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)

Source of Opportunity to Diversify

(Features determined by the operation of natural selection.)

Constraints Imposed by Established Features

(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)

(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.

This sequence (and that of Maynard Smith and Szathmáry 1995) is logically deterministic. If the “tape of life” were to be run again (here or elsewhere), this sequence would be expected.

Knoll and Bambach 2000 *Deep Time* (Paleobiology 26: Supplement to #4)
Outline History of the Earth

"Waiting Time" to each breakthrough

To life as we know it

Prokaryote diversification

Unicellular eukaryote diversification

Aquatic multicellular

Invade land

Int. & Tech.

Diverse study of diversity is available for only the last 550 Myr
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
The PBDB is still adding data and refining its methodology.
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.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Protists</th>
<th>Plants</th>
<th>Fungi</th>
<th>Animals</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrestrial (dry land)</td>
<td></td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Terrestrial (moist habitats, soils)</td>
<td>13</td>
<td>9</td>
<td>5</td>
<td>10</td>
<td>37</td>
</tr>
<tr>
<td>Fresh water</td>
<td>24</td>
<td>2</td>
<td>5</td>
<td>15</td>
<td>46</td>
</tr>
<tr>
<td>Marine</td>
<td>26</td>
<td>1</td>
<td>3</td>
<td>34</td>
<td>64</td>
</tr>
</tbody>
</table>

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.*

Of the estimated 1,750,000 described species, about 250,000 are marine and 1,500,000 are terrestrial.

What about perturbations to biodiversity on a global scale?
Global diversity throughout the next temporal interval was reduced after fifteen of the eighteen Mass Extinctions.

In these events origination was able to replace lost diversity during the next interval only three times.

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.
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.

Shading – Decreasing phase

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

X – extinction event (Barnes et al. 1996)
Evenly distributed in increasing and decreasing phases

• – Mass Extinction (Bambach 2006)
Cluster in decreasing diversity phases ($P = 0.03$)

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 $^{87}\text{Sr}/^{86}\text{Sr}$ ratio fluctuation (dashed line).

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.

E>0, NS
26

E>0, S
3

E<0, NS
20

E<0, S
2

O>0, NS
6
O>0, S
1
O<0, NS
19
O<0, S
25

Origination decreases, but extinction does not have a preferred trend.

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

Gilinsky and Bambach 1987
Paleobiology 13:427–445
What can be learned from the diversity history of individual groups?
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 higher 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 earlier than the mean of the simulations.

The probability of that distribution is just 0.006.
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
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.
Average genus alpha diversity rarefied to 200 specimens has increased.

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

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