A sampling-standardized analysis of Phanerozoic marine diversification and extinction

A Working Group proposed by

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Summary

Our picture of global diversification and extinction on long time scales is mostly based on generalized data for Phanerozoic marine macroinvertebrates. While every effort was made to guarantee the comprehensiveness of this data set, the community has been aware that sampling artifacts may contribute to the observed trends. Until now, we have been unable to remove these effects. Several robust methods for doing this are now available, but these methods use locality-specific data that are not a part of the existing, more generalized compilations. In order to confirm the reality of the major observed patterns, a collaborative data compilation project needs to be initiated. We wish to form a working group to do this. As a first step, we propose a workshop this August involving workers who have specialized in analyzing paleontological diversity data. This workshop will determine the scope, goals, structure, and time table of a database project. Immediately after the workshop, a post-doc who will serve as project coordinator will begin a two-year residency at NCEAS. Over the following two years, experts specializing on particular parts of the fossil record will meet at NCEAS to guide the data collection process. A final meeting will focus on preparing collaborative publications showing how these data influence our picture of marine diversification and extinction.

Problem Statement

Perhaps the most important development in paleoecology over the past two decades has been the compilation of a global database documenting the diversification and extinction of marine invertebrates throughout the Phanerozoic (Flessa and Imbrie, 1973; Sepkoski, 1978, 1993). This database has proven invaluable in: identifying periods of rapid diversification (Sepkoski, 1978, 1984) and mass extinction (Raup and Sepkoski, 1984); documenting the existence of three major "evolutionary faunas" (Sepkoski, 1984); testing models of diversification and extinction (Sepkoski, 1978; Gilinsky and Good, 1991); and contrasting taxonomic diversity trajectories with morphological innovations (Foote, 1993), onshore-offshore trends (Sepkoski and Miller, 1985), and changes in community structure (Sepkoski et al., 1981; Sepkoski, 1988; Jablonski and Sepkoski, 1996). Indeed, the master diversity curve for Phanerozoic marine animals may now be the most widely-reproduced image in the field of paleobiology.

As with any empirical study, it is important to establish that major signals are not artifactual. Some types of bias have been dealt with. For example, the degree of sampling per se (Sepkoski, 1993) and the use of higher-level taxa as proxies for species (Sepkoski and Kendrick, 1993; Wagner, 1995) do not seem to have strongly distorted the Phanerozoic diversity data. Because of such studies, there is a general consensus that the major Phanerozoic trends do accurately reflect at least coarse-scale patterns (Sepkoski et al., 1981).

The purpose of our working group is to grapple with another problem that has long been suspected but not properly dealt with: the fact that diversification and extinction trends may be strongly influenced by sampling biases (Raup, 1976; Sheehan, 1977). A number of paleobiological studies have now shown that sampling effects are often quite important (Raymond and Metz, 1995; Wing and DiMichele, 1995; Alroy, 1996; Miller and Foote, 1996). These effects include variable temporal, geographic, environmental and taxonomic sampling intensities, as well as biases introduced by geological controls such as sea level changes and sequence architectures (Holland, 1995). Addressing these problems has been made feasible by improvements in statistical methods for removing sampling biases (Paul, 1982; Holman, 1985; Marshall, 1990, 1994; Foote and Raup, 1996; Alroy, 1996, in press; Miller and Foote, 1996; Westrop and Adrain, 1998). Developing a protocol for dealing with these factors is the primary goal of the workshop that will initiate this working group.

Goals and Methods

Given the importance of the Phanerozoic marine diversity pattern, it is crucial to establish which of its primary features are real and which are sampling artifacts. How fast were the Cambrian, Ordovician, and Triassic diversification episodes? Was there really a diversity plateau throughout most of the Paleozoic? Has diversity increased exponentially since the early Mesozoic? Are there three dynamically distinct "evolutionary faunas"? Has local species richness increased in tandem with global diversification? How did marine communities recover from the five major mass extinctions? How quickly have extinction rates declined through the Phanerozoic, and why? Does the selectivity of extinction vary with extinction intensity? Are extinction and origination rates periodic, and do they show self-similar or non-linear behavior? These questions about long-term trends only can be addressed firmly by standardizing sampling across the data set.

The reason that the available data do not lend themselves to straightforward sampling bias correction is that they consist only of first and last appearances of taxa on a global basis. More robust sampling correction methods require either knowledge of gaps in age ranges (Lazarus taxa: Paul, 1982; Holman, 1985; Alroy, in press), biostratigraphic ranges through measured sections (confidence intervals: Paul, 1982; Strauss and Sadler, 1989; Marshall, 1990, 1994), or faunal inventories representing individual fossil localities (rarefaction: Raup, 1975; Alroy, 1996; Miller and Foote, 1996). This makes building a new, more detailed compilation of the literature imperative.

Compiling biostratigraphic sections for every part of the Phanerozoic is not a realistic goal. Merely recording global gaps in age-ranges would be of limited utility because this would not address the more complex sampling biases of differential geographic coverage, temporal changes in alpha diversity and biogeographic provincialism, and differential sampling along paleoenvironmental gradients. The most realistic approach is rarefaction, which requires compiling locality-specific faunal inventories and recording geographic, environmental, and geological data for each of these localities, and ideally, abundance data. Because rarefaction attempts to standardize the number of taxonomic records or inventories in each time interval, data collection need only reach a predetermined sampling target in each of these intervals.

Obviously, compiling all published faunal data for the Phanerozoic marine record during a two-year project is not feasible. Our goal is much more focused: because the rarefaction results will only be reliable if the data themselves meet the method's assumptions, we will put a premium on collecting high-quality faunal inventories. Thus, the working group's first major goal will be to define criteria for accepting faunal data, which may include restriction to narrow stratigraphic and geographic contexts, comprehensive taxonomic coverage, and reporting of specimen counts. We will prioritize data compilation by focusing on well-studied and well-preserved taxa, and on geographic regions and environments that are well-sampled in every, or most, major time intervals.

Because useable results must be obtained quickly, data collection will begin with the most promising "module." This initial module might represent a synthesis of faunal lists from just one or two environments on one or two continents, would certainly focus only on marine macroinvertebrates, and would largely rely upon synthesizing pre-existing compilations. In fact, there have been similar, but more limited efforts by others (e.g., Sepkoski and Miller, 1985; Wilson and Palmer, 1990; and especially Bambach, 1977). A quick survey of the literature shows that there are at least 3563 lists in these pre-existing databases (Table 1). Many of these lists could be integrated into the new database, which would minimize the need for primary data compilation.

Nonetheless, there are several reasons why new lists will have to be compiled: 1) certain time intervals, continents, environments, or taxonomic groups have not been surveyed thoroughly; 2) some of the older databases may no longer be accessible; and, 3) some of the databases may not have sufficient information about localities, or might be otherwise incommensurate with our database format.

Based on previous experience, a realistic goal would be to compile about 1000 new faunal lists in two years. Assuming very conservatively that only 500 of the 3563 previously compiled lists prove to be useable, we would have a total of 1500 lists. Following Sepkoski (1984), these might be distributed evenly across the approximately 80 marine stages of the Phanerozoic. This would give us to 15 - 20 faunal lists for each interval, very similar to the rarefaction level used in an analogous study of fossil mammals (Alroy, 1996).

Table 1. Previously compiled data sets that will be useful in this study. Most are restricted to North America, but several are global. Most of the lists pertain to individual faunal horizons in particular outcrops, but some of them pertain to more stratigraphically or geographically generalized collecting localities.

Interval	Group/Environment	Lists	Reference
Phanerozoic	all	386	Bambach (1977)
Phanerozoic	hardground	>63	Wilson and Palmer (1990)
Paleozoic	level-bottom	540	Sepkoski and Miller (1985)
Late Cambrian - Ordovician	trilobites	175	Westrop and Adrain (1998)
Ordovician	all	>400	Miller and Mao (1995)
Ordovician	brachiopods	116	Patzkowsky and Holland (1993)
Middle Mississippian	crinoids	69	Ausich et al. (1994)
Late Pennsylvanian	crinoids	>34	Holterhoff (1996)
Mesozoic	level-bottom	334	Aberhan (1994)
Jurassic	all	331	Tang and Bottjer (1996)
mid-Cretaceous	molluscs	>167	Elder (1989)
Jurassic - Cenozoic	bryozoans	728	Lidgard et al. (1993)
Maastrichtian	bivalves	105	Jablonski and Raup (1995)
Cretaceous - Paleogene	molluscs	>56	Hansen et al. (1993)
Neogene	corals	59	Johnson et al. (1995)

Participants

All of the researchers in the following list have been informally contacted and have expressed strong interest in attending the working group's initial workshop. All of them are experts on analytical methods, relevant field areas, and large paleobiological databases.

- John Alroy, Smithsonian Institution
- Richard Bambach, Virginia Tech
- Karl Flessa, University of Arizona
- Mike Foote, University of Chicago
- Steven Holland, University of Chicago
- Scott Lidgard, Field Museum of Natural History
- Charles Marshall, University of California, Los Angeles
- Michael McKinney, University of Tennessee
- Arnold Miller, University of Cincinnati
- Mark Patzkowsky, Pennsylvania State University
- David Raup, University of Chicago
- Kaustuv Roy, University of California, San Diego

- Jack Sepkoski, University of Chicago
- Peter Wagner, Field Museum of Natural History

Rationale for NCEAS Support

NCEAS provides three crucial elements that ensure the project's viability.

1) Interaction with ecologists. NCEAS has initiated a working group run by Russell and McKinney that will focus on sampling curves (including rarefaction curves), with the participants all being leading researchers in community ecology. This working group's activities will be largely concurrent with, and complementary to, ours. Dr. McKinney also will be a member of our working group, and both he and the on-site program coordinator will serve as liaisons. These and similar interactions will keep the project's goals focused and in tune with current developments in ecological theory and analysis.

2) Infrastructure for long-term support of the data set. The data need to be made available to the larger scientific community, not just during the working group's lifetime but afterwards. Development of software to analyze the data may be computationally demanding, which would require the use of high-performance computers. The Center's staff and computer facilities will prove invaluable for these purposes.

3) Support for meetings of the working group, and for the group coordinator. Members of the group need a forum for meeting face-to-face to make concrete decisions about implementing the project, and for evaluating its results once the data have been compiled. An on-site coordinator will be crucial to the project's ability to collect data in a timely, focused, and consistent manner.

Proposed Activities and Timetable

<u>Project coordinator</u>.--An efficient compilation procedure would have to be overseen by a coordinator at NCEAS. This would best be a postdoctoral researcher with expertise in analytical paleobiology. The coordinator would presumably be available to begin work in late August or September of this year, and would have to continue for two full years in order to compile a complete, useable data module. The coordinator's responsibilities would include converting contributed data into a uniform electronic format, checking contributed data for formatting and other problems, keeping contributors informed about current priorities for data collection, interacting with specialists brought in to NCEAS to participate in the working

group's activities, and interacting with ecological researchers at NCEAS.

Initial workshop.--Major logistical questions need to be resolved before data collection can begin. These decisions need to be made by the researchers who will help to compile the data, and who will eventually analyze them. Therefore, an initial workshop strictly concerned with database issues should begin the working group's activities. This workshop should be held shortly before the coordinator begins residence at NCEAS in August, 1998.

Additional meetings.--At later stages, the working group will be extended to include taxonomic and paleoecological experts specializing in particular parts of the fossil record. We envision bringing together three small groups of experts at six-month intervals to focus on particular time intervals (e.g., Paleozoic, Mesozoic, and Cenozoic), taxonomic groups, or other subsets of the database. These meetings would be held in early 1999, the middle of 1999, and early 2000. Following completion of the data collection phase, we would hold a final meeting in the middle of 2000 to begin work on one or several joint publications presenting the major results to the scientific community.

Anticipated Results and Beneficiaries

We anticipate that the working group will generate both immediate and long-term results. In the short term, we will generate a data module that will show whether the general features of the Phanerozoic diversity and extinction curves are still seen after standardizing for sampling intensity. These high-quality data will be amenable to paleoecological and macroevolutionary analyses at local, regional, and global scales. In the long term, we hope that the database will serve as a nucleus for an ongoing data compilation effort that will involve much of the paleontological community.

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Budget

ITEM	YR.1	YR.2
Travel		
U.S. (# of participants)	30	16
(total travel expenses)	$15,000	$ 8,300
Foreign		
(# of participants)	4	4
(total travel expenses)	$ 5,000	$ 5,000
Expenses (Visitor days x $140.00)	$26,640	$16,800
Salary *** (for Center Fellows)	1	1
Other expenses	None	None

Keywords Worksheet

1. Organizational Focus
(pick 1)

_X Global
__ Ecosystem
__ Community
__ Meta-population
__ Population
__ Organismal
__ Cellular
__ Molecular

2. Regional Focus
(pick all that apply)

__ California
__ United States
  __ Southwest
  __ Northwest

4. Taxonomic Group
(pick all that apply)

__ Plants
_X Invertebrates
  __ insects
  __ other terr. inverts
  _X marine inverts
  __ aquatic inverts
__ Vertebrates
  __ mammals
  __ birds
  __ reptiles/amphibians
  __ fish
__ Microbes
__ Fungi

5. Methods

__ Southcentral
__ Northcentral
__ Southeast
__ Northeast
__ Africa
__ Antarctic
__ Arctic
__ Asia
__ Australia/NZ
__ Canada
__ Central America
__ Europe
__ South America
_X Global

3. Ecological Theme
(rank up to 3)

__ amensalism
_1 biodiversity
__ biogeography
__ commensalism
__ community dynamics
__ competition
__ complex systems
__ dispersal
__ disturbance
__ ecological economics
__ evolution
__ genetics
__ global change
Change/Extinction
_2 methodological innovation
__ microclimate
__ mutualism
__ nutrient cycling
_3 paleoecology
__ plant-animal interactions
__ population dynamics
__ predator-prey interactions
__ primary production
__ soil processes
__ succession
__ parasitism
__ symbiosis
__ Other ________________

(pick all that apply)

_X Statistical modeling
_X Numerical Analysis
__ Simulation model
__ Visualization
_X Meta-analysis
__ Classification and
Mapping
__ Other ________________

6. Research Application
(rank up to 3)

__ acid rain
__ agriculture
__ aquaculture
__ coastal resources
__ conservation
__ ecosystem management
__ energy
__ environmental policy
__ fisheries
__ forestry
__ global warming
__ human population
__ land management
__ ozone
__ pollution
__ reserve siting/design
__ restoration
__ toxicology
_X Other_Global

7. Biomes
(pick all that apply)

_X Marine
__ Benthic
__ Pelagic
__ Intertidal
__ Terrestrial
__ Forest
__ Grassland
__ Desert
__ Wetlands

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Education:

May, 1989	B.A., Biology, Reed College, Portland, Oregon.
March, 1993	M.S., Evolutionary Biology, University of Chicago, Chicago, Illinois.
Aug., 1994	Ph.D., Evolutionary Biology, University of Chicago, Chicago, Illinois. Title: "Quantitative mammalian biochronology, biogeography, and diversity history of North America."

Employment:

July, 1989 - May, 1990	Intern, Evolution of Terrestrial Ecosystems Program, Smithsonian Institution, Washington, D.C.
Sept., 1994 - Aug., 1996	Research Associate, Research Training Group in the Analysis of Biological Diversification, University of Arizona, Tucson, Arizona.
Sept., 1996 - Aug., 1998	Postdoctoral Fellow, Department of Paleobiology, Smithsonian Institution, Washington, D.C.

Grants, awards, and fellowships:

Feb., 1993	Hinds Fund Award, University of Chicago.
April, 1993	Research Grant, Geological Society of America.
April, 1993	Grant-in-Aid of Research, Sigma Xi.
1993 - 1994	William Rainey Harper Fellowship, University of Chicago.
Oct., 1994	Alfred Sherwood Romer Prize, Society of Vertebrate Paleontology.

<u>Papers</u>:

Alroy, J. 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. Paleobiology 18(3):326-343.

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CURRICULUM VITAE

Name: Charles Richard Marshall
Date of Birth: January 13, 1961
Citizenship: Australia / U.S.A. (dual)

EDUCATION

Institution and Location	Degree	Year Conferred	Field of Study
Australian National University, Australia	B.Sc. (Hons)	1984	Math., Paleont., Zoology
University of Chicago, Chicago, IL USA	M.S.	1986	Evolutionary Biology
University of Chicago, Chicago, IL USA	Ph.D.	1989	Evolutionary Biology
Indiana University, IN USA	Postdoc.	1989-1991	Molecular systematics

Employment and Experience

Institution and Location	Position	Dates
Dept. of Earth and Space Sciences UCLA, Los Angeles, CA	Full Professor	July 1997 - present
	Vice Chair	April 1997 - present
	Associate Professor	July 1993 - June 1997
	Assistant Professor	Sept. 1991 - June 1993
Dept. of Biology, Indiana University Bloomington, IN	Postdoc.	Nov. 1989 - Aug. 1991

Affiliations

Research Associate: Invertebrate Paleontology, Museum of Natural History, Los Angeles County (1991 -)
Molecular Biology Institute, UCLA (Member, 1992 -)
Institute for Geophysics and Planetary Physics, UCLA (Member, 1994 -)

Major Grants

Guggenheim Foundation Fellowship	Analytical Paleontology	1997-1998
Petroleum Research Fund Grant (Type AC)	Quantitative Stratigraphy	1996-1998
SGER Grant, Systematic Biology, NSF	Middle Repetitive DNA	1995-1997
Petroleum Research Fund Grant (Type G)	Quantitative Stratigraphy	1993-1995
National Young Investigator Award, NSF	Molecular Paleobiology	1992-1997

Publications (only those most relevant to NCEAS Proposal)

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