Perspectives on Biodiversity Through Time: Trends, Mechanisms, Constraints

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Evolution
has constraints
as well as
opportunities

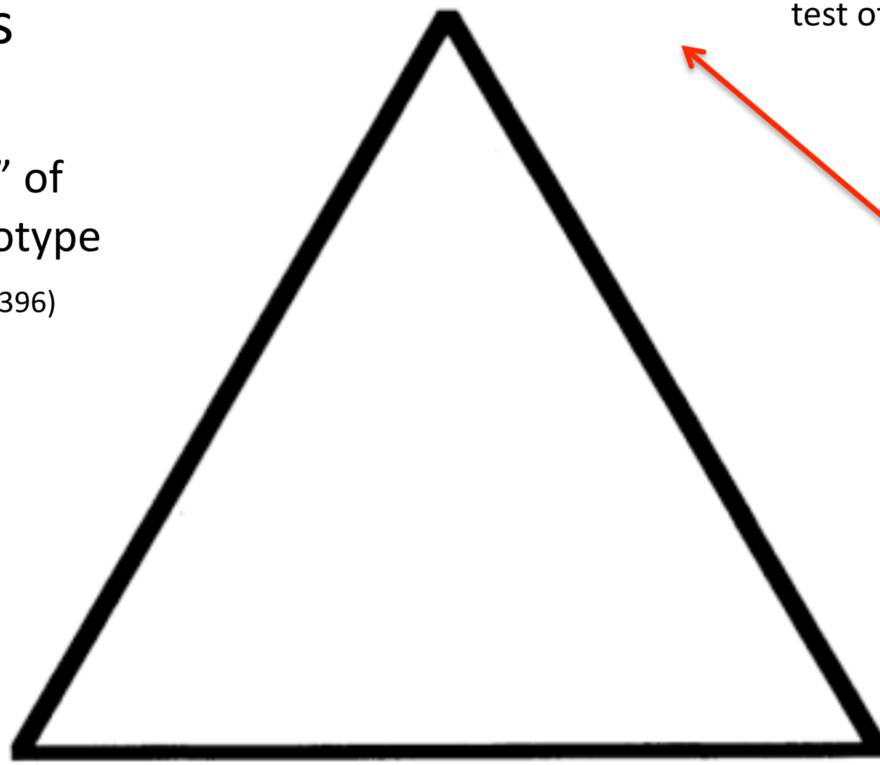
"Seilacher's Triangle" of
determinants of phenotype

(Seilacher 1970 *Lethaia* 3:393–396)

PHYLOGENETIC

(Features determined by
inherited developmental program,
such as lack of mouth parts in trilobites,
presence of dorsal nerve chord in chordates,
test of opaline silica in diatoms)

Constraints
Imposed by
Established
Features



Source of
Opportunity
to Diversify

FUNCTIONAL

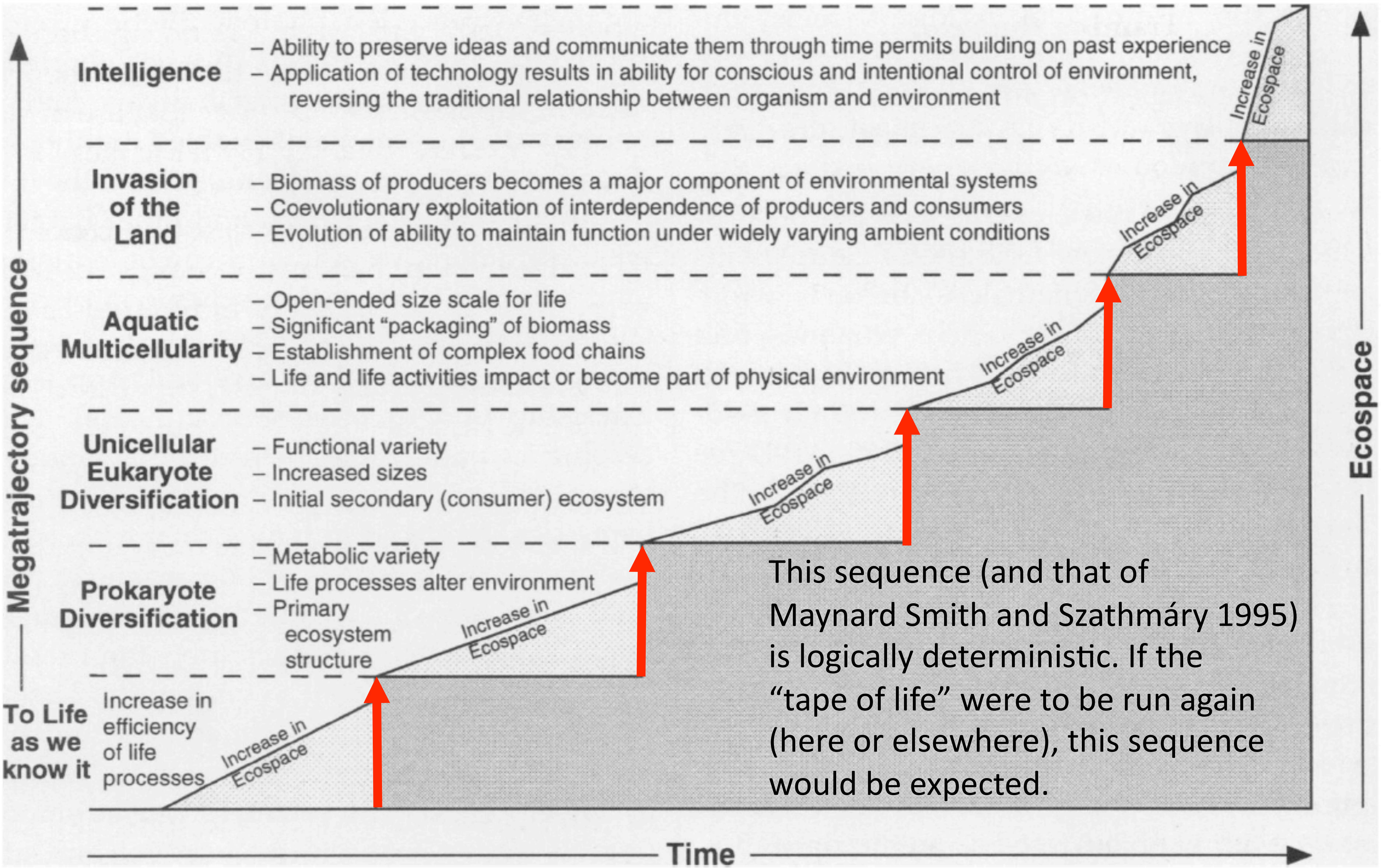
(Features determined by the operation
of natural selection.)

MORPHOGENETIC

(Features related to the structural materials
used, such as hardness and solubility of
calcite or aragonite, diffusion rates in protoplasm,
shear strength of muscle and cartilage.)

Figure from Ross and Allmon 1990 *Causes of Evolution: A Paleontological Perspective*

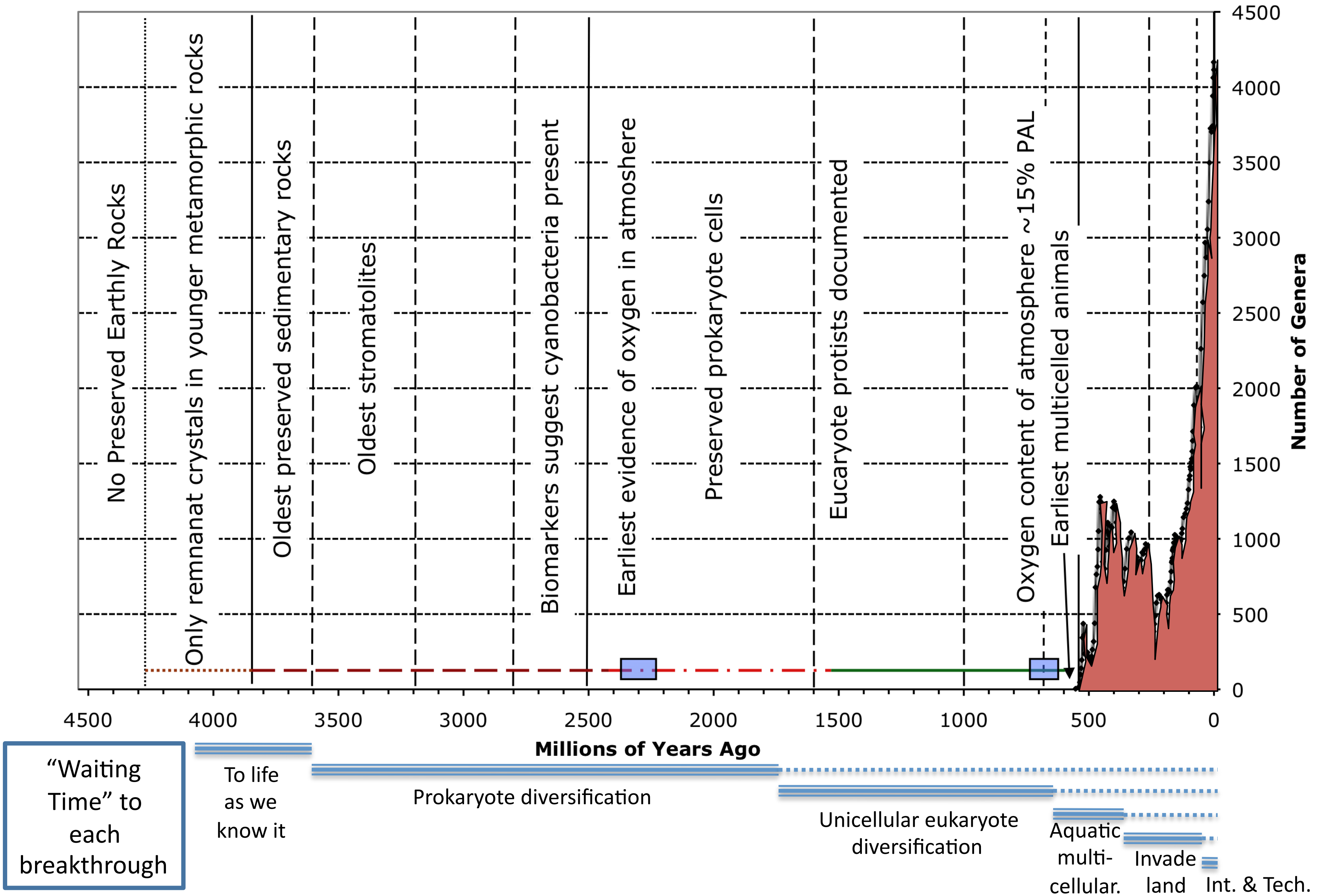
Difficulty in climbing limiting "right walls" are set by phylogenetic and morphogenetic constraints, making the achievement of each step up to the next "megatrajectory" and biodiversity level a chance event.



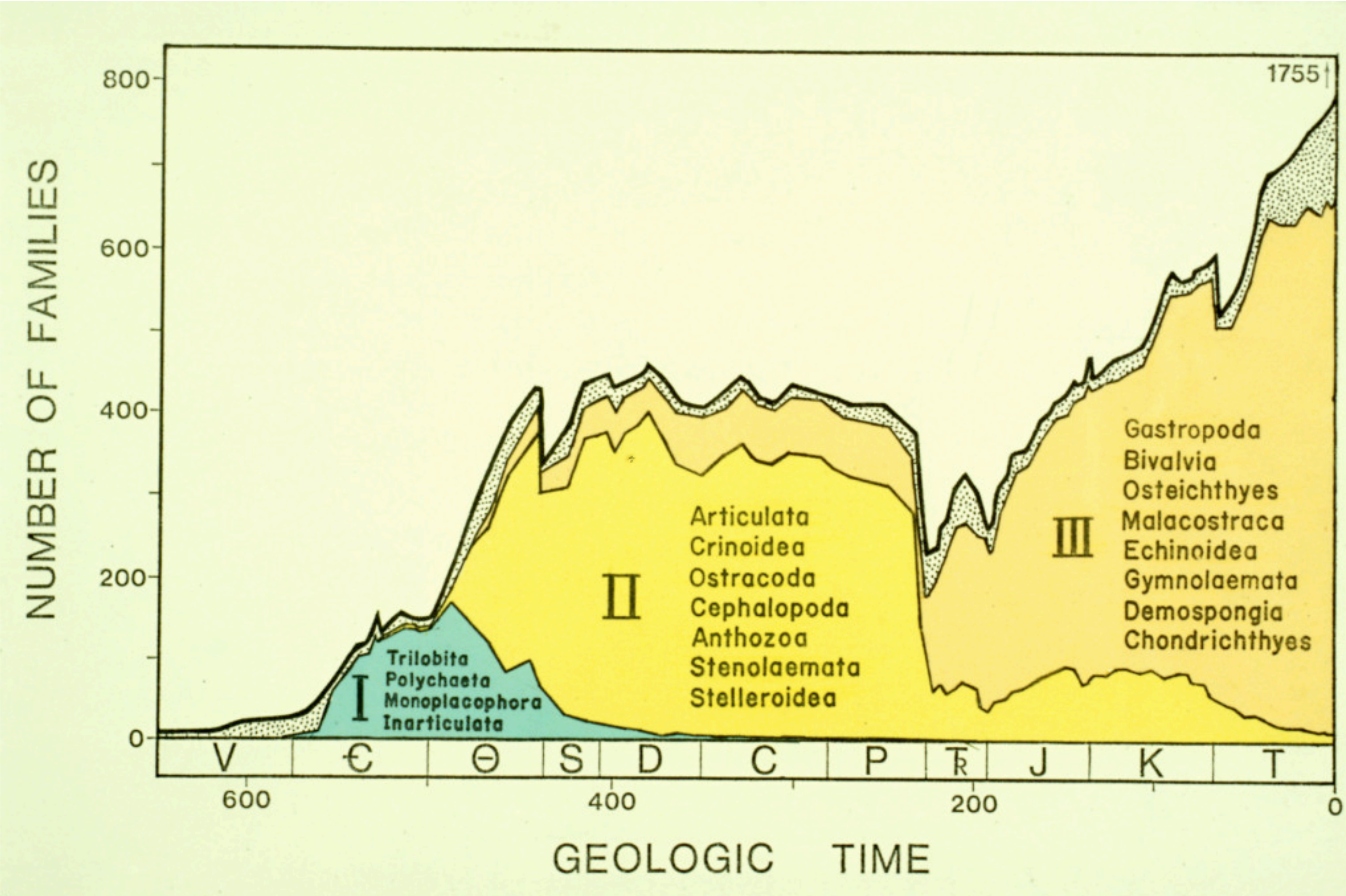
Natural selection and isolation of populations should combine to diversify life fully within each "megatrajectory" as time passes.

Knoll and Bambach 2000 *Deep Time* (*Paleobiology* 26: Supplement to #4)

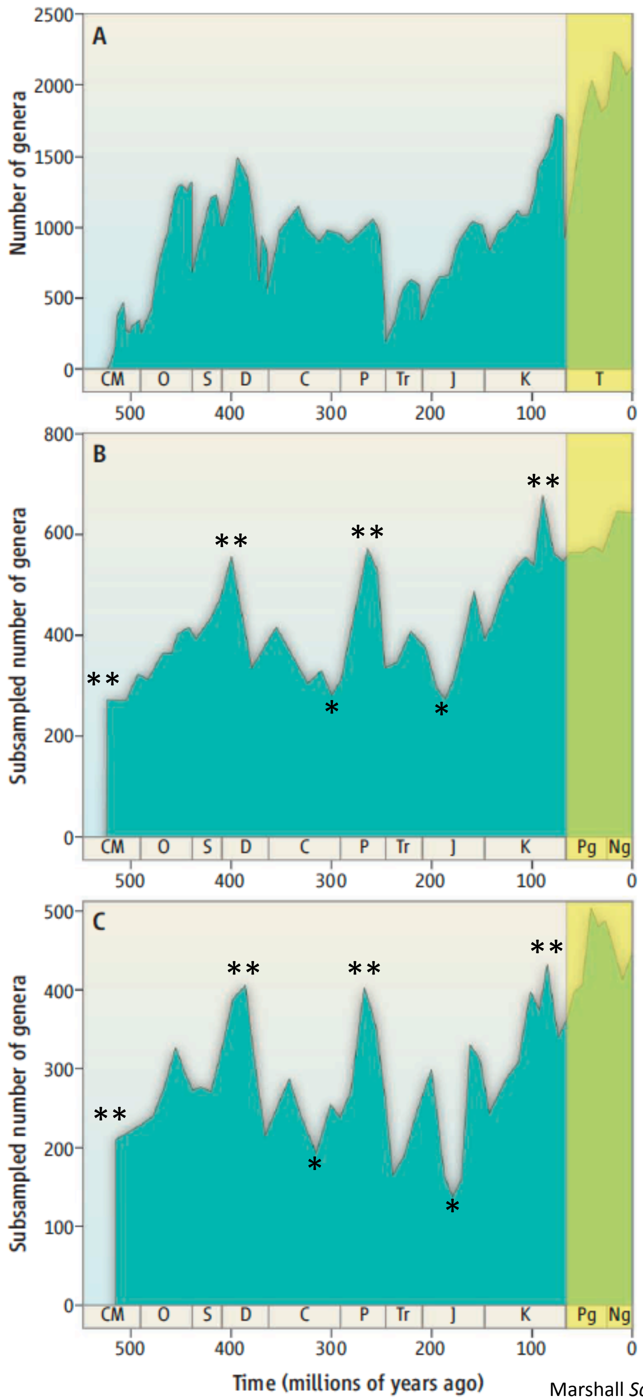
Outline History of the Earth



The iconic illustration of paleobiodiversity — Sepkoski's Family Diversity graph



Jack Sepkoski's *original* "three fauna" figure, used in his talk at the Geological Society of America Meeting in 1980



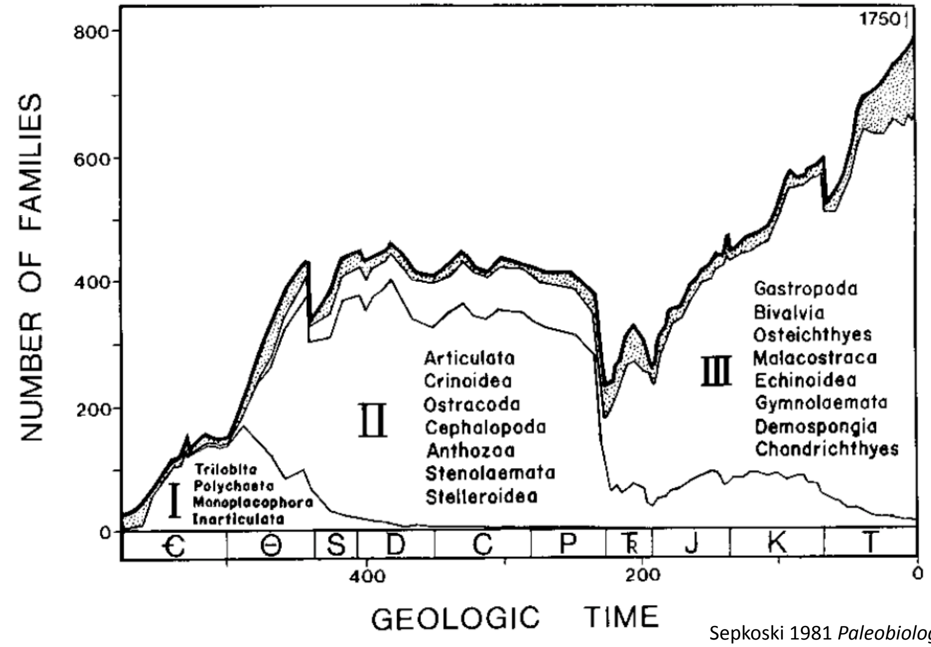
Sepk.
Genera
2002

PBDB
2008

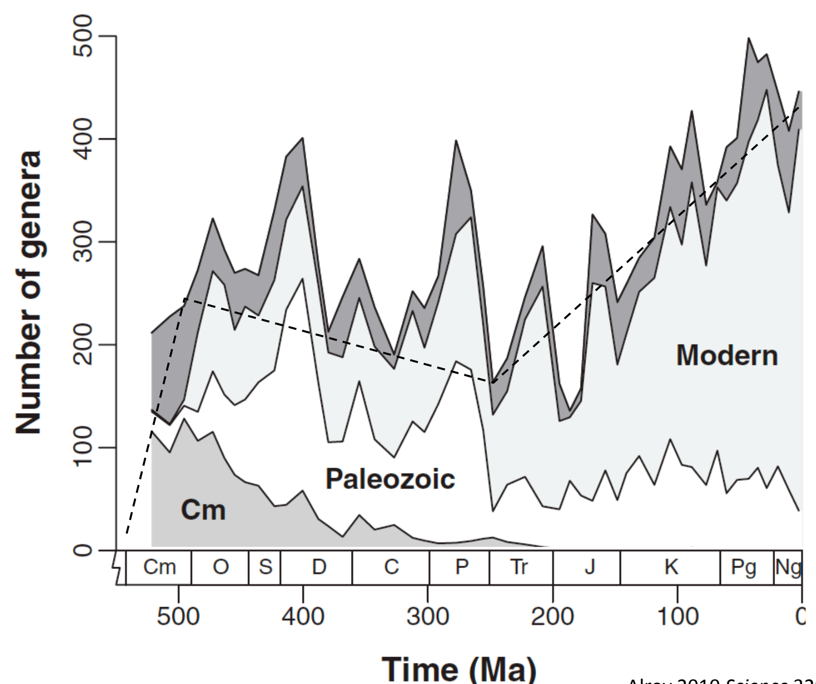
The PBDB
is still
adding data
and
refining its
methodology

PBDB
2010

Marshall *Science* 329:1156–7



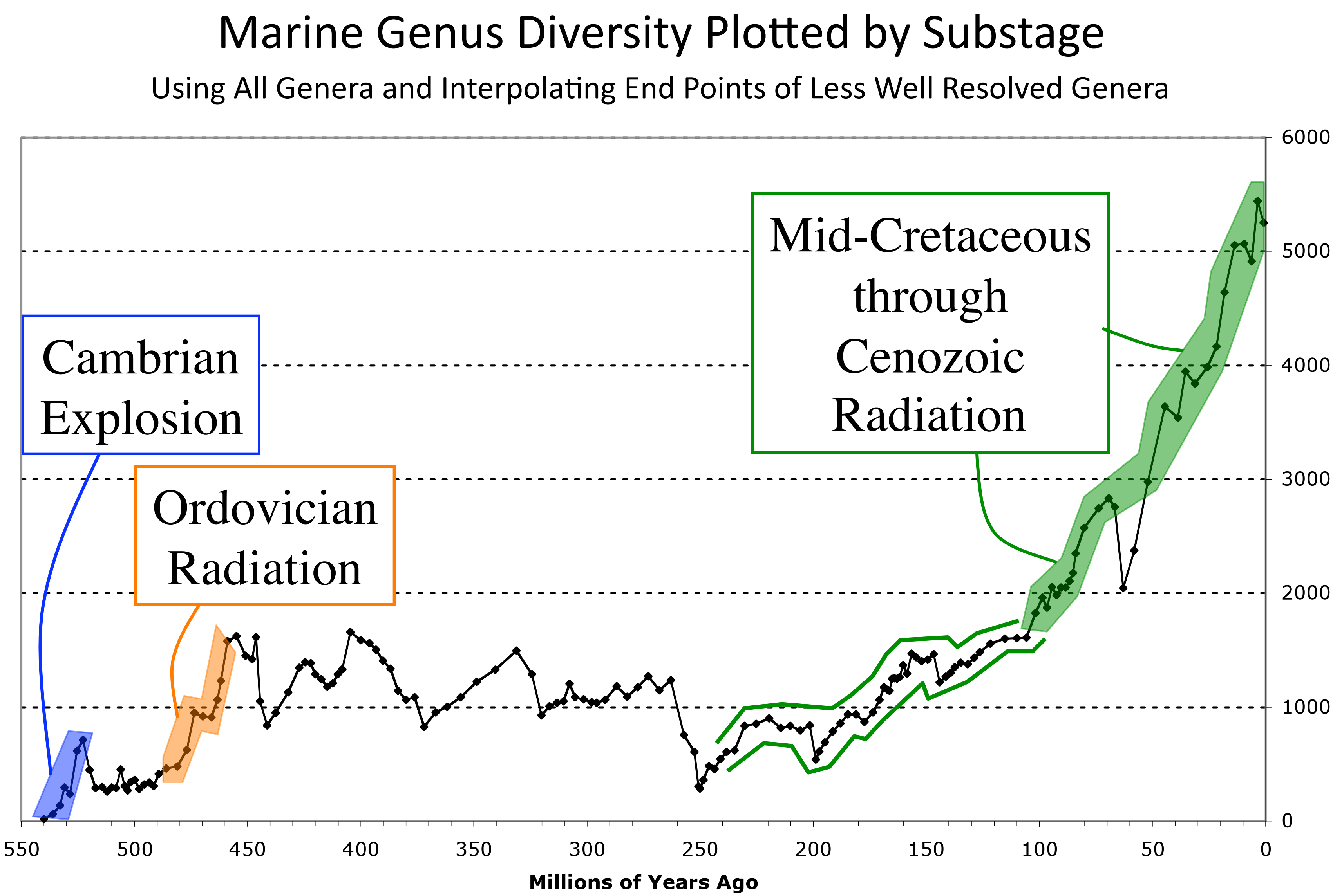
Sepkoski 1981 *Paleobiology* 7:36–53



Despite
differences
a
common
signal
pattern
is
emerging

Alroy 2010 *Science* 329:1191–1194

The first order signal, diversity increase, is from the radiation of the three "evolutionary faunas"



But remember, this is just the "Aquatic Multicellular" "megatrajectory"

An example of the difficulty of "climbing a right wall"

Not all higher phyla are capable of dealing with terrestrial environments

The number of phyla with representatives living freely in different habitat settings.

Habitat type	Protists	Plants	Fungi	Animals	Total
Terrestrial (dry land)		6	2	5	13
Terrestrial (moist habitats, soils)	13	9	5	10	37
Fresh water	24	2	5	15	46
Marine	26	1	3	34	64

Data tabulated from Margulis and Chapman 1998 *Kingdoms and Domains: An Illustrated Guide to the Phyla of Life on Earth*

Living in a dry, low-humidity environment exposed to the atmosphere is extremely difficult.
Few higher taxa have made the transition fully.
Climbing that "right wall" of exposure was far harder
than dealing with osmotic issues in fresh water.

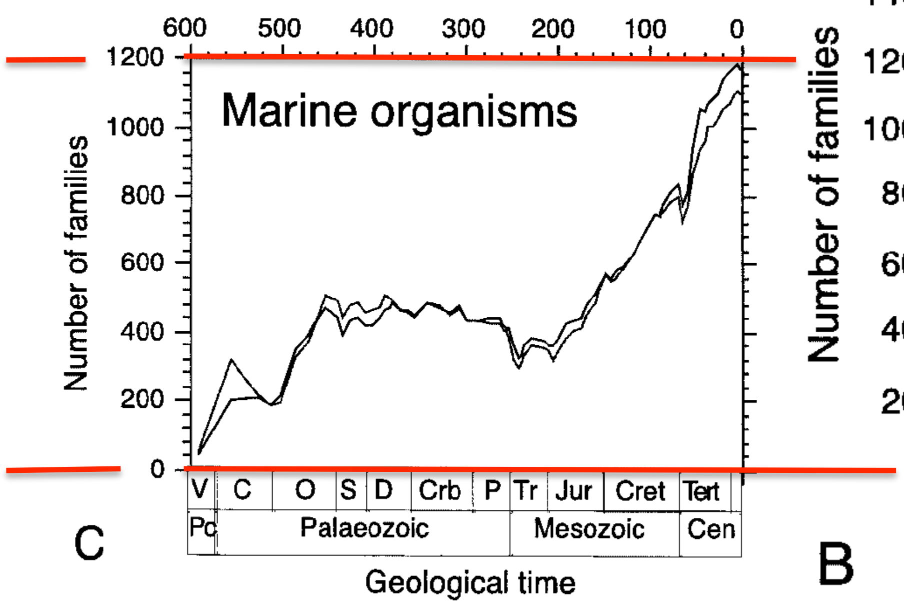
But invasion of the land created vast new opportunities for diversification at lower taxonomic levels

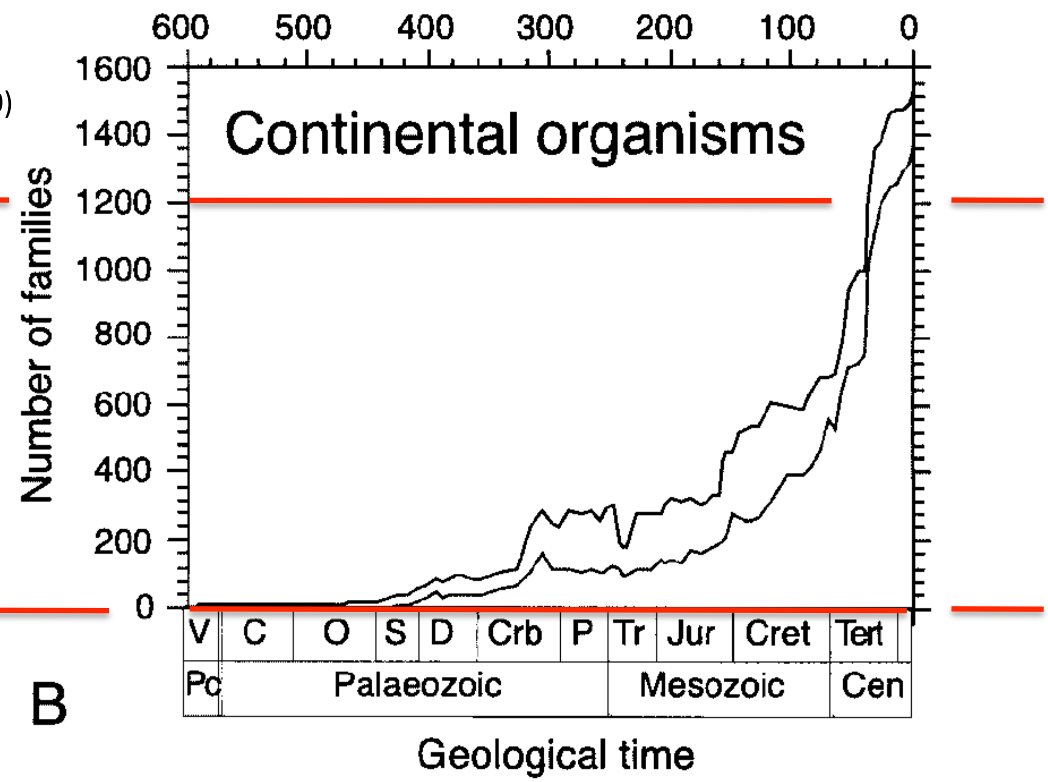
Ease of geographic isolation plus mutualistic interdependences, such as those for feeding and reproduction between angiosperms and arthropods, plus parasitic specializations have led to exceptionally high terrestrial species diversity despite the restricted diversity of higher taxa.

Half to one quarter the number of phyla on land, but more families than in the oceans.

FAMILY diversity

(Graphs from Benton 2001 *Geol. Jour.* 36:211–230)





Of the estimated 1,750,000 described species,

about 250,000 are marine and 1,500,000 are terrestrial.

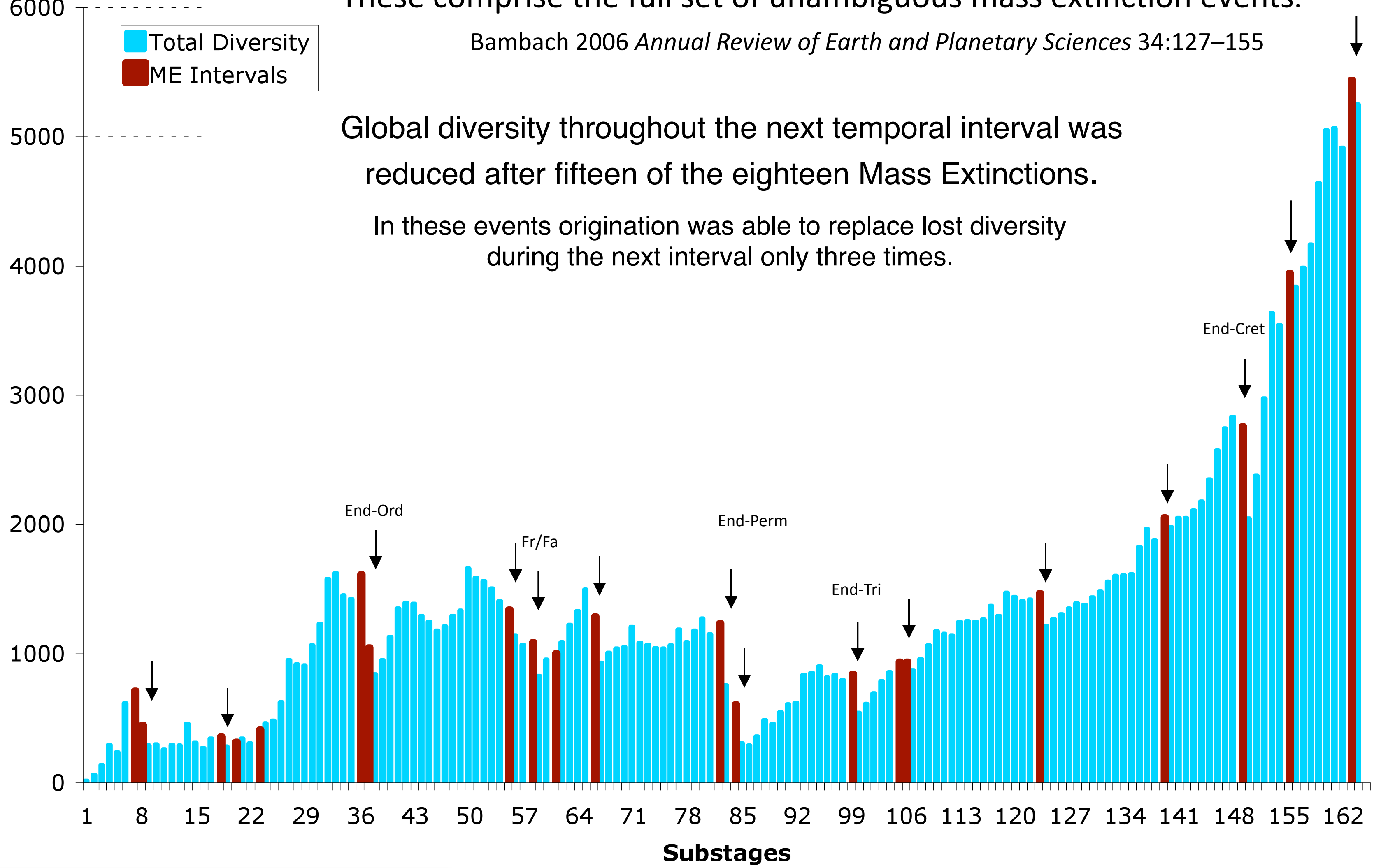
(Groombridge & Jenkins 2002 *World Atlas of Biodiversity)*

What about perturbations to biodiversity on a global scale?

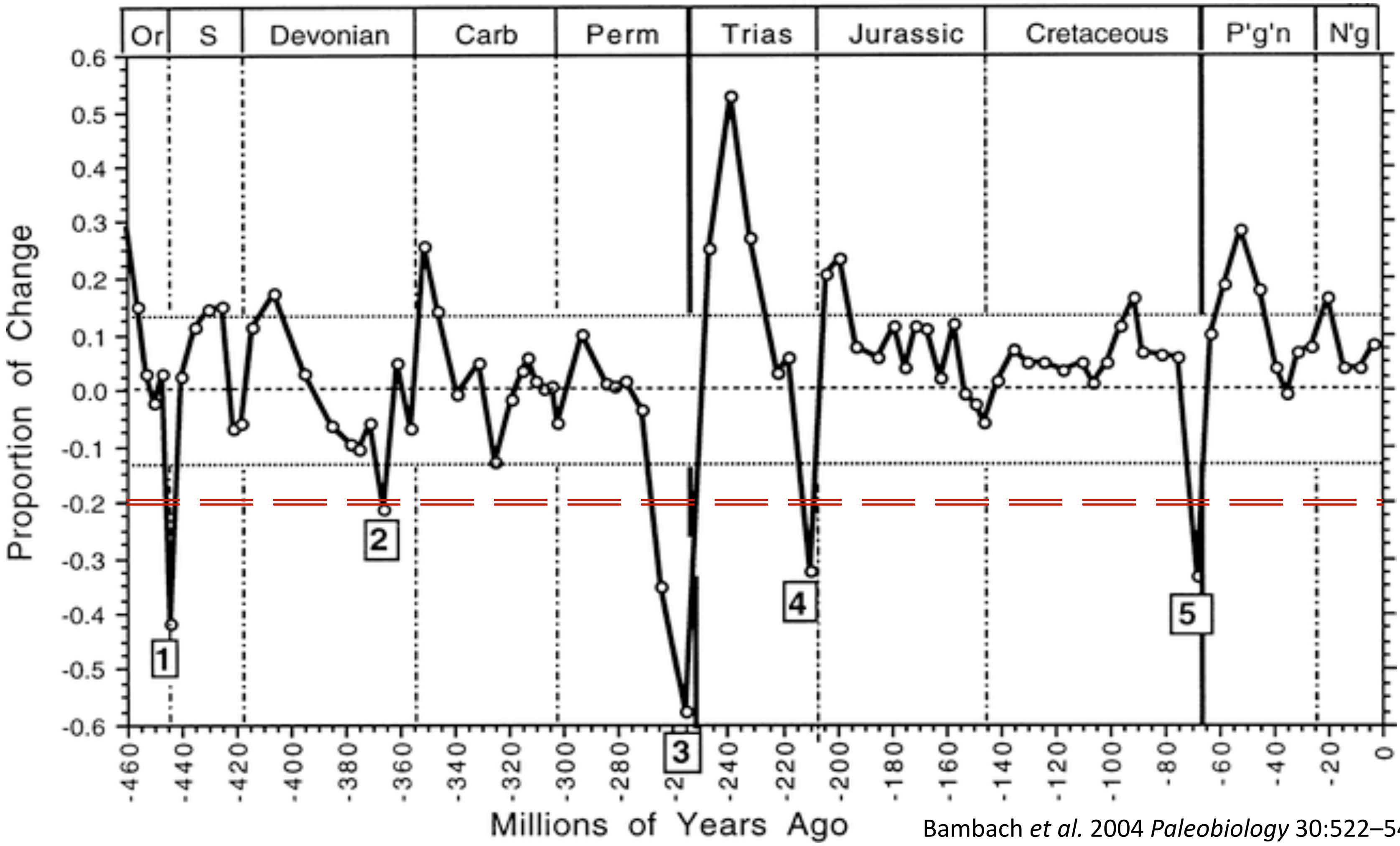
A Diversity of Mass Extinctions

Eighteen substages have peaks of both magnitude and rate of extinction in each of three different styles of evaluating the Sepkoski genus data. These comprise the full set of unambiguous mass extinction events.

Bambach 2006 *Annual Review of Earth and Planetary Sciences* 34:127–155



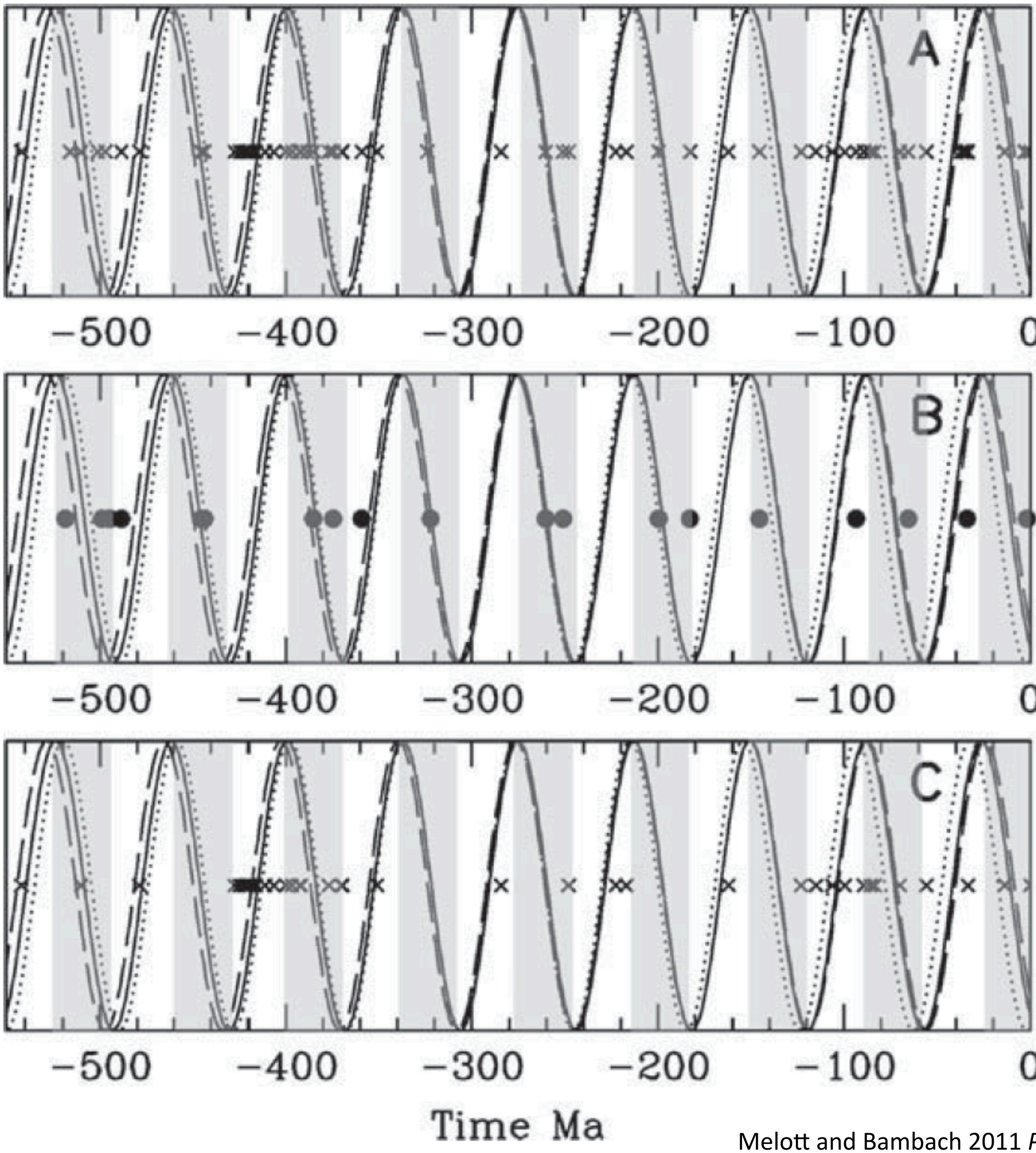
The deeper question is causation. We have some general understanding of the three biggest — (end-Ord, end-Perm, end-Cret) but even for those we do not know enough. *For all we still need more reliable details about timing, selectivity, geographic pattern, and environmental settings.*



Bambach *et al.* 2004 *Paleobiology* 30:522–542

The "Big Five" Mass Extinctions are the ONLY intervals in which marine genus diversity *decreased* by more than 20 percent.

The 62 Myr periodicity to the fluctuation of diversity is ubiquitous in global data



X – extinction event
(Barnes *et al.* 1996)

Evenly distributed in increasing and decreasing phases

Shading – Decreasing phase

• – Mass Extinction
(Bambach 2006)

Cluster in decreasing diversity phases
(P = 0.03)

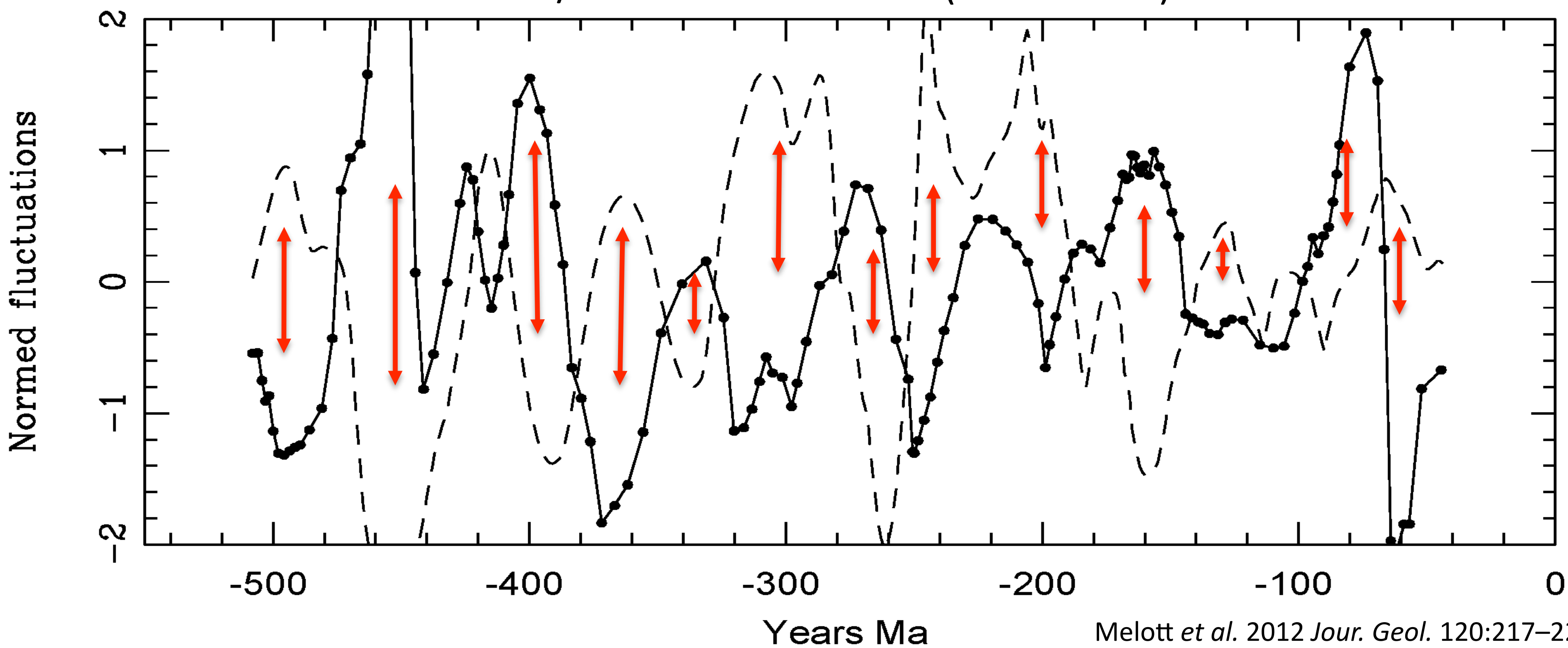
PBDB - Dashed line
R&M (Sep) - Solid line
FR2 - Dotted line

X – non-mass extinctions are preferentially in increasing diversity phases

Melott and Bambach 2011 *Paleobiology* 37:383–408

Marine animal diversity fluctuation also correlates with several geological phenomena

SLG diversity fluctuation (solid line and dots) is *antiphase* to
$^{87}Sr/^{86}Sr$ ratio fluctuation (dashed line)



Melott *et al.* 2012 *Jour. Geol.* 120:217–226

The 62 Myr periodicity in biodiversity also correlates with
a periodicity in the number of marine sedimentary formations.

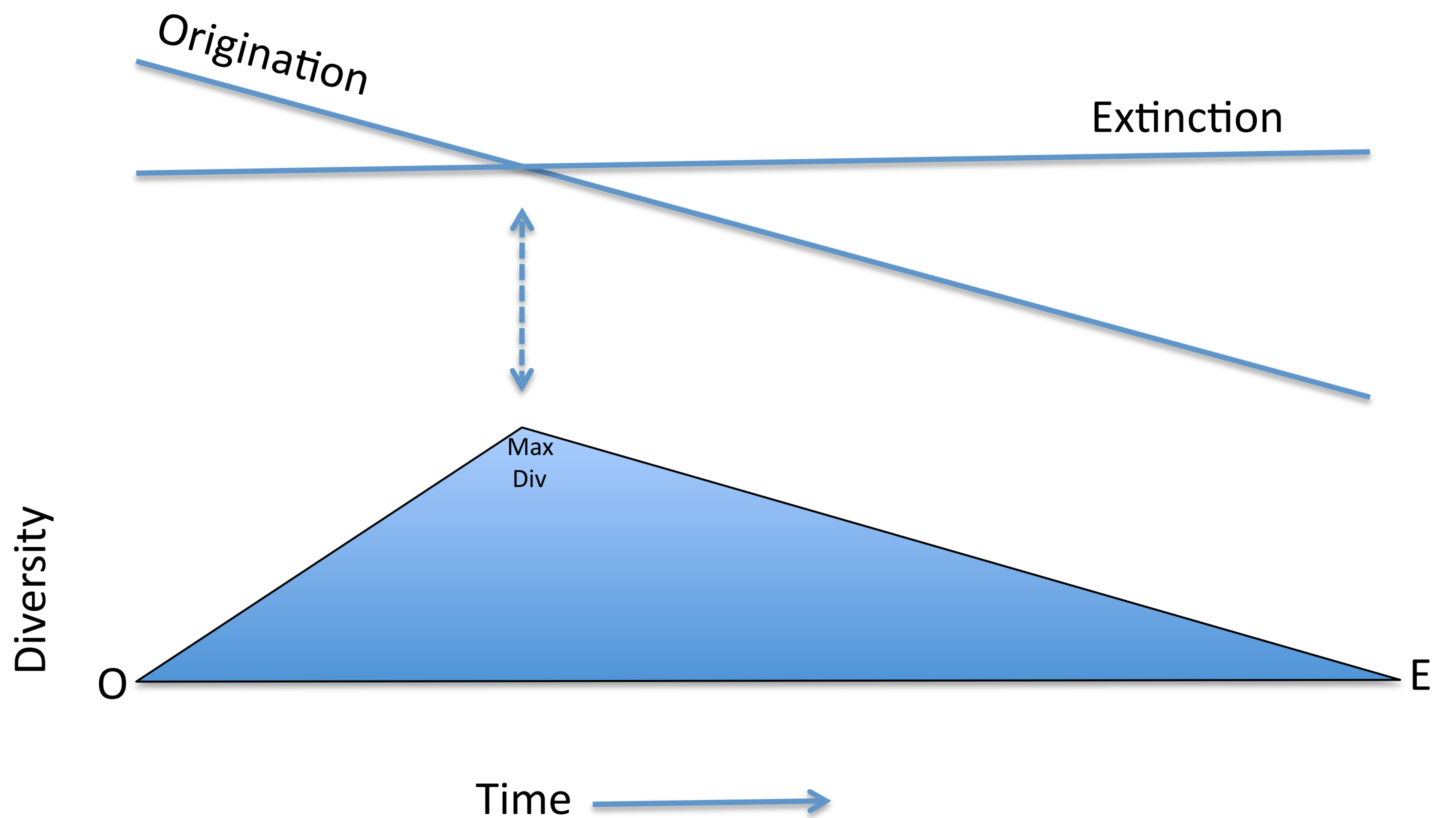
Together these suggest that the periodicity in biodiversity
may be related to a tectonic patterns that can affect endemic faunas.

These patterns may be more regular in timing than previously thought.

Global biodiversity is the sum of the diversity
of all the taxonomic groups present.

What are the controls on diversity
and diversity change within groups?

Diversity within a group is controlled by the interaction of origination and extinction

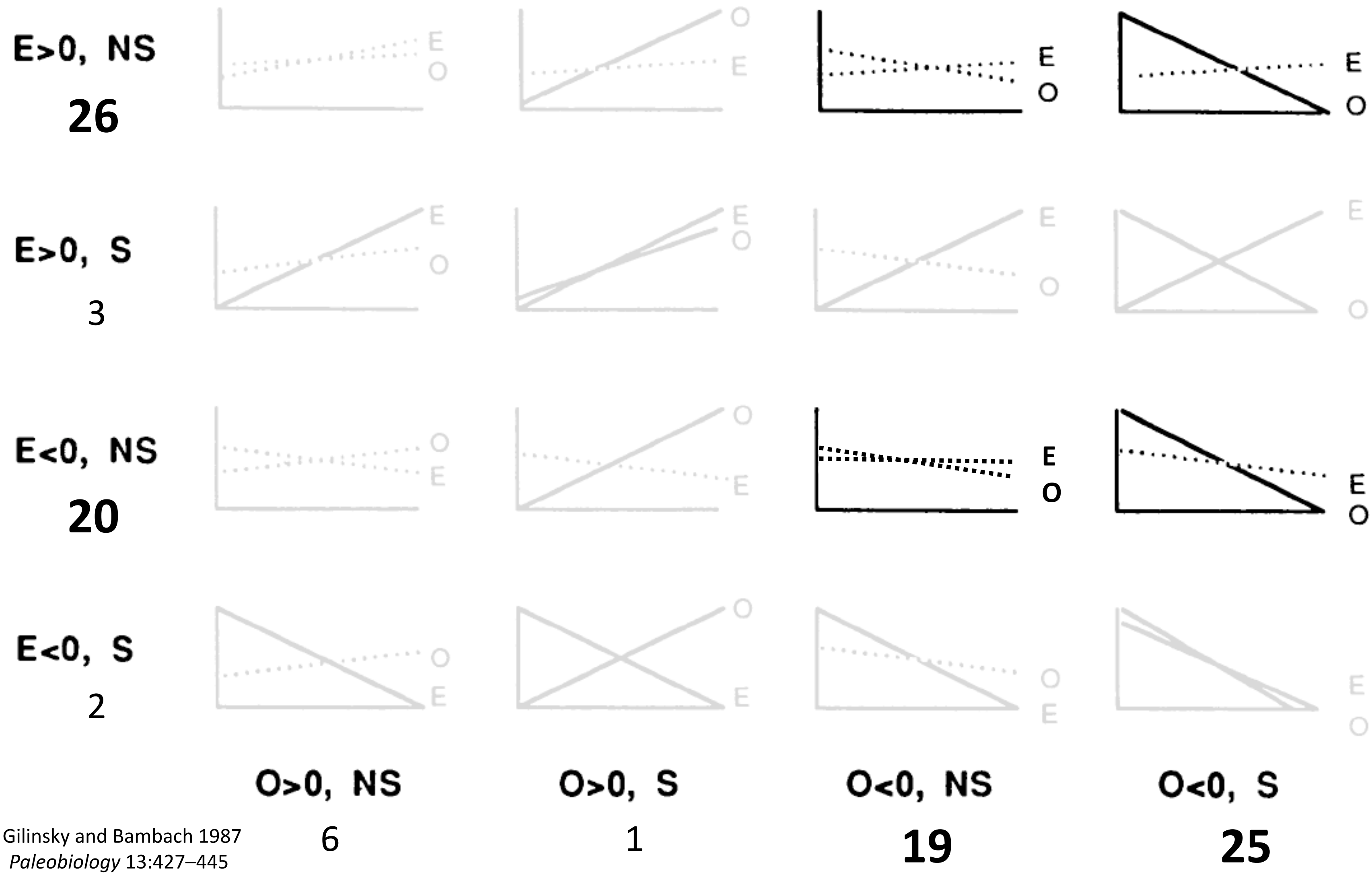


Prior to reaching maximum diversity origination *must* average more than extinction

After reaching maximum diversity origination *must* average less than extinction

Origination and Extinction Trends for 51 Extinct Higher Taxa

Data from first and last intervals omitted to eliminate “small number” enhanced proportions.

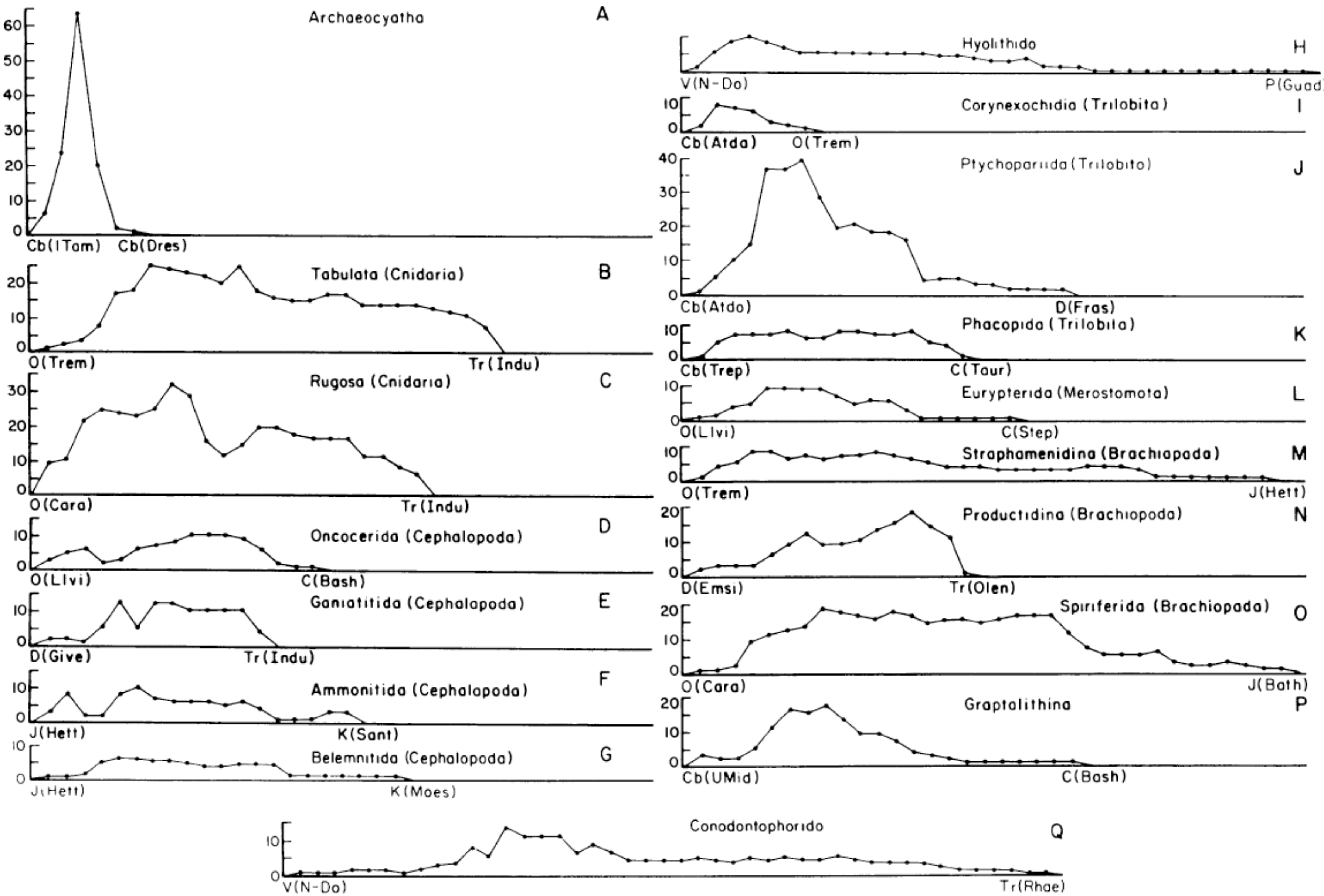


Gilinsky and Bambach 1987
Paleobiology 13:427–445

<u>Origination decreases</u>, but extinction *does not* have a preferred trend.

The 20 holophyletic groups analyzed had exactly the same pattern as the paraphyletic groups.

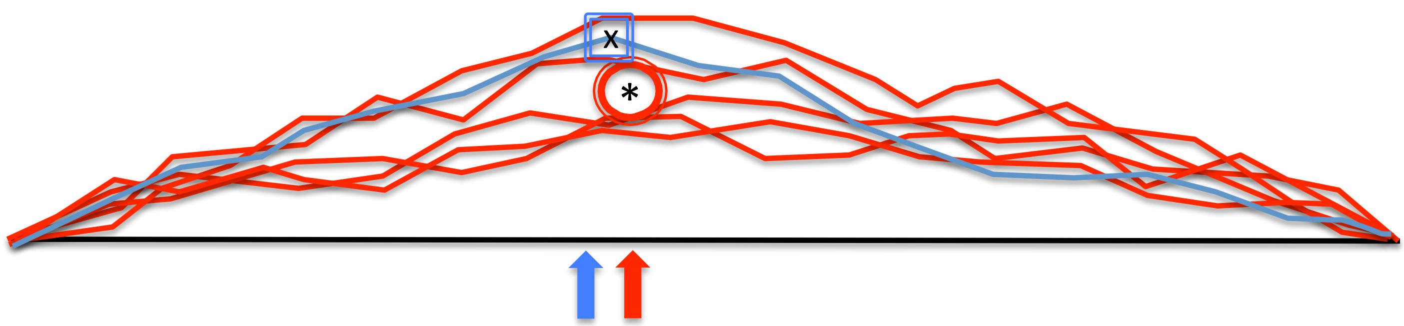
What can be learned from the diversity history of individual groups?



Gilinsky and Bambach 1986
Paleobiology 12:251–268

None of the 17 groups had a maximum diversity significantly different
than the mean of 1,000 bootstrap simulations of the relevant group,
but the distribution of variation about the mean was not symmetrical,
as would be expected if the histories were actually all stochastic phenomena.
Maximum diversity of 15 of 17 groups was <u>higher</u> than the mean of the simulations.

The probability of that distribution is just 0.001.



Only 3 of 17 groups had their center of gravity vary significantly from
the mean of 1,000 bootstrap simulations of each relevant group,
but the distribution of variation about the mean was not symmetrical,
as would be expected if the groups were actually stochastic phenomena.
The center of gravity of 14 of 17 groups occurred <u>earlier</u> than the mean of the simulations.

The probability of that distribution is just 0.006.

Gilinsky and Bambach 1986
Paleobiology 12:251–268

General patterns of clade evolutionary dynamics:

Origination generally decreases over the history of a group.

Extinction has no regular trend. It does not tend to either increase or decrease.

The diversity history of a group is generally not statistically significantly different from the mean of 1,000 bootstrap simulations of the same duration.

Nonetheless, the center of gravity of a real group is *generally earlier in time* and the maximum diversity of a real group is *generally greater* than the mean values for 1,000 bootstrap simulations of that group's history.

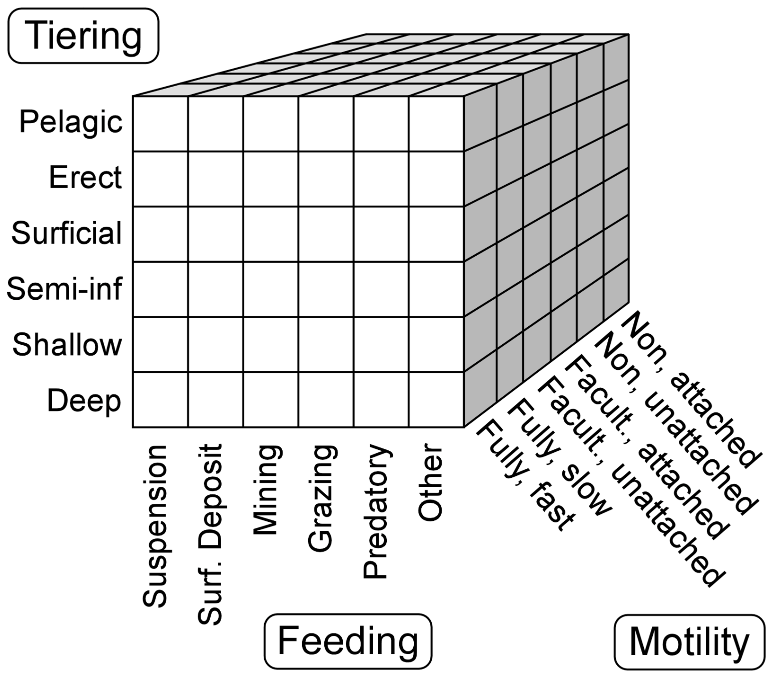
Despite the near stochastic diversity history of individual groups, there is statistical evidence that the typical early high level of origination does produce more diversity than would be expected from chance alone.

Neither origination or extinction is diversity dependent at least where *within* group diversity is concerned.

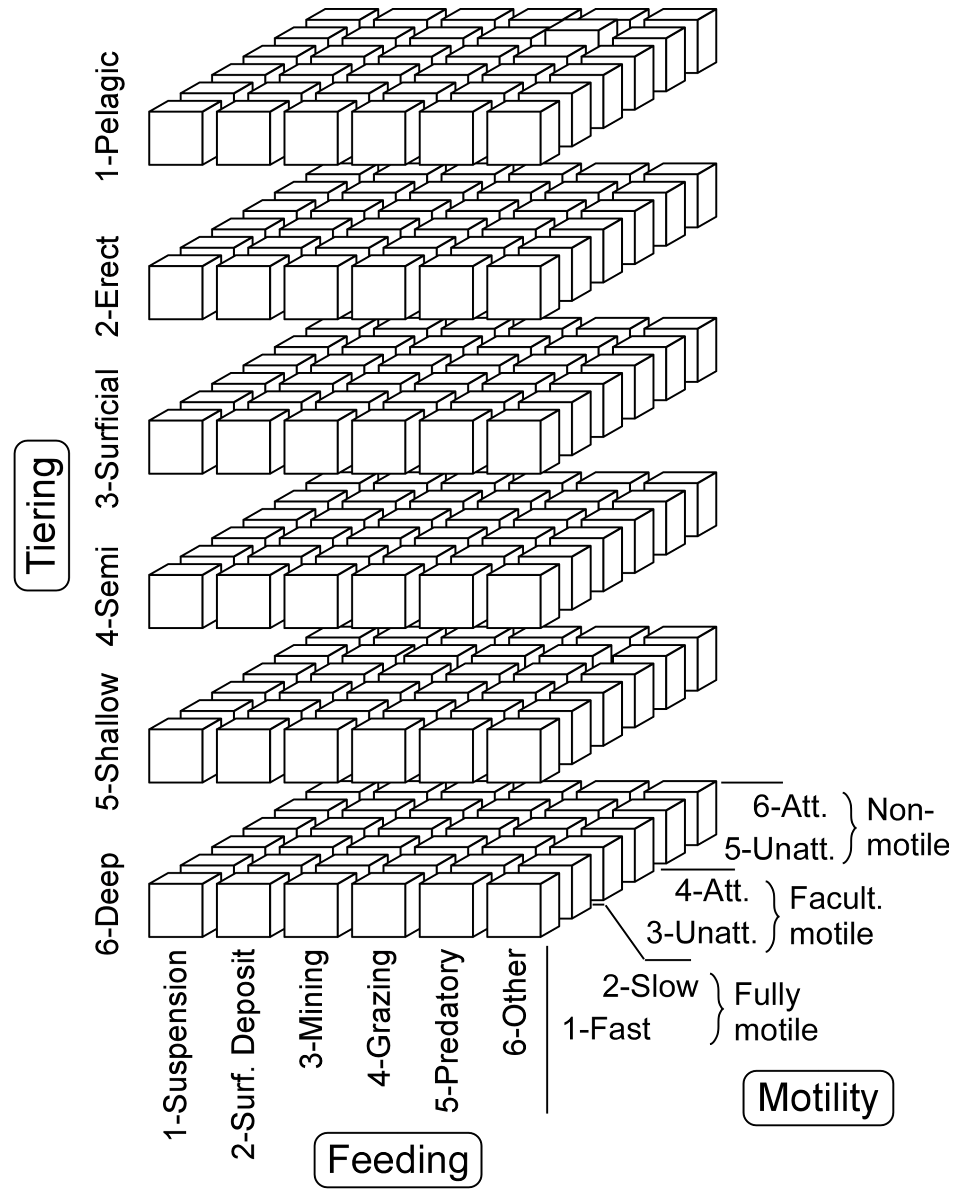
RESEARCH AGENDA: Why does origination decrease over time within a group?
Is it an "aging" of the genome? Or is it a competitive issue as other evolving taxa capture more of the available ecospace formerly open to the group being examined, thus inhibiting successful origination in the group of interest?
The second possibility may explain why incumbents survive, but origination decreases.

What about ecological diversity?

A Theoretical Model of Ecospace

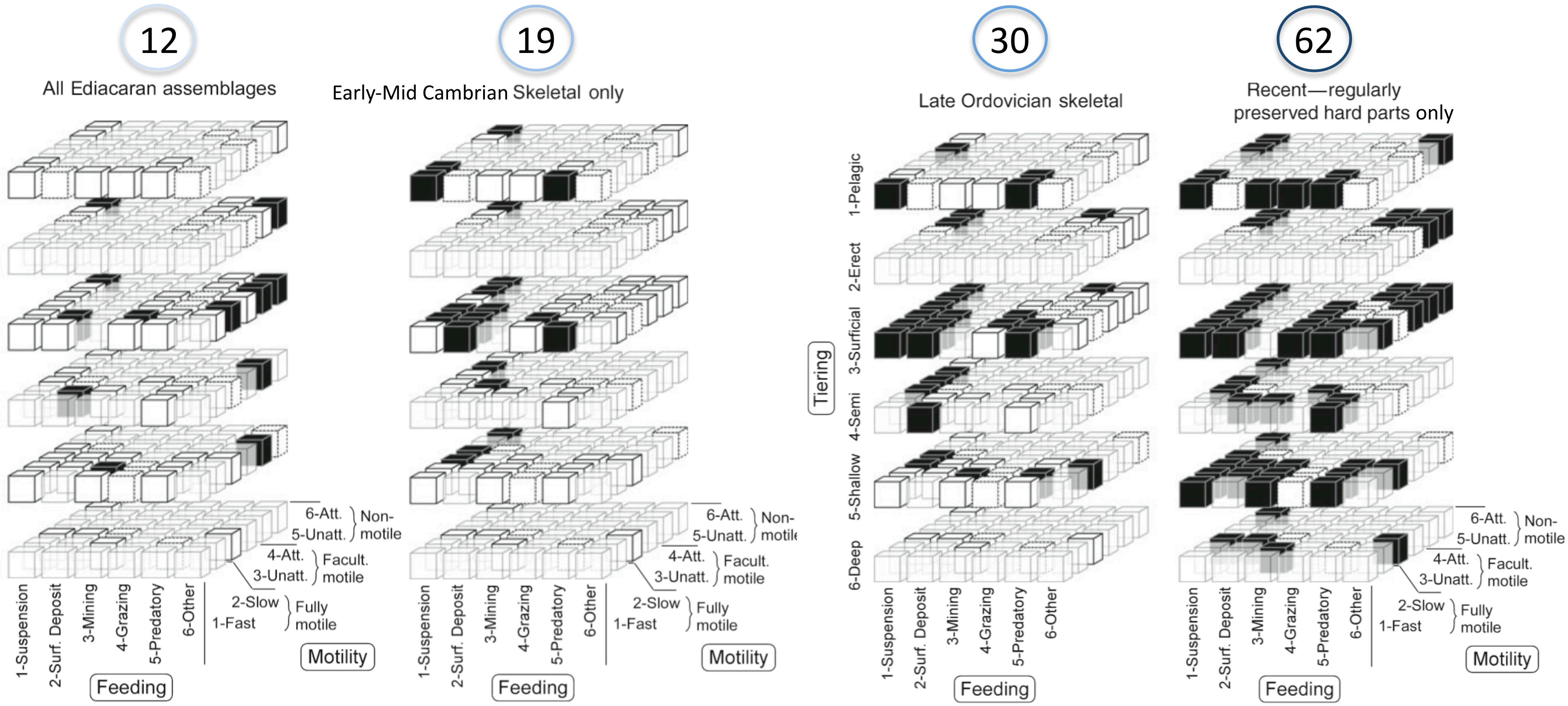


6 x 6 x 6 = 216
Possible
Modes of Life



Bambach *et al.* 2007 *Palaeontology* 50:1–22

Ecosystem complexity increased with the
increase in the number of utilized modes of life through the Phanerozoic



Add modes at all tiers:

more predators,
more motility,
more infauna

Bambach *et al.* 2007 *Palaeontology* 50:1–22

What about the diversity at the local level?

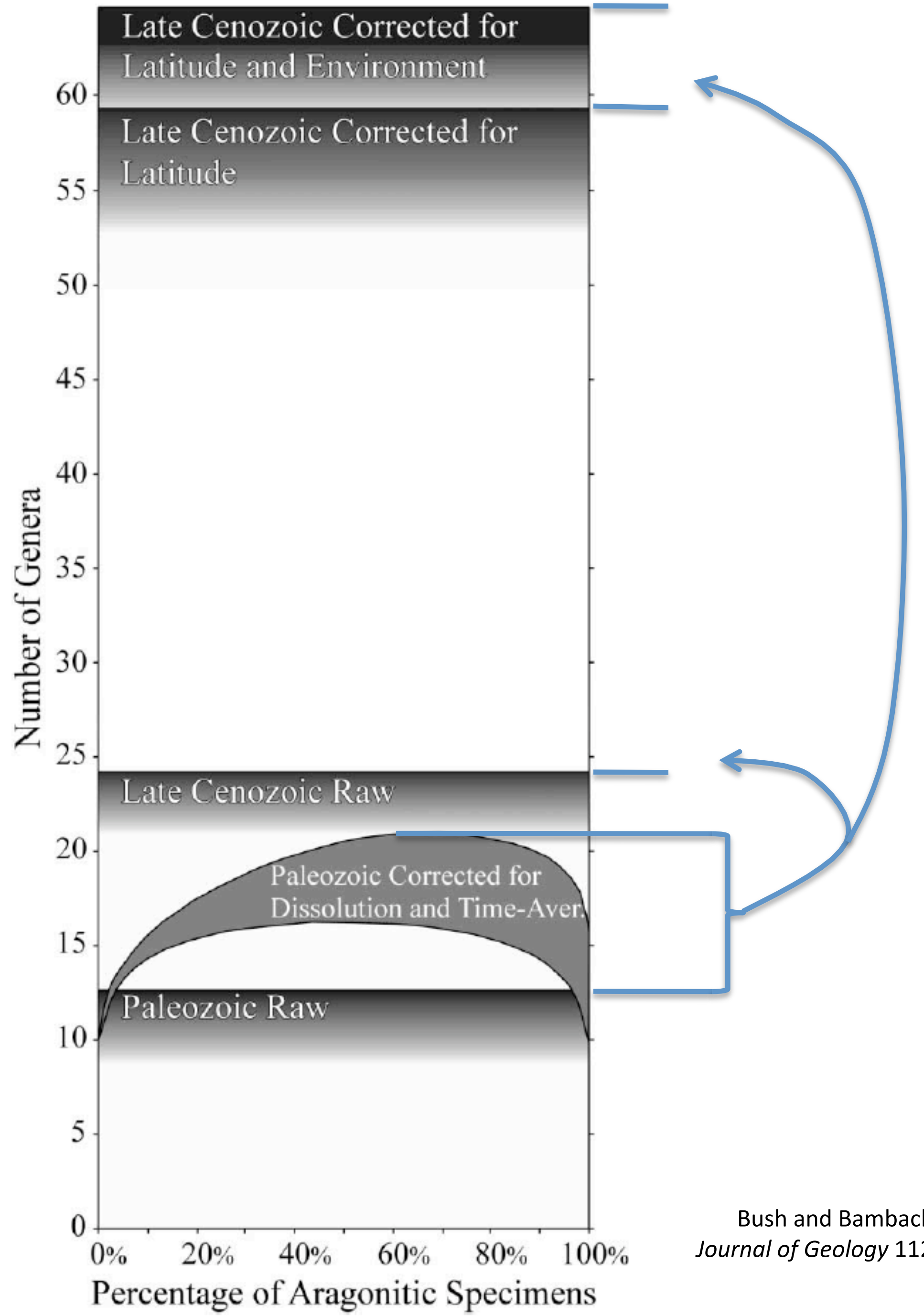
Between the Devonian and the Neogene
within community diversity increased
and
use of ecospace within communities
also increased.

Local ecosystems have become more complex
as community diversity has increased.

These changes are among the likely sources
for observed similar global changes.

Diversity within paleocommunities (untransported fossil assemblages) has increased.

Average genus alpha diversity rarefied to 200 specimens

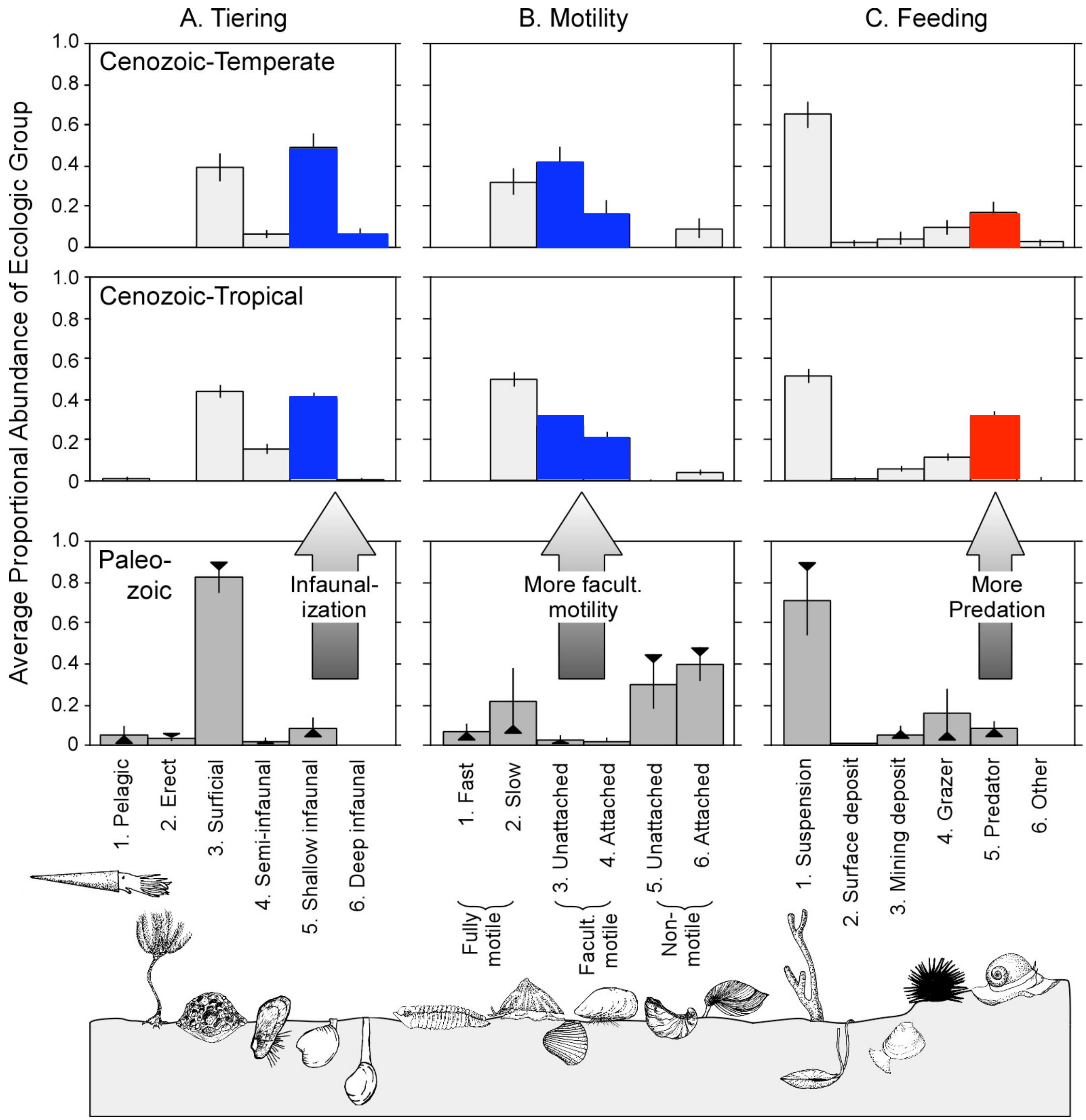


Genus diversity in fossil assemblages increased by as much as a factor of three between the mid-Paleozoic and the Late Cenozoic.

Bush and Bambach 2004
Journal of Geology 112:625–642

Within-community use of ecospace has also increased.

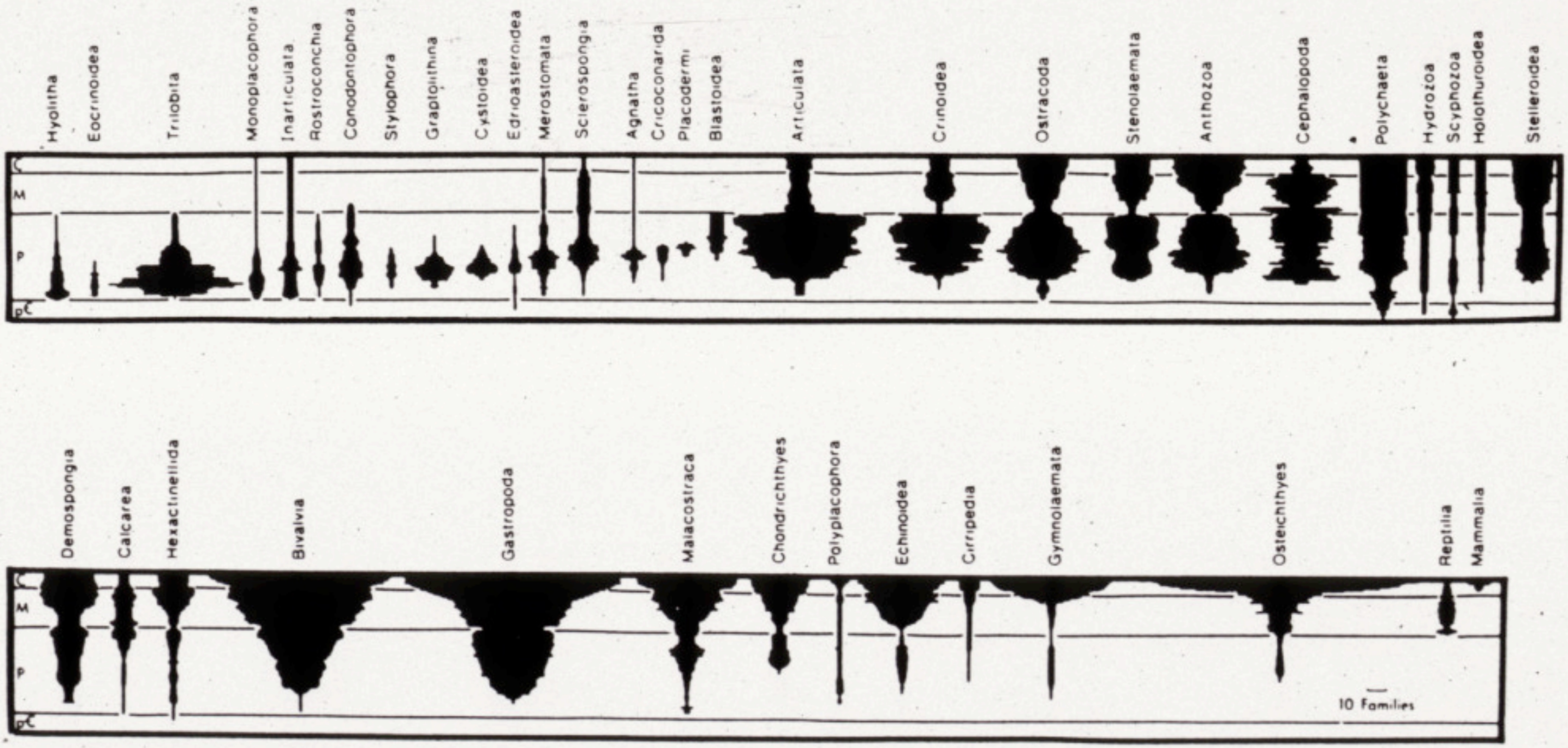
Three trends in ecosystem structure:
Increased predation,
Increased motility,
Increased Infaunalization
are expressed from the community level to the global level.



Bush *et al.* 2007 *Palaeobiology* 33:76–97

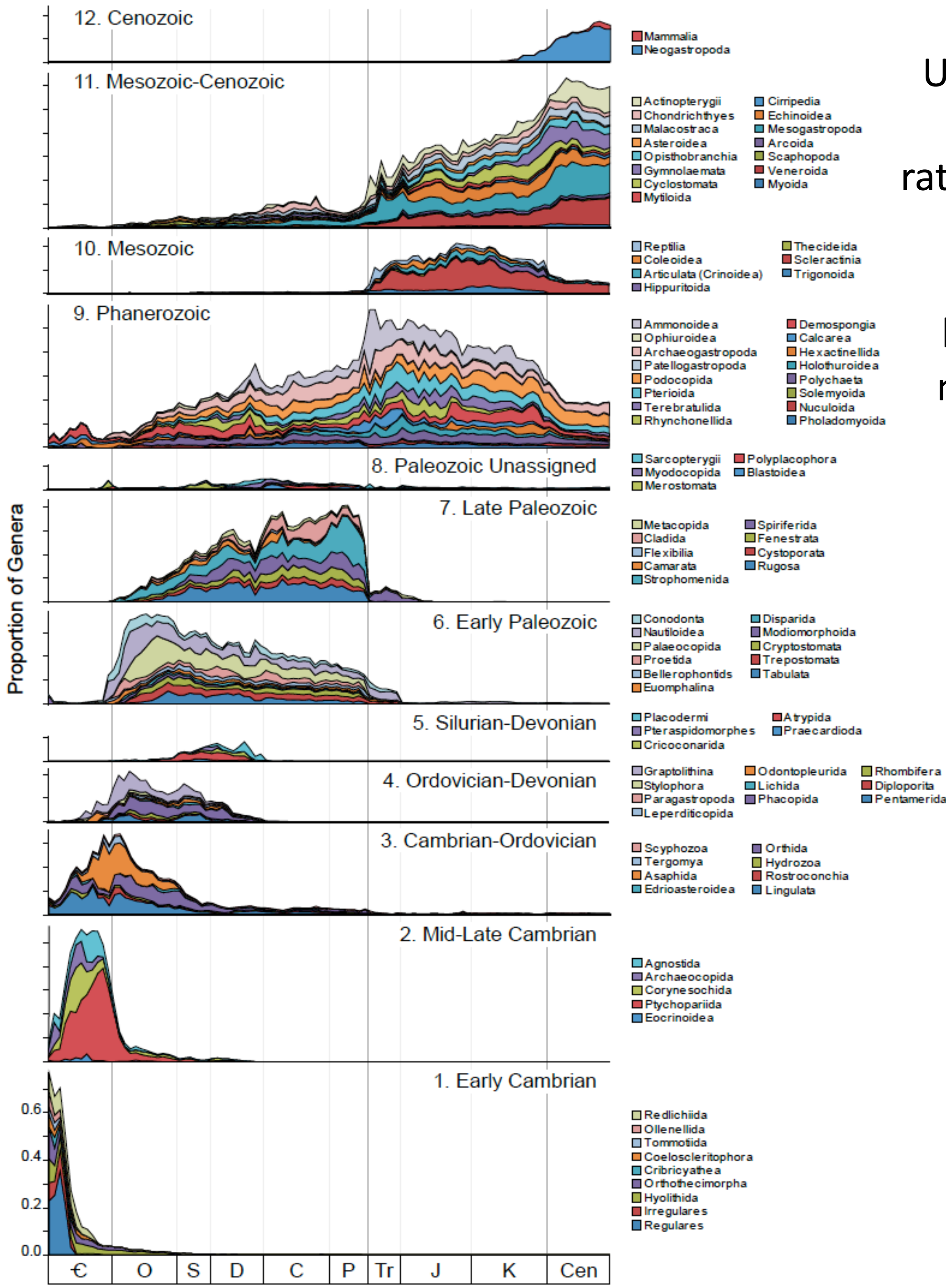
Patterns of diversity change
and ecosystem change
at individual group and community levels
must be integrated together
if we are to understand
how groups interact
and how faunal succession
influences diversity.

The history of diversity on earth has not been a single unified process.
Each group has had its own diversity history.



The context in which the evolution of any group occurs
changes as
other groups wax and wane.

Bambach 1983 after Sepkoski 1981



Using cluster analysis based on a mix of classes, subclasses and orders, rather than just classes as Sepkoski did, the history of faunal succession in the marine realm becomes the succession of twelve, not just three, evolutionary faunas.

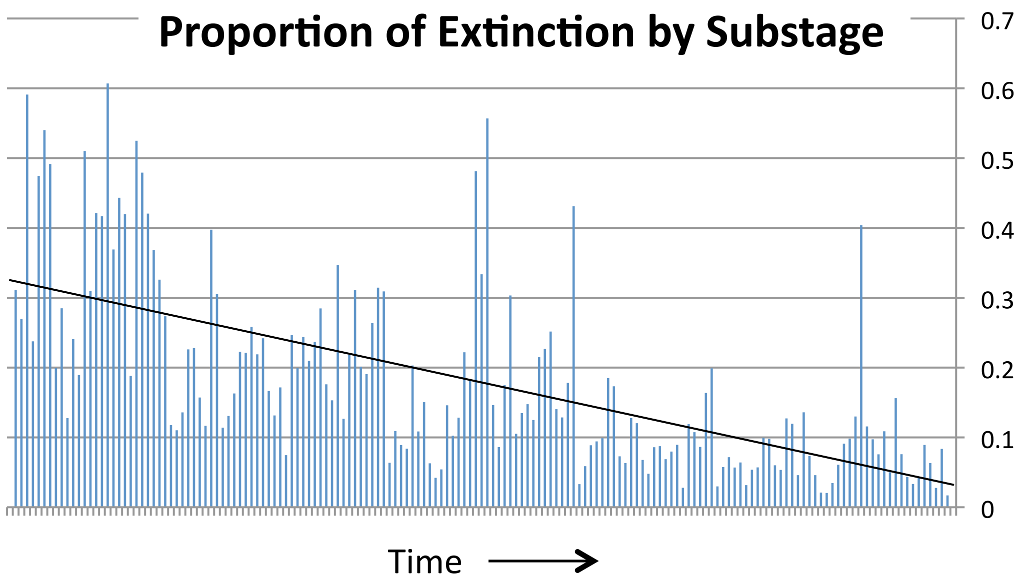
RESEARCH AGENDA:

Why should so many groups have “co-ordinated” histories?

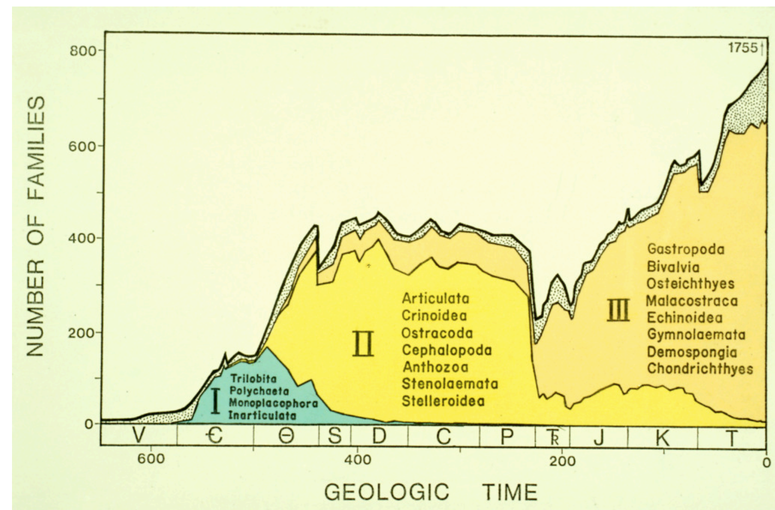
How does ecological interaction affect the fate of these suites of taxa?

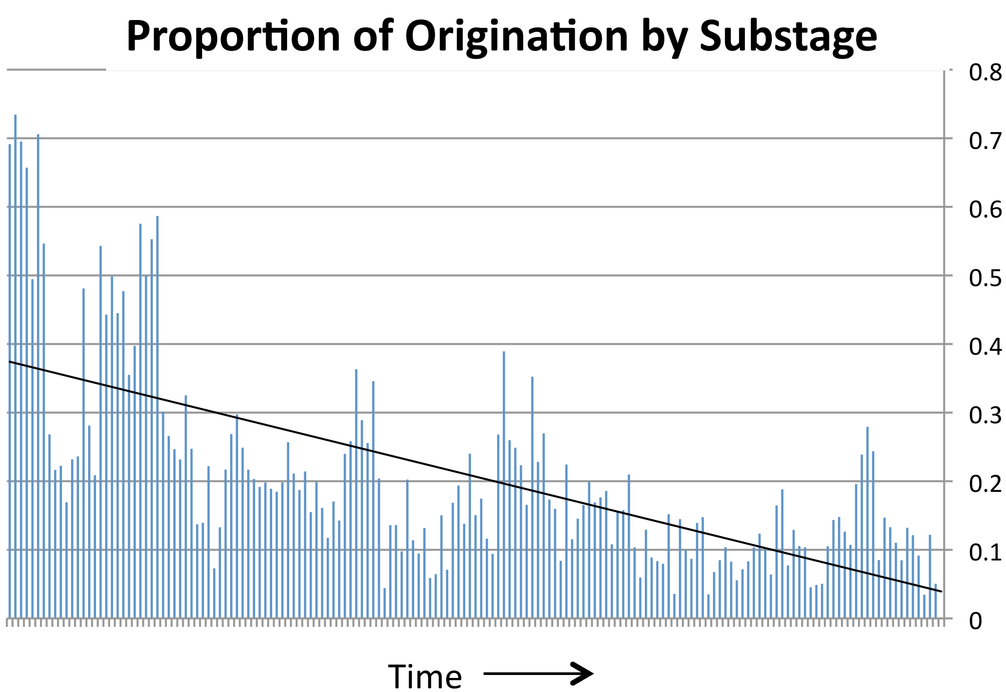
Is this the level at which the ever-present failure of origination within groups is being produced?

Bush and Bambach 2011 *Annual Review of Earth and Planetary Sciences* 39:241–269



Overall extinction decreases with time even though within groups it has no trend. This is because taxon sorting on evolutionary volatility has removed high extinction rate groups.





Origination may decrease overall in part because of increasing diversity, not because origination within individual groups decreases. In effect, initial origination may remain about constant overall, but as diversity increases new taxa become a smaller portion of the total fauna.

Controls, opportunities, and constraints on biodiversity include both geological influences and biotic influences.

Adaptive radiation is part of the early history of most groups,
but chance and physical events also affect diversity trajectories
so most diversity histories vary only slightly from stochastic histories.

Taxonomic succession causes change in ecological context
and each group must either accommodate or fade away.

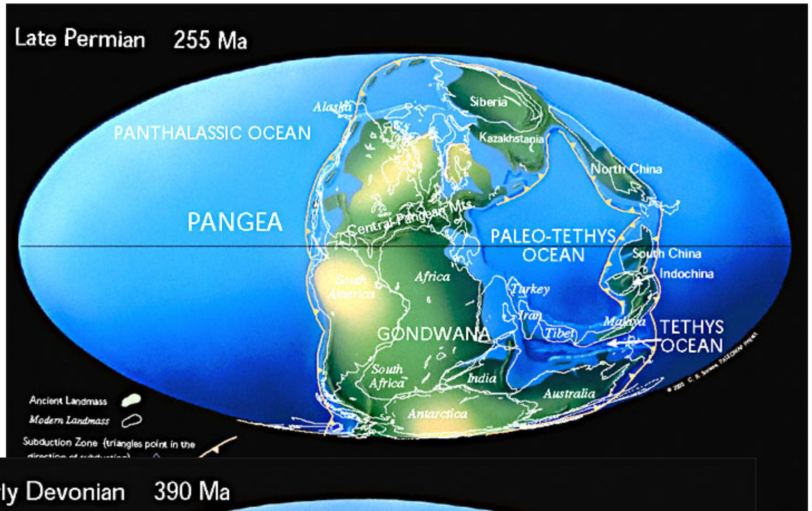
For any established group evolution in other groups tends to lead to competitors.
This may be the source of the universal decrease in origination
with normal attrition causing decline in diversity to eventual extinction.

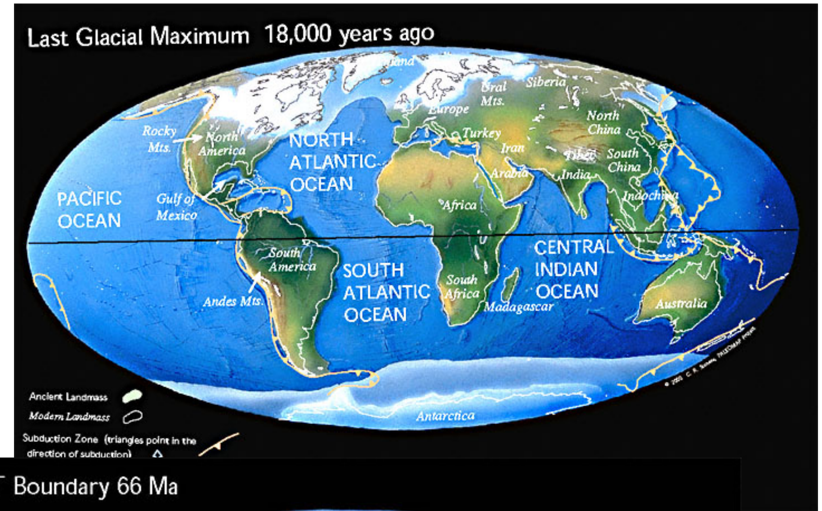
The general succession of major evolutionary transitions
should be similar anywhere life has diversified extensively.

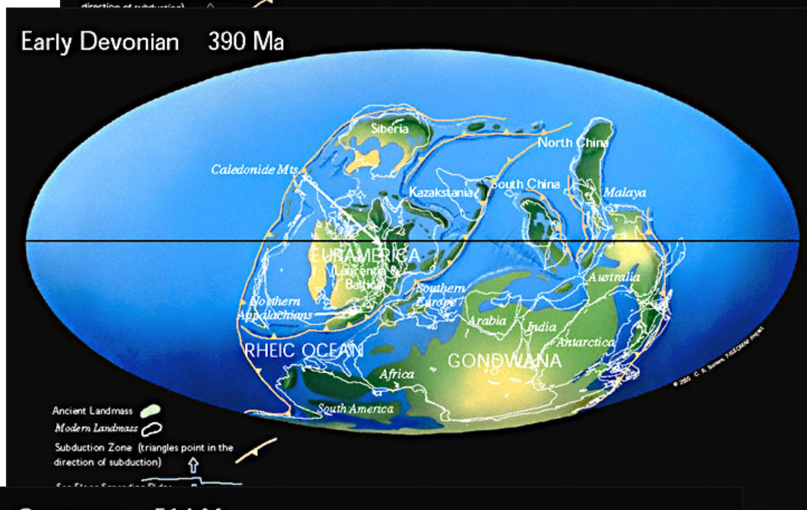
However, the chances of making the major transitions are small,
thus “pond scum” will probably be encountered far more often
than things like active large land animals.

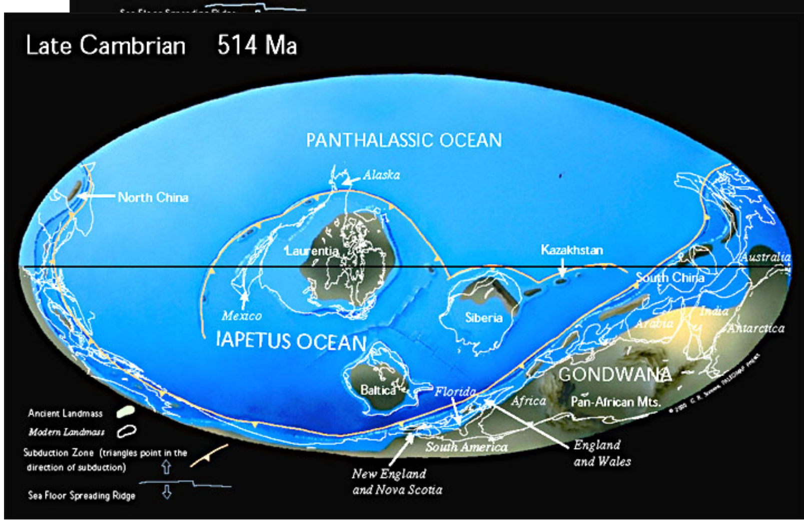
A planet with diverse life forms must have regular, but not excessive,
environmental change to continuously stimulate evolutionary change.

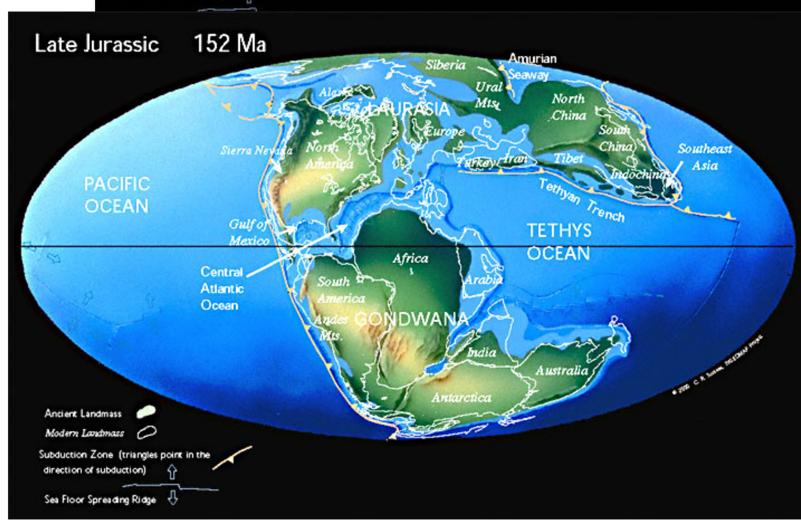
The Earth Changes All The Time











Scotese *PALEOMAP Project*

Finis