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## **Plants – the great survivors!**

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### **Abstract:**

The marine fossil record suggests there have been five great mass extinctions, at the Ordovician-Silurian, Frasnian-Famennian (Late Devonian), Permian-Triassic, Triassic-Jurassic and Cretaceous-Palaeogene transitions. However, the palaeobotanical record tells a rather different story, with only one of these extinctions having significantly disrupted plant evolution. We clearly need to look again at what we really mean by mass extinctions events, especially in the context of the so-called sixth mass extinction occurring today, that appears to be affecting terrestrial as well as marine biotas.

One of the great discoveries in palaeontology has been that life on Earth seems to have suffered five large-scale diversity crises, often termed mass extinctions (marked in red in Fig. 1a). The original model was developed in the 1980s by Chicago palaeontologists David Raup and Jack Sepkoski, based on analyses of large-scale databases of marine fossil faunas. Studies were also attempted on terrestrial faunas and floras, but with mixed results; similarly detailed databases for these groups were not available at the time. This changed in 1993 with the publication of Mike Benton's *Fossil Record 2*, which included family distribution data on all organisms that were preserved as fossils. Based on these and subsequent refinements of the plant data we can now explore vegetation diversity dynamics in the same way as was done for marine faunas (Fig. 1b). This is of course vital for a proper understanding of the terrestrial biosphere – plants are at the base of virtually all terrestrial trophic chains, have a fundamental influence on atmospheres and climates, and are a key element for soil formation and its stabilization; they are the central structural element of land environments.

Plants often break-up during fossilisation and the parts found separately, and so palaeobotanists usually give different species and generic names (known as fossil-taxa) to the different parts. Simply listing fossil-species and -genera will therefore give a highly distorted picture of past plant diversity. The lowest taxonomic rank mostly based on whole plants is the family and so our analyses have been done at this rank. Consequently, when we talk about diversity it is not the same as species biodiversity. Nevertheless, it has been shown that family diversities usually represent reasonable proxies for species diversities, and certainly map the general trajectory of organismal evolution through time. For further discussions on this and other issues relating to sampling and interpretation of fossil floras, see Cascales-Miñana et al. (2013).

### **End-Ordovician (O/S) event**

The earliest (O/S) mass-extinction mainly affected the marine Palaeozoic Fauna, especially corals, brachiopods, stromatoporoids, trilobites and graptolites. Although plant macrofossils of this age are extremely rare, many Ordovician rocks contain dispersed spores indicating a landscape covered by a globally cosmopolitan bryophyte-like flora (Gray's Eoembryophytic phase). There is no evidence of a mass extinction on land ecosystems; rather plants were undergoing a continuous and sustained increase in diversity at this time (Fig. 2).

### **Frasnian–Fammenian (Late Devonian – F/F) event**

This was associated with large-scale anoxia in bottom marine waters and an increase in carbon burial. This particularly affected benthic faunas, especially tropical reef-building organisms; about 20–25% of all marine animal families became extinct.

Land vegetation was in contrast diversifying (Fig. 3). Following the Silurian appearance of rhyniophytes there had been a progressive increase in diversity and complexity of land vegetation, resulting in the Eophytic Flora initially dominated by the herbaceous zosterophylloids, lycopsids and trimerophytopsids. Stems with secondary wood that allowed plants to grow significantly larger appeared during Middle Devonian times, and the first forests had developed by Late Devonian times (Fig. 4a-d). However, the key development was the seed, which freed plants from having to grow in damp habitats to complete their life-cycle (Fig. 4e-g). The resulting pteridosperms and cordaites, together with ferns, and arborescent lycopsids and sphenopsids, formed the Palaeophytic Flora that dominated Carboniferous vegetation, especially in the tropics.

This expansion of forests may have partially caused the decline in marine diversity. Plant roots caused greater chemical erosion and soil development, in turn increasing nutrient flow along rivers into the sea. This may have encouraged algal blooms, causing bottom water anoxia and increased carbon burial – exactly what is observed in the geological record.

### **Pennsylvanian – Permian events**

Palaeozoic global plant diversity peaked during early – middle Pennsylvanian times (Fig. 1). This coincided with the maximum development of the Late Palaeozoic Ice Age, and so much of this plant diversity was concentrated in tropical latitudes, especially in the coal swamps. From Late Pennsylvanian times, however, over the next 55 million years global plant diversity progressively declined. The first significant reduction in diversity (e.g. loss of Chaloneriaceae, Corynepteridaceae, Lyginopteridaceae) occurred when the coal swamps contracted due to a combination of climatic warming (the Late Pennsylvanian Interglacial) and major landscape changes due to the collision of the Gondwana and Laurasia continental plates (Fig. 5a). When the coal swamps returned (mainly in China – the Cathaysian Flora) in latest Pennsylvanian and Cisuralian times, there was a partial recovery in global plant diversity. However, with the final end of the ice age in late Cisuralian – Guadalupian times there was another significant fall in global plant diversity, with the loss of some 26% of plant

families, mostly characteristic forms of the coal swamps such as the Sigillariaceae, Asterothecaceae and Tedeleaceae.

After the end of the Late Palaeozoic Ice Age, other vegetational changes happened. In the tropics, the Mesophytic Flora dominated by conifers, cycadophytes and peltasperms, started to spread significantly into the lowlands and thus become more extensively represented in the fossil record. In higher latitudes, the contraction of polar ice and general climatic warming allowed vegetation to proliferate here, such as the glossopteridalean forests of the southern high latitudes. This resulted in much greater geographical provincialism in land floras. Overall, however, global plant diversity declined (Fig. 5a), suggesting that, as today, maximum plant diversity occurred in tropical areas of high precipitation; the development of forests in the middle and high latitudes could not compensate for the loss of plant diversity in the tropics. It is also notable that there was no corresponding reduction in marine faunal diversity (Fig. 1).

### **Early Triassic (P/T) event**

Among faunas, this was the greatest of the mass extinction events, sometimes called “The Great Dying”. It was likely caused by large scale eruption of flood basaltic lavas in Siberia that produced vast quantities of “greenhouse” gases, triggering intense global warming and marked ocean acidification. The global warming also caused large-scale release of methane from oceanic clathrates that accelerated the warming. The resulting disruption to climates caused some 95% of marine invertebrate species and over half the families to disappear (Fig. 1a), notably among trilobites, eurypterids and blastoid echinoderms. It marked a major reconfiguration of the marine faunas, with the replacement of what Sepkoski called the Palaeozoic Evolutionary Fauna by the Modern Fauna (Fig. 1a). Although evidence from terrestrial faunas is poorer, there also seems to have been a dramatic decline in vertebrates (Fig. 5b) and insects (Fig. 5c).

Until recently it had been assumed that there was also a significant collapse in global vegetation at this time: a spike in fungal spores reported from just above the boundary was interpreted as evidence of extensive rotting of vegetation, and there are abundant undivided spore tetrads thought to have been the result of mutations due to high-levels of ultra-violet radiation. There is also a well-documented absence of coal in the lower and middle Triassic series.

But determining exactly what happened has been hindered by problems of stratigraphical correlation between the marine and terrestrial sequences: did the observed changes in the floras in fact coincide with the changes in the marine faunas? New data is now in fact suggesting that the situation was more complex. There was clearly widespread destruction of forests at the P/T boundary and for several thousand years ferns proliferated. Plant-life then briefly recovered, and for about  $200 \times 10^3$  years was not significantly different from latest Permian vegetation. But then further significant bouts of global warming occurred, probably caused by successive basaltic eruptions in Siberia, and this prolonged stress seems to have had a more pronounced effect on plant diversity. For about 5 million years, vegetation in many parts of the world was impoverished, mainly dominated by shrubby club mosses and conifers. About 55% of plant families became extinct, although this was mainly among the remnant Palaeophytic groups that were already on the wane. A number of groups of Mesophytic seed plants also became extinct (e.g. cordaites, glossopterids, gigantopterids, many voltzialean conifers) but these seem to have been replaced in middle–late Triassic floras by other Mesophytic, and often closely related seed plants such as the bennettitaleans and pinalean conifers. Plant diversity eventually fully recovered after about 20 million years but when it did, vegetation was not so dramatically different from many Late Permian floras.

### **Triassic–Jurassic (T/J) event**

As vegetation progressively recovered during Triassic times, many fern and conifer families found in today's floras appeared for the first time (Fig. 1b); the only major group of extant plants for which Triassic evidence is at best equivocal is the angiosperms. The Triassic Period has in fact become known as the “Heyday of the Gymnosperms” because of the diversity of the seed plants, especially in southern latitudes (Fig. 6). However, the end of the Triassic Period saw another biotic crisis. Extensive volcanism associated with the opening of the Atlantic Ocean (the Central Atlantic Magmatic Province – CAMP) introduced large quantities of CO<sub>2</sub>, SO<sub>2</sub> and CH<sub>4</sub> into the atmosphere, triggering significant global warming. In the oceans, over one-third of the animal genera disappeared; on land, many land reptile groups also became extinct.

Two of the best sections showing terrestrial sequences through the T/J boundary, in southern Sweden and east Greenland, reveal clear evidence of disruption to the vegetation – some 80% of plant species locally disappeared, changing stomatal densities and carbon isotopes indicate a marked increase in atmospheric CO<sub>2</sub>, and abundant fusain suggests

extensive wildfires. However, this ecological stress seems only to have lasted a few decades. In other parts of central Europe (such as Hochalpgaben in Austria), plant diversity in fact increased across the T/J boundary, probably due to climatic warming resulting from redirected oceanic currents. Significantly, very few plant families became extinct at this time, except among some of the southern latitudes gymnosperms. The overall balance of plant groups is essentially similar in Hettangian floras as in Rhaetian floras (Fig. 1b).

### **Cretaceous–Palaeogene (K/T) event**

For many, this epitomises mass extinctions because of its effect on iconic groups such as dinosaurs and ammonites. It was probably caused by a combination of bolide impact in the Chicxulub Peninsula (Mexico) and massive lava eruption in the Indian Deccan Traps. This caused global ecological stress – extensive wildfires, and vast clouds of dust causing global cooling and reduced insolation.

About 70% of marine invertebrate species became extinct due to disruption of shallow marine habitats, and of many of the food-webs that had photosynthetic organisms at their base. On land, there was an extensive die-back of terrestrial vegetation, which lasted for several years, and which had a severe impact on terrestrial herbivores. However, vegetation rapidly recovered, pioneered by ferns (there is a widely documented “spike” in fern spores not far above the K/T boundary), followed by angiosperms and conifers. Terrestrial ecosystems appear to have recovered in just a few decades, in contrast to the marine realm which took millions of years to recover.

Few if any major plant groups became extinct at the K/T boundary; nearly all plant families known from latest Cretaceous floras also range up into the Cenozoic (Fig. 7). Some non-angiosperm seed-plants did not survive such as the Caytoniales, but their remains are already very rare by the Maastrichtian Stage. Another typically Mesophytic group of seed-plants, the Bennettiales, had also become very rare well before the K/T boundary, although there are records of rare Oligocene foliage from Australia. It is most unlikely that the K/T event was the primary cause of the demise of these or any other plant group.

The major change in vegetation had in fact already occurred during Cretaceous times, with the appearance of Cenophytic vegetation dominated by angiosperms and pteridacean ferns (Fig. 1b). This not only had a dramatic effect on plant diversity, but also on the evolution of terrestrial faunas through enhanced herbivory and (mainly with insects) symbiosis; this

symbiosis with insects was probably a more important factor influencing plant evolution at this time than mass extinctions.

### **Plants: the great survivors**

Evidently, most “mass-extinctions” did not significantly disrupt plant evolution. Three of them in fact occurred when terrestrial floras were diversifying: the O/S event with the earliest radiation of land plants; the F/F event when forests were proliferating; and the K/T event with the diversification of the angiosperms. Of the others, the effect of the T/J event on plant evolution was essentially neutral. As the great American palynologist Al. Traverse put it, “Plant evolution dances to a different beat.” This is not to say that these events did not affect plant life; especially at the T/J and K/T events, there is evidence of wildfires and extreme climate change devastated large swathes of vegetation. However, the landscape usually re-vegetated relatively quickly with plants that had much in common with those growing before the event.

So, how do plants survive such ecological catastrophes? Most important is probably their dispersal strategies, which involve spores, seeds and underground structures such as corms, rhizomes and tubers that can often lie dormant in or on the ground for a considerable time before germinating or re-growing. Think what you would find ten years after someone had taken a gun and shot all the elephants in the world: you would find no elephants – they would be extinct. But if someone went out with an axe and cut down all of the oak trees in the world, and came back ten year later, they would find the beginnings of new oak forests – the acorns lying on the ground would have germinated.

The one exception to this was “The Great Dying” after the P/T boundary, where so many plant families became extinct. Why did plants suffer more here than during the other biotic crises? In the short term, the effect of the P/T event on vegetation was not in fact so different from the T/J and K/T boundary events, with plant-life rapidly recovering. However, there then followed a series of other ecological crises during Early Triassic times. This resulted in a much longer time of ecological stress, lasting about 2 millions of years, instead of just a few decades as in the other biotic crises. No matter how robust the seeds and spores were, they cannot survive in the ground for such a long period of time before germinating. The only plants to survive would have been those that could grow in the highly stressed, post-crisis conditions, or in the few refugia habitats that remained. This would have represented a significant evolutionary “bottleneck” for plants and so unsurprisingly many families became

extinct. However, most of the plant families that proliferated in the middle–late Triassic, post-crisis floras seem to have been related to the Permian, pre-crisis Mesophytic groups. Although Early Triassic times did see a significant disruption to the overall trajectory of plant evolution, it was not as profound as the changes to animal evolution: it was the Palaeophytic–Mesophytic floral transition that took place during late Carboniferous and Permian times that changed the overall trajectory of plant evolution, not the P/T event.

The biotic crises known as mass extinctions undoubtedly had a major disruptive effect on the Earth’s biotas. However, most were not really global mass extinctions as they only affected a subset of the Earth’s biota – animals, and mainly marine invertebrates. This is, of course, partly just because the fossil record gives such a biased view of life on Earth. It is important to recognise that there have been different grades of “global mass extinction” that affected different biotas in different ways, and that until now there has in fact been only one truly global mass extinction, in Early Triassic times – the P/T event.

This obviously changes the context of the biodiversity crisis taking place today, which has sometimes been referred to as the sixth mass extinction. As today’s crisis seems to be affecting both terrestrial and marine biotas, we should perhaps be talking about this being only the second global mass extinction that has affected life on Earth during its 3.5 billion year history. Maybe we must think a little more carefully about what we are doing to our world today, especially regarding to vegetation damage.

### **Suggestions for further reading**

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## Figure captions

Fig. 1. Evolutionary Faunas (a; redrawn from Sepkoski *et al.* 1981, *Paleobiology*, **7**, 36–53) and Evolutionary Floras (b; redrawn from Cleal & Cascales-Miñana 2014, *Lethaia*, **47**, 469–484) models compared. Vertical red lines indicate the "Big Five" marine mass extinctions. Vertical green lines indicate the plant End-Carboniferous and Guadalupian biotic crises, respectively. Major extinction episodes: End-Ordovician, Frasnian-Famennian, End-Carboniferous, Guadalupian, End-Permian, End-Triassic and End-Cretaceous.

Fig. 2. Ordovician-Silurian genus-level dispersed spore diversity curves. Redrawn from Cascales-Miñana (2016, *Review of Palaeobotany and Palynology*, **227**, 19–27). Vertical red lines indicate the End-Ordovician marine mass extinctions

Fig. 3. Silurian-Devonian genus-level plant diversity curve. Redrawn from Cascales-Miñana (2016, *Review of Palaeobotany and Palynology*, **227**, 19–27). Vertical red lines indicate the Late Devonian (Frasnian-Famennian) marine mass extinctions

Fig. 4. The Late Devonian saw several key developments in plants. Large plants some 10 m tall started to dominate the landscape, with woody *Callixylon* stems. (a) Transverse section of the secondary xylem of *Callixylon whiteanum* Arnold. Scale bar = 200  $\mu\text{m}$ . (b) Tangential section of the secondary xylem of *Callixylon newberryi* (Dawson) Elkins & Wieland. Scale bar = 200  $\mu\text{m}$ . (c) Reconstruction of *Archaeopteris* sp. Scale bar = 1 m. (d) Leafy branch of *Archaeopteris roemeriana* (Göppert) Lesquereux. Scale bar = 1 cm. Also important was the appearance of the seed, which allowed plants to expand into a larger range of habitats. (e) Cupules of *Moresnetia zalesskyi* Stockmans. Scale bar = 5 mm. (f) is a fossil of such a seed cluster (specimen NMW 2013.38G.1; type locality, Elkins, Randolph County, West Virginia, USA; scale bar = 10 mm). Artwork by Annette Townsend (formerly of National Museum Wales). (g) Reconstruction of *Elkinsia polymorpha* Rothwell *et al.* Scale bar = 5 cm.

Fig 5. Apparent family-level diversity patterns during the early configuration of terrestrial ecosystems compared. (a) Plants (redrawn from Cascales-Miñana *et al.* 2016. *Historical Biology*, **28**, 1066–1074). (b) Tetrapods (redrawn from Sahney *et al.* 2010. *Biology Letters*, **6**, 544–547). (c) Insects (redrawn from Clapham *et al.* 2016. *Proceedings of the Royal Society*

B, 283, 20152476). Red lines indicate the accepted marine mass extinctions. Green lines indicate the end-Carboniferous and Guadalupian plant extinctions.

Fig. 6. Mesophytic vegetation. (a) Reconstruction of vegetation in middle Mesozoic fluvial habitat, including ginkgophyte, bennettites and tempskya fern trees, and herbaceous ferns and horsetails. (b) Conifer shoot *Elatides* sp., Rhaetian Stage, Penarth Head, South Wales (NMW 2002.36G.1). (c) Part of bennettites leaf *Otozamites* sp., Rhaetian Stage, Penarth Head, South Wales (NMW 2008.40G.1). (d-f) *Ginkgo huttonii* (Sternberg) Heer leaf, Scalby Formation (Bathonian), Scalby Ness, Yorkshire, UK (NMW 30.432.G67.2). Artwork by Annette Townsend, formerly of National Museum Wales. Photographs of fossils by James Turner (National Museum Wales). All scale bars = 10 mm.

Fig. 7. Cenophytic vegetation dominated by flowering plants. (a) Leaf bed with *Alnus*, Frechen Mine, near Köln, Germany; scale bar = 10 mm (NMW 76.6G.32). (b) Flowers of *Magnolia campbellii* Hook.f. & Thomson. (c) Palaeocene (Danian) fossil flower *Notiantha grandensis* Jud *et al.*, Rancho Grande, Chubut, Argentina; scale bar = 1 mm. (d) Grass flowers, *Poa* sp. Fossil in (a) photographed by James Turner (National Museum Wales); fossil in (c) reproduced with permission from Jud *et al.* (2017, *PLoS ONE*, 12, e0176164.); living plants in (b) and (d) photographed by Ingrid Jüttner (National Museum Wales).











