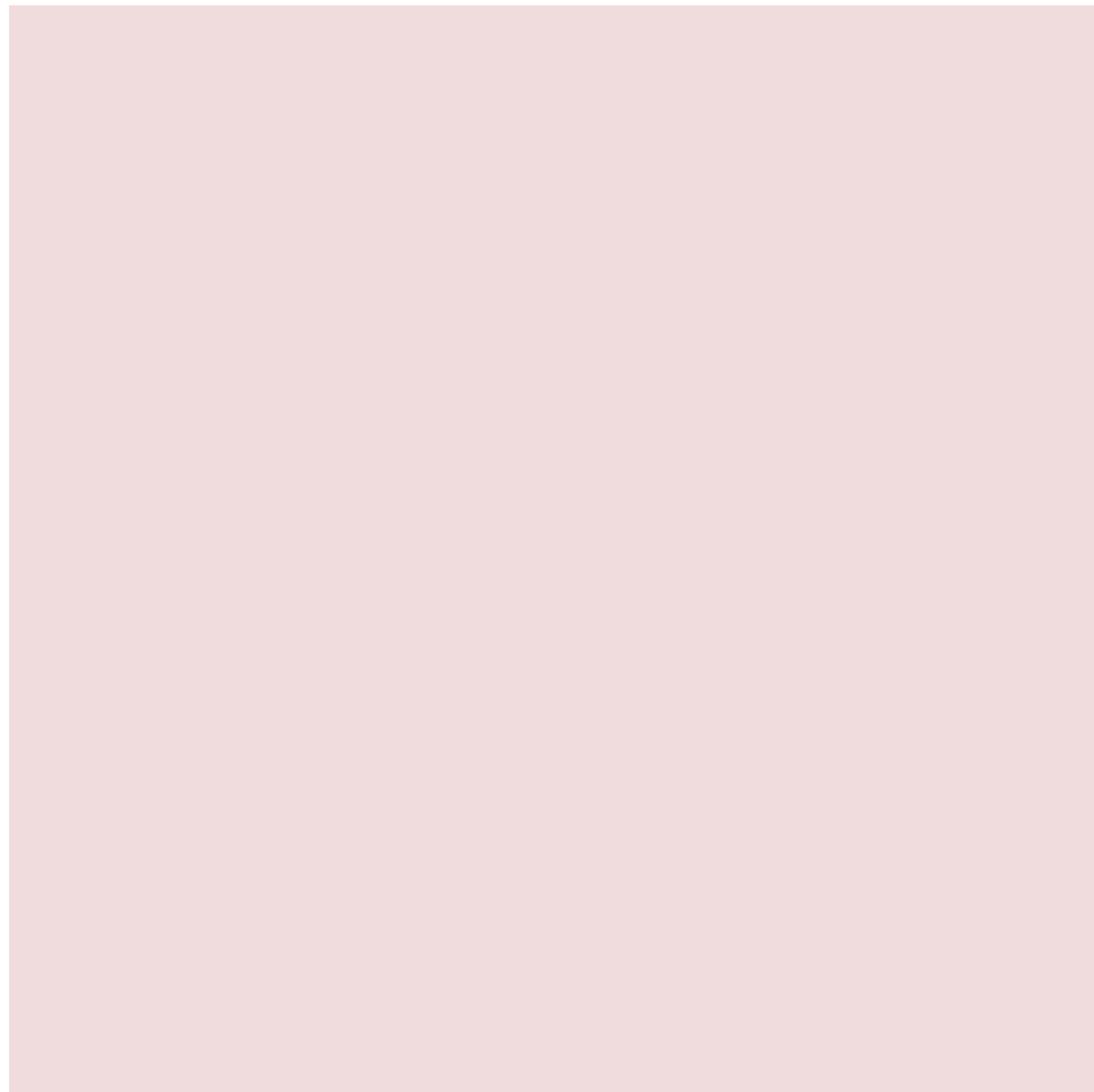


Massive extinctions in geological time

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At least five times in the past, a large number of species have disappeared in a short period of time [\[1\]](#). The study of these five major extinctions brings paleontologists, climatologists, geochemists and ecologists closer together and provides comparative references for ongoing ecological changes. All different, each extinction has profoundly reshaped biological diversity, changed the course of living history... and our scientific conceptions.

All species die out sooner or later. Paleontologists estimate that, **on average**, the life span of a paleontological species does not exceed a few million years (and sometimes much less). The "normal" disappearance of a species can have various causes: the morphology of a population can change sufficiently for paleontologists to decide to defining a new species; a population can split into one or more others which, by diverging genetically, will separate sufficiently to constitute distinct species; ecological competition between species can lead to the ecological exclusion of one of them, etc. Extinction is therefore a normal process in the history of life.

But **fossil records**, studied since the early 19th century, suggested very early that living communities have undergone major changes during Earth history, during which many forms seem to have disappeared simultaneously, while others have appeared afterwards. These upheavals (at least apparent) are at the basis of the major divisions of the **geological time scale**.

1. Mass extinctions: an old idea, rejected and rediscovered

1.1. Cuvier's "Globe Revolutions" against Lyell's theory of "Causes now in operation"

"There is therefore nothing in the known facts to support in the least the view that the new genera I have discovered or established among the fossils, nor those that have been discovered or established by other naturalists [...] may have been the strains of some of the animals of today [...]" [2]

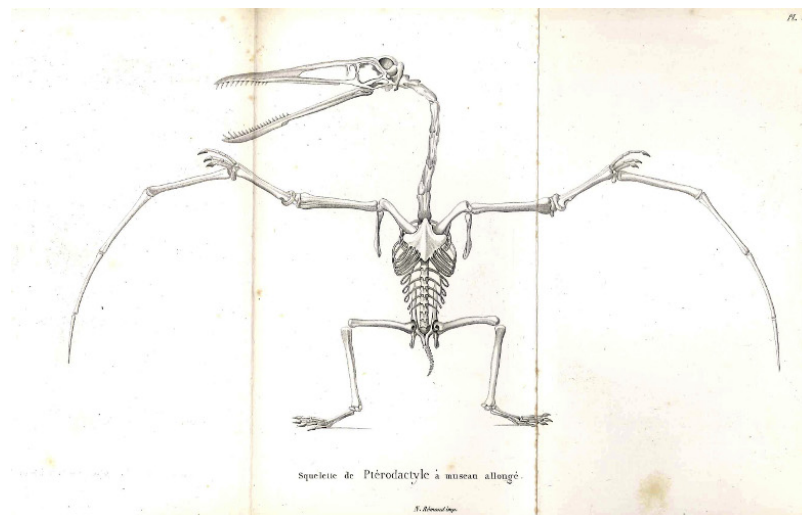


Figure 1. *Pterodactylus longirostris*, an example of a species identified by Cuvier as extinct and not directly related to current animals.
[Source : © C. Langlois]

It is in these terms that the anatomist Georges Cuvier (1769-1832) (See [Focus Georges Cuvier](#)) affirmed at the beginning of the 19th century that some fossils correspond to organisms that have completely disappeared today. For Cuvier, who rejected the idea of species evolution, these disappearances, which he saw repeatedly in the geological terrains described at the time in Europe, involved repeated upheavals of the earth's surface, which he called "revolutions": *"We are now at least in the middle of the fourth succession of terrestrial animals"* he wrote in one of the last paragraphs of his *"Discourse on the revolutionary upheavals on the surface of the globe"* (Figure 1).

With the emergence of the **theory of evolution**, formalized by Charles Darwin (see [Focus Darwin](#)) in 1859 and consolidated in 1942 with the "synthetic theory of evolution" - which finally reconciled the progress of population biology with that of genetics - the idea that cataclysmic events could suddenly and randomly transform biological communities was rejected:

On the one hand, according to the position defended by geologist Charles Lyell [3] and Darwin, geological phenomena, violent or not, observable today (erosion, absence of deposits, volcanism, earthquakes, sea level change...) were sufficient to explain the ancient events recorded in rocks [4];

On the other hand, according to Darwin, biological evolution, the adaptation of populations to their environments, was a slow and continuous process.

Cuvier's "catastrophism" was therefore abandoned in favour of Lyell's "actualism" (Charles Lyell's theory of "causes now in

operation" is often referred to as the "principle of actualism" or "uniformitarianism", even if uniformitarianism was first formulated by geologist James Hutton, 1726-1797). The idea of a biological crisis was thus banished from the scientific discourse of the 1950s and 1980s.

1.2. Speed and extent of disappearances, key markers of a crisis

Nevertheless, changes in fauna and flora were well documented in fossil records, and provided landmarks for cutting out sediments and constructing the geological time scale (**the chronostratigraphic scale**). But there were relatively slow changes, which could be explained by changes in sea level and plate tectonic movements.

Indeed, the majority of fossil species are marine organisms living in the shallow seas of the continental margins (the continental shelf). Sea level variations modify the area of these submerged edges (wider in periods of high sea level, more restricted in the opposite case), and therefore the quantity of species they can support. This surface also decreases when the continents come together in a supercontinent, as it was the case in Permian, 300 million years ago. On the contrary, it increases when the continental blocks diverge and separate.

It was when the rocks could be dated and assigned numerical ages (by radiochronology [5]) that the relative brevity of some of these episodes, and the disappearance of a large number of species in relatively short time intervals, could be demonstrated. At the same time, some paleontologists made an effort to identify all known marine fossils and to quantitatively assess **paleo-biodiversity** and its fluctuations (See Focus [The species for the palaeontologist](#)).

2. The massive extinctions of the past

2.1. Paleo-biodiversity is not biodiversity

Biodiversity (see [What is biodiversity?](#)) is a concept forged by and for biologists and ecologists; relevant to describe the current biosphere with modern technical means, including genetic analysis. It is not directly transferable to fossils [6]. Only morphology is accessible to the paleontologist, and it is often deformed or incomplete. The researcher can therefore only describe **morpho-species** (See Focus [The species for the paleontologist](#)), and the quantities of fossil species counted cannot be directly compared to those recorded in the current biosphere.

The American researcher John J. Sepkoski (1948-1999) devoted most of his career to identifying marine invertebrate fossils described in the literature and preserved in museum and university collections around the world. This huge database, with more than 31,000 genera [7], and the paleo-marine biodiversity curve derived from it, have become references. Other researchers, such as the British M. J. Benton, began similar collections for vertebrates and continental organisms. Since the 2000s, a collective effort to identify fossils, using recent collaborative computing, standardized descriptions and modern statistical analysis tools, has enabled paleontologists to build a new database, the **Paleobiology Database** [8].

2.2. Five crisis in fossiliferous times

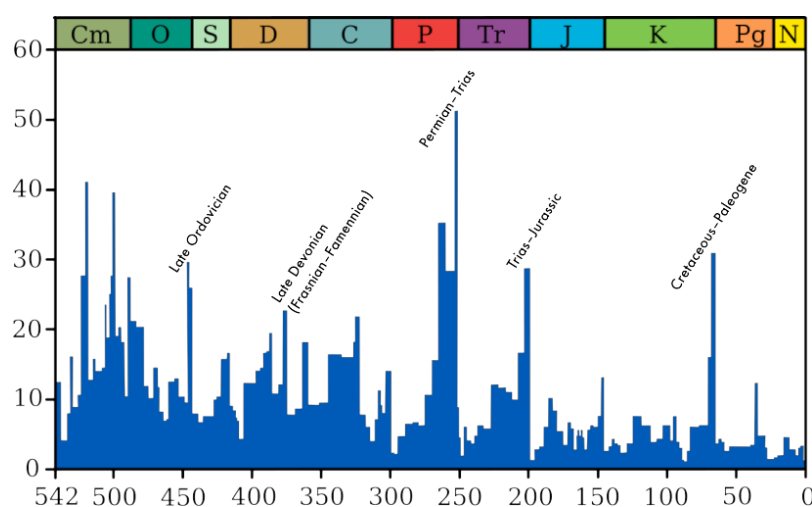


Figure 2. The extinction rate (in %) in multicellular marine invertebrates during fossiliferous time, derived from the analysis of the Sepkoski Compendium. The main peaks correspond to the five massive extinctions classically mentioned. Abbreviations: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; N, Neogene. Scheme adapted from Rohde & Muller [9]. [Source: Dragons flight (CC-BY-SA-3.0), via Wikimedia Commons]

All this work indicates that paleo-diversity has varied considerably over the 541 million years since a reliable fossil record has

been maintained. When we examine the **extinction rates** (number of extinctions per million years) of marine invertebrates, several peaks stand out (Figure 2) [9]. These peaks in extinction rates correspond to the more or less simultaneous disappearance of a large number of different groups in many parts of the world; these characteristics justify the designation of these events as "crisis", since they are rapid, non-selective and of great scope. Five of these crisis [10] are classically considered major ones [11]. The most intense took place at the end of the Permian era, 251 million years ago (Table 1). It is such a disruption of marine fauna that geologists have placed the boundary between two major geological periods, the **Paleozoic** (the "ancient life", from 541 to 251 Ma) and the **Mesozoic** (the "intermediate" life, from 251 to 66 Ma) [13]. More generally, and even before they were identified as large-scale disasters, all these episodes of species extinction (and later appearance) were used to fix the main divisions of the fossil time scale (Figure 2).

Table 1. The "five major" crisis of fossiliferous times (Adapted from Barnosky *et al.* [12]).

Name of the event	Date and estimated duration	Intensity	Proposed causes
Ordovician	- Ended ~443 Myr - Within 3.3 to 1.9 Myr	- 57 % of genera were lost - an estimated 86 % of species	Onset of alternating glacial and interglacial periods, marine transgressions and regressions, Appalachian orogeny affecting atmospheric CO ₂ , and Sequestration of CO ₂ .
Late Devonian	- Ended ~359 Myr - Within 29 to 2 Myr	- 35 % of genera were lost - an estimated 75 % of species	Global cooling (followed by global warming), diversification of land plants, with associated changes in biogeochemistry, and the drawdown of greenhouse gases, leading to widespread deep-water anoxia and the Frasnian-Famennian transgressions. Timing and importance still debated.
Permian-Triassic	- Ended ~251 Myr - Within 2.8 Myr to 160 Kyr	- 56 % of genera were lost - an estimated 96 % of species	Siberian volcanism. Global warming. Sea level rise. Anoxia in shallow waters. Elevated CO ₂ and H ₂ S concentrations in terrestrial realms. Ocean acidification. Still debated.
Triassic-Jurassic	- Ended ~200 Myr - Within 8.3 Myr and 600 Kyr	- 47 % of genera were lost - an estimated 80 % of species	Activity in the Central Atlantic Magmatic Province (CAMP) may have elevated atmospheric CO ₂ levels, leading to global warming, higher temperatures and led to a calcification crisis.
Cretaceous-Paleogene	- Ended ~66 Myr - Duration 2.5 Myr	- 40 % of genera were lost - an estimated 76 % of species	Bolide impact in the Yucatan (Chicxulub crater), global cataclysm and caused rapid cooling. Terrestrial biota may have been declining owing to volcanic activity and volcanism contemporaneous with global warming, altering biogeography and accelerating extinctions. Contributing to ocean eutrophication and anoxia just before extinction, drop during extinction event.

Myr, million years; Kyr, thousand years

3. Explanations for mass extinctions

3.1. Cataclysmic volcanism, a systematic cause?

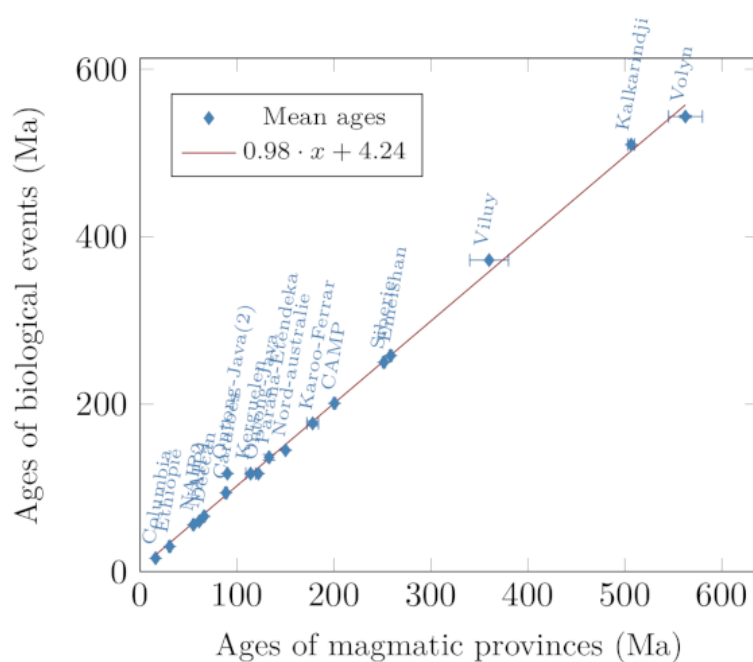


Figure 3. Comparison of the age ranges of the major magmatic provinces and biological events over the last 600 million years. A clear correlation appears. Does it involve causality? [Source: scheme © C. Langlois (data from ref. [13,14])]

Since the end of the 20th century, hot debates on the possible causes of extinctions have led to suspicions about the involvement of major and infrequent geological phenomena. Quite naturally, volcanism was quickly mentioned; this suspicion stimulated research and study of the major continental and underwater volcanic regions. These regions were therefore identified and dated (see Figure 6 below). Since the early 2000s, the dates of effusion of these gigantic lava masses - interpreted as the rise from the depths of the Earth's mantle, and the partial melting by decompression of a large "plume" of rocks - have shown a clear correlation with those of the major and minor upheavals in palaeo-biodiversity (Figure 3) [14],[15].

Is this volcanism the cause, or one of the causes, of extinctions? By which mechanisms could it have affected the biosphere? These questions have fuelled research on the effects of volcanoes. The 1991 Pinatubo eruption made it possible to monitor by satellite the fate of aerosols and gases projected at high altitude by this type of explosive volcano located at low latitudes. It was also possible to observe climate changes in the years that followed. These observations have inspired interpretations of other episodes of climate change that have occurred in historical times [16].



Figure 4. Siberian Trapps portion, near Lake Dyupkun (southwestern part of the Putorana Plateau, northern Siberia). [Source: Photo: © Dougal Jerram (see reference [17])]

However, not all these findings are directly applicable to the very intense volcanic episodes identified in the past. Indeed, in the latter cases, the magma emitted was mainly in the form of lava, and not clouds of ash. In addition, the volume of magma emitted

was considerably higher (estimated at several million cubic kilometres of lava, spread over one to several million square kilometres). Consequently, the volume of gas and aerosols produced was probably also considerable. And this volcanism continued for years (about a million years for the most important episodes) to build huge plateaus of superposed lava flows, called *traps* (Figures 4 & 5) [17].

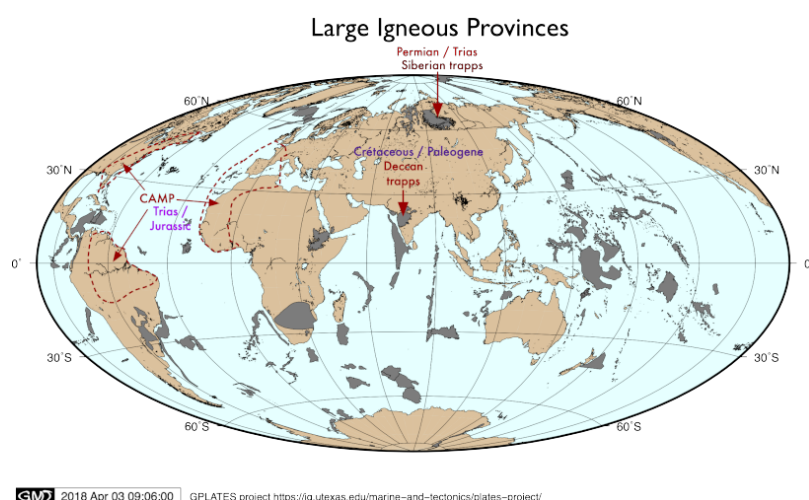


Figure 5. Current position of the large magmatic provinces that may have contributed to the massive extinctions. [Source: © C. Langlois]

In addition, we know that these lava flows have crossed and heated carbonated soils and coal beds, which have therefore burned, thus releasing carbon dioxide. Estimates put the amount of CO₂ emitted directly and indirectly by this volcanic event at more than 100,000 billion tonnes (for comparison, the present annual CO₂ emissions due to human activities are about a thousand times lower).

Such an event is therefore disproportionate compared to the explosion of a single Indonesian volcano. Its consequences have probably been unparalleled with what has been observed so far. Paleo-climatologists therefore try to imagine these effects, model them and look for potential traces. Figure 6 summarizes this scenario, distinguishing between the products probably emitted by volcanism and the direct and indirect pathways through which these emissions could lead to the observed result, a massive disappearance of organisms, both marine and continental. [18]

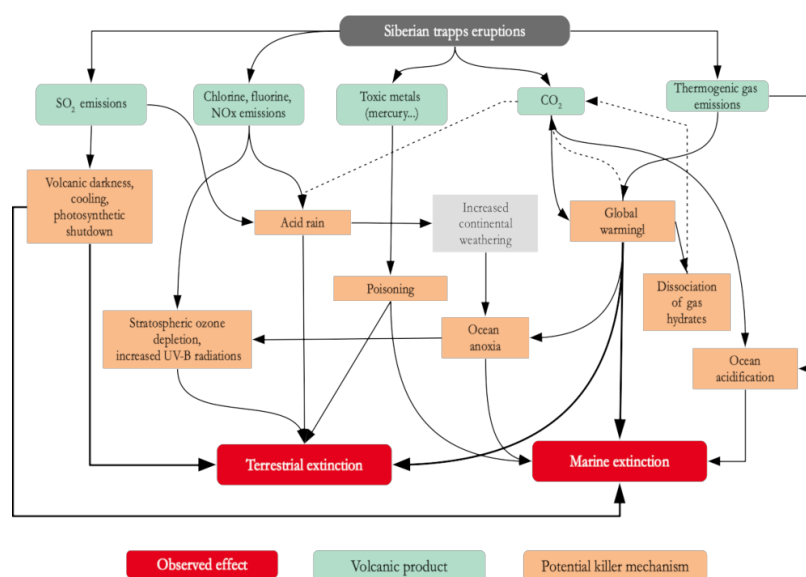


Figure 6. Diagram of possible mechanisms linking cataclysmic volcanic eruption and marine and terrestrial biological extinctions, with the case of the Siberian traps. [Source: © C. Langlois (adapted from ref. [18])]

While these eruptions probably played a major role, they would not explain all the major extinctions on their own. They have probably contributed to the collapse of ecosystems that have been previously or simultaneously weakened by other phenomena.

Thus, at the end of the Permian, 251 million years ago, the cascading effects of volcanism identified in northern Siberia (see Figures 5 & 6), affected a planet where all continents were gathered into a single supercontinent [19]. This land arrangement had reduced the area of the submerged continental shelves, which are home to most of the marine biodiversity. In the emerged areas, the climate had therefore become very continental and even arid in the interior. The high mountains produced by the collision of continents (the so-called Variscan, or Hercynian, mountain range), had also reduced biological diversity [20]. Glaciation evidence also suggests that this supercontinent supported an ice cap near the South Pole: the Permian climate was therefore colder than that of the Carboniferous period preceding it.

3.2. The Cretaceous-Paleogene crisis and the impact of a meteorite

The crisis at the end of the Cretaceous, 66 million years ago, was the one that saw the disappearance of dinosaurs (see Introductory Figure) [21], with the exception of birds that were part of it and had appeared a hundred million years earlier. Many other organisms disappear during this episode, including other reptiles (flying pterosaurs, marine mosasaurs...), many microorganisms (foraminifera), but also bird and mammal species! A volcanic cause is also considered here, since this period corresponds to the eruption of the Deccan traps in India (see Figure 5). However, in this particular case, several clues detected in the sediments deposited during this transition from the Cretaceous period to the next, the Paleogen, led to another hypothesis in the early 1980s: the impact of a relatively large asteroid (See [Focus The Cretaceous-Paleogene crisis](#)).

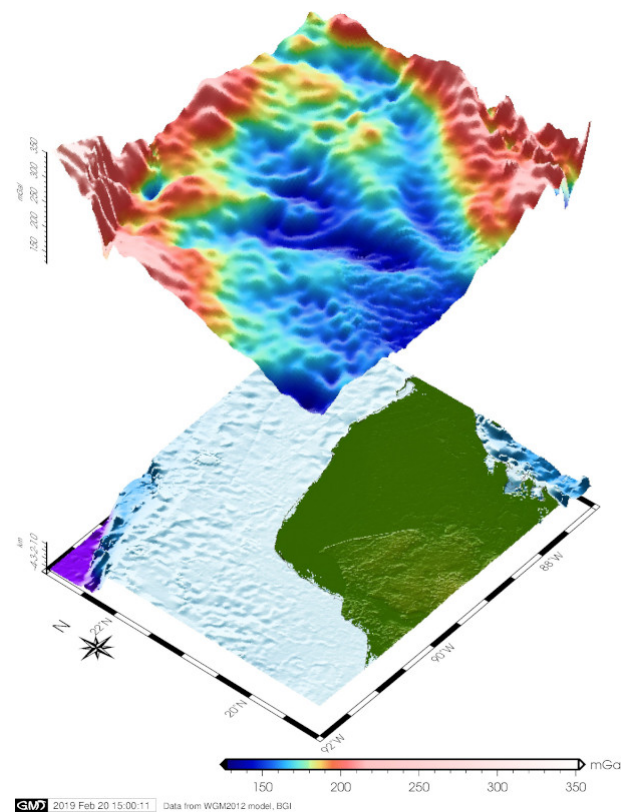


Figure 7. The Yucatan Peninsula (currently very flat area, bottom map) has a gravimetric anomaly (blue regions drawing a rounded cavity in the center of the top image). This basin of intensely disturbed rocks, invisible on the surface, is interpreted as the impact crater of a meteorite that hit the Earth 66 million years ago. [Source: © C. Langlois. Data: WGM 2012 model, Bureau Gravimétrique International]

The effects of this impact would have been quite similar to those of volcanism: darkening of the atmosphere, causing sudden cooling and affecting photosynthesis, large tsunamis, fires, acid rain, degassing of toxic molecules... The greenhouse gases (methane and carbon dioxide) released by fires and by carbonaceous and carbonated soils affected by the impact would have led to significant global warming in the longer term. Recent studies of the lava layers of the Deccan even suggest that the meteorite impact, through the seismic waves it generated, could have increased the vigour of the volcanic eruption that had begun some time earlier.

In the early 1990s, a meteorite impact site was identified by gravity measurements in the northeast of the Yucatan Peninsula in South America, in Chicxulub Province (Figure 7) [22]. Currently very flat, the edge of the Yucatan Peninsula has a roughly circular mass deficit in its subsoil of about 200 km in diameter (Figure 7, top part). This gravimetric anomaly corresponds to a decrease in land density compared to neighbouring regions. It is explained by an intense fracturing of the rocks hidden under the more recent, intact deposits. Drilling in this area has indeed recovered volcanic glasses and breccias, *i.e.* melted or crushed rocks, which the study has shown to have suffered an intense shock. In the absence of volcanism on this peninsula, the most plausible explanation for these observations is the impact of a meteor, whose size is estimated at about ten kilometres. The age of the

affected lands and the distribution of impact products in the rest of the world suggest that this crater corresponds to the impact of the end of the Cretaceous (66 million years ago), although some debates remain.

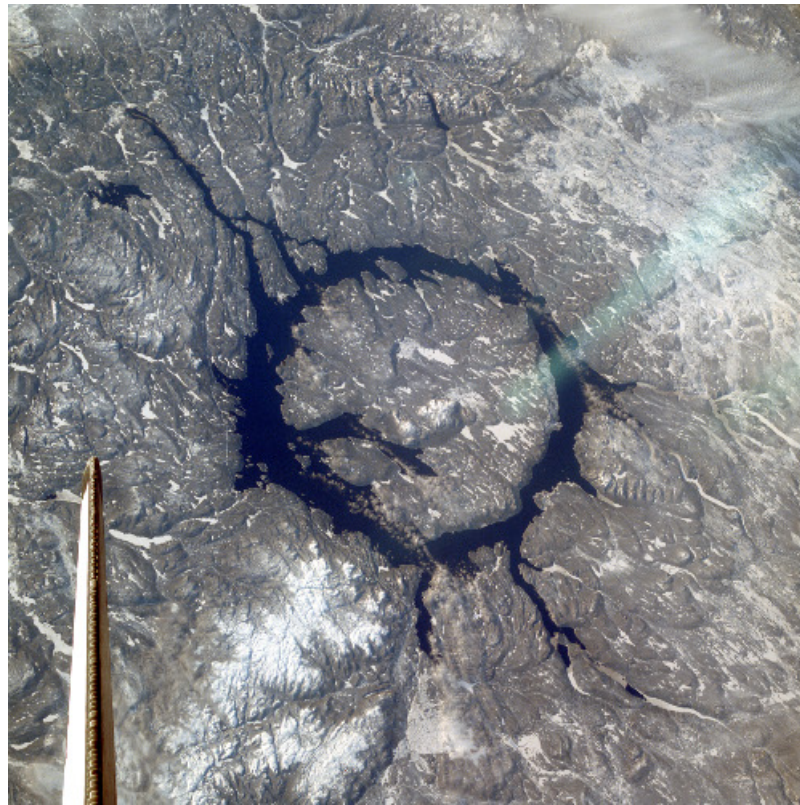


Figure 8. Aerial view of the Manicouagan crater, Canada. Currently, the water fills the rim of the crater as well as fractures radiating outwards. With a diameter of 70 km and a date of 210 million years (i.e. prior to the Triassic-Jurassic boundary crisis), this meteorite impact probably affected the biosphere). [Source: © National Aeronautics & Space Administration [Public domain], via Wikimedia Commons]

This implication of a cosmic phenomenon in the evolution of life was initially difficult to accept. Subsequently, this explanation was proposed for other massive extinctions (Permian-Triassic, Fin Devonian), without the advanced indices having won the support of the scientific community. So far, the Cretaceous-Paleogene crisis remains the only one for which the impact of a meteorite seems to be proven and adds its effects to those of an intense volcanism already underway. Among the particular effects of this exceptional event are tsunamis caused by the impact, and widespread fires, documented by fossil pollen analysis [23]. North American forests would have been replaced by ferns and pioneer plants for perhaps a thousand years (Figure 8).

3.3. Extinctions caused by the evolution of life?

The meteorite cause of the extinction of the late Cretaceous appears to be an exception; however, the other major crisis are of comparable or even more intense importance. Perhaps volcanism then had more effects, in tectonic and ecological contexts different from those of the Cretaceous. Or other factors, climatic or biological, have been added.

This idea is put forward for two of the crisis of the Paleozoic era: the end of the Ordovician and the end of the Devonian (see Table 1). In both cases, extinctions concern marine organisms, while continents are just beginning to be colonized by plants (in the Ordovician) or forests are spreading there (in the Devonian). The colonization of the land, by organisms more complex than the microorganisms certainly already present, is likely to have disrupted the very functioning of the Earth's surface envelopes.

Thus, experiments suggest that even very simple plants (mosses and lichens) promote the alteration of the rocks on which they settle and release the elements they contain into the runoff water. Conversely, vegetation reduces mechanical erosion (particle disintegration) of rocks. Rivers then bring more dissolved elements and less sediment to the sea. The implantation of plants therefore modifies the relative shares of chemical dissolution and physical disintegration of rocks: rivers thus bring less particles to the sea, but more dissolved elements.

This new operation could have encouraged the proliferation of marine microorganisms which, by consuming the oxygen dissolved in surface waters, would have deprived organisms living on the bottoms of the continental margins, causing some of them to disappear. By modifying carbon exchanges between air, water, the biosphere and soil (see [A carbon cycle disrupted by human activities](#)), these transformations may also have influenced climate (for example, by reducing atmospheric CO₂ levels,

promoting climate cooling; the end of the Ordovician is indeed marked by the development of an ice cap at the South Pole). (Read, to complete, [The first terrestrial ecosystems](#) and [The Biosphere, a major geological player](#)).

4. Past extinctions, current extinction: are they comparable?

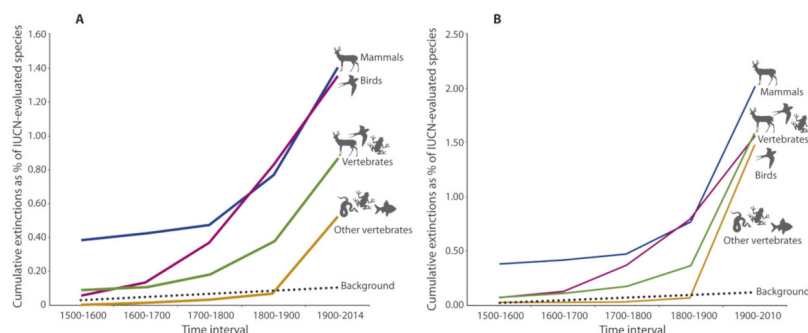


Figure 9. Extinction rates of animal species recorded by the International Union for Conservation of Nature (IUCN), by century interval, according to two estimates. Note that the scales of the two vertical axes are different. The dotted "base level" assumes a natural extinction rate of 2 species per 100,000 per century, or 2 species per million years. [Source: C. Langlois, adapted from Ceballos et al. [17] (Licence CC BY-NC)]

Five major crisis have reworked the maps of living history over the past 540 million years. Others probably preceded them. Today, an increasing number of scientific studies indicate a rapid decline in biological diversity. Many species are at risk of extinction in the very near future; a number of them have already become extinct in historical times (Figure 9). Some authors no longer hesitate to speak of a massive "**sixth extinction**", whose direct and indirect cause is the grip of industrialized human societies on the environment.

While this term "sixth extinction" is intended to highlight the extent of the phenomenon and its catastrophic nature, it is also misleading since it suggests that this disappearance of species (and more broadly this degradation of ecosystems) is comparable to previous ones.

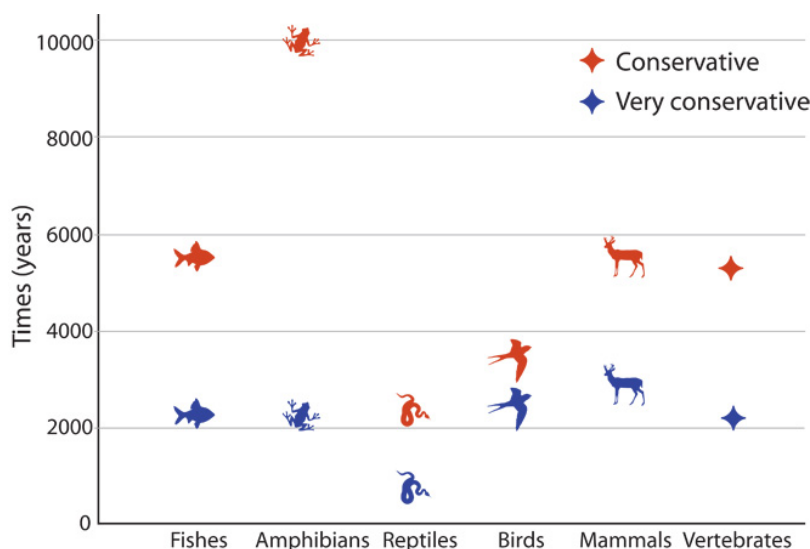


Figure 10. Theoretically necessary times to reach the quantities of extinction observed today in vertebrates with an overall natural extinction rate of 2 species per 100,000 per century. The extinctions suffered by all vertebrates over the last four centuries should have taken between 800 and 10,000 years with a "natural" extinction rate. [Source: C. Langlois, adapted from Ceballos et al. [17] (CC BY-NC License)]

However, the current evolution **differs from past crisis in its speed** (Figure 10), since it is perceptible over only five centuries and has accelerated in recent decades. The proportion of extinct vertebrate species among those officially recognized by the *International Union for the Conservation of Nature* (IUCN) is estimated for the last five centuries and compared to the expected evolution of an extinction rate considered "normal" of 2 extinct species per million species per year (see Figure 9). It is

immediately apparent that the number of extinctions has considerably exceeded this baseline level, particularly since the 19th century, regardless of how species extinction is assessed. In Figure 11, these results are presented in a different way. Assuming the natural extinction rate of 2 species per million per year, the authors calculated the time it would have taken to arrive at the quantity of species actually extinct over the past 500 years: the extinctions suffered by all vertebrates over the past four centuries should have taken between 800 and 10 000 years with a "natural" extinction rate. A duration that is still well over 500 years, proof that the disappearance of species observed is indeed abnormally rapid (and varies according to the organisms considered). This speed justifies the term "crisis" for the current evolution of the biodiversity of vertebrates (but also of other animal and plant groups).

Only the meteorite impact of the Cretaceous period could have had such brutal effects. But the current case is also exceptional in that it is due to processes that we can study, understand, model and act on, unlike previous crisis, which are inevitable and unpredictable.

5. Messages to remember

The existence of past biological crisis has once again become a subject of reflection and an active research topic since the discovery of chemical traces of a large-scale meteorite impact at the end of the Cretaceous period, 66 million years ago.

All the fossils listed around the world make it possible to estimate fluctuations in past biological diversity and ecosystem disturbances. These studies show many episodes of declining diversity over the past 541 million years, and particularly five major episodes of biological community disruption, affecting many groups of organisms, including groups then flourishing.

Their causes are probably always plural, with perhaps, in each case, the intervention of an intense volcanic episode, linked to the arrival on the surface of a large plume of deep material.

The latest crisis, that of the Cretaceous-Tertiary boundary, is most likely related, in addition to the Deccan volcanism in India, to the impact of a large meteorite, which could correspond to the crater identified at Chicxulub, Mexico.

These five "great extinctions" have each modified the evolutionary history of life, making certain groups disappear and encouraging the diversification of others.

The study of these events makes it possible to study how ecosystems have been affected by these unusual phenomena, and to understand the complexity of interactions between biological communities and their geological environment. These past extinctions provide reference points for understanding changes in current ecosystems and measuring the extent and speed of disturbances due to human activities.

References and notes

Cover image. Trix, Tyrannosaurus fossil (see reference [20]). [Source: Photo By Rique (CC BY-SA 4.0), from Wikimedia Commons]

[1] For geology, "short" means a few million years at most. That is, a duration that may only be represented in the field by a boundary between two layers of rock.

[2] Cuvier G. (1840) *Discours sur les révolutions de la surface du Globe*, 8^e édition, Paris, H. Cousin.

[3] Charles Lyell (1809-1882), British geologist, close friend of Darwin. He is the author of the *Principles of Geology* published from 1830 to 1833 and subtitled "*being an inquiry how far the former changes of the earth's surface are referable to causes now in operation*".

[4] A sudden transition between fossil species in two successive layers could be explained, for example, by a temporary interruption of deposition at this location.

[5] Radiochronology refers to all dating techniques based on the decay of certain radioactive isotopes of "parent" chemical

elements, giving isotopes of another "son" element. Since the decay rate of the parent isotope is only a function of the amount of the parent isotope, measurements of the concentrations of the parent isotope or son isotope in a rock or crystal of an appropriate mineral provide the time elapsed since that object (the rock or mineral) incorporated the parent isotope, which has slowly disintegrated. The best known of these techniques is ^{14}C ("father" element giving nitrogen 14 "sons"), or radiocarbon, mainly used in archaeology. Geologists use other father-son pairs, such as rubidium 87 - strontium 87, potassium 40 - argon 40, uranium 238 - lead 207, etc.

[6] With a few exceptions, in the case of relatively recent fossils (frozen mammoths from Siberian permafrost, teeth and bones of neanderthals or archaic *Homo sapiens*...) in which some molecules (DNA or proteins) are still recoverable and identifiable.

[7] Since fossil species are difficult to identify and differentiate with certainty, it is easier to count the higher levels of taxonomy, genera (e.g. lion, tiger and leopard) or families (e.g. *Felidae* family).

[8] <https://paleobiodb.org/#/>

[9] Rohde R.A. & Muller R.A. (2005) *Cycles in fossil diversity*. Nature 434, 208-210.

[10] These are the "Big Five", the five major crisis of Anglo-Saxon literature.

[11] The Cambrian and Ordovician extinction peaks (between 542 and 450 million years ago in Figure 2) could be explained by the ecological upheavals produced by the diversification of organisms during this period, during which the main groups of animals appear and transform their environment, building new networks of interactions and new ecological niches.

[12] Barnosky A.D. *et al.* (2011) *Has the Earth's sixth mass extinction already arrived?* Nature 471, 51-57

[13] The Cretaceous-Paleogene crisis also corresponds to the passage from the Mesozoic to the Cenozoic (the "recent life").

[14] Courtillot V. & Reindeer P. (2003) *On the age of flood basalt events*. Comptes Rendus Géoscience 335, p. 113-140. <https://www.sciencedirect.com/science/article/pii/S1631071303000063>

[15] Bond D.P.G. & Wignall P.B. (2014) *Large igneous provinces and mass extinctions: An update*. Geological Society of America Special Papers 505: 29-55. <http://specialpapers.gsapubs.org/content/505/29.abstract>

[16] For example, the unusually harsh and disturbed European climate of the 1816-1820s, now attributed to the explosion of the Tambora volcano in Indonesia in April 1815. Henrik H.

[17] Jerram Dougal A., Svensen, Planke Sverre, Polozov Alexander G., Torsvik, Trond H. (2016) The onset of flood volcanism in the north-western part of the Siberian Traps: Explosive volcanism versus effusive lava flows, Palaeogeography, Palaeoclimatology, Palaeoecology, Volume 441, Part 1, , Pages 38-50, ISSN 0031-0182, <https://doi.org/10.1016/j.palaeo.2015.04.022>.

[18] Bond D.P.G. & Grasby S.E. (2017) *On the causes of mass extinctions*. Palaeogeography, Palaeoclimatology, Palaeoecology 478, 3-29.

[19] This supercontinent was named Pangea ("all the earth" in Greek) by meteorologist Alfred Wegener (1880-1930) who had proposed its existence in 1912. He explained it by his hypothesis of "continental drift", whose arguments were then incorporated into the current theory of plate tectonics, accepted since the late 1960s.

[20] The over-rection of a mountain represents a reduction in the available surface area and that high-altitude regions generally support fewer species than plains.

[21] The Tyrannosaurus Trix (cover photo) was discovered in 2013 in Montana, USA, by a team of paleontologists from the *Naturalis Biodiversity Center* in Leiden, the Netherlands. It is the oldest known Tyrannosaurus specimen, a female over thirty years of age, and considered to be the third most complete Tyrannosaurus found, with between 75% and 80% of its bone volume recovered.

[22] Alan R. Hildebrand, Glen T. Penfield *et al* (1991) *Chicxulub Crater: A possible Cretaceous/Tertiary boundary impact crater on the Yucatán Peninsula, Mexico*. Geology v. 19, pp. 867-871.

[23] Recent analyses -Field D.J. *et al* (2018) *Early Evolution of Modern Birds Structured by Global Forest Collapse at the End-Cretaceous Mass Extinction*. Current Biology 28, p1825-1831.e2- suggest that these fires would have caused the disappearance of most of the many bird species that existed in North America at the time. A new diversification of birds would have taken place after this episode, from a few surviving groups living on the ground.

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