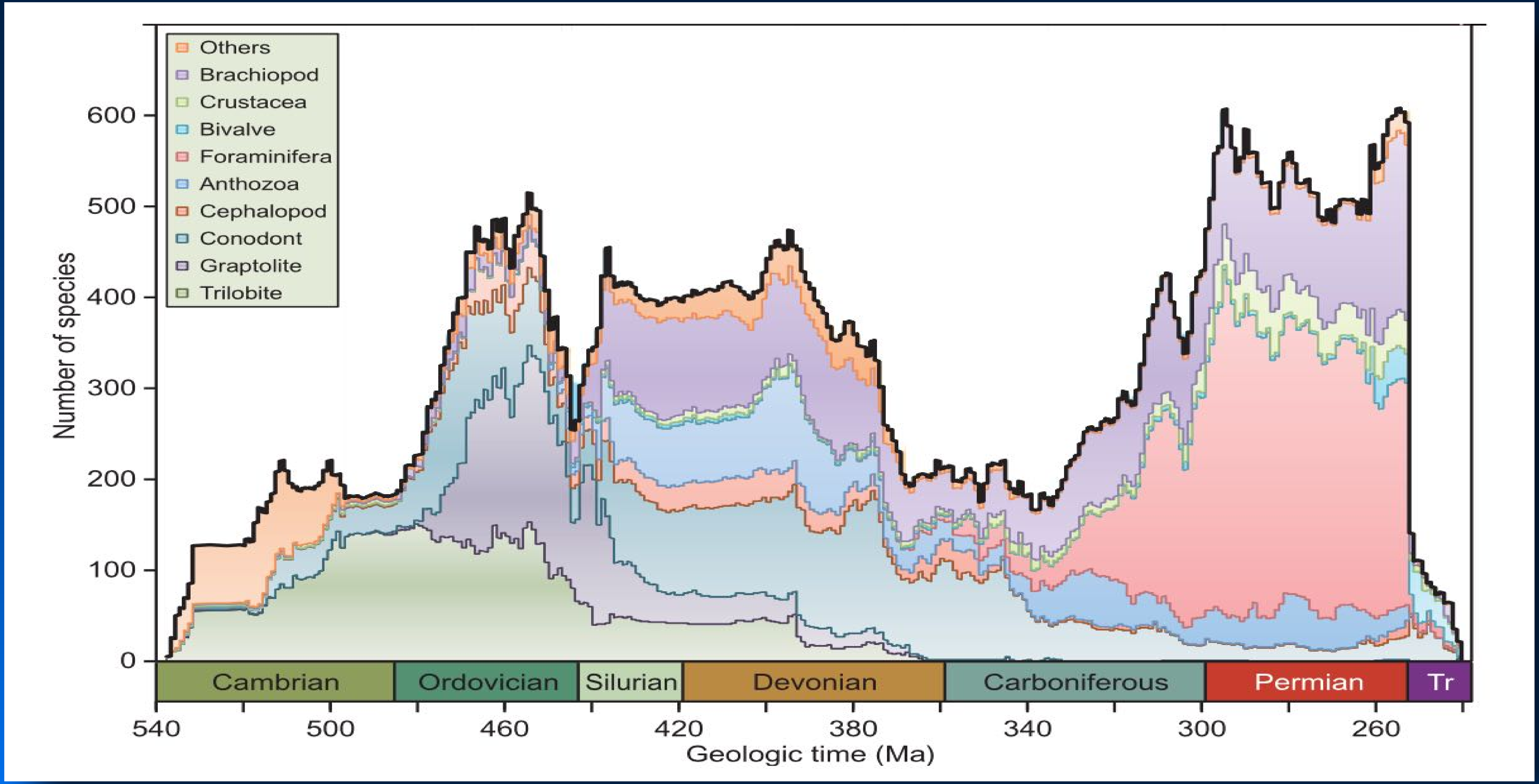
NJU Course

Principles of Paleobiology

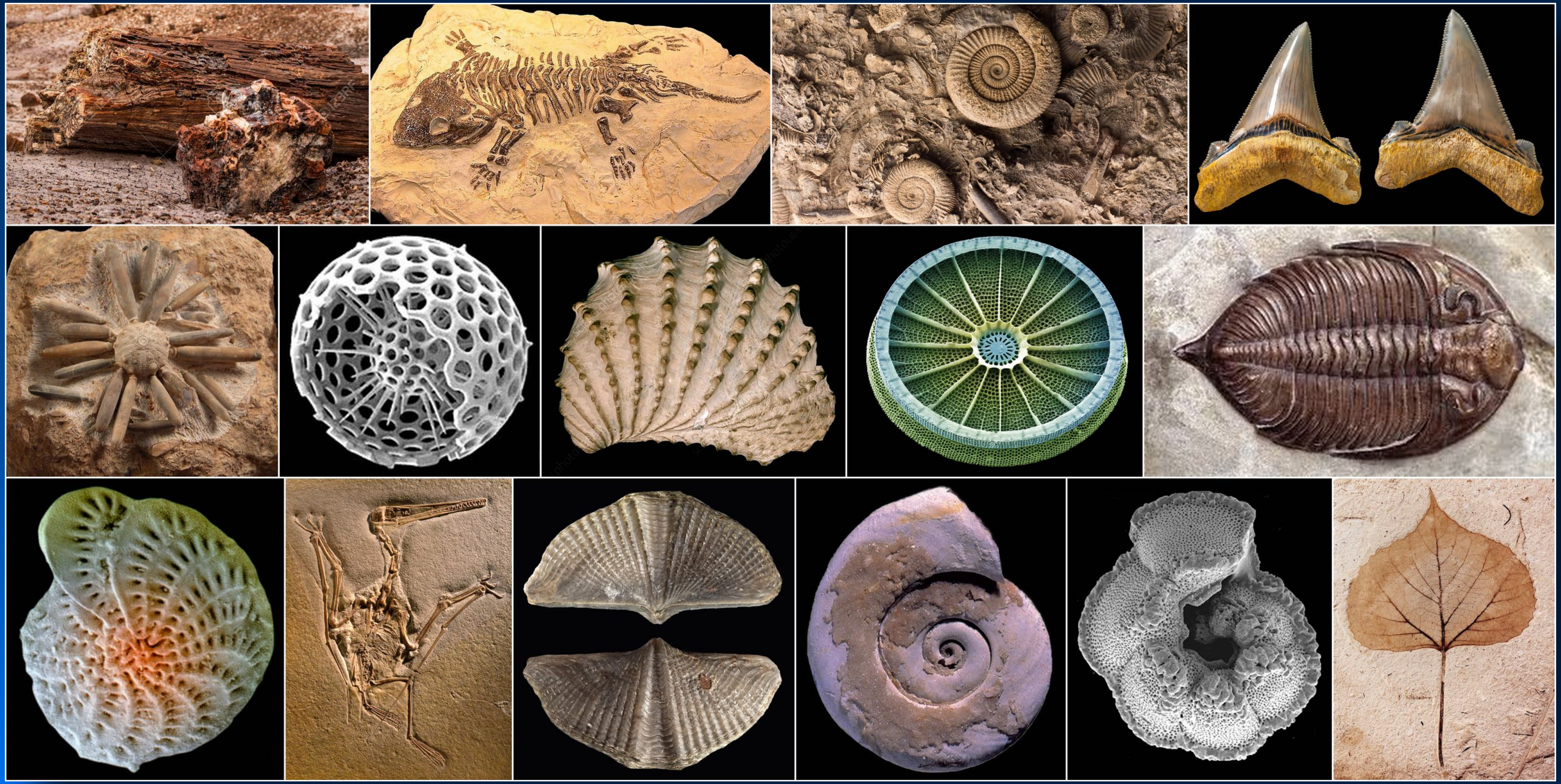
Paleobiodiversity



Paleobiodiversity

Definition

The study of the kinds and distribution of life on Earth with special reference to taxa that lived in the geological past.



Paleobiodiversity

Biodiversity

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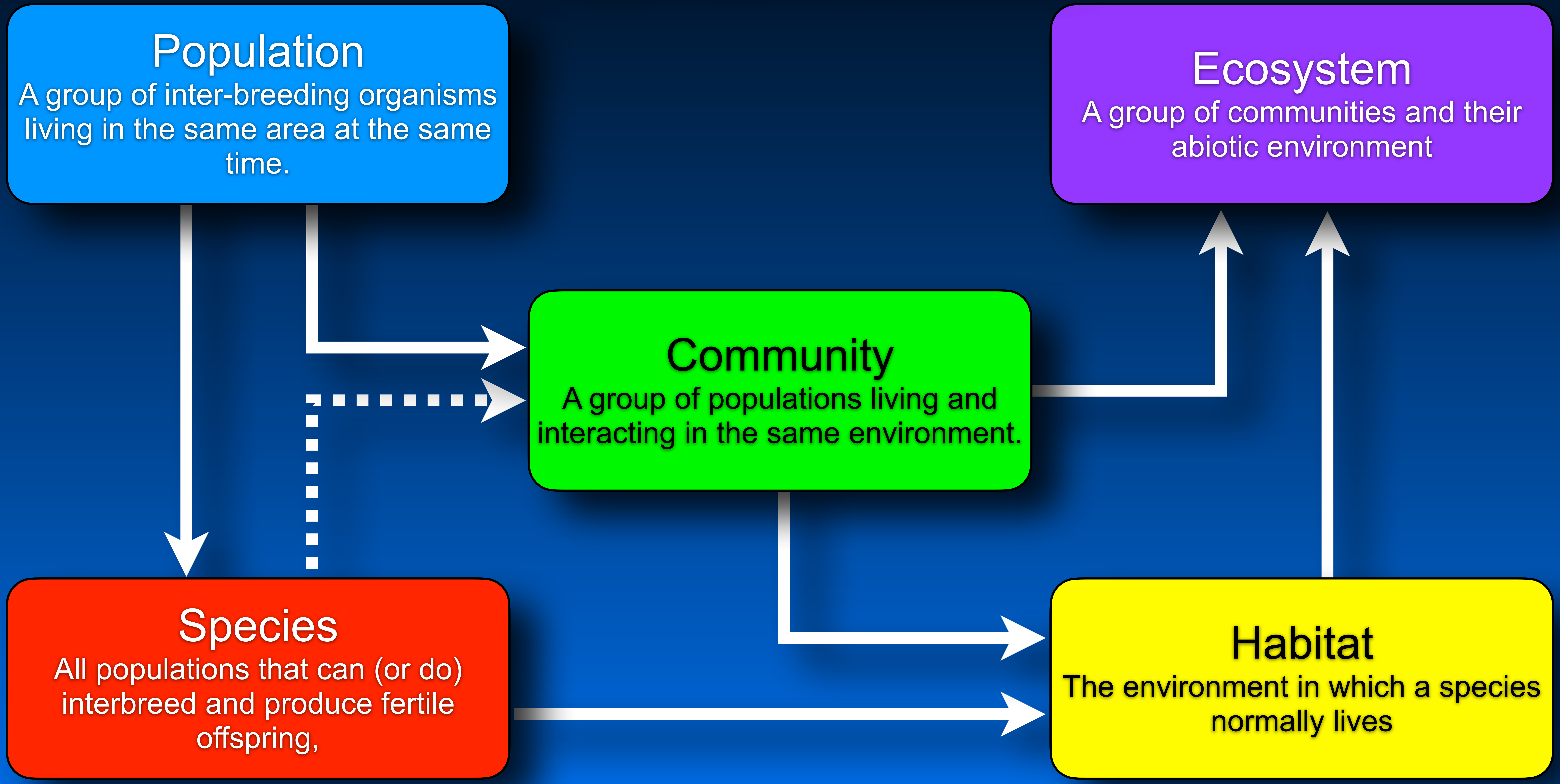
Organization of Levels



Population
A group of inter-breeding organisms living in the same area at the same time.

Ecosystem
A group of communities and their abiotic environment

Community
A group of populations living and interacting in the same environment.

Species
All populations that can (or do) interbreed and produce fertile offspring,

Habitat
The environment in which a species normally lives

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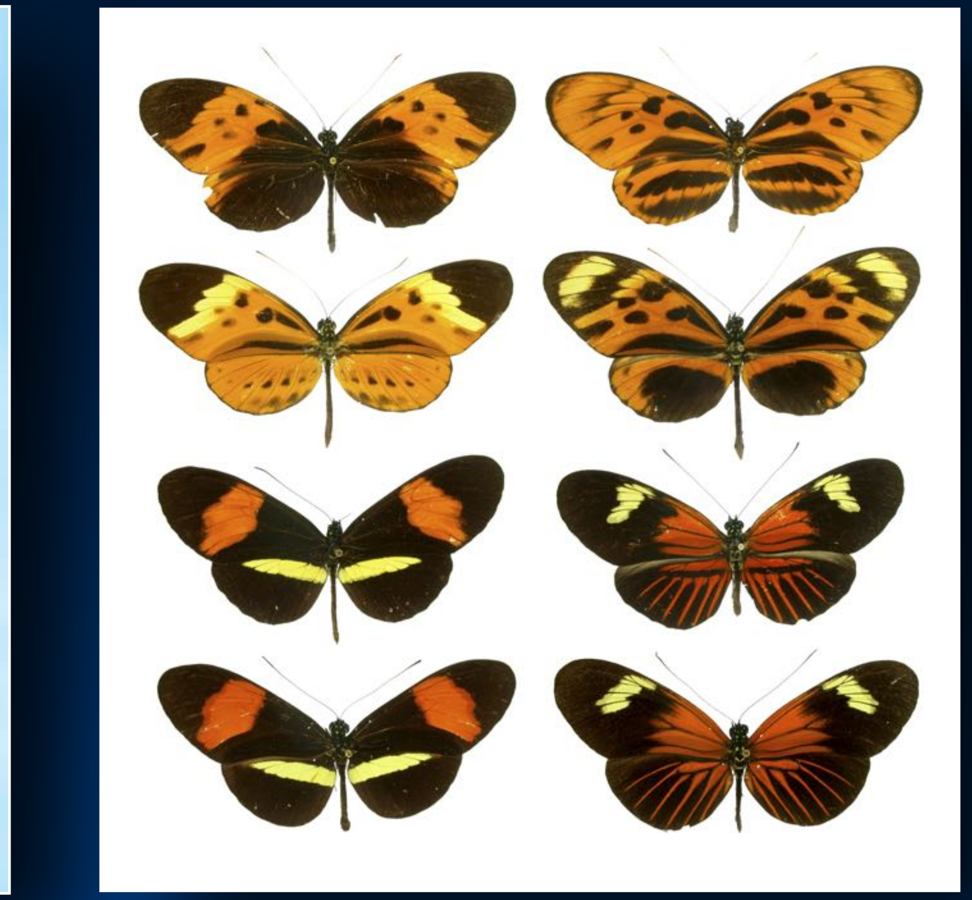
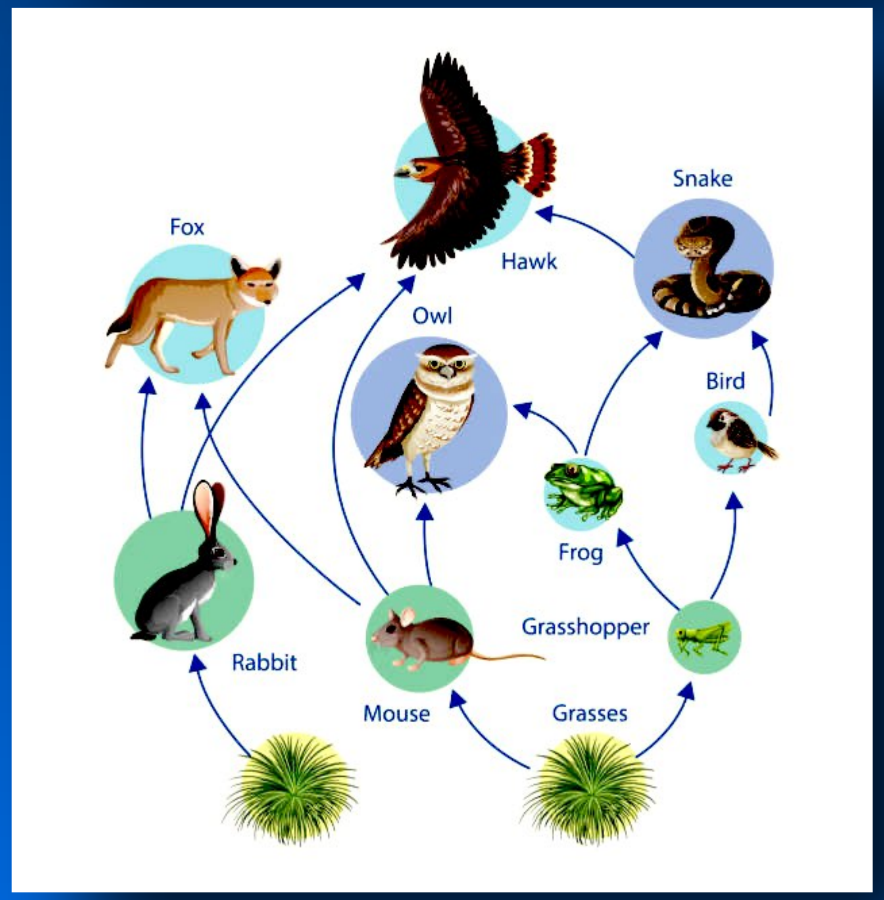
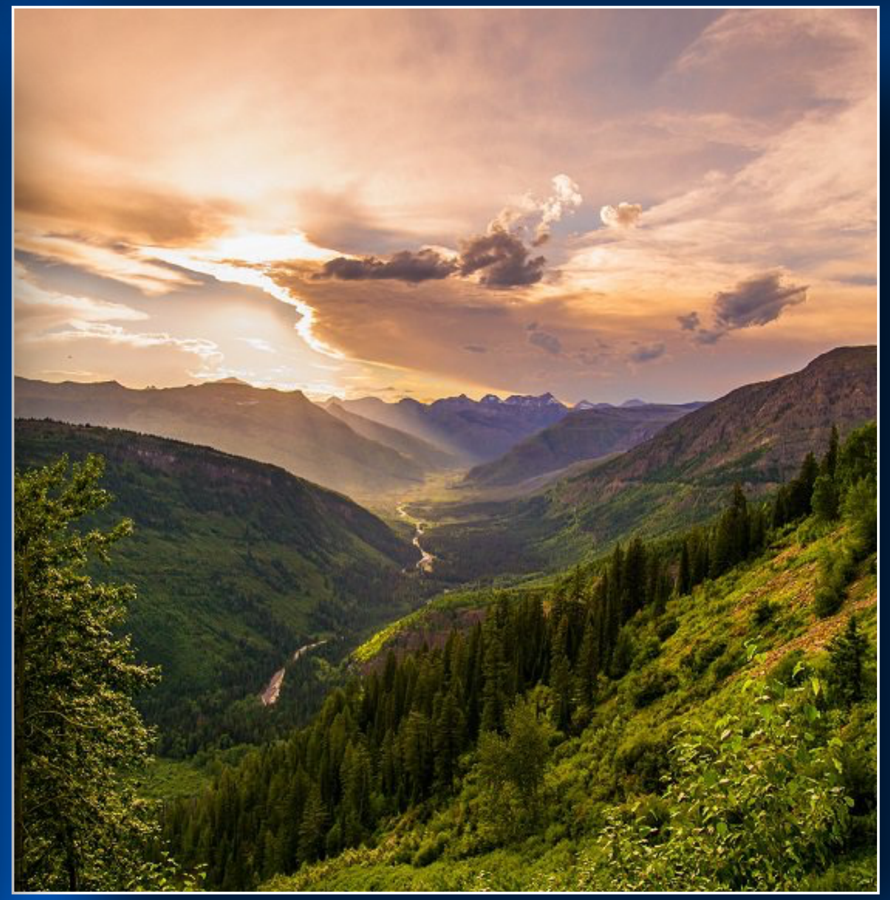
Components

- Diversity of genes - variety of alleles and genes in species.
- Diversity of species - variety of species in habitats.
- Diversity of ecologies - variety of biotic interactions, dependencies and trophic relations among species in a region.
- Diversity of ecosystems - variety of both the physical factors and biotic constituents of regions and biomes.







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Genetic Diversity

- Total number of genetic characteristics of a population or species.
- The primary way populations adapt to changing environments.
- Basic Theories:
    - Neutral Theory of Evolution - diversity results from accumulation of neutral substitutions.
    - Diversifying Selection - different populations in different environments may diversify by being subjected to selection at different alleles.
    - Frequency-Dependent Selection - selection tends to operate more intensely on common alleles.

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Species Diversity

- The number and abundance of different species in a given community, environment, ecosystem or dataset.
- Aspects:
  - Richness - the sum total of different species.
  - Evenness - the degree to which the abundances of different species are equal or depart from equality
  - Phylogenetic Distance - the sum of the branch lengths of the cladogram that encompasses all species.
  - Disparity - morphological uniqueness.

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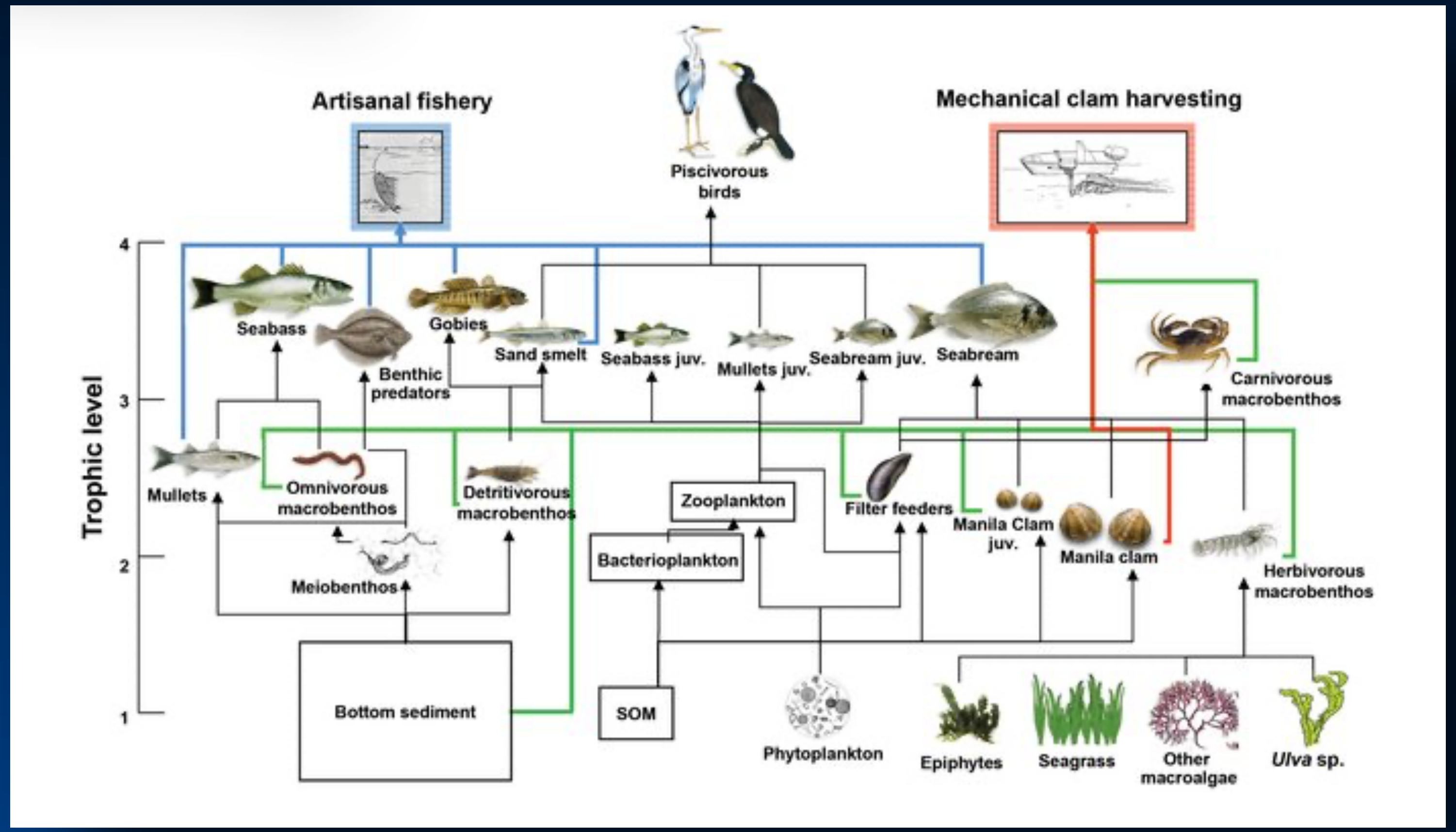
Ecological Diversity



- The diversity of relations between living organisms.
- Basic Types:
  - Competitive - mutually exclusive interaction to acquire the same resource.
  - Predatory - feeding interaction in which one species (predator) kills and eats another (prey) in order to survive.
  - Commensal - a category of symbiosis in which one species benefits from an interaction and others are unharmed.
  - Mutualistic - a category of symbiosis in which all species benefit from an interaction.
  - Parasitic - a category of symbiosis in which one species benefits from an interaction and other are harmed.

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Ecosystem Diversity

A combination of biodiversity and the diversity exhibited by the abiotic environment (geodiversity) of a regional or global set of communities.

- Types:
  - Mountain
  - Desert
  - Grassland
  - Forest
  - Wetland
  - Aquatic
  - Neritic
  - Continental slope
  - Abyssal
  - Pelagic

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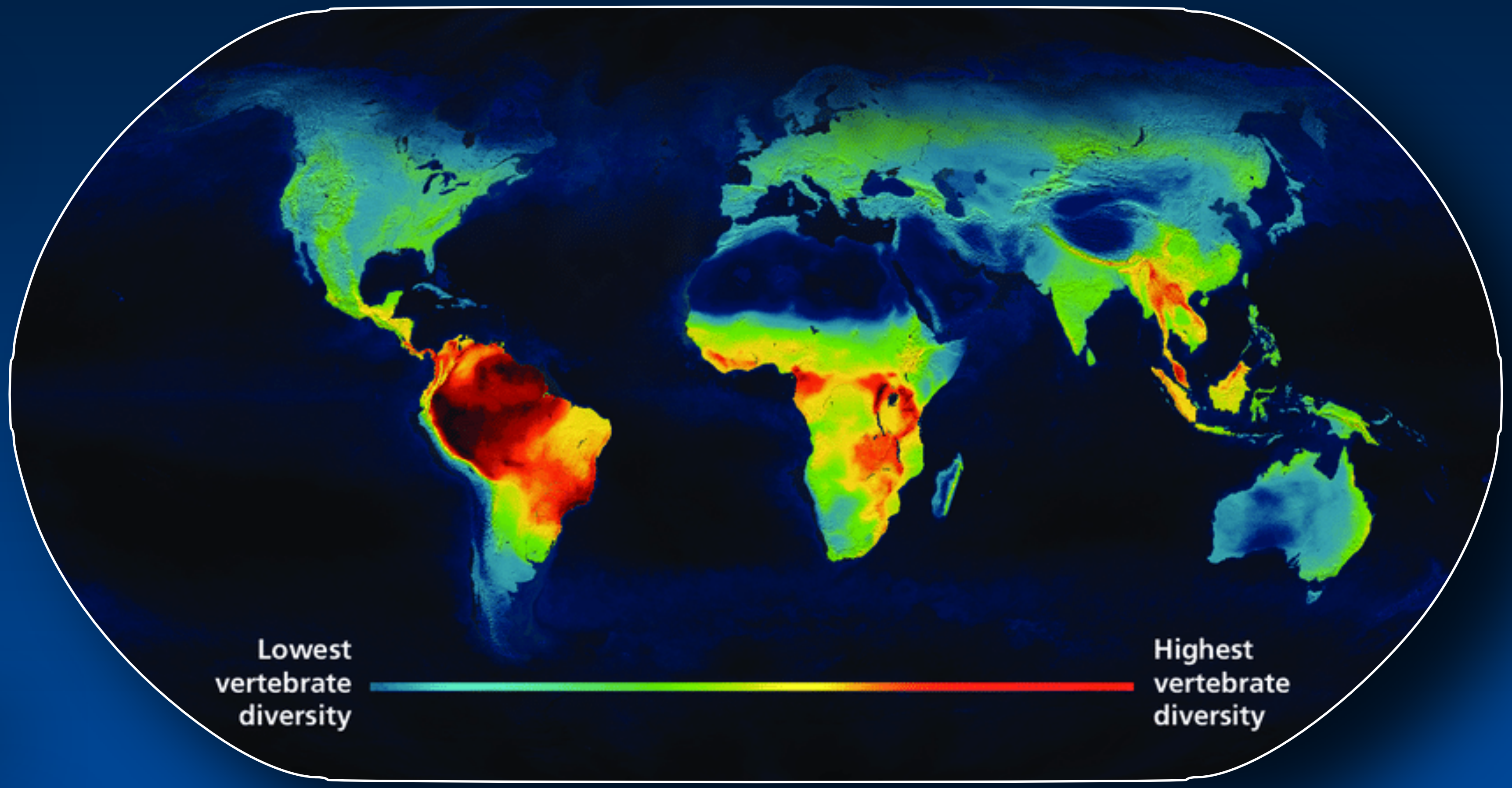
Biodiversity Trends (or Biological Rules)

Spatial Rules



- Latitudinal Diversity Gradient - Species richness is maximal in the tropics decreases towards both poles.
- Bergmann’s Rule - body sizes in populations and species increase toward both poles.
- Alan’s Rule - body sizes and shapes in endotherms vary to minimize heat loss in cold climates and maximize heat loss in warm climates.
- Foster’s Rule - on islands body sizes become larger or small depending on the level of resource available.
- Golger’s Rule - within species of endotherms heavily pigmented forms tend to be found in more humid environments.
- Jordan’s Rule - in aquatic species an inverse relation exists between water temperature and eristic characters (e.g., fin rays, vertebrae, scale numbers).

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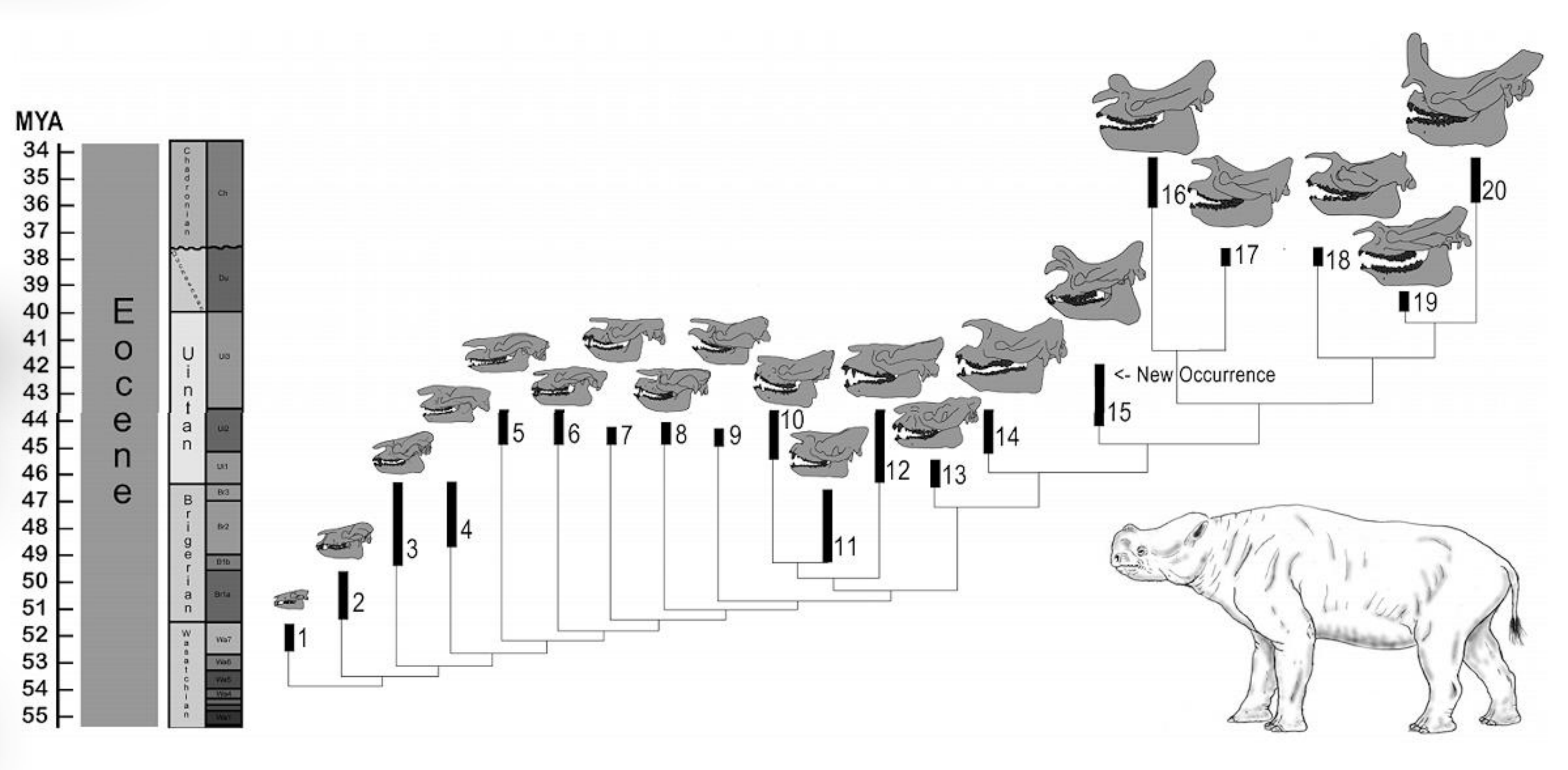
Biodiversity Trends (or Biological Rules)

Temporal Rules

- Cope's Rule - within animal lineages body size tends to increase over time.
- Dollo's Law - within lineages morphologies never return to their previous states irrespective of the state of the environment.
- Gause's Law - two species that compete for the same resource cannot co-exist at a constant abundance ratios; there is always a winner and a loser.



- Hennig's Rule - species with the most primitive character states occupy geographic regions at or close to the lineages center of origin.
- Williston's Law - within lineages, and over time, body parts tend to become reduced in number and specialized in function.

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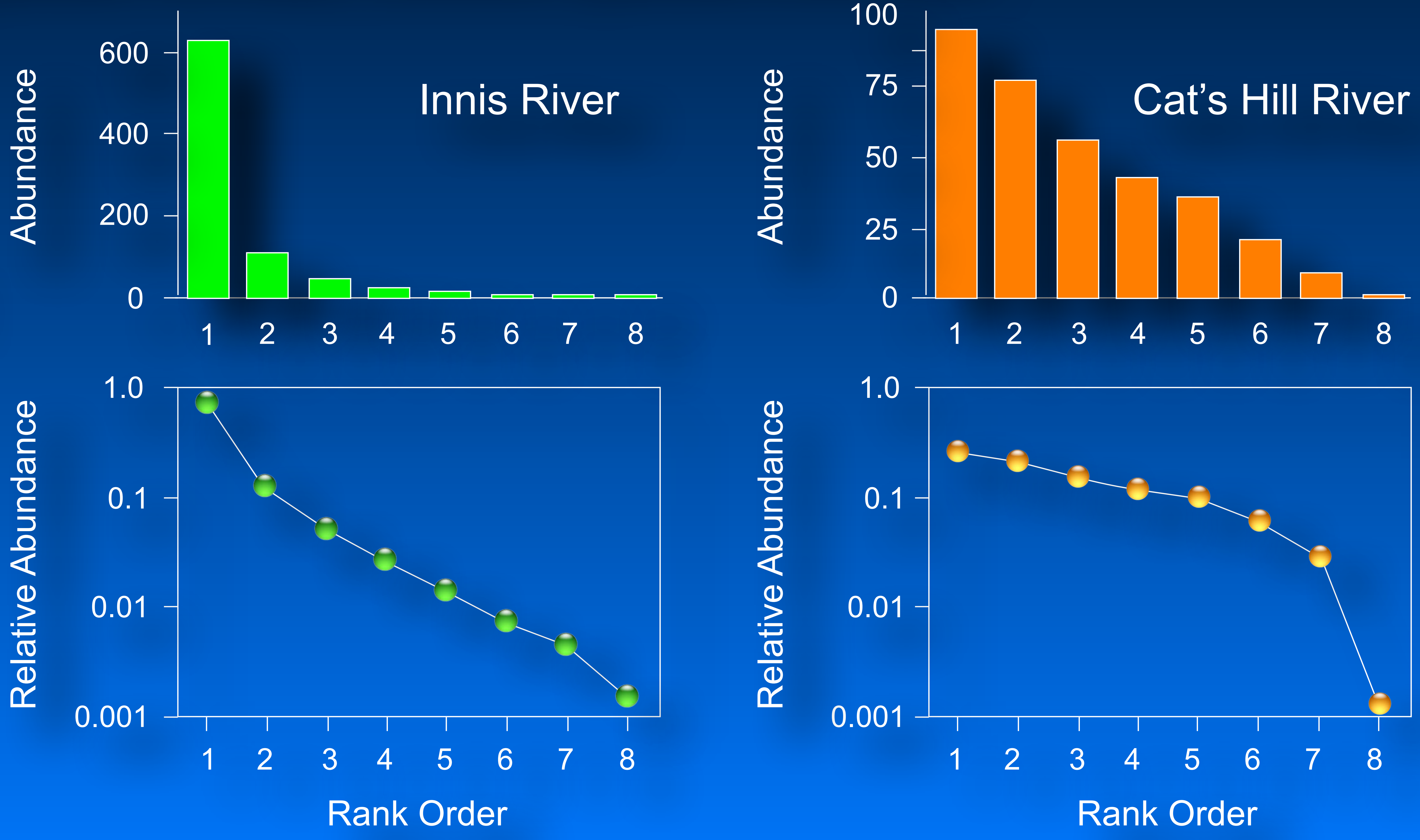
Measurement of Diversity

Whittaker Plots

Same species richness, different species evenness.

There exists a tendency among paleobiologists to focus on counts of taxa (e.g., species, genera, families) and regard that as a measure of “diversity”. This is incorrect. The ecological concept of diversity encompasses both taxon counts (richness) and abundance (evenness).



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Measurement of Diversity

Theoretical Models

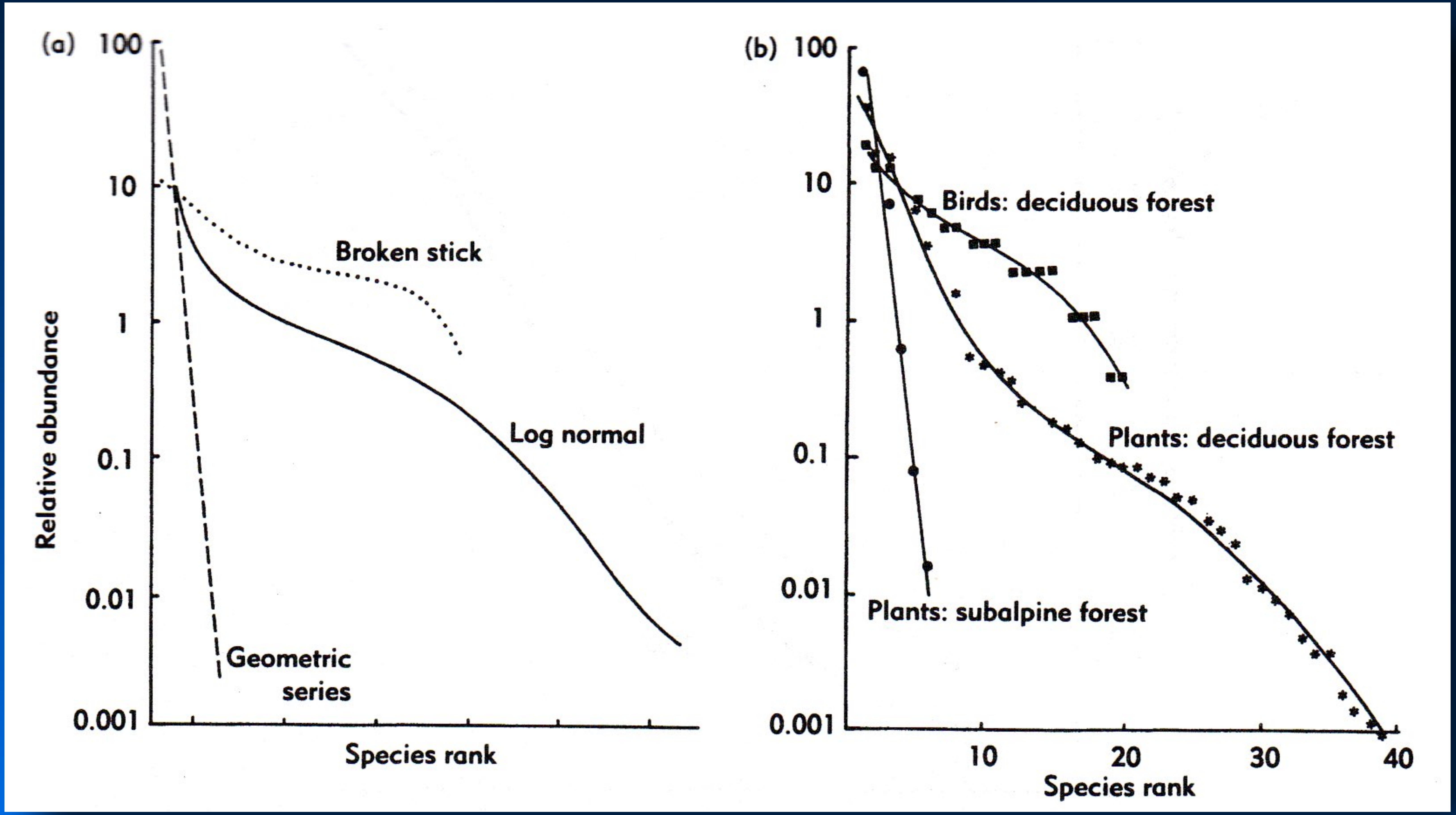

Diagram from Magurran (2004)

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Diversity Indices

Simpson Diversity Index* (λ)

A measure of the degree to which individuals are concentrated into different types (= species).

$$\lambda = \sum_{i=1}^{n} p_i^2$$

where: p_i = proportional abundance of species i.
n = number of species.

A simple measure of relative evenness that has been employed widely across many different fields (e.g, computer science, economics).

* Also known as the Herfindhl Index and Herfindahl-Hirschman Index.

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Diversity Indices

Shannon Diversity Index (H')

A measure of the variability (uncertainty or unevenness) in species abundance data

$$H' = -\sum_{i=1}^{n} p_i ln p_i$$

where: p_i = proportional abundance of species i.
n = number of species.

Although the equation refers to the base of natural logarithms, any logarithm base can be used.

* Also known as the Shannon-Wiener Index and Shannon Entropy Index.

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Diversity Indices

Simple Diversity Index (D)

The inverse of the weighted sum of proportional species abundances. Used for data expressed as a percentage.

$$D = \frac{1}{\sqrt[q-1]{\sum_{i=1}^{n} p_i {p_i}^{q-1}}}$$

where: p_i = proportional abundance of species i.
n = number of species.
q = weighting coefficient.
  q = 0; D = harmonic mean
  q ➝ 1; D = exponential of Shannon entropy
  q = 2; D = arithmetic mean

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Diversity Indices

Kempton-Taylor Diversity Index (Q)

A complex, statistical, and robust approach to diversity estimation that avoids bias introduced by abundant or rare species.

$$Q = \frac{\frac{1}{2}n_{R1} + \sum_{R1+1=0}^{R1-1} n_r + \frac{1}{2}n_{R2}}{ln\frac{R2}{R1}}$$

where: n_r = number of species with abundance R.

$R1$ = 25% quartile.

$R2$ = 75% quartile.

n_{R1} = number of species in 25% quartile.

n_{R2} = number of species in 75% quartile.

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Diversity Indices

Kempton-Taylor Diversity Index (Q)

For the Kempton-Taylor diversity (Q) quartiles are chosen according to the following equations.

$$\sum_{1}^{R1-1} n_r < \frac{1}{4}S \leq \sum_{1}^{R1} n_r \qquad \sum_{1}^{R2-1} n_r < \frac{3}{4}S \leq \sum_{1}^{R2} n_r$$

where: S = total number of species in the sample.

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Diversity Indices

Clarke-Warwick Diversity Index (Δ^+)

A phylogenetic index that summarizes the pattern of relatedness in the sample.

$$\Delta^+ = \frac{\left[\sum \sum_{i<j} \omega_{i,j}\right]}{[n(n^{-1})/2]}$$

where: n = number of species in the sample.
ω_{ij} = phylogenetic path length between species i and j.

This index is based on the Simpson (H) index and measures the degree of phylogenetic distinctiveness of the sample. It has come be an important measure of diversity in conservation biology.

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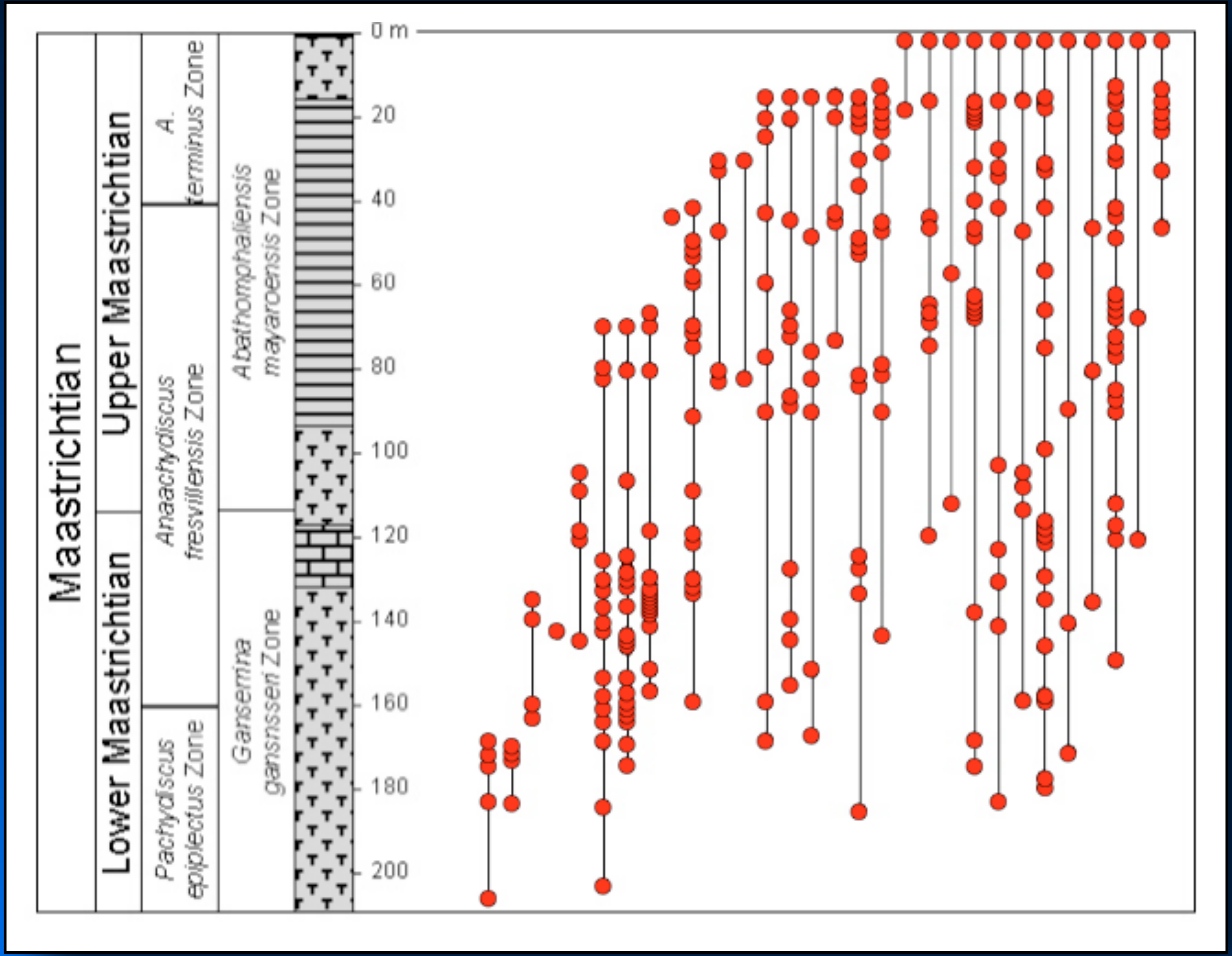
Taxic Richness

Range-Through Approach to Estimating Stratigraphic Ranges



Redrawn from Marshall and Ward (1996)

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Taxic Richness

Issues of Concern

- **Boundary Crossing** - use of only boundary-crossing taxa dampens the effect of taxa confined to a single interval which may be the result of preservation problems (see Bambach et al. 2004).

- **Singletons** - single occurrences of taxa are inherently problematic. It may be that these taxa are genuinely short-lived, or or may be that they have abundances so low as to fall below the detection threshold given the sample sizes collected. Additionally, such taxa may have inherently low preservation potentials. Eliminating singletons from the dataset avoids these sources of ambiguity.

- **Pull of the Recent** - Given the range-through method of determine stratigraphic intervals of occurrence the inclusion of Recent taxa is problematic owing to the much better sampling of the Recent (and near-Recent) biota and the fact that taxa with very low preservation potential can be found in the extant biota. Inclusion of Recent taxa can dramatically extend stratigraphic ranges (e.g., Coelocanth) and so inflate richness estimates.

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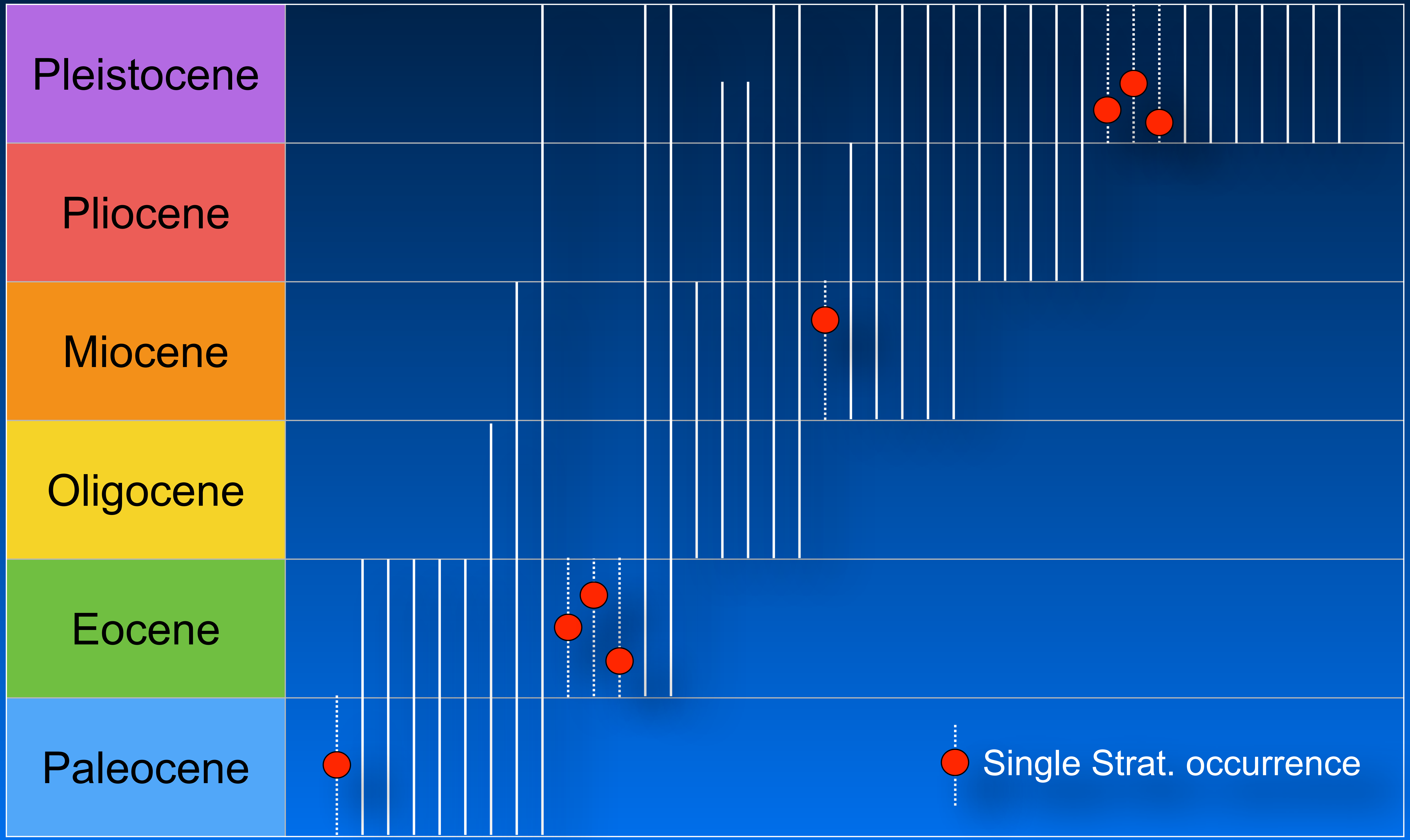
Taxic Richness

Hypothetical Stratigraphic Ranges



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Taxic Richness

Pull of the Recent

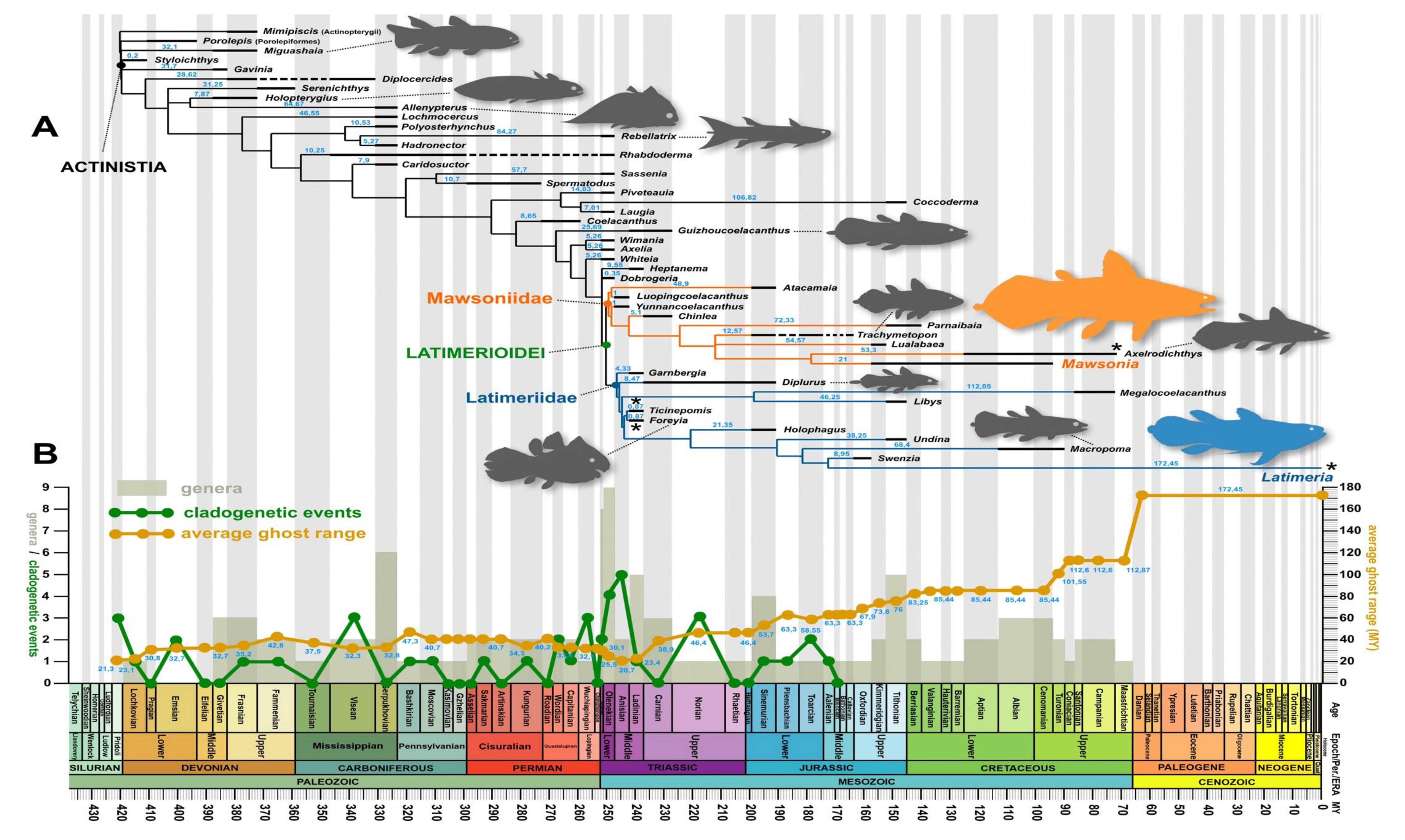

Diagram from Torino et al. (2021)

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Taxic Richness

Taxic Richness Variables

Var.	Definition
d_t	richness in interval t
$d_{t\text{-}1}$	richness in previous interval (t-1)
$d_{(t/t+1)}$	richness at boundary between intervals t and t-1
$n_{orig(t)}$	number of originations in interval t
$n_{ext(t)}$	number of extinctions in interval t
$n_{ext(t\text{-}1)}$	number of extinctions in previous interval (t-1)
n_{single}	number of singletons in interval t

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Taxic Richness

Taxic Richness Indices

Standard Method

$$d_t = x_{t-1} + n_{orig(t)} - n_{ext(t-1)}$$

Boundary-Crossing Method

$$d_{t/t+1} = d_t - n_{ext(t)}$$

Depending on the situation and the data it may be permissible to remove singleton and/or Recent taxa.

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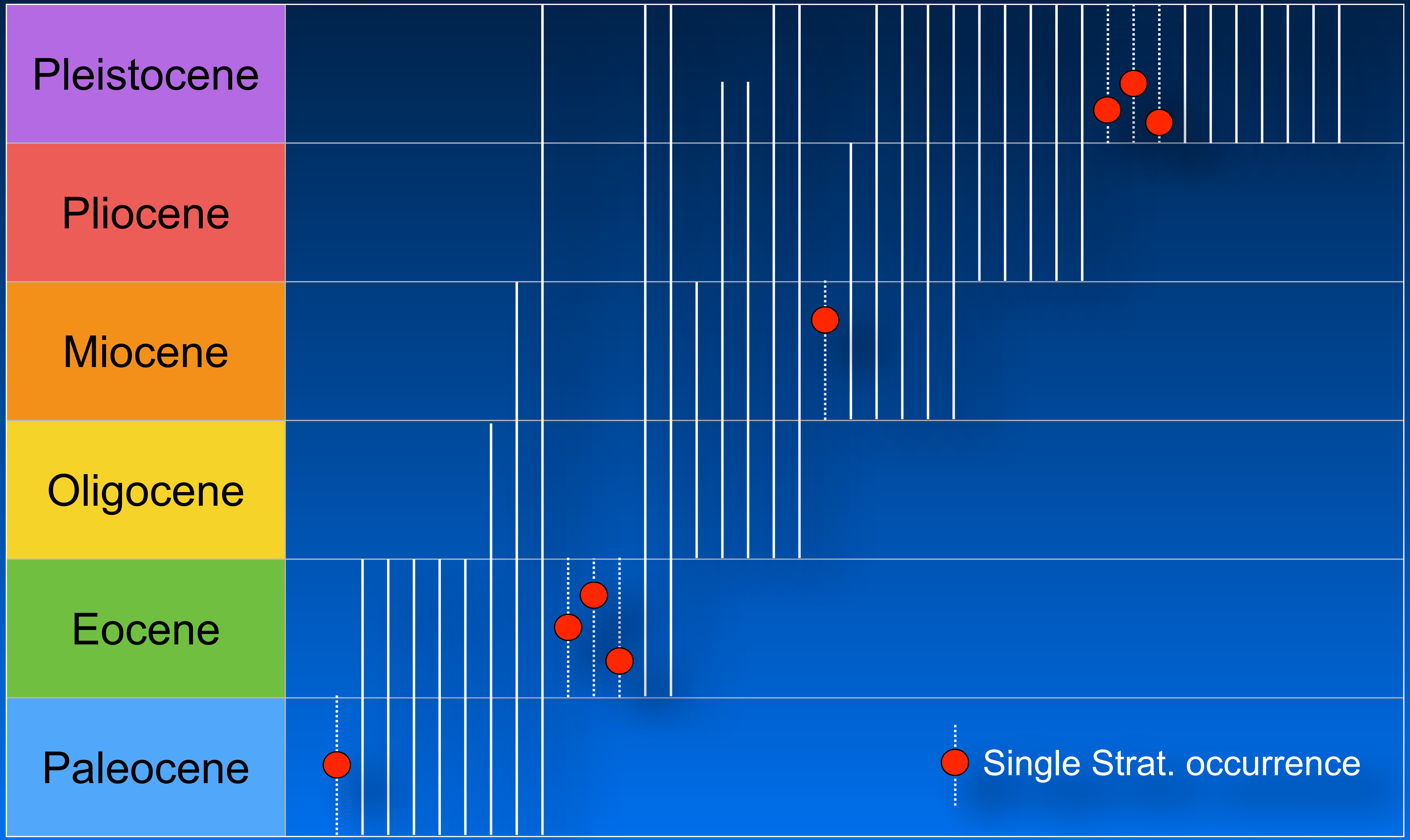
Taxic Richness

Hypothetical Stratigraphic Ranges



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Taxic Richness

Hypothetical Stratigraphic Ranges

Data	All Data		w/o Singletons		w/o Recent	
Taxic Richness	d_t	$d_{t/t+1}$	d_t	$d_{t/t+1}$	d_t	$d_{t/t+1}$
Pleistocene	26	26	23	21	5	2
Pliocene	17	16	17	17	3	2
Miocene	15	12	14	14	6	3
Oligocene	10	9	10	9	7	5
Eocene	13	5	10	4	10	7
Paleocene	9	8	8	8	8	7

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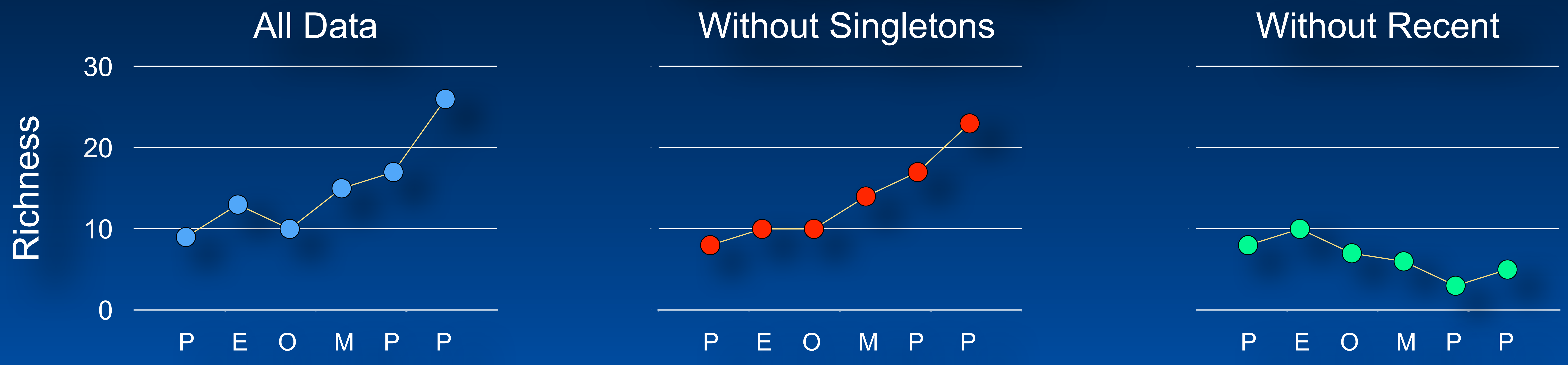
Taxic Richness

Hypothetical Stratigraphic Ranges

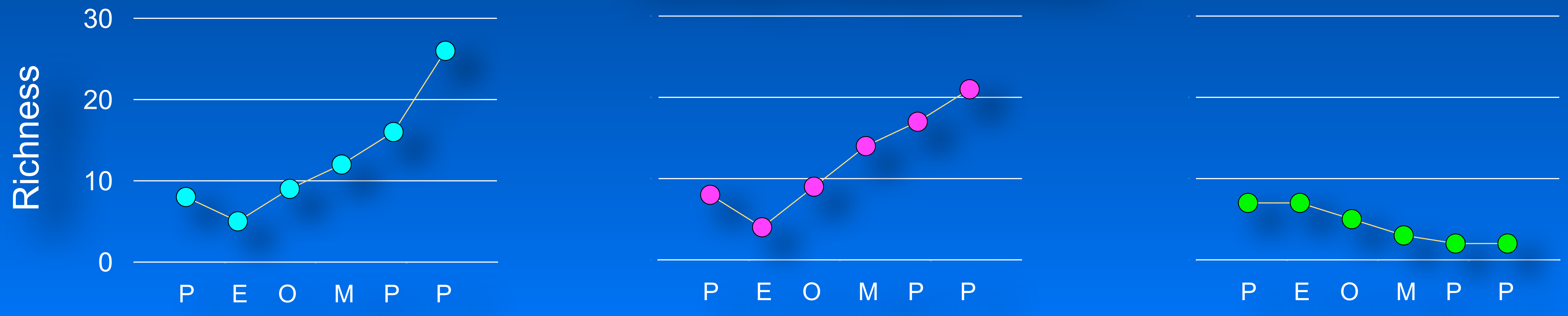
Standard Richness


All Data

Without Singletons

Without Recent

Boundary-Crossing Richness



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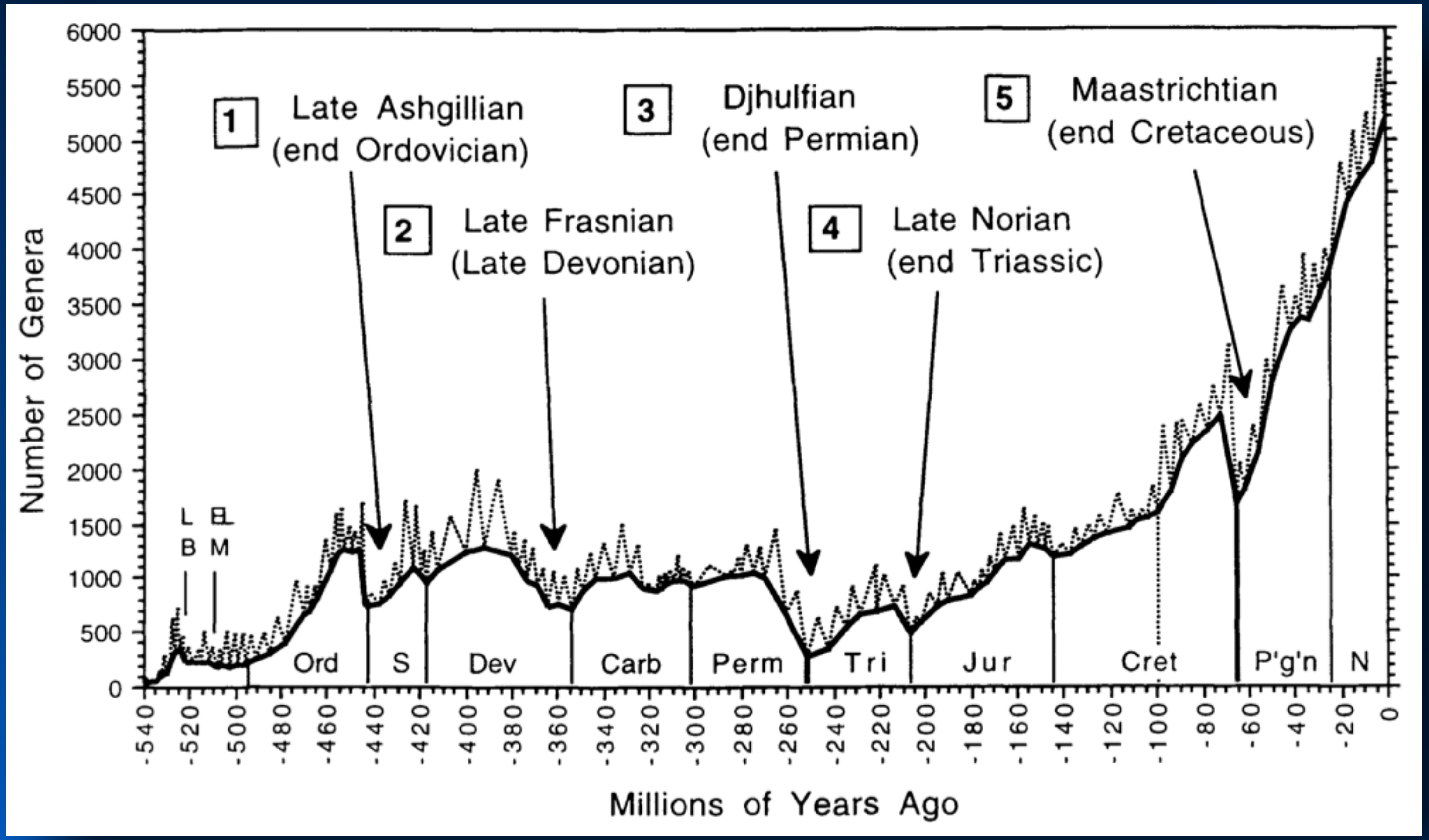
Interpretation of Taxic Richness

Dynamic Interplay Between Origination, Extinction and Richness

Taxic richness over any stratigraphic interval represents a combination of …

- … taxic richness at the beginning of the interval;
- … number of taxic originations during the interval;
- … number of taxic extinctions during the interval.



When interpreting the causes of the pattern of richness increase or decrease based on paleontological data the distention between originations and extinctions must always be kept in mind.

Diagram from Bambach et al. (2004)

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Interpretation of Taxic Richness

Dynamic Interplay Between Origination, Extinction and Richness

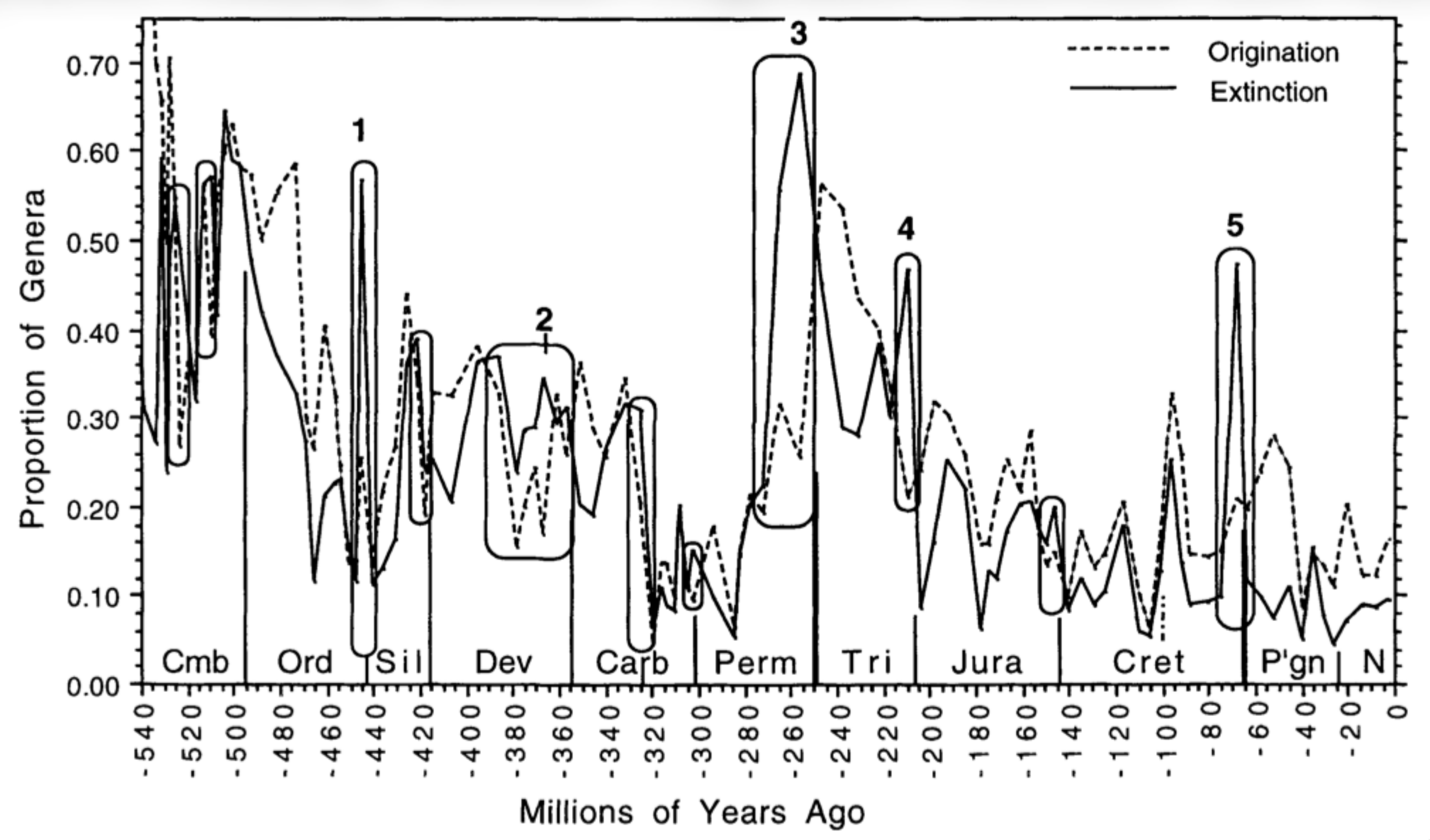

Diagram from Bambach et al. (2004)

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Interpretation of Taxic Richness

Dynamic Interplay Between Origination, Extinction and Richness

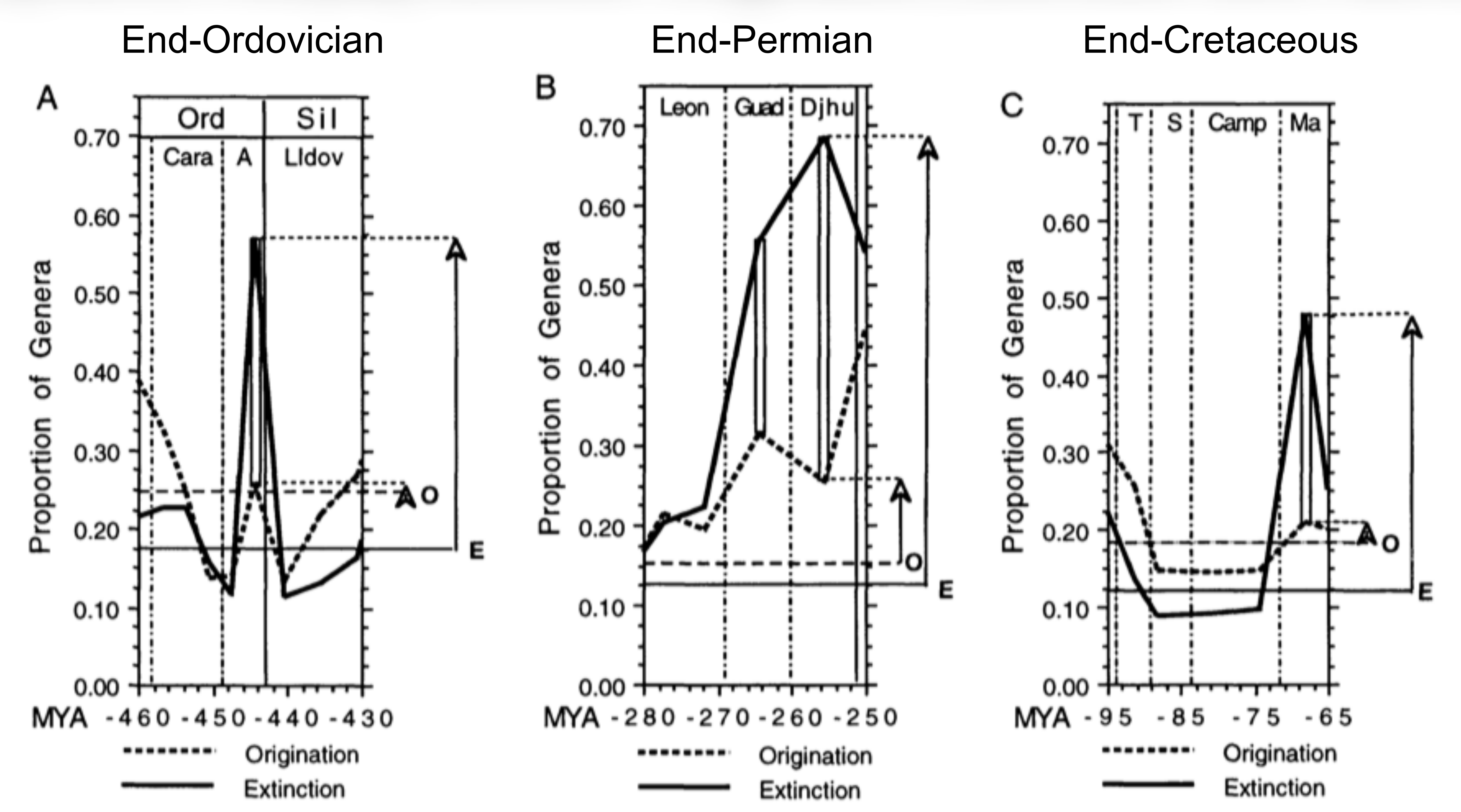

Diagram from Bambach et al. (2004)

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Interpretation of Taxic Richness

Dynamic Interplay Between Origination, Extinction and Richness

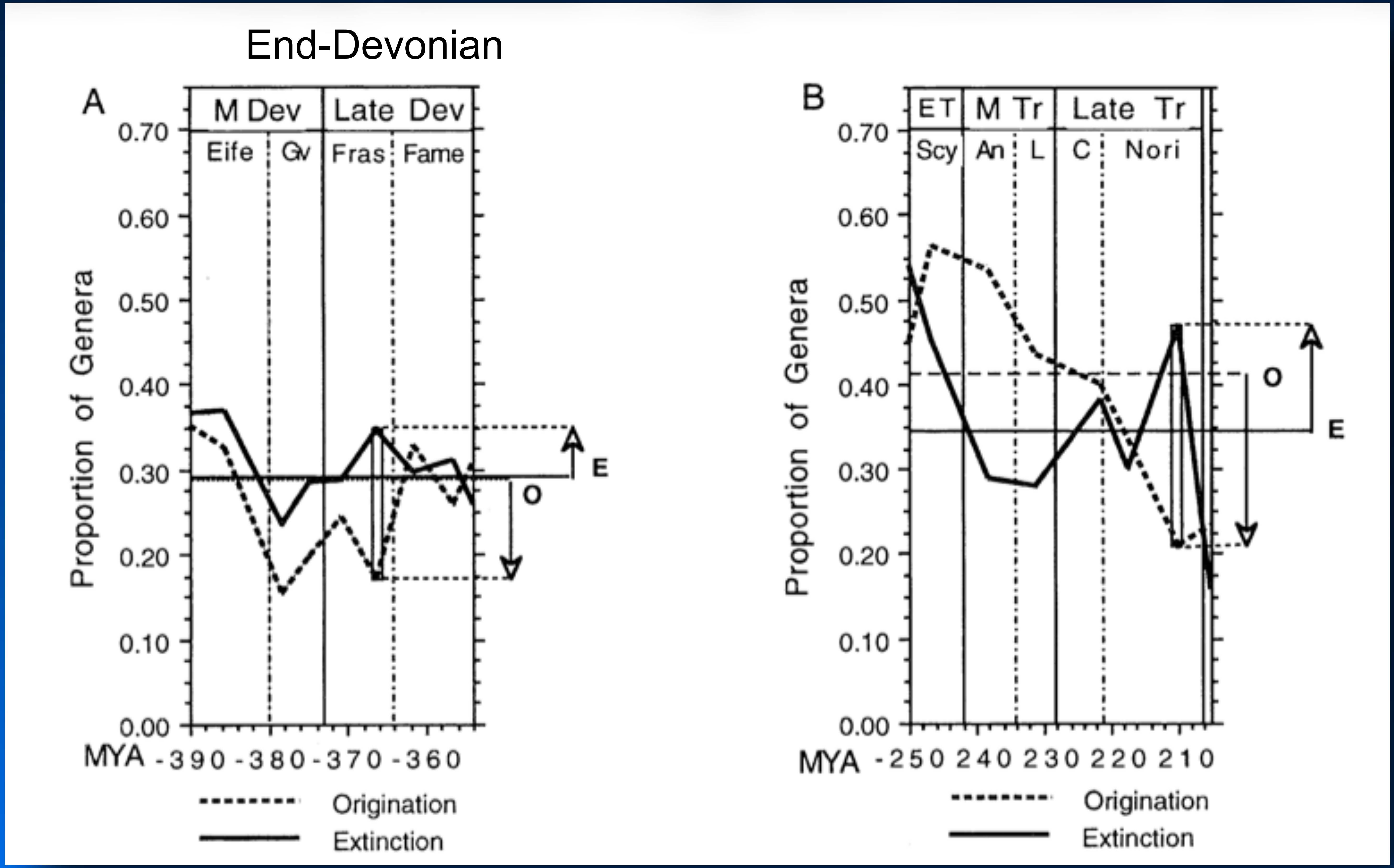

Diagram from Bambach et al. (2004)

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Comparisons Between Samples

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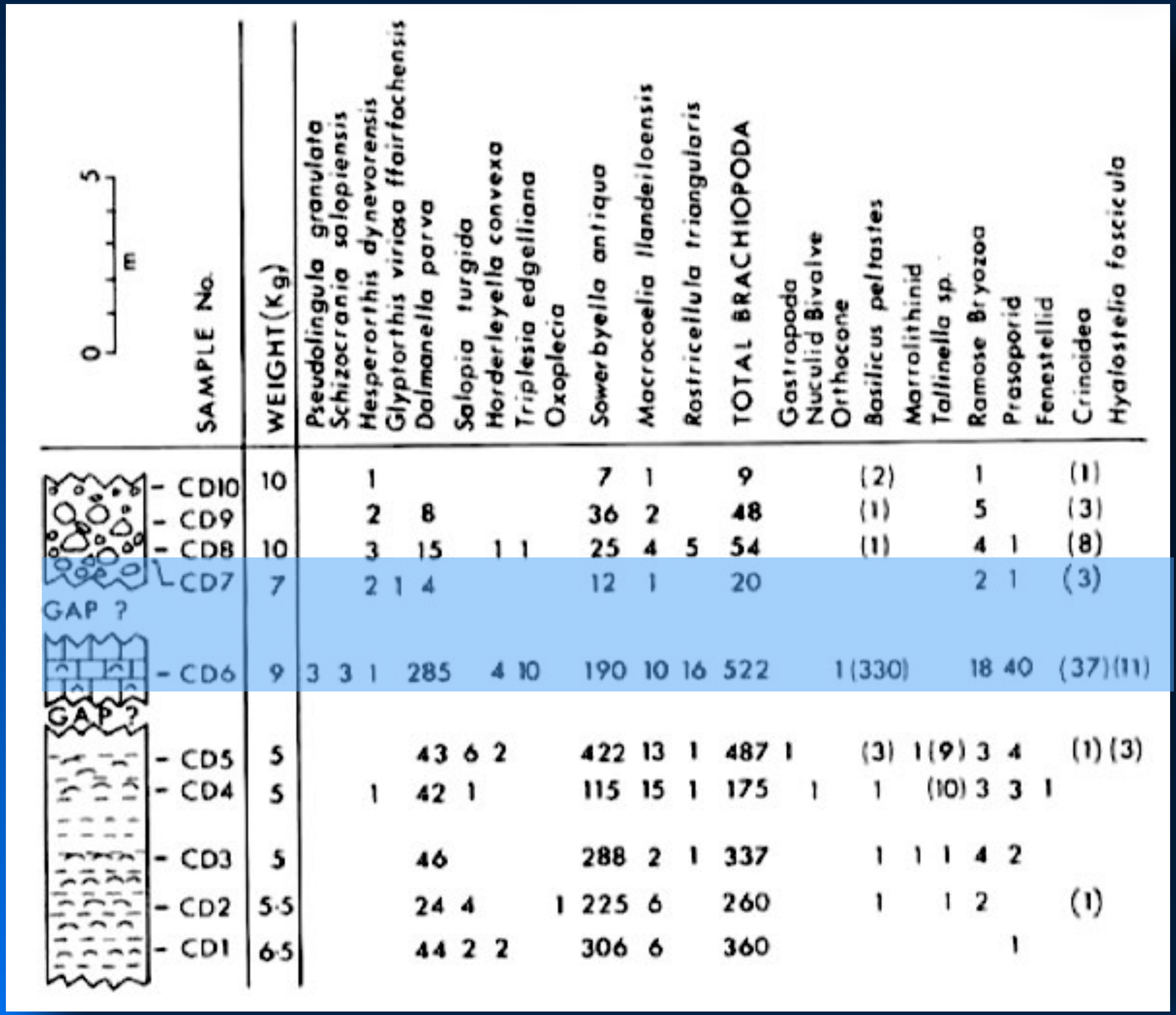
Taxic Richness Comparison

Has species richness changed across the hiatus?



SAMPLE No.	WEIGHT (Kg)	Pseudolingula granulata	Schizocrania salopiensis	Hesperorthis dynevorensis	Glyptorthis viriosa ffairfachensis	Dalmanella parva	Salopia turgida	Horderleyella convexa	Triplesia edgelliana	Oxoplecia	Sowerbyella antiqua	Macrocoelia llandeiloensis	Rostricellula triangularis	TOTAL BRACHIOPODA	Gastropoda	Nuculid Bivalve	Orthocone	Basilicus peltastes	Marrolithinid	Tallinella sp.	Ramose Bryozoa	Prasoporid	Fenestellid	Crinoidea	Hyalostelia fascicula
CD10	10			1							7	1		9				(2)			1			(1)	
CD9				2		8					36	2		48				(1)			5			(3)	
CD8	10			3		15		1	1		25	4	5	54				(1)			4	1		(8)	
CD7	7			2	1	4					12	1		20							2	1		(3)	
GAP ?																									
CD6	9	3	3	1		285		4	10		190	10	16	522			1	(330)			18	40		(37)	(11)
GAP ?																									
CD5	5					43	6	2			422	13	1	487	1			(3)	1	(9)	3	4		(1)	(3)
CD4	5			1		42	1				115	15	1	175		1		1		(10)	3	3	1		
CD3	5					46					288	2	1	337				1	1	1	4	2			
CD2	5·5					24	4			1	225	6		260				1		1	2			(1)	
CD1	6·5					44	2	2			306	6		360								1			

Sample	No. Taxa	Sample Size
CD7	8	26
CD6	17	702

Diagram from Williams et al. (1981)

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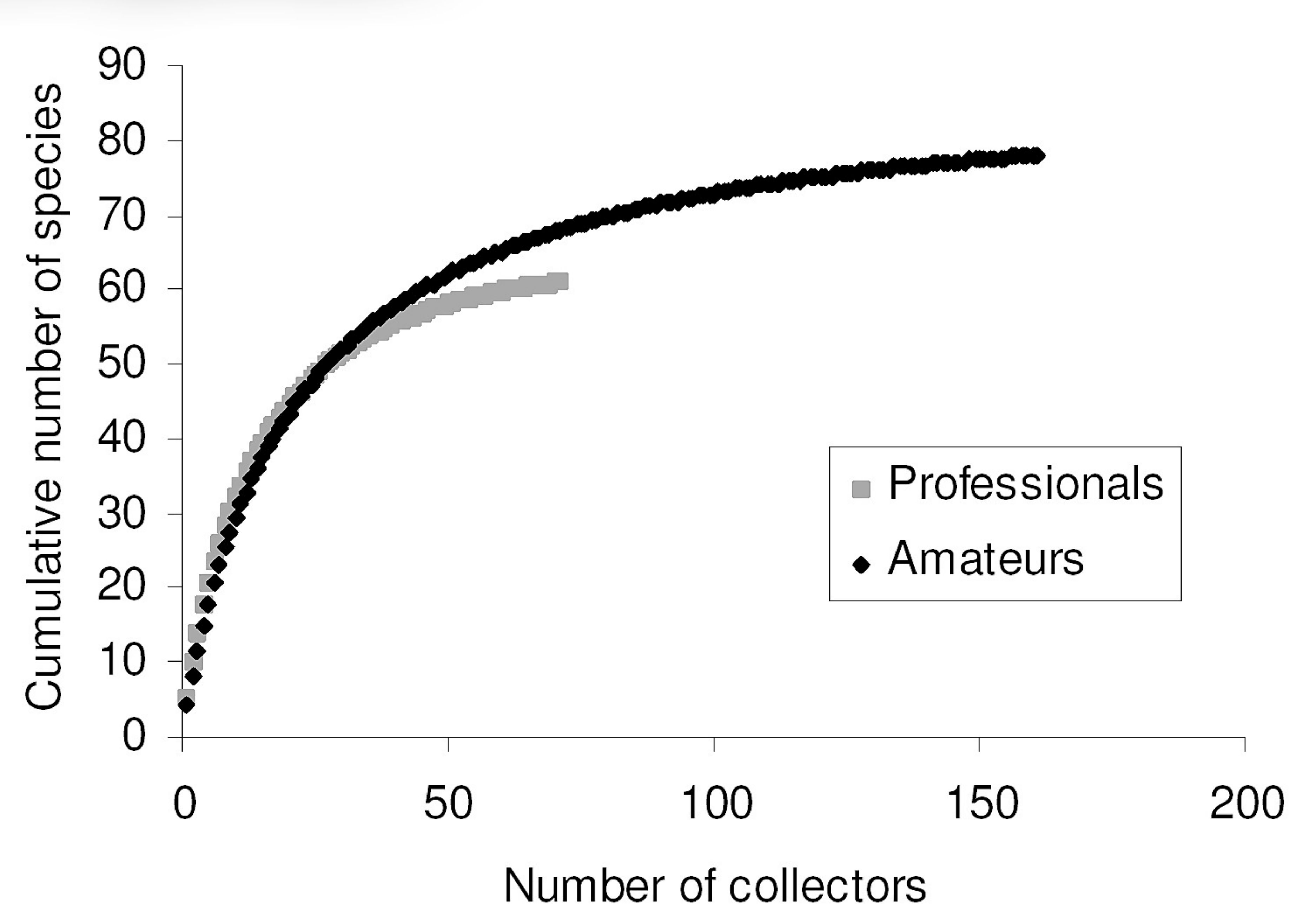
Taxic Richness Comparison



The number of taxa that will be recovered in any sampling program depends on …

- the size of the sample collected;
- the number of collections made;
- the skill/experience of the collectors;
- accuracy of the taxonomy.

Collector curves can be used to determine whether additional collecting effort is warranted. However …

- all the taxa present in a sample will rarely (if ever) be collected;
- differences in sample sizes must be taken into account when comparing taxic richness values.

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Taxic Richness Comparison

Rarefaction

A simple numerical procedure for estimating the number of groups that would be expected to be recovered at sample sizes smaller than the ones to hand.

Sample CD 6

Taxon	*n*
Pseudolingula granulata	3
Schizocrania salopiensis	3
Hesperorthis dynervorensis	1
Glyptorthis viriosa ffairfachensis	-
Dalmanella parva	285
Hordoerlyella convexa	4
Triplesia edgelliana	10
Sowerbeyella antiqua	190
Macocoelia llandeiloensis	10
Rostricellula triangular	16
Orthocone Cephalopod	1
Basilicus Peltastes	330
Ramose Bryozoa	18
Prasoporid sp.	40
Crinoid sp	37
Hyalostelia fascicula	11
Richness	15
Sample Size	959

Sample CD 7

Taxon	*n*
Pseudolingula granulata	-
Schizocrania salopiensis	-
Hesperorthis dynervorensis	2
Glyptorthis viriosa ffairfachensis	1
Dalmanella parva	4
Hordoerlyella convexa	-
Triplesia edgelliana	-
Sowerbeyella antiqua	12
Macocoelia llandeiloensis	1
Rostricellula triangular	-
Orthocone Cephalopod	-
Basilicus Peltastes	-
Ramose Bryozoa	2
Prasoporid sp.	1
Crinoid sp	3
Hyalostelia fascicula	-
Richness	8
Sample Size	26

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Taxic Richness Comparison

Rarefaction

A simple numerical procedure for estimating the number of groups that would be expected to be recovered at sample sizes smaller than the ones to hand.

$$E(S_n) = \sum_{i=1}^{S} 1 - \left[\frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right] \qquad \binom{N}{n} = \frac{N!}{(N-n)!n!}$$

where: N = number of Individuals in the whole sample.
S = number of taxa in the whole sample.
N_i = number of individuals in the i^{th} taxon.
n = number of individuals in the estimated sample.

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Taxic Richness Comparison

Rarefaction

A simple numerical procedure for estimating the number of groups that would be expected to be recovered at sample sizes smaller than the ones to hand.

Variance Associated with the $E(S_n)$ Estimate

$$Var(S_n) = \binom{N}{n}^{-1} \left[\sum_{i=1}^{S} \binom{N-N_i}{n} (1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} + \right.$$

$$\left. 2 \sum_{j=2}^{S} \sum_{i=1}^{j-1} (\binom{N-N_i-N_j}{n} - \frac{\binom{N-N_i}{n}\binom{N-N_j}{n}}{\binom{N}{n}}) \right]$$

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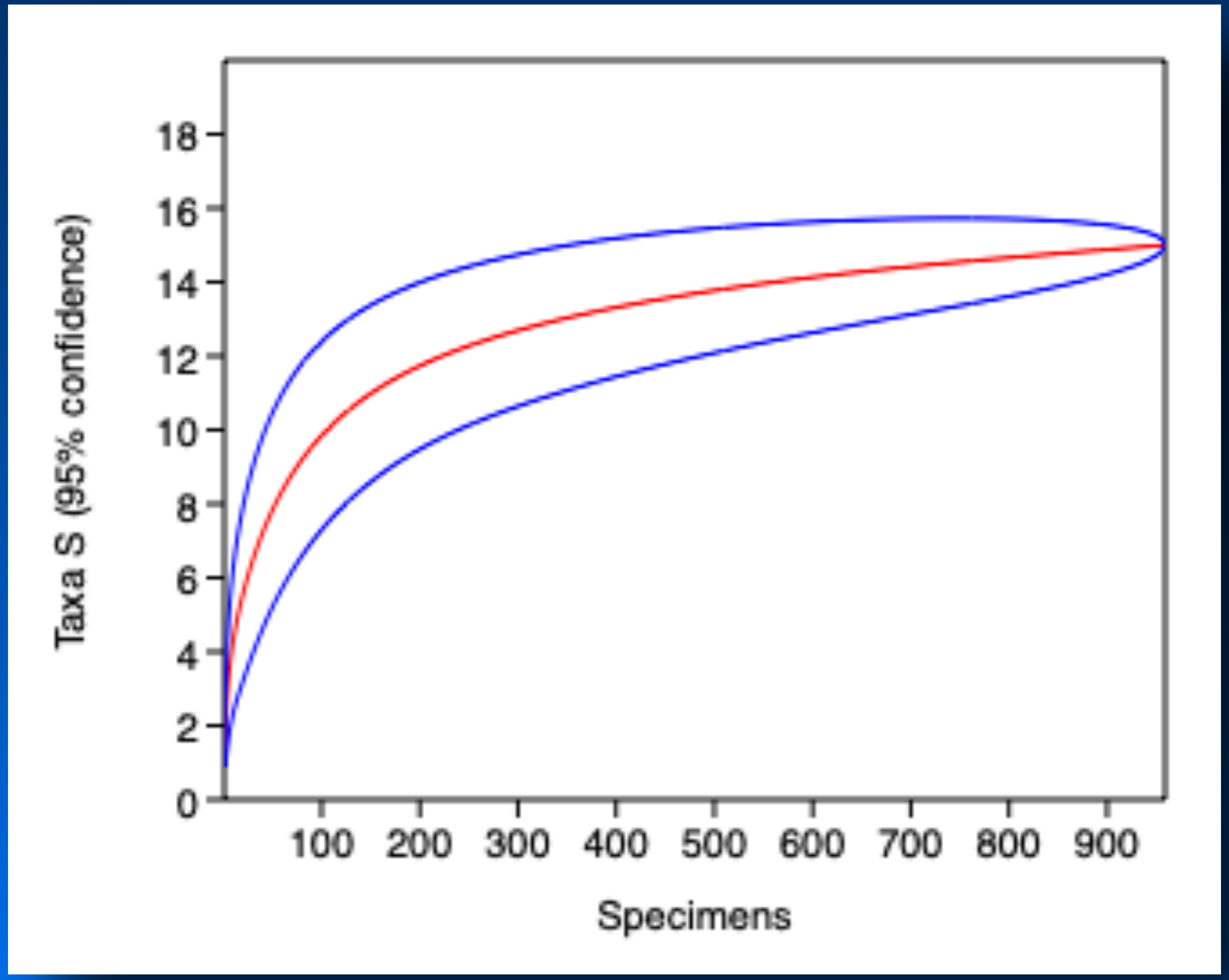
Taxic Richness Comparison

Rarefaction

A simple numerical procedure for estimating the number of groups that would be expected to be recovered at sample sizes smaller than the ones to hand.

Sample CD 6



Rarefaction Result

n	Est. (S_n)	Variance
17	5.229	1.156
18	5.341	1.172
19	5.449	1.187
20	5.554	1.200
21	5.656	1.213
22	5.756	1.224
23	5.853	1.235
24	5.947	1.244
25	6.040	1.253
26	6.130	1.261
27	6.218	1.269
28	6.304	1.276
29	6.389	1.282
30	6.471	1.288

CD 6 (*n*=26)

Sample	CD 6
Est. S_n	6.130
Var.	1.261
95% $\text{CI}_{\text{(upper)}}$	8.602
95% $\text{CI}_{\text{(lower)}}$	3.621

Sample	CD 7
S_n	8

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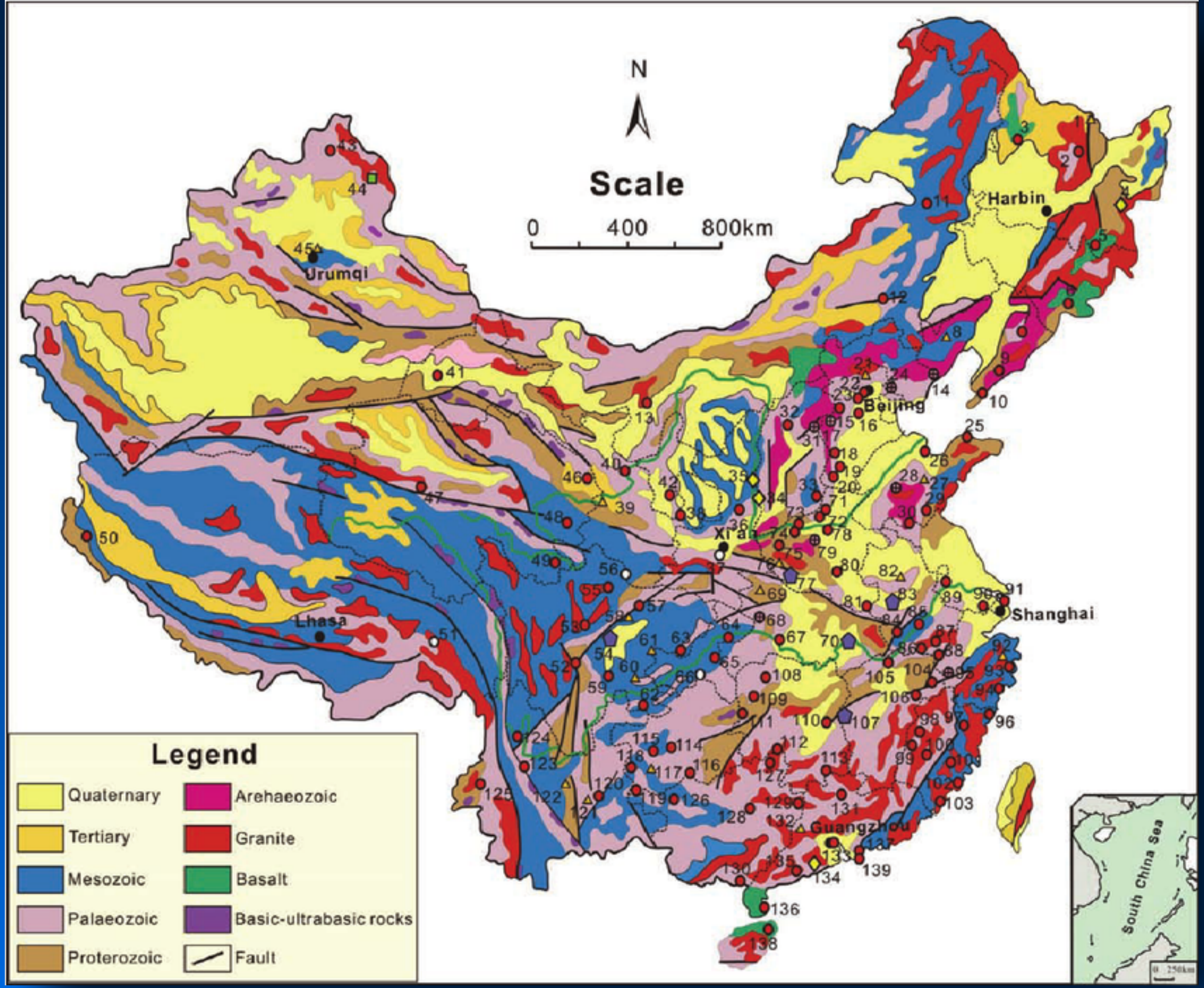
Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness



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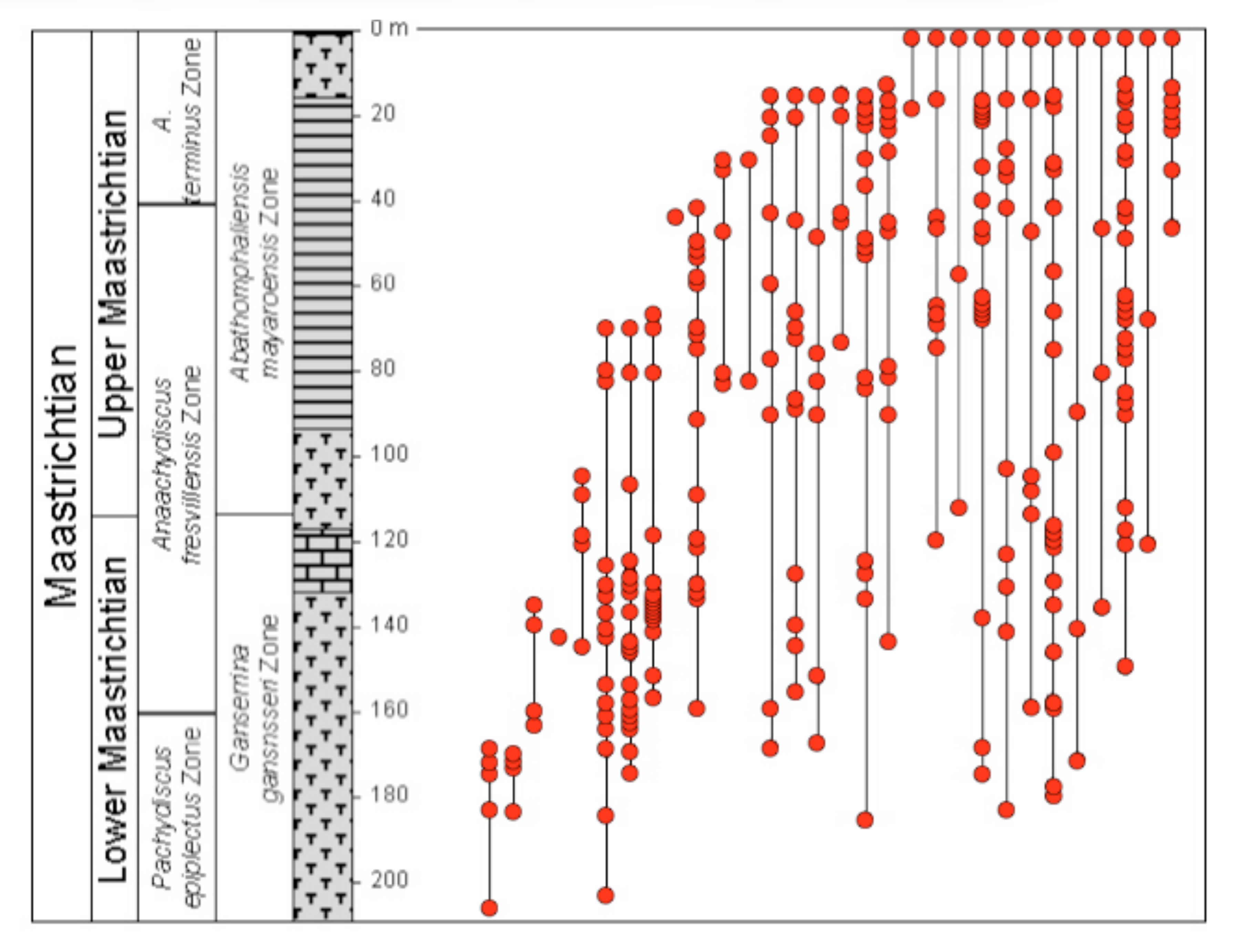
Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness

If it is inappropriate to compare richness counts for two samples of different sample sizes, it is also inappropriate to compare richness counts of different time intervals in which the frequency of fossil occurrences may differ for a wide range of reasons:

- uneven outcrop area;
- differences in outcrop accessibility or geographic sampling;
- differences in the range of facies or depositional environments preserved;
- presence of Lagerstätten;
- uneven taxonomic resolution.



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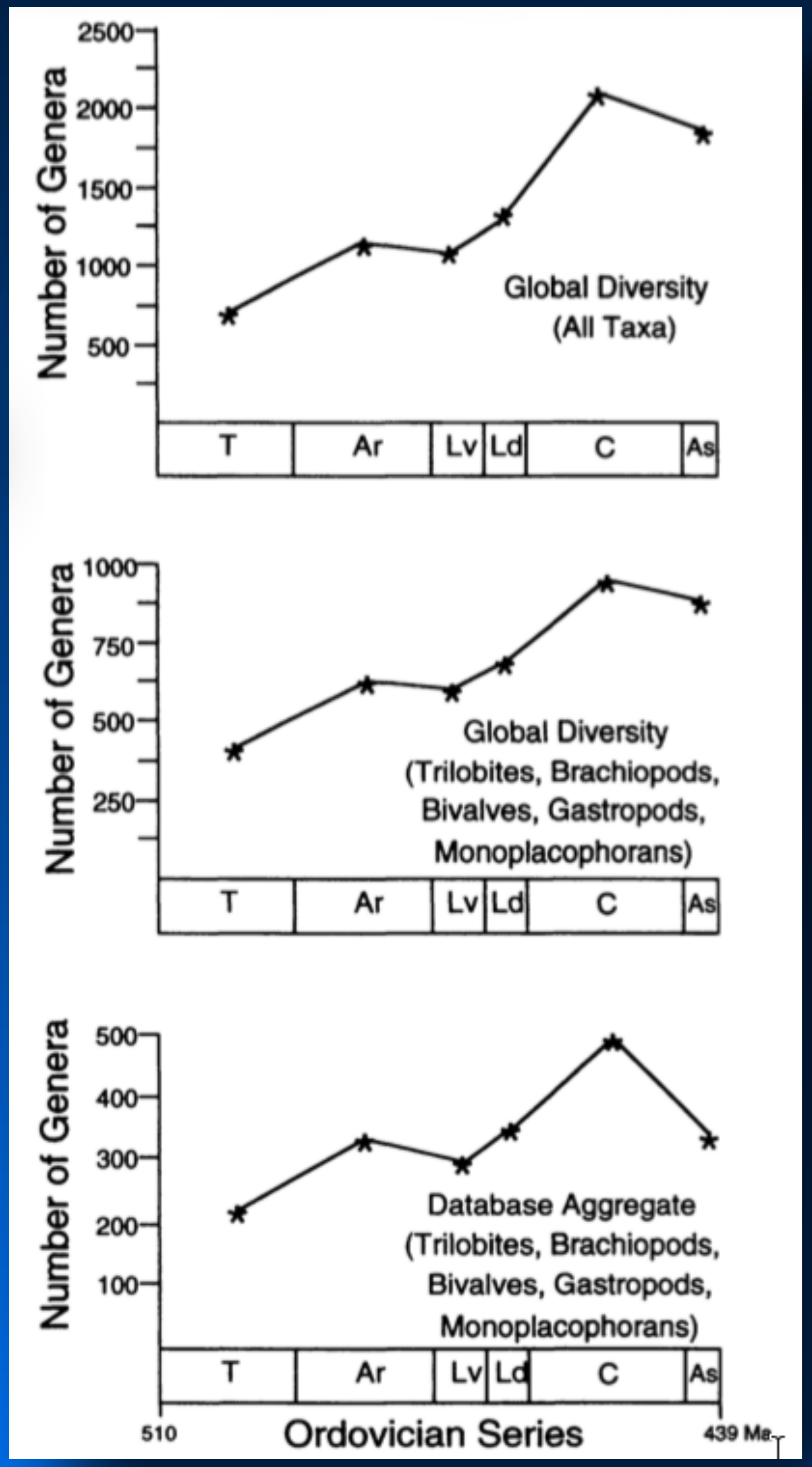
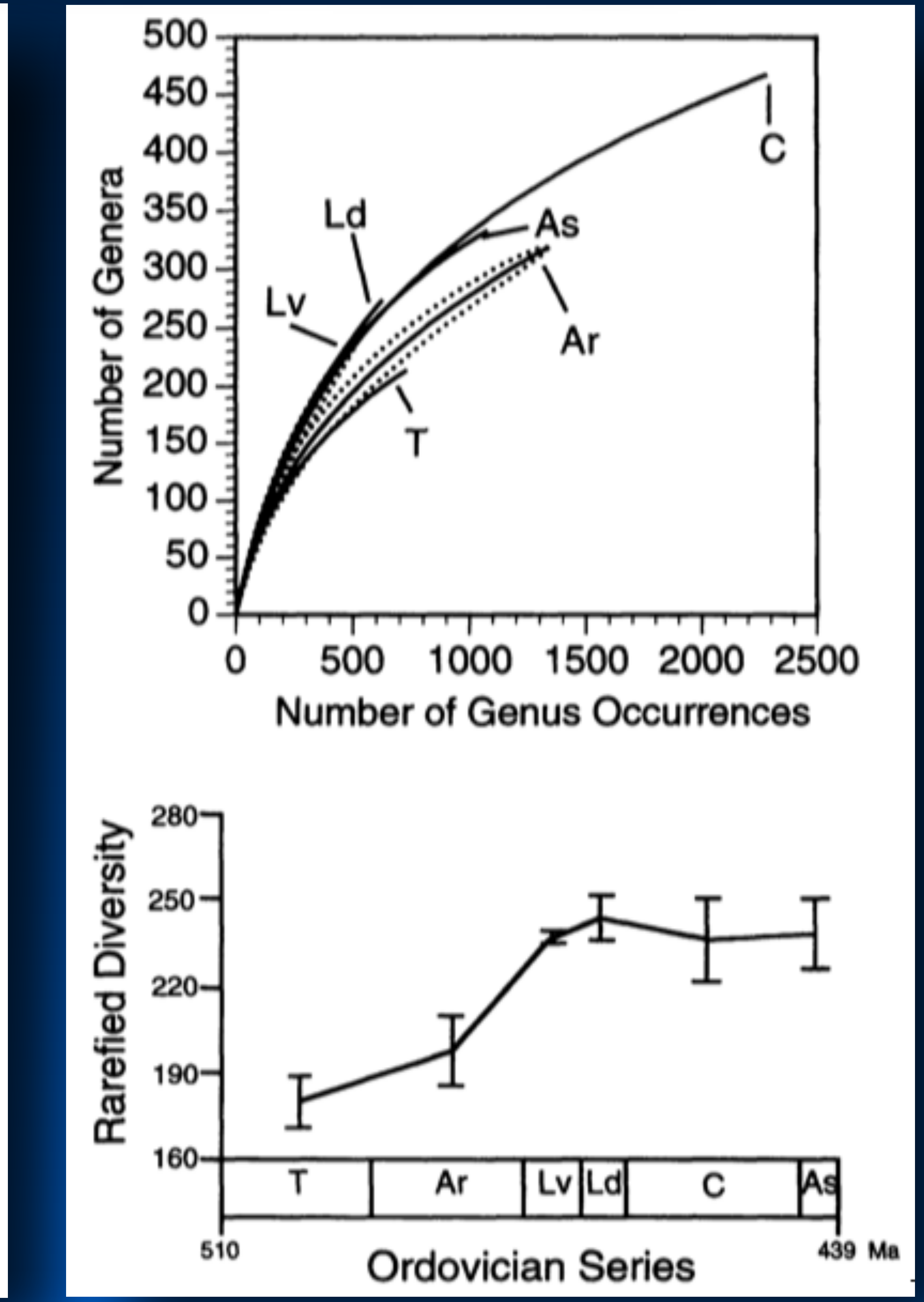
Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness

Miller & Foote (1996) showed how rarefaction of marine invertebrate occurrence data could be used to correct taxic richness estimates for differences in sampling intensities that characterize different Ordovician stages.

In this context the rarefaction technique represents of form a subsampling.



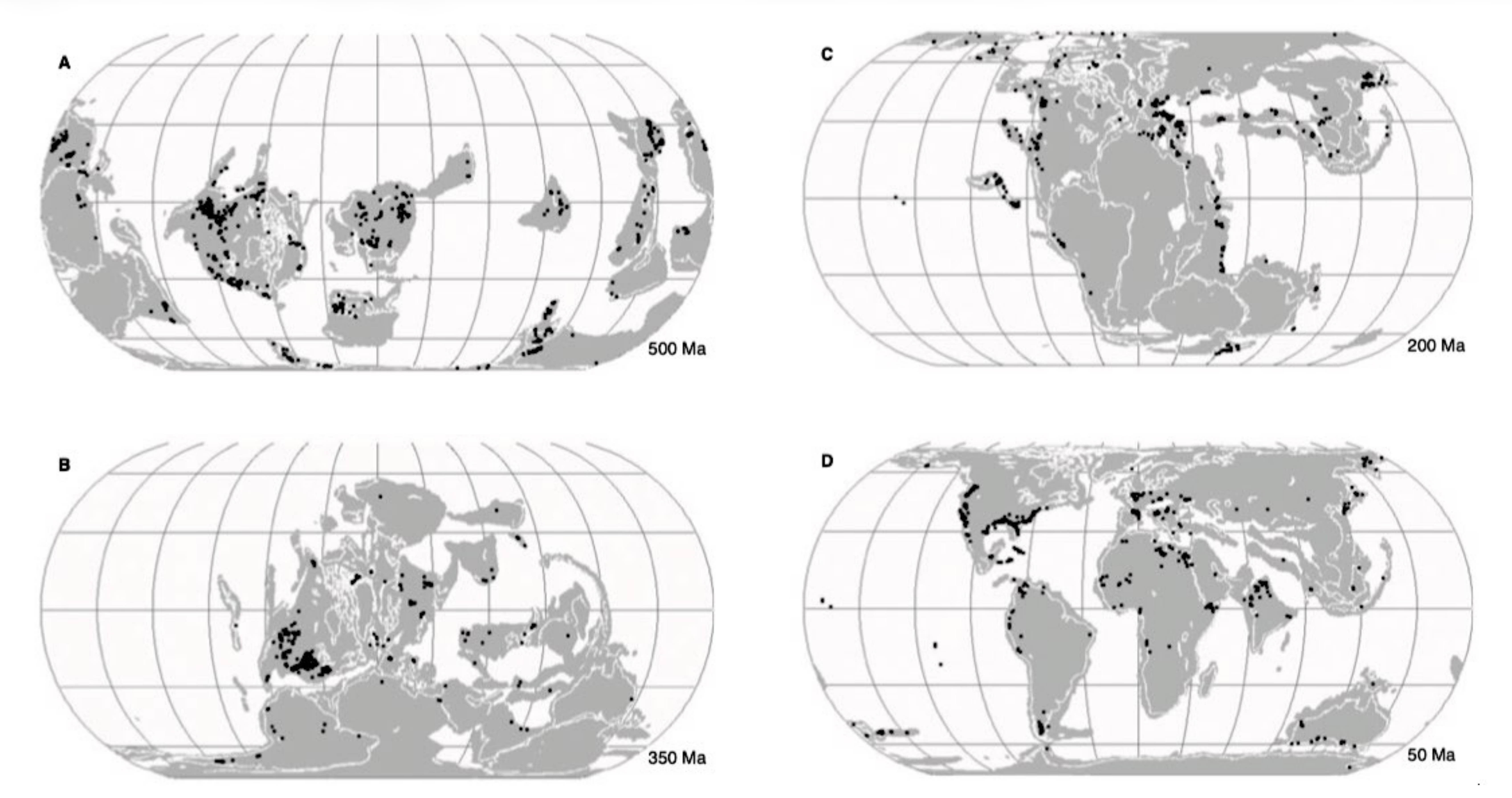


Diagrams from Miller & Foote (1996)

Paleobiodiversity

Taxon Richness Measurement

Dynamic Interplay Between Preservation, Access and Richness



Diagrams from Alroy (2010)

Paleobiodiversity

Taxon Richness Measurement

Dynamic Interplay Between Preservation, Access and Richness

The Problem

Traditional rarefaction or extrapolation to equal-sized samples can misrepresent the relationships between the richnesses of the communities being compared because a sample of a given size may be sufficient to fully characterize the lower diversity community, but insufficient to characterize the richer community. Thus, the traditional method systematically biases the degree of differences between community richnesses.

Chao & Jost (2012)

The Solution(s) (Provisional)

“It is not sufficient to scale taxon counts back to a common sample size (via rarefaction). Instead, the sizes of the samples should be adjusted to the point where the completeness of their representation, or “coverage” is equal relative to the statistical populations of interest.”

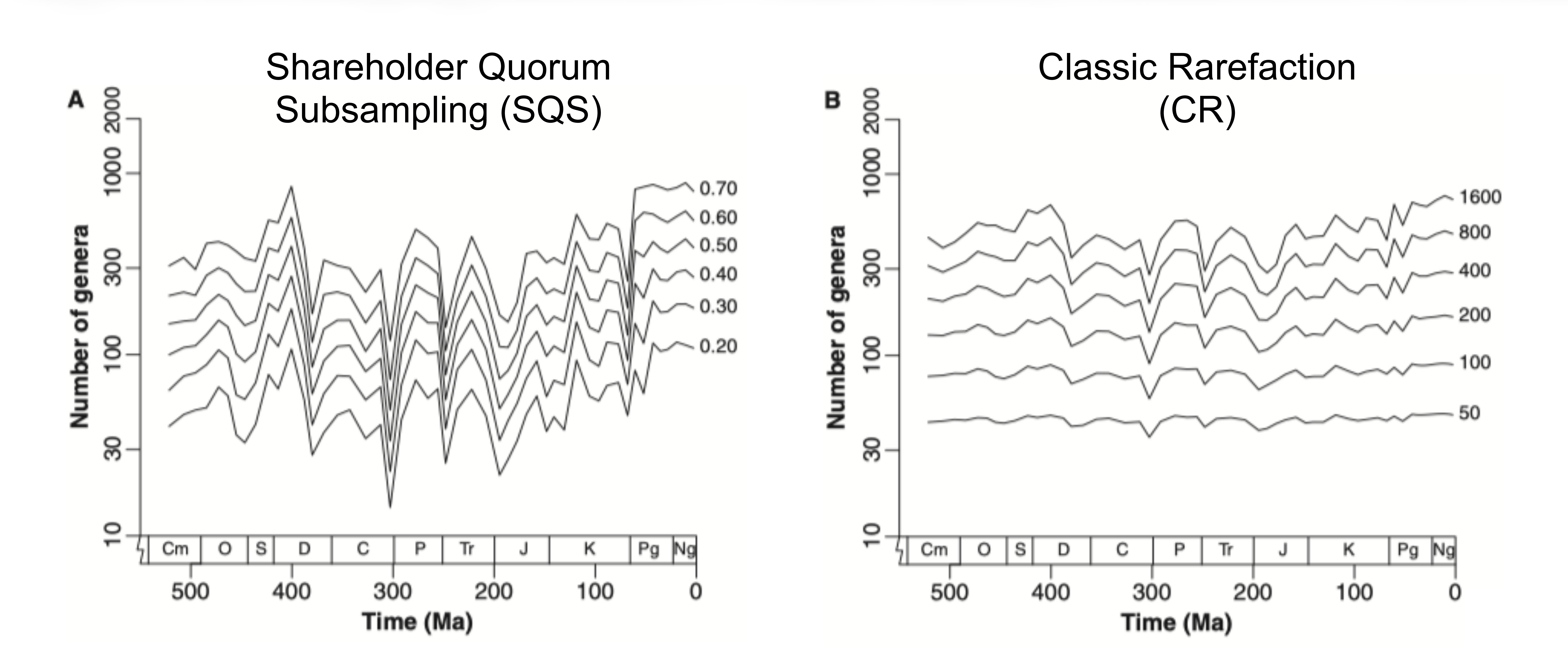
MacLeod & Shi (in press)

Such adjustments can be made by increase the size of underrepresented samples or, statistically, but adjusting oversized samples back to a common “coverage” value.

Paleobiodiversity

Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness



Shareholder Quorum Subsampling (SQS)

Classic Rarefaction (CR)

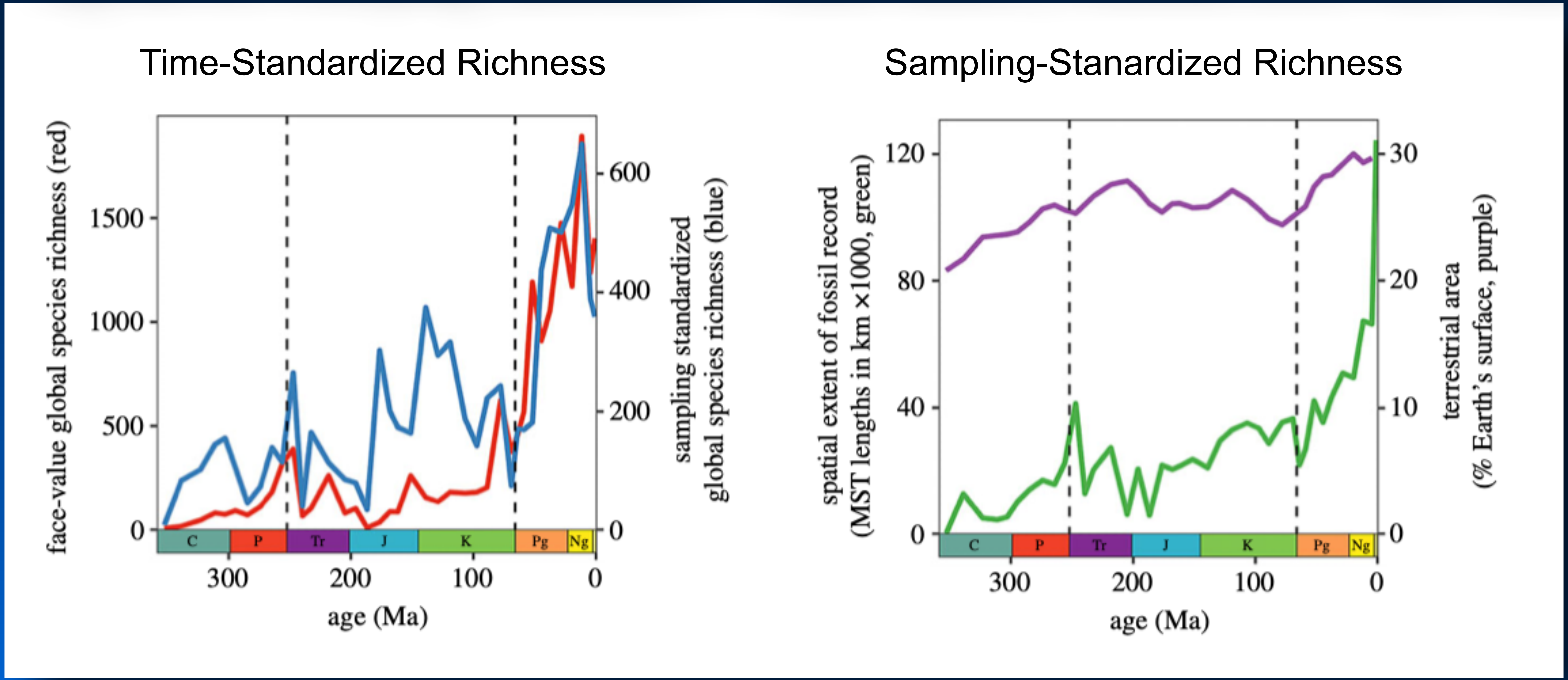
Phanerozoic taxic richness curves estimated by different subsampling methods at different sampling levels

Diagrams from Alroy (2010)

Paleobiodiversity

Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness



Time-Standardized Richness

Sampling-Stanardized Richness

Taxon Counting

Time-Interval Standardized (SQS)

Sampling Standardized (equal area grid)

Sampling Standardized (habitable area)

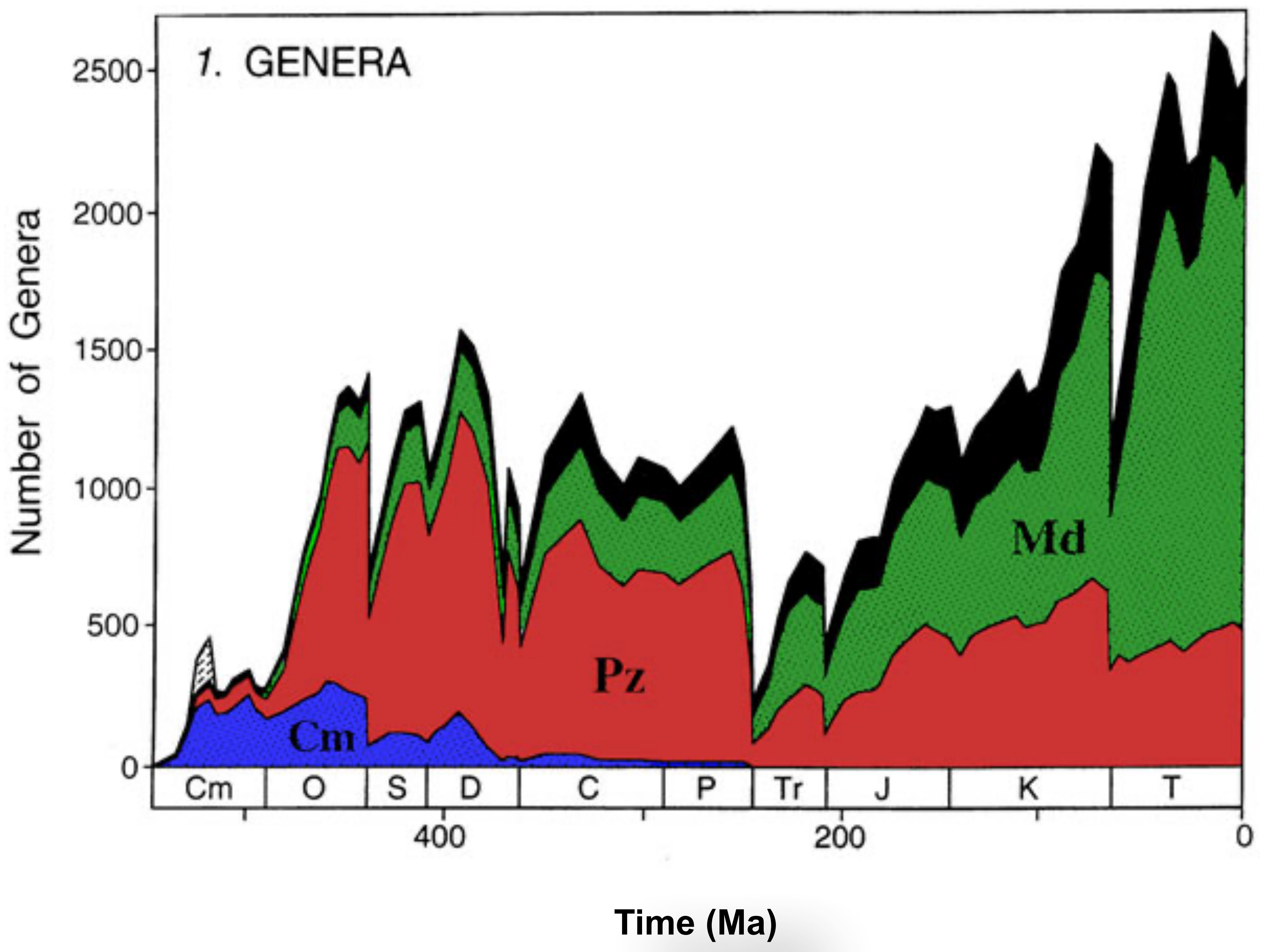
Diagrams from Close et al. (2020)

Paleobiodiversity

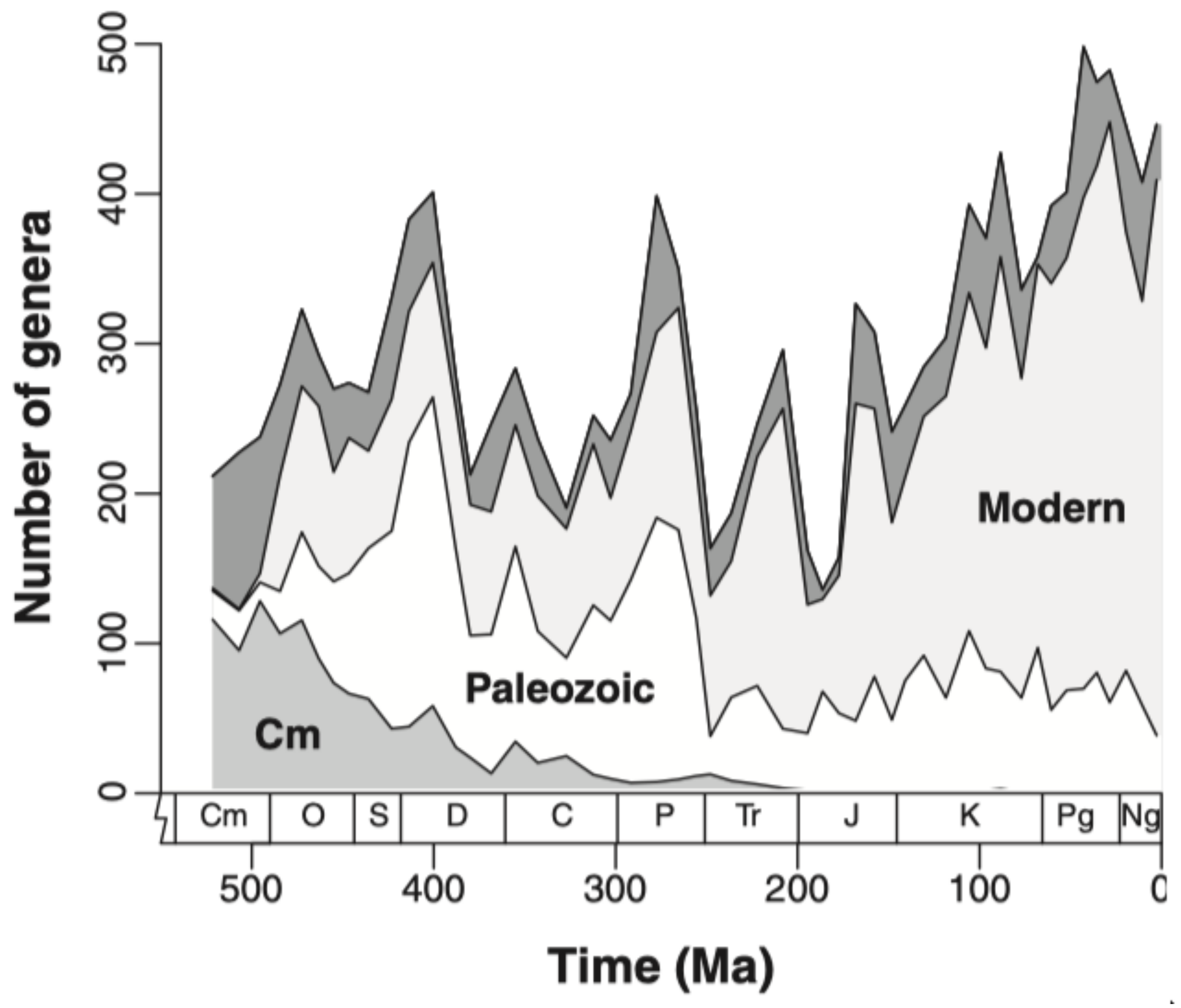
Bias in Taxon Richness Estimates

Dynamic Interplay Between Preservation, Access and Richness

Taxon Counting Richness



Sampling Stanardized Richness



Diagrams from Sepkoski (2001, left) and Alroy (2010, right)

Paleobiodiversity

Interesting Ideas & Issues

Paleobiodiversity

Interesting Ideas & Issues

It has long been known that terrestrial species richness in the Recent far exceeds marine species richness (see Vermeij & Gosberg 2010). But the fossil record indicates this was not always so.

- When did terrestrial species richness exceed marine species richness?
- Was there something special about that time; could it have happened earlier or later?
- What attribute(s) do terrestrial species have – or marine species lack – that allows them to, or retards them from, the accumulation of species?

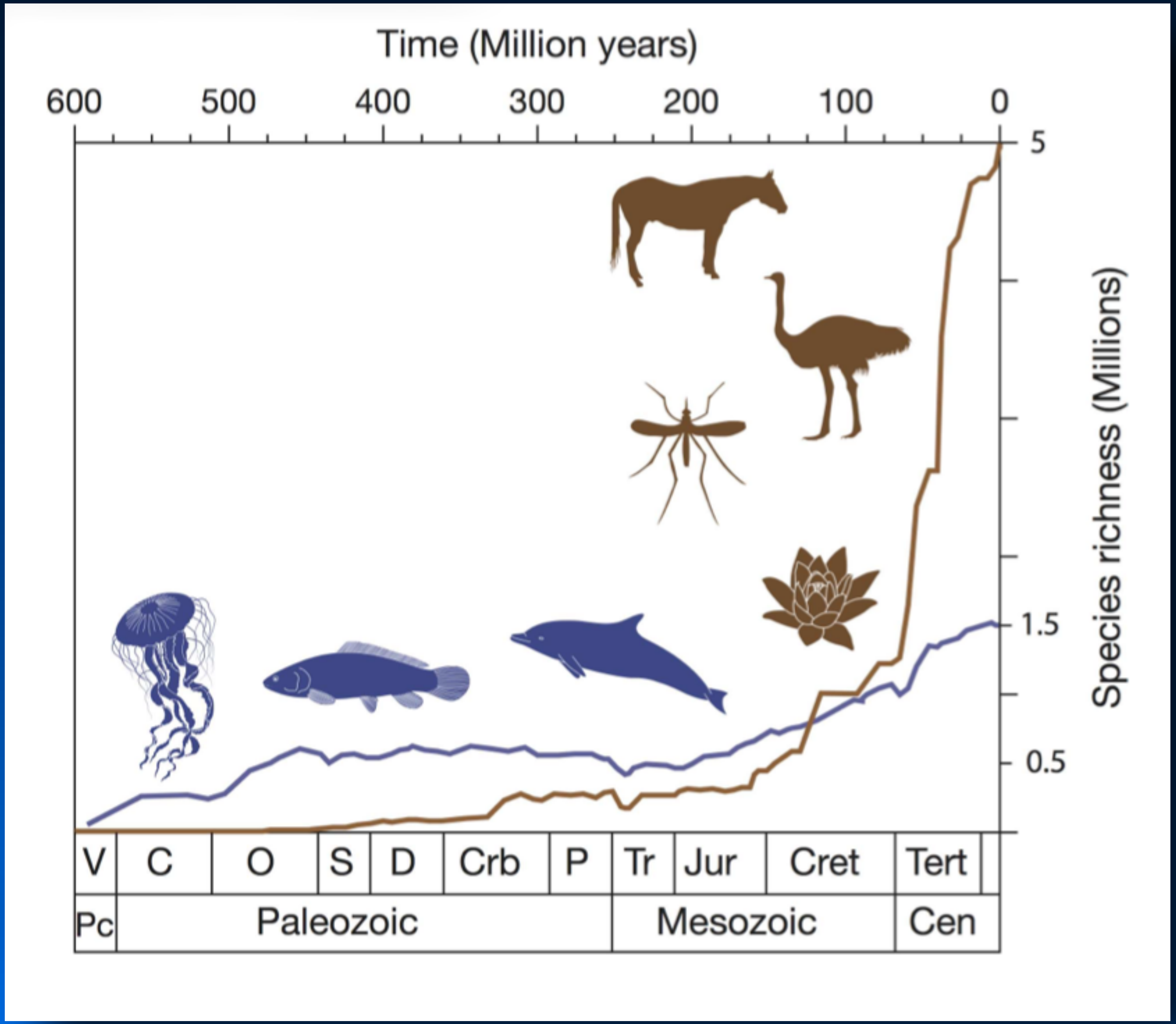


Diagram from Benton (2016)

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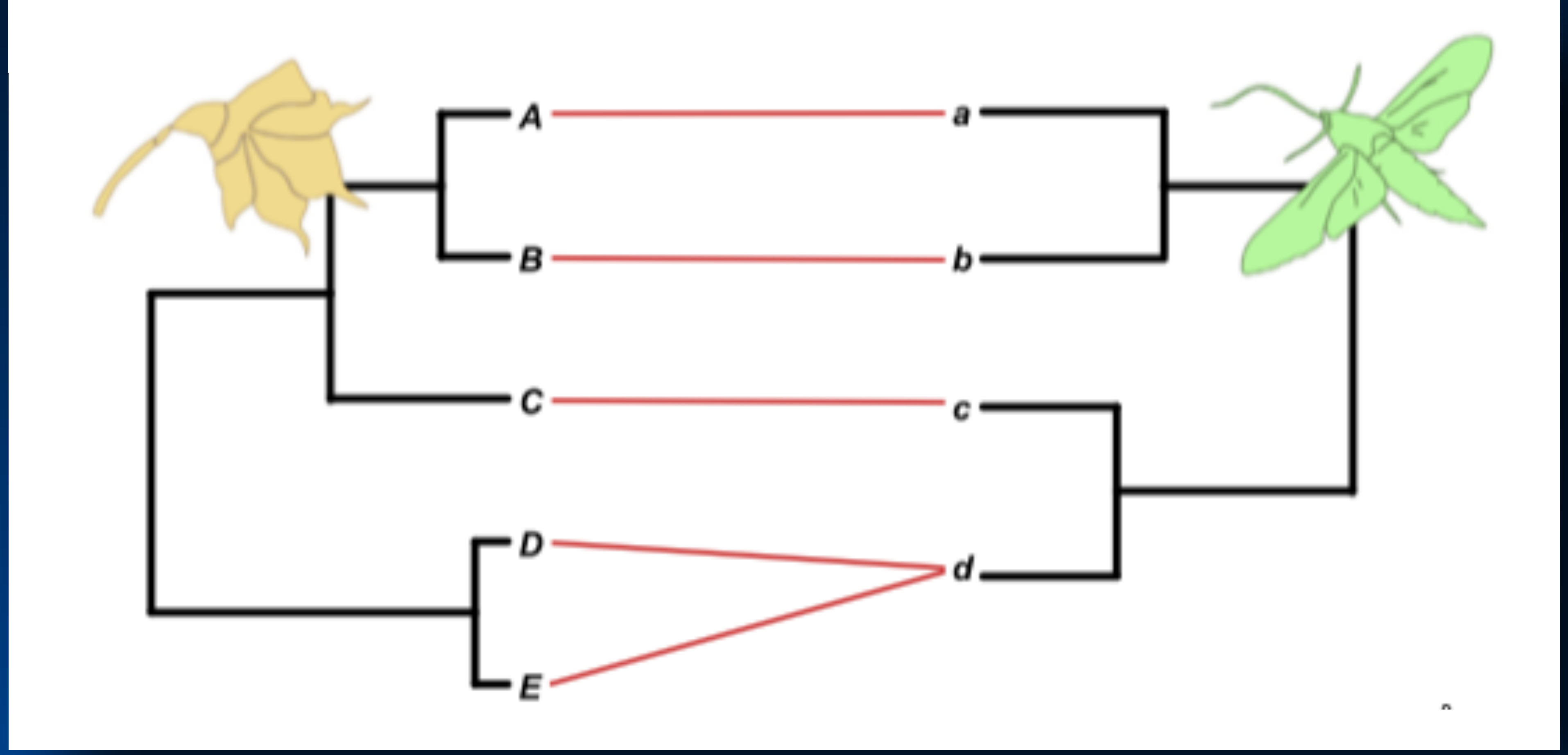
Interesting Ideas & Issues

Co-phylogeny provides a powerful way to understand eco-evolutionary relations among species and explore datasets for the presence of such relations.

To date this technique has been used to document host-symbiont relations, but it has potential for a much wider range of applications.

Such studies focus on understanding patterns of taxic diversification via the establishment evidence for links between patterns of diversification and mechanisms that promote (or inhibit) diversification (see Blasco-Costa (et al., 2021 for a recent review).



Symbiont

Host

	a	b	c	d
A	1	0	0	0
B	0	1	0	0
C	0	0	1	0
D	0	0	0	1
E	0	0	0	1

Diagram from Blasco-Costa et al. (2021)

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Interesting Ideas & Issues

The Relation between Morphological Novelty and Ecological Innovation

Cladograms (if sufficiently robust) can be used to generate a wide range of hypotheses concerning the relation between the patterns and mechanisms of evolutionary diversification.

Here, a well corroborated xiphosurid cladogram has been used as the basis of making predictions regarding the life-history mechanisms (e.g., paedomorphosis, peramorphosis) that were employed to bring these changes about. The consistency with which these life-history data reflect the major clades within this group helps to both verify the accuracy of the phylogenetic analysis and gain insight into the developmental mechanisms employed to realize diversification.

It also raises an interesting question regarding whether the ultimate cause for the evolution of this clade was a developmental "push" or an ecological "pull".

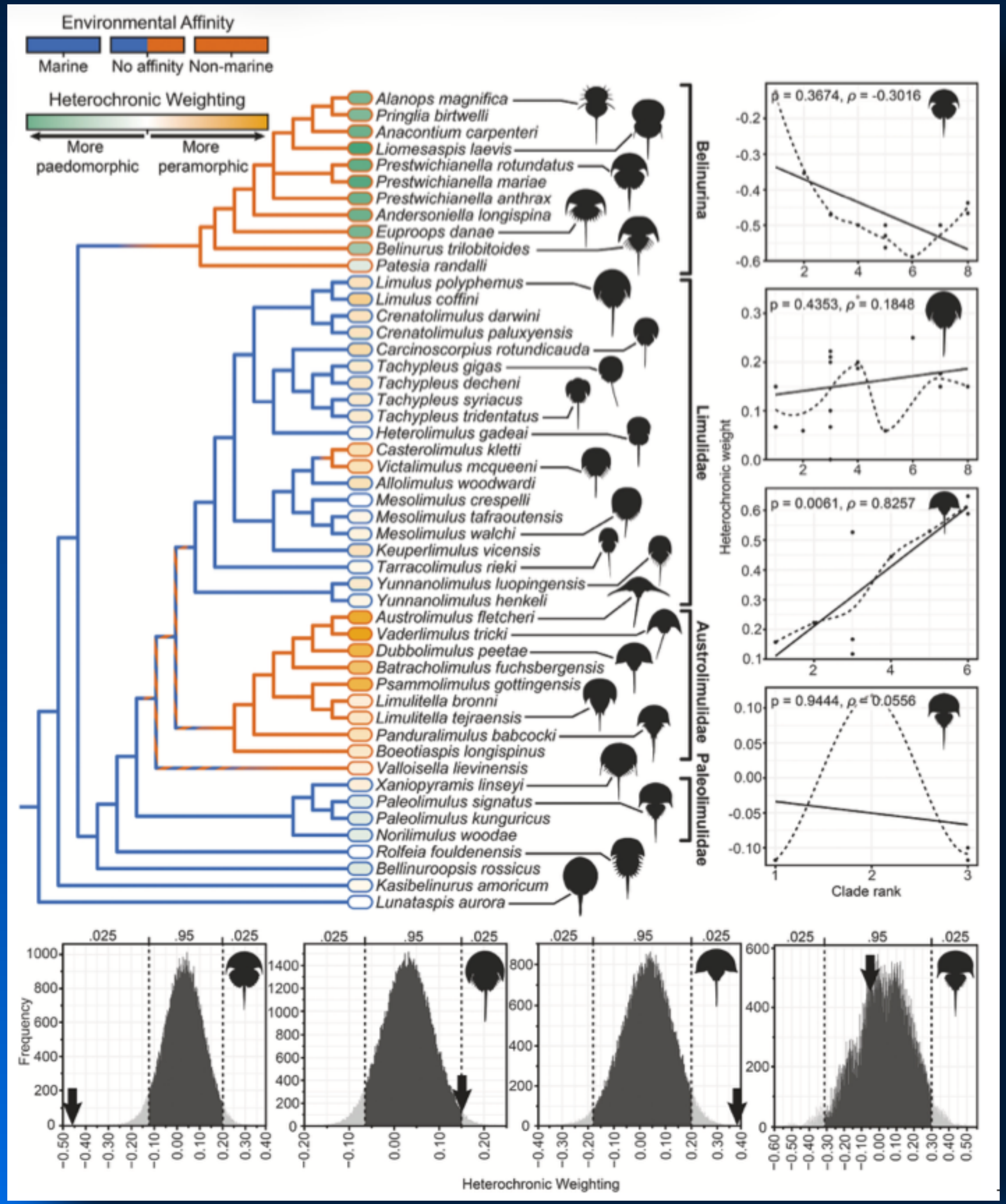

Diagram from Lambsdell (2021)

Paleobiodiversity

Interesting Ideas & Issues

The Relation between Morphological Novelty and Ecological Innovation

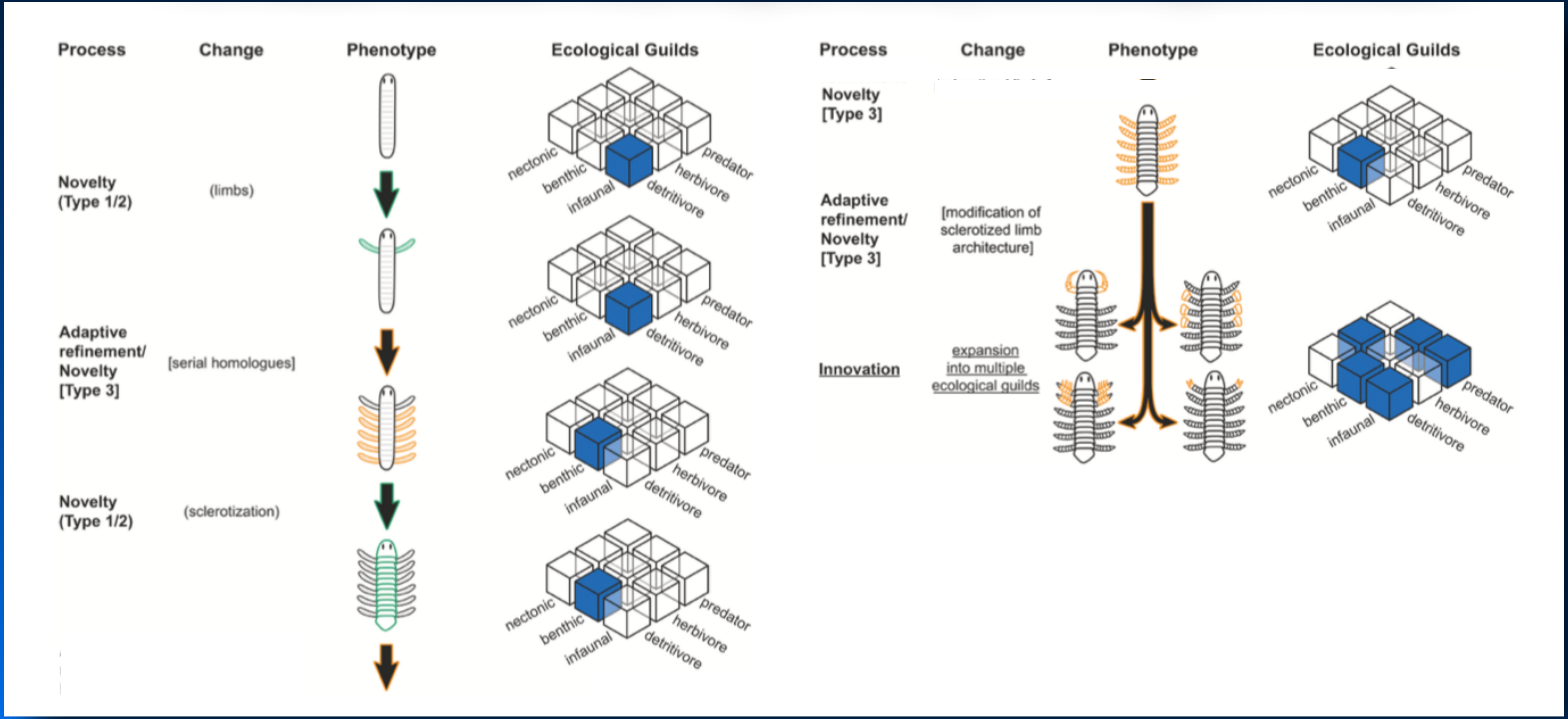

Diagram from Lambsdell (2021)

NJU Course

Principles of Paleobiology

Paleobiodiversity