SOME IMPLICATIONS OF MASS EXTINCTION FOR THE EVOLUTION OF COMPLEX LIFE

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ABSTRACT. Extinction has the destructive effect of eliminating estab-
lished lineages from an evolutionary system and the constructive effect
of vacating ecospace into which new lineages can evolve. Mass extinc-
tions, which are times of unusually intense extinction, have been con-
sistently followed by major radiations of new lineages. Extraterrestrial
impacts associated with extinction events and a periodic recurrence of
these events implicates an extraterrestrial forcing mechanism as the
ultimate cause of mass extinction. This suggests that the extraplane-
tary environment has played an important, active role in the development
of complex life on Earth.

1. IMPORTANCE OF EXTINCTION IN MACROEVOLUTION

Large-scale evolutionary patterns in the history of life are often ana-
lyzed in terms of three basic processes (Huxley, 1958): *cladogenesis*,
the production (or diversification) of evolutionary lineages; *anagenesis*,
the transformation of morphology or other characters within established
lineages; and *stasigenesis*, the persistence of lineages and their char-
acters. In recent years it has become increasingly apparent that stasi-
genesis and its opposite, extinction, play a very important role in
evolution (Eldredge and Gould, 1972; Gould, 1984). In this contribution
I will consider some of the effects of extinction, and especially mass
extinction, on evolutionary systems.

1.1. Effects of Extinction

Extinction has two basic effects on evolutionary systems. Most obvi-
ously, it terminates lineages and therefore eliminates specific genes
and gene combinations, and the specializations they produce, from the
system. These, then, no longer play a role in the course of evolution,
unless partially re-evolved through convergence in related lineages.
    A second, more subtle effect is that extinction makes room for new
specializations to appear within evolutionary systems. Stanley (1975,
1979) has argued that anagenesis within established lineages operates
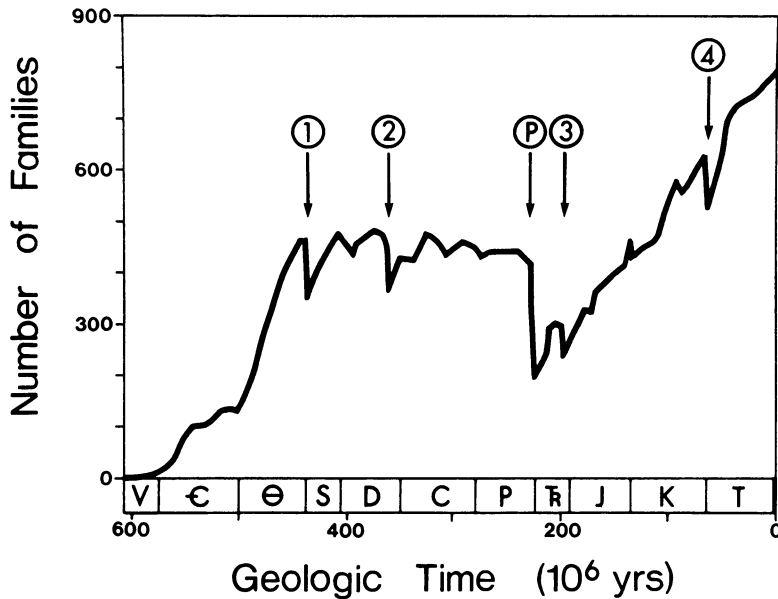
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Figure 1. Diversity of animal families in the oceans
through the Phanerozoic Eon. Arrows indicate five
major mass extinctions (P = Late Permian; 1 = terminal
Ordovician; 2 = Late Devonian; 3 = Late Triassic; 4 =
terminal Cretaceous). Symbols along the ordinate indi-
cate geologic systems. (After Sepkoski, 1982)

too slowly to produce the major changes in morphology, etc. evident in
the history of life. Instead, cladogenesis, and the appearance of
evolutionary novelties within new lineages, must be responsible for
most evolutionary trends and breakthroughs. However, cladogenesis can-
not proceed indefinitely in the absence of extinction. Ecosystems are
not infinite, and therefore the number of lineages within them is
limited by their limited resources. Thus, new lineages often are
introduced only after some previous lineages have been eliminated by
extinction.

1.2. Diversity and Major Mass Extinctions

Perhaps the best-known example of the appearance and expansion of new
lineages after an extinction event is the rapid radiation of modern
mammalian orders in the wake of the extinction of dinosaurs at the end
of the Cretaceous Period. Another example of this phenomenon is
offered in Figure 1. This graph illustrates the diversity of marine
animal families through the Phanerozoic Eon, from 600 ma to the pre-
sent. Families, rather than species, are graphed because families
represent the lowest taxonomic level for which we have accurate, com-

prehensive data from the whole of the fossil record. Marine animals, rather than terrestrial animals or plants, are used because the fossil record from the oceans is more complete and more thoroughly studied.

Figure 1 shows that the diversity (or, equivalently, complexity) of the marine biosphere has increased considerably over the last 600 ma. But this increase has been episodic rather than continuous. The three principal intervals of diversification are the Early Cambrian (575 to 540 ma), the Ordovician (500 to 438 ma), and the Jurassic to the present (213 to 0 ma). The first two intervals were followed by extended periods of reduced diversification or near steady state, reflecting partial saturation of the world-ocean ecosystem. The third diversification appears to be tapering and presumably will approach steady state in the future (Sepkoski, 1984).

Superimposed upon the pattern of expansion and stabilization are several episodes of mass extinction. Mass extinctions are geologically short (less than 15 ma and generally much less than 5 ma) intervals during which unusually large numbers of taxa disappear. Five such events are visible in Figure 1; these occur at the end of the Ordovician (at 438 ma), within the Late Devonian (around 367 ma), through the Late Permian (263 to 248 ma), near the end of the Triassic (around 215 ma), and at the end of the Cretaceous (at 65 ma).

Each extinction event is manifested in a sharp drop in familial diversity (with losses ranging from 17 to 57% and probably higher at the species level). These drops are then followed immediately by rapid rebounds, representing radiations of new lineages into the "ecospace" cleared by the mass extinctions. The radiations occur at rates comparable to the Early Cambrian and Ordovician diversifications and proceed over 15 ma or longer until the previous configuration of the system has been regained: the near steady state in the case of the earlier mass extinctions and the long expansion in the case of the later events. The only event that might be interpreted as fundamentally changing the configuration of the system is the great Late Permian mass extinction. However, I have argued elsewhere (Sepkoski, 1984) that this change is probably illusionary--that the system in fact was changing well before the Permian and that the long-term expansion following the mass extinction represents a combination of the expected rapid rebound and a previously initiated, much slower diversification.

1.3. Resilience of the Biosphere

From the somewhat cursory analysis above, it appears that mass extinctions do promote rapid cladogenesis following the removal of established lineages. It also appears that the biosphere as a whole is rather resilient to the perturbations that cause mass extinction. This observation has important implications with respect to the relationship of the Earth's biosphere to its extraplanetary environment. There is now compelling evidence that the mass extinction at the end of the Cretaceous Period was associated with an impact of a large extraterrestrial body. Occurrence of a global iridium anomaly (A. Alvarez et al., 1980), altered microtektites (Montanari et al., 1983), and shock-metamorphosed quartz grains (Bohor et al., 1984) in sediments at the top of the

Cretaceous all indicate impact of a large ($\sim$10 km) body. Climatic
models (e.g., Pollack et al., 1983) suggest that the ejected dust and
atmospheric alteration produced by the impact would have caused several
months of global darkness followed by several years of subfreezing tem-
peratures, both of which would have shut down primary productivity over
the Earth. Yet, if we look at the large-scale evolutionary effect of
this catastrophe, it does not appear as disasterous as might be expected.
Marine familial diversity dropped only about 17% and then took approxi-
mately 15 ma to recover (Figure 1). This resilience suggests that the
evolution of complex life on Earth could have proceeded even if the
extraplanetary environment were considerably more hostile.

2. PERIODICITY OF MASS EXTINCTIONS

The marine biosphere has been subjected to more mass extinctions than
are visible in Figure 1. Familial diversity, sampled over geologic
stages (with average durations of 6 to 10 ma), tends to dampen smaller
fluctuations in evolutionary rates (cf. Raup, 1979) with the result
that only the largest mass extinctions are evident. Other methods of
examining the data, however, provide more detailed pictures of the
history of extinction and suggest a periodic recurrence of mass extinc-
tions.

2.1. Record of Smaller Mass Extinctions

Figure 2 illustrates one of several possible measures of extinction
intensity through time. The curve shows the percentage of marine fami-
lies becoming extinction in each of 43 geologic stages relative to the
total number of families at risk (i.e., the standing diversity in the
stage). Only the last 270 ma of geologic time, over which the familial
data are most accurate and the sampling intervals shortest, are illus-
trated.
    The curve in Figure 2 exhibits a number of peaks (local maxima) in
extinction intensity that significantly exceed the level of local, back-
ground extinction (i.e., the extinction intensity of "normal" intervals
of time). The three highest peaks correspond to the last three major
mass extinctions visible in Figure 1: the Late Permian, Late Triassic,
and terminal Cretaceous events. Five other significant peaks occur in
the Early Jurassic (Pliensbachian Stage at 194 ma), Late Jurassic
(Tithonian Stage at 144 ma), "middle" Cretaceous (Cenomanian Stage at
91 ma), Late Eocene (at 38 ma), and Middle Miocene (at 11 ma). All of
these peaks are manifested in local outcrops and deep-sea cores by
unusually large numbers of extinctions of local species (Sepkoski and
Raup, 1985), indicating that they do indeed correspond to definite, if
small, mass extinctions. Note that this total of eight significant mass
extinctions is smaller than the 12 "extinction events" identified over
the same time interval by Raup and Sepkoski (1984).
    Although the eight peaks in Figure 2 vary considerably in magnitude,
their timing appears rather regular. This impression has been confirmed
with a variety of statistical tests, including Fourier analysis and
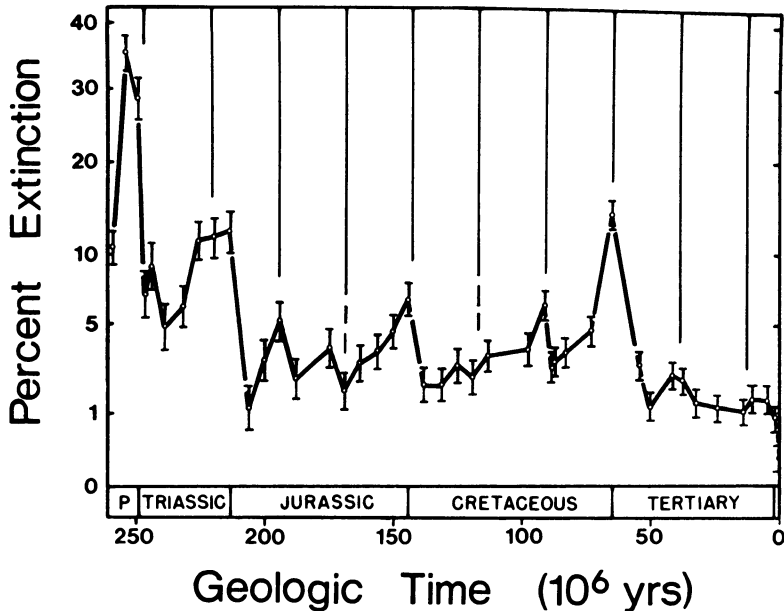
Figure 2. Percent of marine animal families becoming
extinct in each of 43 geologic stages from the Late
Permian to the present. Error bars indicate one stan-
dard error on either side of the observation. Vertical
lines drawn from the top of the graph illustrate the
best-fit position of the 26.2 ma periodicity in mass
extinctions. (Modified from Sepkoski and Raup, 1985).

nonparametric bootstrap procedures (Raup and Sepkoski, 1984; Rampino and
Stothers, 1984; Sepkoski and Raup, 1985), which indicate that the tem-
poral distribution of mass extinctions is decidedly nonrandom and, in
fact, fits a periodic distribution rather well. The best estimate of
the period length in this distribution currently is 26.2±1 ma (Sepkoski
and Raup, 1985).

   The vertical lines in Figure 2 illustrate the 26.2 ma period super-
imposed over the data in the best-fit position. Most of the predicted
times of mass extinction correspond to observed peaks in extinction
intensity rather well. Deviations that exist derive from three sources:
possible errors in the estimated time scale; smearing of peaks resulting
from incomplete sampling of the fossil record (probably of particular
importance for the Late Triassic, Late Eocene, and Middle Miocene peaks);
and existence of "gaps" where extinction peaks should occur. Gaps,
indicated by partially dashed lines in Figure 2, are present where the
fifth and seventh predicted extinction events should fall. These gaps
may result either from the forcing mechanism of mass extinction occas-
sionally "missing a beat" (i.e., occurring at such low intensity that
its effects on the biosphere are minimal) or, more probably, from limi-
tations in the resolution of the data on marine families. Preliminary

data on marine genera and on subfamilies of ammonoids (cephalopod mol-
luscs) suggest a small extinction event occurred in the Aptian Stage of
the Early Cretaceous, about where the fifth event is predicted, and
a possible event occurred in the Callovian Stage of the Middle Jurassic,
near to where the seventh event is predicted. Both events, if real, are
smaller than those evident in Figure 2, which is consistent with the
pattern of variable magnitude but regular timing in marine mass extinc-
tions.

2.2. Mechanisms of Periodic Mass Extinction

The observation of a 26.2 ma periodicity in mass extinctions indicates
that the environment of the Earth's biosphere has not been constantly
benign over long time intervals but rather has been subjected to geolog-
ically frequent perturbations. However, the nature of these perturba-
tions is far from clear. Our knowledge of the short-term stability of
the biosphere is very limited, and we know little about the proximate
causes of mass extinction (or even of background extinction). However,
several lines of evidence suggest that the Earth's extraplanetary envi-
ronment may have played a role in mass extinctions:
   a. Known terrestrial processes with periodic behaviors have cycle
      times that are far too short (<1 ma) to account for the 26.2 ma
      periodicity in mass extinctions.
   b. Evidences of impacts of extraterrestrial objects (including iridium
      anomalies) have now been discovered in association with three of
      the eight well-documented mass extinctions: the terminal Creta-
      ceous event (noted above), the Late Eocene event (Glass and Zwart,
      1977; W. Alvarez et al., 1982), and the Late Permian event (Sun
      Yi-Ying et al., 1984).
   c. Analyses of the ages of terrestrial impact craters indicate these
      also exhibit a statistical periodicity with a phase relationship
      and cycle time (estimated to be 28.4±1 ma by W. Alvarez and Muller
      {1984} and around 27 ma by Sepkoski and Raup {1985}) that are con-
      gruent with the periodicity in mass extinctions.
The last two observations implicate perturbations of the Oort Cloud as
the agent of mass extinctions. Gravitational perturbations could pro-
duce showers of up to a billion comets into the inner solar system, from
which a variable number and size distribution would impact the Earth
(Hills, 1981). Three potential sources of gravitational perturbations
have been suggested (see review in Sepkoski and Raup, 1985):
   a. The spiral arms of the Milky Way Galaxy, which are crossed quasi-
      periodically during the Sun's galactic orbit (Shoemaker, 1984)
      (although this mechanism would induce a periodicity of approxi-
      mately twice the length observed for mass extinctions and terres-
      trial impact craters);
   b. Large molecular clouds concentrated near the galactic plane, which
      would be encountered during the Sun's z-oscillation about the plane
      (Rampino and Stothers, 1984) (although, again, the half period of
      oscillation {approximately 33 ma} and the phase relationship {the
      Sun is currently very near the galactic plane} do not fit the
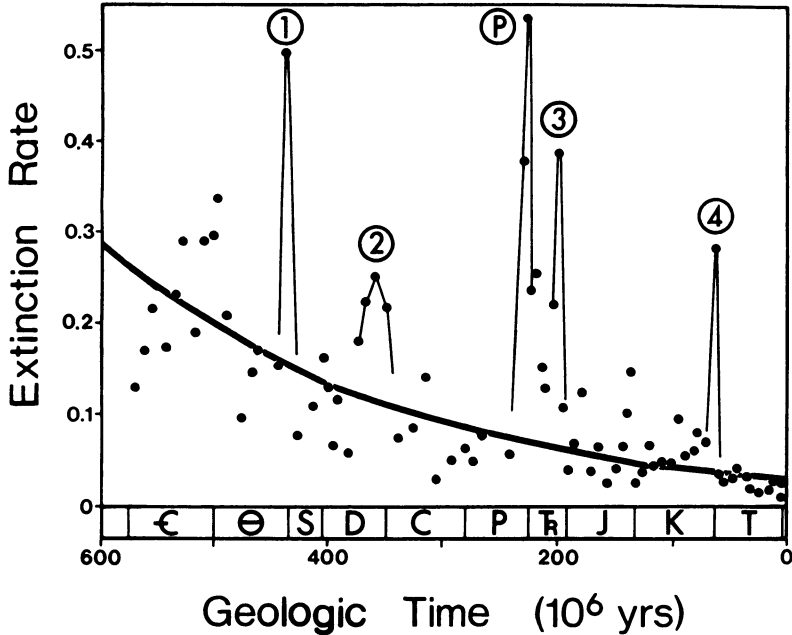   extinction periodicity well);

Figure 3. Per-capita rate of extinction of marine
families through the Phanerozoic Eon. The solid line
represents an exponential function fit to the data
(with the major mass extinctions eliminated). Numbers
identify the major mass extinctions evident in Figure 1.
(Modified from Raup and Sepkoski, 1982)

   c. An undected binary companion of the Sun, which might have a highly
      eccentric orbit that would bring it through or near the Oort Cloud
      every 26 to 28 ma (Davis et al., 1984; Whitmire and Jackson, 1984;
      Muller, this volume).
These suggestions must be considered speculative at this time, and more
work is clearly needed to convert them into a consistent series of hypo-
theses and observations. But taken together, they implicate the Earth's
extraplanetary environment as being more than simply a benign province
in which evolution can operate; rather, it may have played an active
role in patterning some important aspects of the history of life.

3. IMPLICATIONS FOR UNIVERSAL ASPECTS OF EVOLUTION

The geologically-frequent mass extinctions seen in the history of the
biosphere indicate that a planetary environment need not be completely
or continuously stable in order to support complex life. In fact, the
evolutionary resilience of the Earth's marine ecosystem suggests that it
could have tolerated even more frequent and severe perturbations without
collapsing entirely. This suggests that estimates of the probabilities

of complex life evolving elsewhere in the Universe need not be confined
to the domain of planetary systems throught to be similar to ours;
planetary systems embedded within multiple star systems or surrounded by
considerably more unaccreted debris (as the Earth was in the early
Archean) may still be capable of supporting complex life.

But even more fundamentally, it may prove that total stability is
actually detrimental to the evolution of complex life. Some suggestion
of this comes from the Earth's fossil record. Figure 3 illustrates
another measure of the intensity of extinction in the marine biosphere
over the whole of the Phanerozoic. The graph shows the per capita rate
of familial extinction (i.e., the percent of families becoming extinct
in a given stage divided by the estimated duration of that stage)
plotted against geologic time. As evident, there has been a strong
secular decline in the average, background rate of extinction, with the
current rate being considerably less than that of the early Phanerozoic
(Raup and Sepkoski, 1982; Van Valen, 1984). This decline is depicted
in Figure 3 as an exponential function, fitted to the data less the
five major mass extinctions (indicated by the "peaks" in extinction
rate). Extrapolation of the exponential curve into the future suggests
that rates of background extinction should continue to decline asymptot-
ically toward zero. In the absence of mass extinction, this situation
would mean that macroevolution would be confined to the slow process of
anagenesis and evolutionary novelties would appear rarely at best (see
also Gould, 1984). Only mass extinction would break this stagnation by
clearing ecospace for the radiation of new lineages. Thus, over the
long histories of evolutionary systems, perturbations of the biotic
environment may not just be tolerated but may actually be essential to
ensure the continuation of evolutionary experiment and the further
development of complex life.

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