Patterns of Extinction and Biodiversity in the Fossil Record

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Life has existed on the Earth for more than three billion years. Until the Cambrian explosion about 540 million years ago however, it was restricted mostly to single-celled micro-organisms that were, for the most part, poorly preserved in the fossil record. From the Cambrian explosion onwards, by contrast, we have a substantial fossil record of life's development which shows a number of clear patterns, including a steady increase in biodiversity towards the present, punctuated by a number of large extinction events which wiped out a significant fraction of the species on the planet and in some cases caused major reorganizations amongst the dominant groups of organisms in the ecosphere.

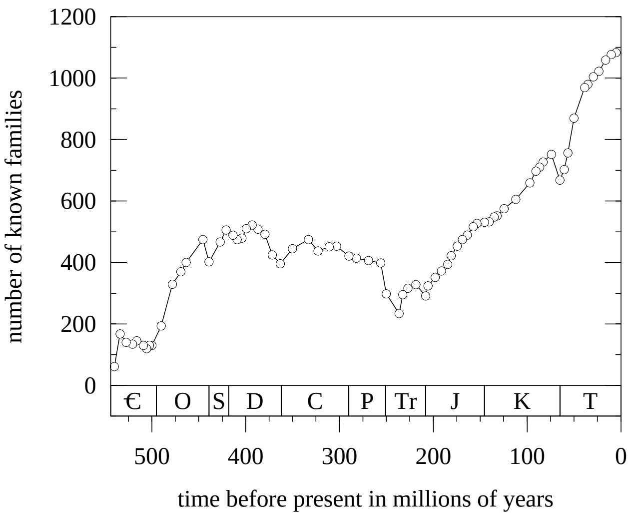

Figure 1: Number of known marine families alive over the time interval from the Cambrian to the present. The data are taken from Sepkoski (1992).

The history of life on the Earth begins in the oceans during the Archean eon, somewhere around 3.8 billion years ago, probably with the appearance first of self-reproducing RNA molecules and subsequently of prokaryotic single-celled organisms. At the start of the Proterozoic eon, around 2.5 billion years ago, the atmosphere changed from reducing to oxidizing as a result of the depletion of stocks of elemental iron in the Earth's crust, and oxygen-breathing life become possible. Eukaryotes, multicellular life, and sexual reproduction all appeared for the first time during the Proterozoic, although the exact order and dates are still in dispute, since the fossil record of this period is poor. The earliest firm evidence of multicellularity dates from about 575 million years ago.

About 540 million years ago, for unknown reasons, an enormous increase in the diversity of multicellular animals took place. This event, known as the Cambrian explosion, produced all the major body-plans of animals seen today, as well as a number of others which have since become extinct. The first land-dwelling plants appeared during the Silurian period, about 430 million years ago, followed shortly afterwards by the first land-dwelling animals, which were insects, and then the first land-dwelling vertebrates during the Devonian. About 250 million years ago at the end of the Permian period the largest mass extinction of all time took place, killing at least 90% of all species on the Earth, and ending the era that we know as the Paleozoic.

The Paleozoic was followed by the Mesozoic, colloquially known as the Age of the Dinosaurs. In addition to dinosaurs the Mesozoic also saw the first appearance of mammals and of flowering plants. It ended about 65 million years ago with the Cretaceous–Tertiary (KT) extinction event, which wiped out the dinosaurs along with about 70% of all other species then alive. The interval from the KT event until the present, known as the Cenozoic era, saw the radiation of the mammals to fill many of the dominant land-dwelling niches and, eventually, the evolution of mankind.

This information comes from geological studies and from the substantial fossil record of extinct lifeforms. The current known fossil record includes about a quarter of a million species, mostly dating from the time interval between the Cambrian explosion and the present. There are numerous biases in the fossil record which make accurate quantitative investigations difficult, including the following:

1. Older fossils are harder to find because they are typically buried in deeper rock than more recent ones.
2. Accurate dating of fossils is difficult. Radio-carbon dating, for example, is not useful for rocks which are hundreds of millions of years old. Radioactive isotopes other than carbon with longer half-lives are used for most of the geologic time-scale, but resolution of dates using these isotopes can be poor.
3. Particularly rich fossil beds, or particularly zealous in-

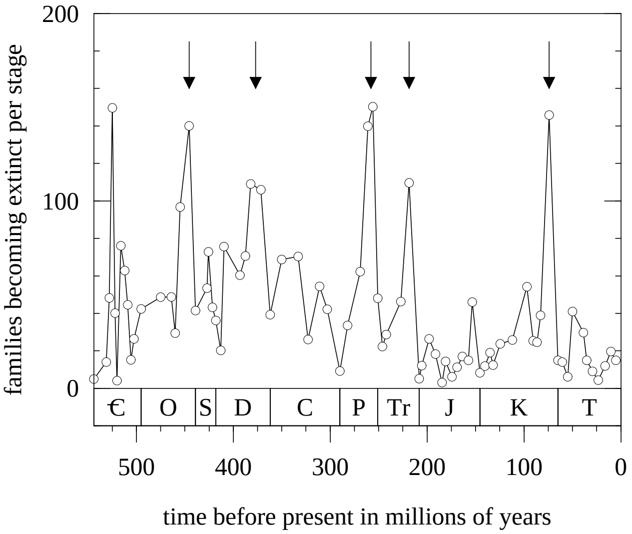

Figure 2: Estimated extinction marine animals in families per stratigraphic stage since the Cambrian. The arrows indicate the positions of the “big five” mass extinction events discussed in the text.

extinction	*genus loss (observed)*	*species loss (estimated)*
end Ordovician	60%	85%
late Devonian	57%	83%
late Permian	82%	95%
end Triassic	53%	80%
end Cretaceous	47%	76%

Table 1: Extinction intensities at the genus and species level for the big five mass extinctions of the Phanerozoic. Estimates of genus extinction are obtained from directed analysis of the fossil record while species loss is inferred using a statistical technique called “reverse rarefaction”. Figures are taken from Jablonski (1991).

vestigators, may produce very complete records for some time periods or groups of organisms, while other periods or groups may be comparatively poorly researched.

4. Prehistoric environmental disturbances can upset the deposition processes by which fossils are formed and give rise to time periods in which the fossil record is poor.
5. Marine organisms tend to be much better preserved than land-dwelling ones, because deposition is much more uniform and reliable in the oceans than it is on land.

Despite these biases, a number of trends are clear from the fossil record.

In Figure 1 we show a plot of the best estimate of the number of living families of marine organisms, as a function of time since the start of the Cambrian. As the plot shows, diversity appears to increase substantially over time, and this is believed to be a real trend. On average there have been more families, and indeed more species, alive in recent times than there were at earlier times. Over the course of the plot, diversity appears increase by a factor of about five, although some of this increase is an artifact of the greater availability of fossils of recent species in more easily accessible rocks.

Figure 2 shows the extinctions, again of marine organisms, as a function of time over the same interval. The graph gives the number of families becoming extinct per stratigraphic stage. Stages are uneven intervals of time based on recognizable geological and paleobiological markers, with typical length about seven million years. As the figure shows, there has been considerable variation in the intensity of extinction over prehistoric time. Of particular note are the five large peaks in extinction marked with arrows. These are the “big five” mass extinction events which marked the ends of the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods. A sixth peak in the Cambrian is also visible, but this is thought probably to be an artifact of poor fossil preservation during that period rather than a real extinction event. The basic features of the big five extinctions are as follows. (See also Table 1.)

The end-Ordovician event about 440 million years ago appears to have occurred in two bursts, separated by about a million years, which between them wiped out about 85% of then-living species. The event was confined to marine species, since multicellular life had not yet colonized the land. Particularly affected were brachiopods, bivalves, echinoderms, bryozoans, and corals. The immediate cause of extinction appears to have been the continental drift of a significant land mass into the south polar region, causing a global temperature drop, glaciation, and consequent lowering of the sea level, which destroyed species habitats around the continental shelves. The sea level rose again with the end of the glacial interval about a million years later and caused a second burst of extinction.

The late-Devonian extinction around 360 million years ago is complex and rather poorly understood. It is probably in fact composed of a number of separate events—as many as seven—spread over about 25 million years, including particularly notable extinctions at the ends of the Givetian, Frasnian, and Famennian stages. Overall, about 80% of living species died out in the late Devonian. Particularly hard hit were corals, brachiopods, bryozoans, ammonoids, and fish. The causes of these extinctions are unclear. The leading theories suggest that changes in sea level and ocean anoxia, possibly triggered by global cooling or oceanic volcanism, were most likely responsible, although the impact of an extraterrestrial body such as a comet has also been considered.

The late-Permian extinction around 250 million years ago was the largest extinction event of all time, killing some 95% of marine species and about 70% of land-dwelling ones. Like the end-Ordovician event, it seems to have been composed of two bursts, separated by an interval of about 10 million years, the second being the larger of the two. Notable extinction happened again amongst brachiopods, ammonoids, and corals, as well as gastropods and, unusually, insects. Despite an enormous amount of research of the subject, the causes of the late-Permian event are still a subject of debate. It is clear however that the sea level rose during this period, levels of oxygen in the oceans were low, and carbon dioxide levels were high. There is some suggestion that a cometary impact may have been involved, or a shift in ocean circulation driven by climate change, or CO_2 and sulfur release following large-scale volcanic activity. The late-Permian event had a profound effect on the terrestrial ecosystem which is still being felt today, a quarter of a billion years later. A particularly notable example amongst marine faunas is that of the bivalves, a relatively minor group during the Paleozoic that took advantage of the ecological vacuum left by the extinction to establish a solid grip on shallow-water environments, leading to their dominance over the previously very successful brachiopods and gastropods.

The end-Triassic extinction around 210 million years ago is probably the most poorly understood of the big five extinction events. It appears to have killed about 80% of species then living, either in one burst or possibly in two, separated about about 20 million years. Major extinction is observed particularly amongst ammonoids, bivalves, gastropods, and brachiopods. Leading theories of the causes of the end-Triassic event are ocean anoxia, massive volcanism, or possibly a bolide impact.

The end-Cretaceous event, usually called the Cretaceous–Tertiary or KT event, has attracted the most popular interest of any extinction because it saw the death of those perennial movie stars, the dinosaurs, but it was in fact the smallest by quite a wide margin of all the big five. The KT event appears to have been a single pulse of extinction around 65 million years ago, which wiped out about 70% of all species then living. It particularly affected large-bodied animals such as the dinosaurs, but also extinguished many other land-dwelling vertebrates along with large numbers of (marine) bivalves, gastropods, and foraminifera. The proximal cause of the KT event was, almost certainly, the impact of a large comet or meteor near the present site of the town of Puerto Chicxulub on the Yucatán peninsula in eastern Mexico, with an associated drop in sea level and possibly short-term cooling or heating, or acid rain.

The fossil record can give us valuable insight into the nature of extinction and the effects of large-scale environmental change. It also indicates that recovery from extinction is a slow process by human standards, typically taking on the order of five or ten million years. Thus it is important to fend off such extinctions before they happen, rather than hoping that the ecosystem will prove robust enough to take care of itself.

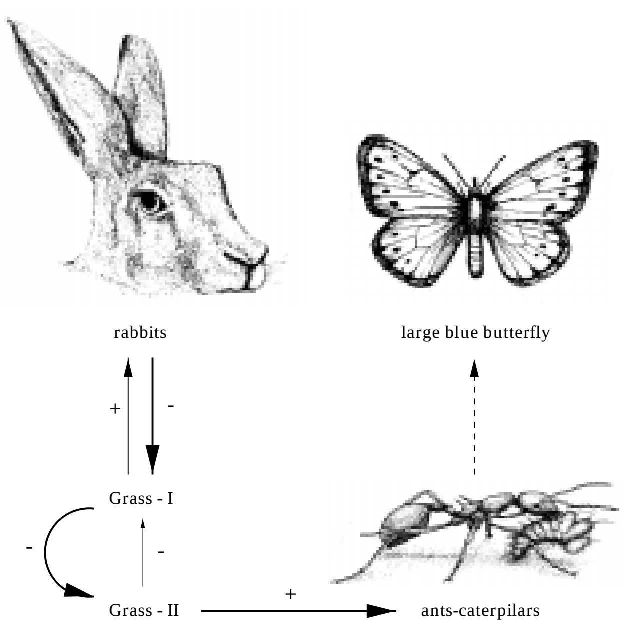

Figure 3: An example of coextinction: the introduction of the myxoma virus to rabbit warrens in England triggered the extinction of the Large Blue butterfly (*Maculina arion*), an already endangered, endemic species. Myxomatosis caused a dramatic decline in rabbit populations and a consequent surge in the abundance of a species of grass on which the rabbits previously grazed (grass–I). Another previously dominant species of grass (grass–II) was unable to compete and declined substantially in its abundance, giving rise to a shortage of nesting material for certain variety of ant (*Myrmica*). As a result of a symbiotic dependence between the butterfly *Maculina* and this species of ant, the butterfly then became extinct.

Comparison between fossil and present-day extinction is not straightforward since, as mentioned above, the fossil record consists largely of marine organisms, whereas interest in contemporary extinction focuses mostly on land-dwelling organisms. Also, specimens of recently extinct or currently endangered species tend to be rare, whereas the fossil record primarily reflects the most abundant and numerous biotas. Still, there are a number of general patterns in the fossil extinction record which may help us in the conservation of modern-day biodiversity.

First, we note that habitat loss, such as the destruction of shallow-water environments on the continental shelf as a result of changes in sea-level, appears to have been an

	fossil record	*present day*
time resolution	$\simeq 10^5$–10^6 years	$\simeq 1$ years
most affected biotas	tropical biotas	coral reefs, rainforests
selectivity on size	small-bodied species favored	small-bodied species favored
loss of endemic species	not well known	widespread
effects of habitat loss	widespread	widespread
time scale of recovery	$\simeq$ 5–10 million years	not known
indirect extinction via food webs	not known	substantial
extinction levels	75–80%	$\simeq 10^4$ species/year

Table 2: Comparison between different features of past mass extinction events and present-day, human-driven mass extinction. In both cases, habitat loss and fragmentation has widespread effects, but the causes of habitat loss were different. In the major mass extinctions of the fossil record sea-level and climatic changes and bolide impacts seem to be the major causal factors, whereas modern day extinction is primarily the result of human-driven habitat destruction. Estimates of species loss are from Jablonski (1991) and Wilson (1992).

important cause of extinction again and again. A rise in sea-level as a result of global warming over the next century, for example, could be devastating for reef communities. Habitat fragmentation—the division of a habitat into spatially isolated sub-areas—can also result in extinction. The division of even a large population into a number of weakly connected sub-populations could substantially increase extinction risk. For example, it is believed that human-driven habitat fragmentation enhanced the extinction of large-bodied mammals during the Pleistocene, with 75% of them ultimately becoming extinct. Area reduction during glacial cycles also led to widespread habitat fragmentation and seems to have produced extinction. And a considerable number of current plant species are found only in small areas because of confinement during the last Ice Age; it seems plausible that many others became extinct for the same reason.

Second, most past extinction events appear to have been selective to some extent. The end-Ordovician event, which was associated with a period of global cooling and glaciation, particularly favored species which were well adapted to cold-water conditions, and was particularly harsh on those which were not, for obvious reasons. The KT boundary event, as mentioned previously, appears to have come down especially hard on large-bodied animals. A number of explanations for this latter effect have been put forward. Large-bodied animals have smaller populations and greater area requirements, and are thus more sensitive to habitat loss or fragmentation. Moreover, their trophic requirements and low rates of population growth make them slow to recover from environmental change. It has been suggested that the loss of large herbivorous faunas could trigger major changes in biogeographic vegetation patterns that could in turn trigger further extinctions.

This last observation leads us to an additional question: to what extent do interactions between species affect the response of an ecosystem to environmental stress? Ecological interdependence between species may have heightened the impact of some of the mass extinctions; some studies, for example, have suggested that the collapse of marine food chains at the end-Cretaceous contributed to the KT extinction event. The KT event had a rapid effect on most biotas and a subsequent long-term effect perhaps related to a decrease in primary productivity. This seems particular likely in the case of marine biotas, which show a marked dip in the rate of accumulation of carbonates following the KT boundary, indicating a decrease in productivity. The resulting decrease in food supply would then produce extinctions at higher trophic levels. Similar mechanisms may also have been at work during the end-Pleistocene extinctions of mastodons and mammoths in North American, which were associated with widespread changes in vegetation patterns and the disappearance of many other species. One may well ask whether the current extinction of large herbivorous species in African ecosystems will result in similar concurrent extinctions. It is also believed that symbiotic and parasitic species are particularly vulnerable to extinction, as a result of their dependence upon a partner or host. Many living species may in fact already be doomed to extinction, because of the loss of a partner in an essential symbiotic relationship (Figure 3). The situation with parasites may be even worse, since most parasites are specific to a single species of host, and extinction amongst parasites often goes unnoticed, even though their importance in maintaining diversity has been stressed by many studies. Since all known animals and plants have some parasitic load, extinctions of parasites must be widespread in evolutionary history. The eggs of what are believed to be ectoparasitic mites have been discovered on fossilized dinosaur remains, indicating that coevolutionary parasitism, and hence coextinction (the coupled extinction of ecological partners) is an ancient phenomenon. Estimating extinction rates for parasites is unfortunately difficult, since they are poorly represented or difficult to identify in the fossil record, and internal parasites are basically not preserved at all.

Overall, recent extinction rates in most plant and animal taxa are relatively low, but for some groups they do approach the levels associated with prehistoric mass extinction events. These observations have led some researchers to suggest that the biosphere may be on the verge of another such event. Some claim that the world has already entered a sixth period of mass extinction, driven primarily by the human population explosion. Theoretical studies of long-term ecological responses to habitat destruction suggest that steady increases in extinction rates are to be expected in the near future. Paleontological studies indicate that rare, localized, or specialized species that have evolved to survive in particular niches are the mostly likely to become extinct, while widespread or adaptable species, or opportunistic colonizers are likely to prevail. The fossil record is thus more than a cautionary tale. As paleontologist David Jablonski has put it: "The lessons from the past are inevitably blurry at a coarse scale. At the present stage of knowledge, the fossil record is more revealing for potential long-term consequences than for immediate solutions. However, the history of life of Earth provides an array of worst-case scenarios. . . that are sufficiently spectacular to militate against inaction."

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