

The timing and pattern of biotic recovery following the end-Permian mass extinction

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The aftermath of the great end-Permian period mass extinction 252 Myr ago shows how life can recover from the loss of >90% species globally. The crisis was triggered by a number of physical environmental shocks (global warming, acid rain, ocean acidification and ocean anoxia), and some of these were repeated over the next 5–6 Myr. Ammonoids and some other groups diversified rapidly, within 1–3 Myr, but extinctions continued through the Early Triassic period. Triassic ecosystems were rebuilt stepwise from low to high trophic levels through the Early to Middle Triassic, and a stable, complex ecosystem did not re-emerge until the beginning of the Middle Triassic, 8–9 Myr after the crisis. A positive aspect of the recovery was the emergence of entirely new groups, such as marine reptiles and decapod crustaceans, as well as new tetrapods on land, including — eventually — dinosaurs. The stepwise recovery of life in the Triassic could have been delayed either by biotic drivers (complex multispecies interactions) or physical perturbations, or a combination of both. This is an example of the wider debate about the relative roles of intrinsic and extrinsic drivers of large-scale evolution.

Life came closest to complete annihilation 252.3 Myr ago during the end-Permian mass extinction (EPME), which occurred just before the Permo–Triassic boundary (PTB). This largest crash in global biodiversity of the past 500 Myr (refs 1–3) markedly redirected the course of evolution during the Mesozoic and Cenozoic eras, and is responsible for much of the structure of marine and terrestrial ecosystems today^{1,4–6}.

The disappearance of ~90% of skeletonized marine species⁷ marked the end of Palaeozoic marine faunas and the rise of the replacing ‘modern fauna’¹. Formerly dominant denizens of the deep, such as brachiopods, crinoids, trilobites and tabulate and rugose corals, either disappeared or were massively reduced in diversity. Other groups that were already present, but were minor components of ecosystems, such as bivalves, gastropods, malacostracans (crabs and lobsters), echinoids (sea urchins), scleractinian corals and bony fishes, took their places. These are still the dominant groups in the sea, so modern marine ecosystems date back to the Triassic recovery. On land too, basal tetrapods gave way to archosaurs including dinosaurs, as well as the ancestors of modern frogs, turtles, lizards, crocodiles and mammals.

Many aspects of biotic recovery following the EPME, in the Early and Middle Triassic, have been puzzling, including its tempo and mechanism^{8–11}. There are three elements: timing; roles of intrinsic and extrinsic processes; and significance of trophic levels in ecosystems. In terms of timing, some clades seemed to bounce back relatively rapidly, within 1–2 Myr (refs 12–14), whereas others experienced a long delay of 5–10 Myr (refs 8,9,15–17; Fig. 1). The relative roles of intrinsic (ecosystem dynamical) and extrinsic (physical environmental) processes as drivers of the recovery depend on the timing of recovery. If the recovery was slow, there are questions about whether the delay was imposed by continuing poor-quality environments^{8,15,18–21}, complex ecosystem interactions^{9,14,22,23} or a combination of both. Finally, trophic level might be crucial, and we outline a multi-step recovery model involving the addition of progressively higher trophic levels within marine ecosystems and spanning some 8 Myr.

Because the EPME was the most extreme of several mass extinctions in the past 500 Myr, the post-extinction recovery began

from a much more devastated planet and biota than the others. With only some 10% of species surviving, the EPME was much harsher than the other mass extinctions, during which global species diversity reduced to only about 50% of the pre-extinction total^{1,2,24–26}. This means that the Triassic recovery has two profound implications: first, it may show qualitative, as well as quantitative, differences from the other post-extinction recoveries; and, second, it can act as an exemplar of what to expect, at its most extreme, when global biodiversity is pushed to the brink. There are obvious implications for current concerns about biodiversity loss and recovery resulting from human impacts^{27,28}.

In the past ten years, attention has focused on the sedimentary successions in south China. These are enormously laterally extensive, with some formations extending more than 2,000 km from the Zhejiang to Yunnan provinces. The huge exposures, length of the sections and improving dating open up the opportunity to explore physical environmental and biotic changes through the extinction and recovery times in varied marine habitats, and compare these with patterns elsewhere in the world (Fig. 1). A fine-scale, forensic analysis of this extraordinary time in Earth’s history now becomes possible.

The end-Permian mass extinction

The EPME killed 80–96% of marine animal species and 70% of terrestrial vertebrate species^{10,24,29,30}. In the intensively sampled Meishan section in South China, 280 out of 329 marine invertebrate species disappeared near the PTB, indicating an abrupt, one-stage extinction pattern³¹. Closer study at Meishan and adjacent areas indicates that the EPME may have followed a two-stage pattern, with each crisis step separated by approximately 0.2 Myr (refs 32–35).

A number of potential triggers for the crisis have been identified: increased CO₂ concentrations and global anoxia, euxinia (anoxic and sulphidic conditions), hypercapnia (CO₂ poisoning), a bolide impact, rapid global warming and plume-induced volcanic eruption³⁶. The most widely accepted model^{7,10,37,38} begins with eruption of the Siberian traps, huge volumes of basaltic lava that produced CO₂, which led to global warming and the short-term

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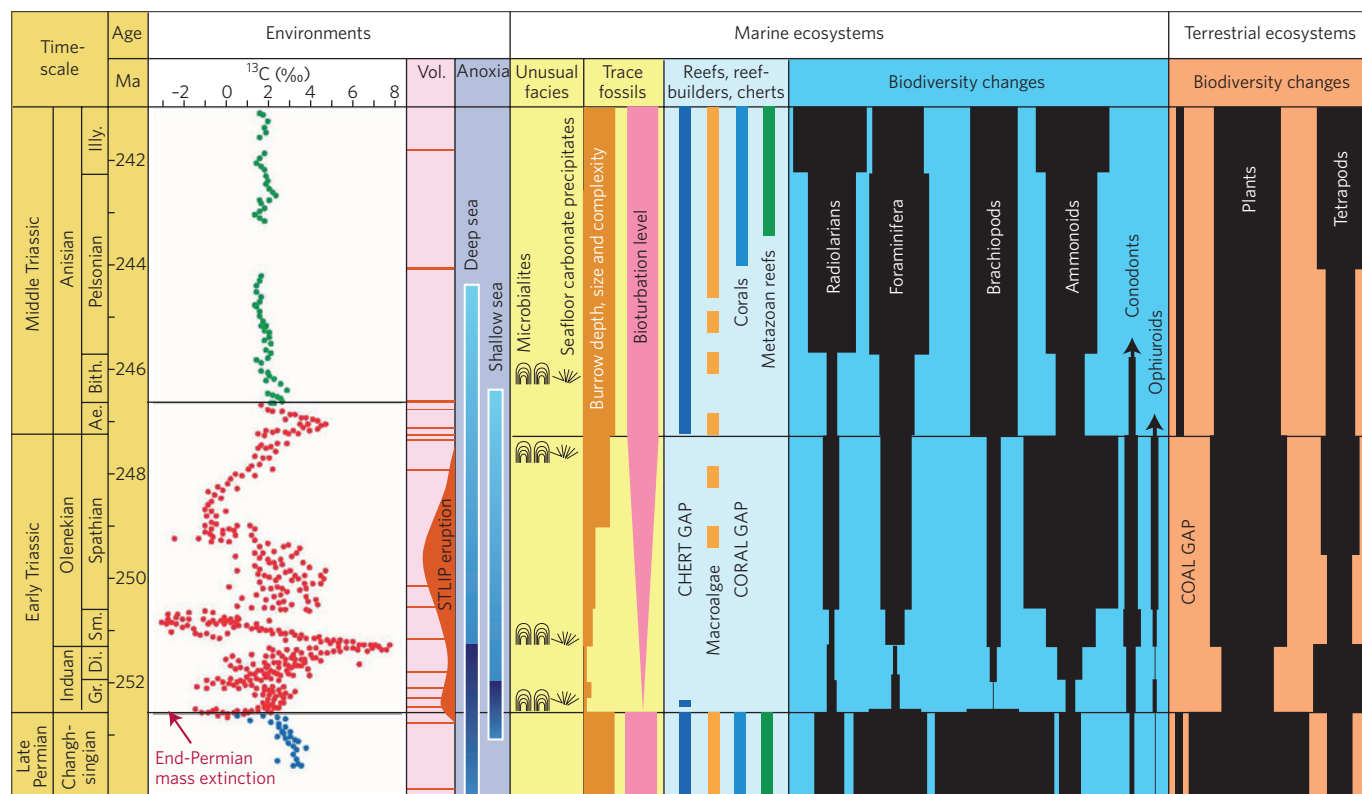


Figure 1 | Environmental changes and biodiversity variations from the latest Permian to Middle Triassic. Arrows indicated on the conodont and ophiuroid range bars show increasing data into the Middle Triassic; detailed data on genus diversity and principal authors are listed in Supplementary Table S1. The timescale was based on new radiometric dates outlined in Supplementary Information S2. Carbon isotope fluctuations, Siberian Traps large igneous province (STLP) eruption, anoxia ranges, trace fossil data, and reef, reef builder, chert and coral gap data from references in Supplementary Information. Ae., Aegean; Bith., Bithynian; Di., Dienerian; Gr., Griesbachian; Illy., Illyrian; Sm., Smithian; Vol., volcanism.

production of acid rain. The acid rain killed plants on land, which led to massive erosion as soil was released, all associated with a shift from fine-grained sediments deposited in lakes and meandering rivers to conglomeratic braided fluvial facies^{39,40}. The massive erosion was associated with wildfires, perhaps triggered during the unusually arid conditions³⁵. Sedimentation rates in terrestrial successions increased⁴¹ and there was an abrupt, increased influx of terrigenous siliciclastics to the oceans^{42,43}, associated with soil-derived biomarkers⁴⁴.

In marine environments, heightened CO₂ levels led to ocean acidification; at the same time, global warming and raised inputs of nutrients into the sea caused ocean anoxia, indicated by widespread black sediments and sulphides⁴⁵. Furthermore, interaction between Siberian-trap magma and organic-rich sedimentary rocks could have greatly increased release of CO₂ and other greenhouse gases. The warming could also have triggered the release of methane from deep ocean reserves and coals, which would have exacerbated the global warming and ocean anoxia³⁷.

The extinction and recovery episodes are well dated, especially in marine sections. High-resolution fossil biozones from the PTB beds and Triassic sequences of south China enable correlation of the EPME and its aftermath^{35,46}. The EPME was calibrated to the base of a volcanic ash bed just below the PTB in the Meishan section, south China³¹, the world standard for the PTB (ref. 46). In south China (Fig. 1), this crisis has been dated at 252.3 Ma (ref. 35) and the Early–Middle Triassic successions are constrained by high-resolution radiometric ages⁴⁸ and astrochronology⁴⁹. Terrestrial successions are harder to date accurately, but a combination of radiometric dating, magnetostratigraphy and chemostratigraphy is improving the situation^{35,47,48}.

Physical environments in the aftermath of the EPME

Environmental conditions in the Early Triassic were poor. This is indicated by unusual biosedimentary features (including abundant microbialites, wrinkle structures and seafloor carbonate precipitates) that reflect the absence of metazoans devastated by the EPME, combined with episodes of low oxygen and high chemical precipitation⁴³. These unusual conditions are matched by the ‘coral gap’, when there were no reefs built by colonial metazoans in shallow water^{3,43}, and the ‘coal gap’^{50–52} on land, during which forests, and hence coal deposits, were absent (Fig. 1).

Anoxia has long been documented as a key element of the EPME^{35–45}, and it seems to have been a recurring condition throughout the Early Triassic^{19,36}. Upwelling of CO₂ from anoxic deep-ocean waters during the EPME may have increased the acidity of surface waters for a short time, causing elevated mortality among carbonate-secreting organisms⁷. Oceanic euxinia (anoxic and sulphur-rich stratified ocean) is indicated by the loss of dissolved oxygen and free H₂S in the water column, as shown by biomarkers, pyrite framboid sizes, S-isotopic compositions and Ce anomalies^{43,53}. The massive release of sulphides into the oceans adds H₂S toxicity to the cocktail of potential killers⁵⁴.

Redox changes may have been caused either by chemocline-upward excursions^{53,54} or by upwelling of deep anoxic water masses^{43,55}. These massive changes in seawater chemistry are attested by repeated C-isotopic excursions¹⁹, but the origins of these are uncertain. Clues may come from correlations with fluctuations in other geochemical proxies, such as ²⁹C/³⁰C hopane and 2-MHP biomarker ratios, and increased concentrations of ³⁴S-depleted pyrite^{53–55}, which can indicate upwelling of ¹³C-depleted, sulphidic deep waters.

Negative excursions in carbon isotope ratios, indicating repeated greenhouse crises⁵¹, occurred as many as five times during the 5 Myr of the Early Triassic and early Anisian age (Fig. 1). It is uncertain how such repeated light-carbon excursions could be generated so frequently: one spike could exhaust the global reserves of methane stored in deep ocean gas hydrates. Either the methane reserves could recharge faster than had been assumed, or large volumes of CO₂ were repeatedly released from coal beds⁵¹ or frequent volcanic eruptions³⁶.

The pattern of Triassic recovery

The recovery of life began rapidly, within the first 1–3 Myr of the Triassic. For example, among marine organisms, ammonoids¹² and conodonts^{56,57} diversified in the first 2 Myr of the Early Triassic, reaching apparently stable local diversities. Further, some earliest Triassic body and trace fossil assemblages are more diverse than predicted^{58–61}. The best example comes from foraminifera in the south China sections, where recovery began 1 Myr into the Triassic, and was not much affected by Early Triassic crises¹⁴. This early phase of recovery was short-lived for most groups, and there were further extinctions at the end of the Smithian and Spathian sub-stages, both in the sea^{19,20,56,62} and on land^{11,16,21}, so global species and ecosystem stability had not yet been achieved.

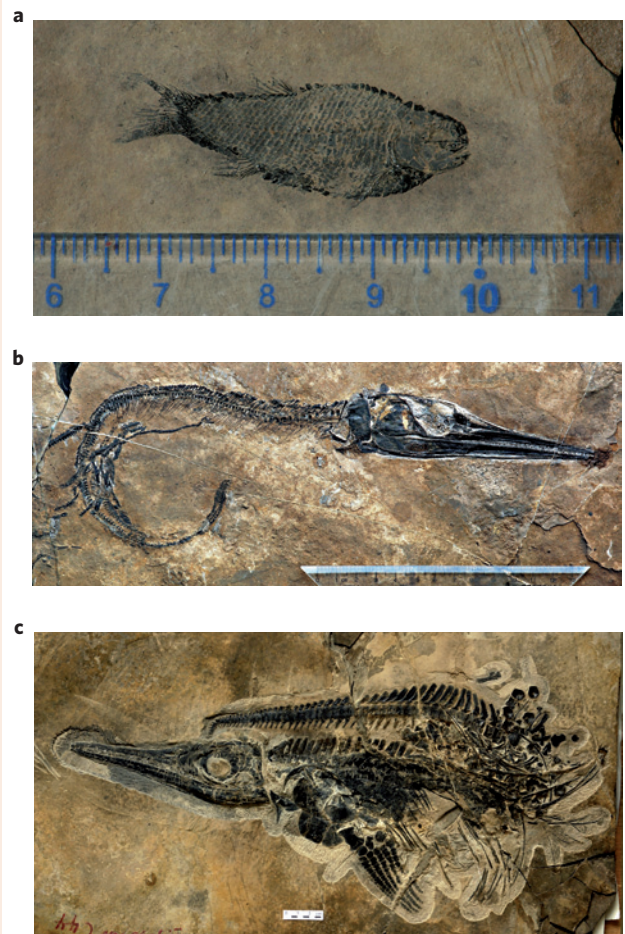
The recovery of life on land indicates similar patterns^{11,16,21,51}. Plants declined rapidly in diversity through the EPME and rebounded in the Smithian, but did not return to pre-extinction levels until the Late Triassic (Fig. 1). However, extinction was limited; rather, temporary ecological replacements arose, driven by environmental changes. The spore spike in many sections before the EPME was the first sign of environmental deterioration, when stable gymnosperm-dominated floras were replaced by rapidly growing, early successional communities dominated by lycopods and ferns^{62–64}, resulting in reduced sequestration of organic matter in terrestrial facies during the Early Triassic coal gap^{50–52}. A further spore spike occurred in the middle Smithian, preceding the end-Smithian extinction when the lycopods were replaced by woody gymnosperms, indicating a switch from warm and equable climates to latitudinally differentiated climates^{62,63}.

Tetrapods also underwent massive extinction through the EPME (Fig. 1), with the destruction of complex latest Permian ecosystems dominated by herbivorous pareiasaurs and dicynodonts, and carnivorous gorgonopsians. Dicynodonts recovered to become major herbivores again, passing through a bottleneck at the PTB, and smaller groups, such as procolophonids and therocephalians, survived the EPME. Tetrapod ecosystems in Russia, at least, showed considerable volatility until the Ladinian age¹¹. Further, the key tetrapod groups had changed and new clades, the archosaurs and cynodonts, became dominant, with dinosauromorphs originating earlier than had been thought, in the maelstrom of the Spathian to Anisian recovery^{65,66}.

Marine ecosystems had recovered substantially in the early to middle Anisian, 8–9 Myr after the crisis, and perhaps at the same time (or even later) on land. Importantly, this was the time when the coral and coal gaps ended (Fig. 1).

The EPME was positive in the emergence of new organisms. Most striking were the marine reptiles (ichthyosaurs, thalattosaurs, pachypleurosaurs, nothosaurs and placodonts) that emerged in the Olenekian and Anisian ages, and decapod crustaceans (crabs and lobsters). These added new top trophic levels, creating a typical Mesozoic, or even 'modern', ecosystem — seen especially in China (Box 1). These reptiles and decapods are new clades and so technically not part of the recovery — where 'recovery' means the return to a previous state — but these new predators were key components of Mesozoic ecosystems. On land, too, major new groups appeared in the aftermath of the extinction, including frogs, dinosauromorphs (and eventually dinosaurs)⁶⁵, rhynchosaurs and diademodont cynodonts.

Box 1 | The Luoping biota



The Triassic of south China is marked by several exceptionally preserved fossil assemblages, in which a wide array of organisms, those with skeletons and those without, are preserved. One recently discovered example, the Luoping biota of the Yunnan Province, southwest China⁹⁶, dated as mid-Anisian, documents the final stages of recovery from the EPME. The Luoping biota is dominated by lightly sclerotized arthropods, associated with fishes, marine reptiles, bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, foraminifers and conodonts⁹⁶. So far, some 20,000 specimens have been collected. Unusually, the commonest animals were arthropods (including decapods), comprising 94% of all finds. The 25 species of fishes and diverse marine reptiles, comprising together 4% of finds, show multiple new predatory levels in the ecosystems, and match closely with well-known marine faunas from the Middle and Late Triassic elsewhere in the world. The Luoping biota seems to represent a stable, typically Mesozoic marine ecosystem.

The photographs above show exceptionally preserved fishes (a,b) and reptiles (c) from the Luoping biota, Yunnan, southwest China: a, eugnathid fish; b, *Saurichthys*; c, ichthyosaur.

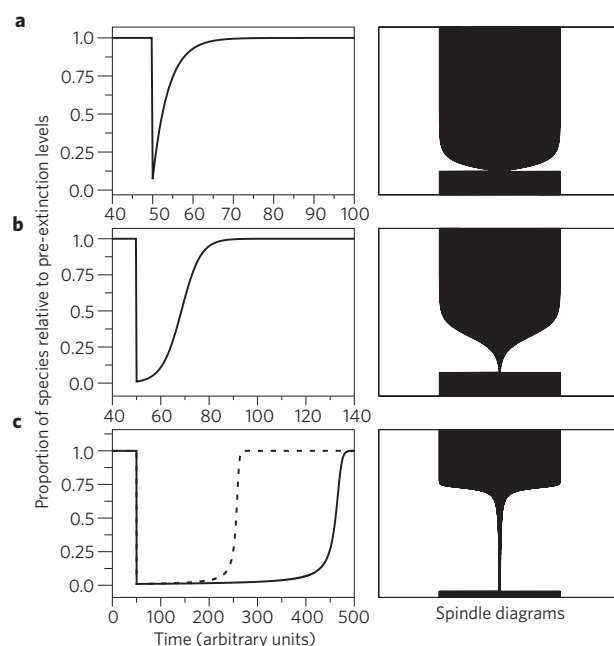
Trace fossils (burrows and trails) provide alternative evidence for recovery patterns, especially in the sea^{67,68}. Although several diversity spikes among trace fossils have been recognized from the Induan age^{59,69,70}, multiple lines of evidence, including diversity, burrow size, complexity, tiering levels and bioturbation levels, show that trace fossil assemblages recovered in the Spathian^{67,68,71–73} (Fig. 1).

Box 2 | Models of recovery

From an evolutionary point of view, biotic recoveries following mass extinctions are characterized by a complex set of dynamics, including the rebuilding of whole ecologies from low-diversity assemblages of survivors and opportunistic species. Biodiversity recovery could follow one of three trajectories²³: **a**, an immediate linear response; **b**, a logistic recovery; or **c**, a simple positive feedback pattern of species interaction that follows a hyperbolic trajectory. In theoretical modelling²³, the lag time to biotic recovery increases significantly as biotic interactions become more important in the recovery process, an example of positive feedback⁹. These models are developed with equilibrium assumptions — of the world before and after extinction having a fixed carrying capacity — that have been questioned⁹⁹.

The three models can characterize different trophic levels, with producers recovering first, according to a linear model, and consumers taking longer to recover. Long delays in recovery are expected at higher trophic levels in the food chain^{23,95}, with predators taking longer to recover than primary consumers (herbivores). Theoretical modelling supports the last model, but it will be important to tease apart the effects of three possibly interacting variables during recovery from mass extinction: the magnitude of the extinction and consequent scale of the immediate recovery faunas; the effects of continuing or repeated low-quality physical environments; and the effects of species interactions throughout the recovery time. If such interactions are absent, the linear or logistic model might be expected; if they are present, the hyperbolic model might be followed. If species interactions are indeed important during post-extinction diversification, then the length of delay before the onset of rapid recovery should scale with the speciation rate²³. Further, if there is environmental inhibition of recovery, it might be possible, with excellent dating and thorough sampling of fossil records, to identify such a lag from the subsequent recovery²⁰.

A further interesting theoretical question is whether diversifications following mass extinctions differ from other kinds of clade expansions. In other words, are there differences



in the dynamics and macroecological impacts of recoveries when compared with ‘adaptive radiations’, contrasting opportunistic versus adaptive drivers? Broader macroecological questions for all kinds of diversifications¹⁰⁰ concern the timing: whether ecosystems rebuild themselves in a wholesale manner or step-by-step; whether the recovery passes up through the trophic chain from producers to top carnivores; whether there is an ‘early burst’ of diversification of disaster taxa and then a decline; and how different sub-clades fare relative to each other.

Several benthic assemblages were found to be rather diverse in the aftermath of the EPME, indicating an earlier benthic recovery^{58,74}. However, benthic communities in most areas of the world remained at low diversity through the Early Triassic^{17,75,76}.

A final ecological aspect of the Triassic recovery was the ‘Lilliput effect’ (dwarfing) shown by marine organisms, not only during the EPME, but also through the entire Early Triassic^{14,77,78}; although, body sizes of some clades (for example, gastropods⁶¹) remained unchanged or slightly increased in the Early Triassic. The dwarfing may have been driven by reductions in food supply, reductions in oxygen levels during greenhouse crises, or changing ecological pressures, and recovery of normal sizes corresponds to the return of stable conditions in the early Anisian¹⁹.

Slow or fast recovery?

A key question concerns the timing of Triassic recovery. The standard view^{8,15,18–21,43,79} is that the recovery lasted some 5–9 Myr, whereas others^{14,61,80} concentrate on the first 1–3 Myr after the EPME. There are issues concerning definitions of terms and possible sampling bias.

Early phases of recovery may be indicated by recovery of species numbers within 1 Myr of the EPME (Fig. 1), and yet these ecosystems were often unbalanced. For example, earliest Triassic terrestrial faunas may have contained as many species as before the crisis⁸¹, but species ‘evenness’ (the similarity of relative abundances of species) was unbalanced, with individuals of the dicynodont *Lystrosaurus*

in huge abundance (>90%), together with rare amphibians, but without diverse herbivores and top predators^{11,16,82}. Most would call this a ‘disaster fauna’, a short-term community composed of opportunistic species that did not form the basis for the balanced, even ecosystems typical of later times. The same case has been made concerning earliest Triassic marine faunas²⁰.

Delayed recovery could reflect poor sampling in the Early Triassic¹². Perhaps the reefs and marine reptiles that emerged in the Anisian are actually present in earlier Triassic rocks, but have yet to be sampled. There is no test to distinguish true absence from simply a lack of sampling or fossilization⁸³. Sampling of the Early Triassic of south China, and other well-documented long sections, has improved enormously in the past twenty years. Evidence has yet to be found showing that lithologies or quality of exposure are sufficiently different between, for example, the earliest Triassic and the Anisian for early appearing reefs or marine reptiles to be missed.

If ecosystems recovered in a stepwise and steady fashion, then individual taxonomic groups show major differences. Fast-evolving taxa, such as ammonoids and conodonts, apparently recovered fast after the EPME. Their high rates of speciation were associated with considerable evolutionary volatility: both groups had suffered extinctions (particularly the ammonoids) during the EPME, as well as during crisis intervals throughout the Early Triassic^{12,56}. The story is not quite so simple, however. Although ammonoids recovered relatively rapidly, reaching a higher diversity by the Smithian than in the Late Permian¹², much of this Early Triassic radiation was within

a single clade, the Ceratitina, and the global diversity of ammonoids did not reach maximum levels until the mid Anisian⁷⁹.

A more slowly evolving group, the benthic foraminifera, took 10 Myr to recover to pre-extinction diversity levels, even though their recovery began 1 Myr after the EPME, and they were apparently not much affected by the environmental shocks of the Early Triassic¹⁴. Among other slowly evolving groups (Fig. 1; Supplementary Table S1), brachiopods had been the commonest animals in Permian oceans, but experienced a sharp decline in the Early Triassic and their diversity did not rebound until the early Middle Triassic^{84,85}. Corals suffered a major diversity loss in the EPME and did not re-occur until the middle Anisian⁸⁶. This is also true for radiolarians, a clade that suffered a large depletion in diversity during the Early Triassic and early Anisian^{87,88}. Among echinoderms, crinoids were absent for much of the Early Triassic and rebounded at the end of the Spathian⁸⁹, whereas ophiuroids experienced diversity increase and geographic expansions immediately after the EPME (ref. 90).

Habitat may also matter. It has been argued^{14,20} that pelagic taxa such as ammonoids and conodonts recovered before benthic forms: pelagic recovery began immediately in the Induan, and then benthic forams and others began to recover more slowly from the beginning of the Olenekian¹⁴.

Most studies of Triassic recovery have used global or regional diversity counts, typically numbers of genera or species. Such palaeodiversity metrics cannot indicate all aspects of recovery⁸, and a wider ecological approach is essential³. For example, ammonoid diversity rose in the Smithian (Fig. 1), but their morphological disparity (range of form) did not expand until the end-Spathian⁹¹. This diversity-first model may not be ubiquitous, however, and many tetrapod groups in the Triassic show the more typical disparity-first pattern^{92–94}. For ammonoids, then, the diversity-first model indicates rapid speciation of similar disaster taxa filling ecospace, followed by more steady adaptive evolution into new sectors of morphospace as ecosystems and community interactions stabilized. The disparity-first pattern seen among tetrapods indicates that clades explored the limits of morphospace early, and then later filled the space by specialization. Perhaps the two patterns reflect overall rates of evolution (fast in ammonoids), or whether a clade reacts in a ‘disaster-taxon’ way (diversity-first) or in a long-term ecosystem-stabilizing manner (disparity-first). The distinction between fast- and slow-evolving taxa may relate to ecology, distinguishing opportunistic species that show high rates of reproduction, many offspring and limited parental care (r-selected), and those that produce few offspring infrequently and invest in their nurture (K-selected). These studies show the need to consider more than palaeodiversity in seeking to understand the real richness of diversification.

Multi-step trophic model of recovery

There is some debate over whether trophic levels predict recovery rates or not — the standard view^{22,23,57} is that lower trophic levels recover before higher levels, and this is supported by fundamental ecological assumptions (Box 2). However, the fact that ammonoids and conodonts began to recover early, and that predatory fishes such as *Birgeria* and *Saurichthys*, as well as the first ichthyosaurs, occur in the Olenekian, indicates that trophic level is not on its own a guide to the timing of recovery¹⁴, but ought to be considered together with intrinsic rates of evolution of each clade^{22,57}. Here, we broaden the ecological network model^{23,95} to explore the complete trophic structure of fossilized ecosystems during the Permo-Triassic transition (Fig. 2), as a means of assessing the recovery.

During the Late Permian and Early Triassic, primary producers, forming the lowest trophic level, were microbes. The middle part of the food web comprises primary and meso-consumer trophic levels, the former dominated by microorganisms such as foraminifera, and the latter by opportunistic communities (that is, disaster taxa and tracemakers), benthic shelly communities and reef-builders. These

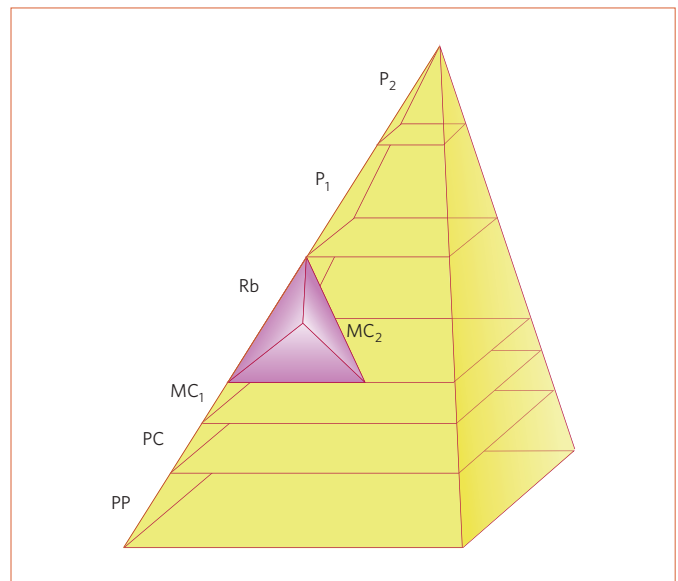


Figure 2 | Outline trophic pyramid of a fossilized marine ecosystem in the Permian or Triassic. From the bottom, the trophic levels are: primary producers (PP), mainly microbes; primary consumers (PC), such as foraminifera; meso-consumers (MC₁), such as endo-faunal trace-markers; meso-consumers (MC₂), such as benthos; reef-building meso-consumers (Rb); predatory invertebrates (P₁), such as gastropods; and predatory fishes and reptiles (P₂).

were consumed by invertebrate and vertebrate predators, the top trophic level (Fig. 2).

We track the recovery through rich evidence from the Late Permian to Middle Triassic of south China (Fig. 1). Latest Permian ecosystems usually had a healthy trophic structure from primary producer to top predator. Marine assemblages were dominated by brachiopods, fusulinid foraminifera, corals and crinoids (Fig. 3a), and had low abundance, high diversity and low evenness⁷⁶. These ecosystems collapsed during the EPME.

Marine ecosystems immediately after the extinction were either microbialite build-ups, formed from microbes associated with tiny gastropods and ostracods (Fig. 3b), or high-abundance, low-diversity communities dominated by disaster taxa (Fig. 3c). Thus, marine ecosystems were degraded to a low level, typified by primary producers or opportunistic consumers (Fig. 3b,c). These two types of ecosystems prevailed through most of the Early Triassic.

In the Spathian, marine ecosystems (Fig. 3d) comprised ever more diverse trace fossil assemblages, as well as biodiversity increases of some clades. This epoch was also marked by the emergence of some high-tiering organisms such as crinoids, as well as rare predatory fishes and the first ichthyosaurs. However, benthic communities were still of low diversity and high abundance¹⁷.

After prolonged loss of dominance in Early Triassic marine communities, Palaeozoic holdover faunas of brachiopods and crinoids became significant again in the Anisian. Corals and metazoan reefs also reappeared in the Anisian, when marine assemblages shared similar community structural indices with pre-extinction communities¹⁷ (Fig. 3e). In the middle-late Anisian, marine ecosystems were characterized by the common occurrence of reptile- and fish-dominated communities (Fig. 3e), such as the Luoping biota in Yunnan, southwest China⁹⁶ (Box 1), in which marine reptiles (ichthyosaurs, pachypleurosaurs, thalattosaurs and prolacertiforms) diversified as top predators. With these top predators, Middle Triassic ecosystems added a new trophic level not seen in the Permian, when sharks, and not reptiles, had been top predators. Thus, ecosystems were constructed step by step

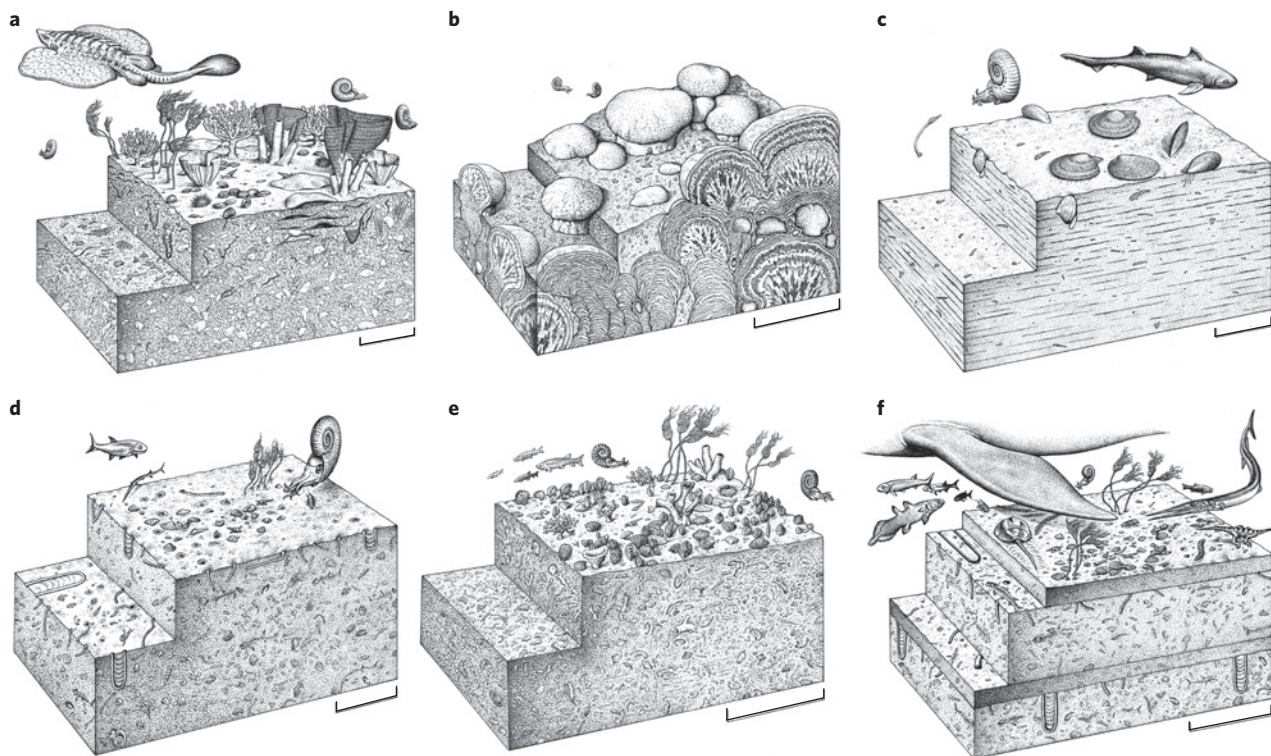


Figure 3 | Reconstructed marine ecosystems before and after the end-Permian mass extinction in south China. **a**, Pre-extinction marine benthic ecosystem in the latest Permian; low abundance, high diversity and dominated by brachiopods, corals, crinoids and fusulinid foraminifers. Scale bar, 10 cm. **b**, Microbe-dominated ecosystem immediately after the EPME in early Griesbachian (early Induan); primary producers dominate. Scale bar, 10 cm. **c**, Opportunist-dominated ecosystem in Griesbachian-Dienerian (Induan); high abundance, low diversity and dominated by disaster taxa (for example, the bivalve *Claraia*). Scale bar, 5 cm. **d**, Tracemaker-dominated ecosystem in Spathian (late Olenekian), indicating recovery of tracemakers. Scale bar, 6 cm. **e**, Mid Anisian (Middle Triassic) benthic ecosystem; low abundance, high diversity and dominated by brachiopods and crinoids. Scale bar, 8 cm. **f**, Mid-late Anisian ecosystem; dominated by marine fishes and reptiles, marking the rebuilding of top-predator trophic structure. Scale bar, 10 cm. Drawings © John Sibbick.

from low to top trophic levels through Early–Middle Triassic times (Fig. 4) following logistic growth of biotic recovery, based on theoretical modelling^{23,95}.

Reasons for delayed recovery

Life began to recover quickly in the Early Triassic, but full recovery took some 8–9 Myr^{8,15,18–20,97} in the sea, and the same or longer on land^{11,16,21}. A key question is whether this delay resulted from complex ecosystem dynamics or from continuing grim physical environmental conditions, or a combination of both. Current theoretical models for recovery (Box 2) indicate that a recovered ecosystem should be at equilibrium, showing high biodiversity, low turnover, resistance to invaders and a complex trophic structure⁹⁵, resistant to environmental perturbation. According to these models, delay to recovery is proportional to the amount of interaction between species²³.

Even though biotic interactions may have played a role and some taxa were little affected by extrinsic perturbations^{12,14,22,61,80}, it is widely accepted^{13,7,15,19,21,22,51,57,67,97} that poor environmental conditions in the post-extinction world slowed full recovery. An exception may be the benthic foraminifera¹⁴, which radiated slowly through the Early Triassic, and at most were affected by the end-Smithian event⁶². In a further example, metazoan reefs have been reported⁸⁰ from the Smithian, within 1.5 Myr of the EPME, and these supposedly plug the coral gap. However, these ‘reefs’ are microbial mats associated with sponges and serpulid worms, and their occurrence is transient; they do not indicate the permanent re-emergence of coral reefs, delayed for some 8–9 Myr after the EPME.

Paradoxically, high productivity might have delayed recovery^{32,97} by favouring bacteria. Observed bursts of primary productivity

immediately after the EPME³² and later in the earliest Triassic⁴³ seem to relate to phases of terrestrial erosion and flushing of sediment into the sea⁴³. Increased fluxes of nutrients to marine systems would have created eutrophic conditions that favoured stromatolitic microbes over corals and other filter feeders.

Testing models of evolution

The distinction between early and late phases of recovery reflects groups and habitats. Fast-evolving taxa such as ammonoids and conodonts recovered pre-extinction diversity fast, but continued to show volatile responses to continuing environmental shocks in the Early Triassic. More slowly evolving taxa, such as foraminifera and brachiopods, began to re-emerge in the first 1–2 Myr of the Early Triassic, but took 5–10 Myr to achieve pre-extinction global diversity, and were less subject to repeated turnovers. On land, plants were slow to recover, and tetrapods rebuilt local diversity very fast, but ecosystems remained unbalanced and unstable until the Middle Triassic.

The ecosystem stepwise recovery pattern, however, must be tested in a broad range of well-dated, high-quality fossil records from different geographic regions. This requires correlation of fossil records in various facies and latitudes worldwide, which is in progress at present through the International Geological Correlation Program 572: Permian–Triassic ecosystems (2008–12).

There are several key concepts and predictions that may be explored in the Triassic aftermath of the EPME, as well as in other recoveries. The length of time for recovery is proportional to the depth of the extinction, but this is not linear. Recovery is slowest if extinction is global in scale, not restricted to climatic belts. Recovery on land may be slower than in the sea, perhaps because

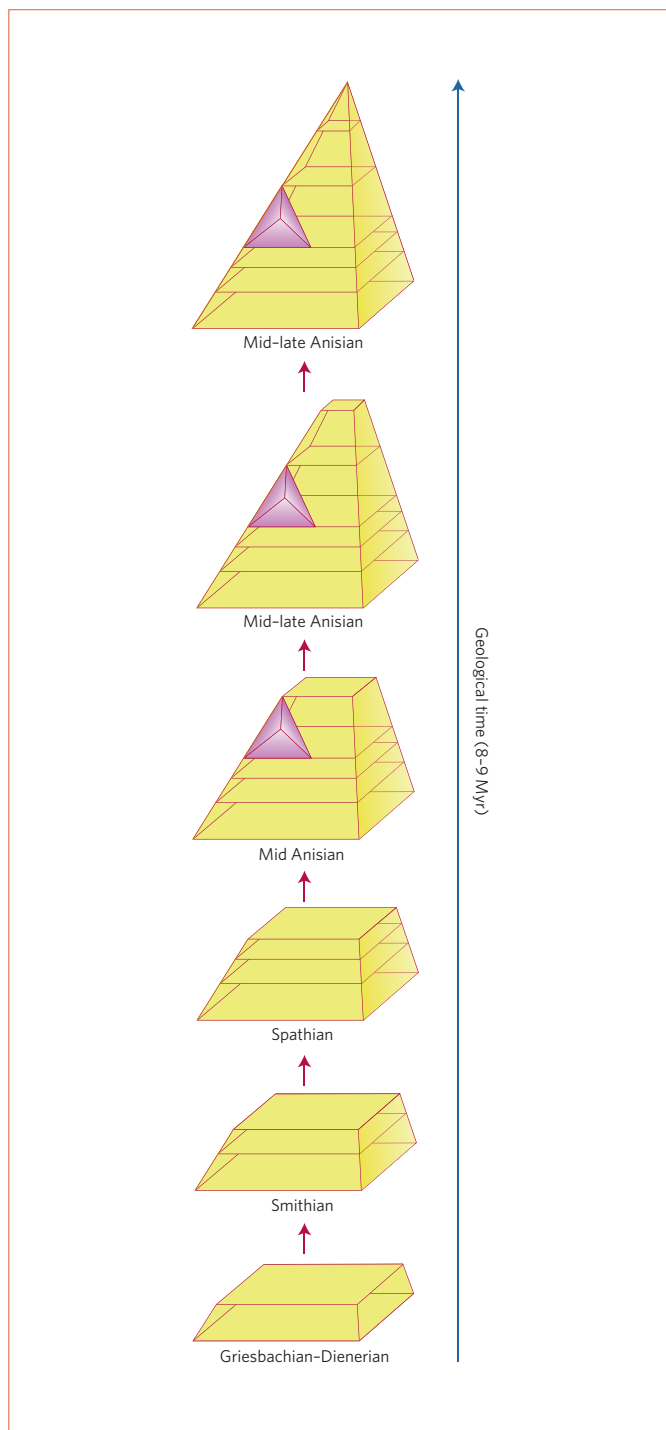


Figure 4 | Stepwise rebuilding pattern of marine ecosystems from low to top trophic levels in the aftermath of the EPME. Immediate post-extinction ecosystems in the Griesbachian-Dienerian show only the lowest trophic level. Further levels are added from Smithian to Anisian, with the topmost level, of reptiles and large fishes that fed on other vertebrates, fully achieved only by the mid-late Anisian, 8–9 Myr after the mass extinction event.

terrestrial environments take longer to stabilize than marine ones. Surviving taxa will not all recover equally well — some may adapt rapidly to new environmental conditions, whereas others may not. Lower portions of food chains will probably recover first, followed by ever higher trophic levels. High-level consumers may recover early if they are fast speciators (for example, ammonoids), but they may have to feed on unusual diets until full recovery occurs.

Disaster taxa may show diversity-first responses, whereas others may show the more usual disparity-first patterns. Full recovery is identified only when ecosystems are complete at all trophic levels, and represent the longer-term stable pattern.

The contrast between the extrinsic and intrinsic models exemplifies a wider debate about macroevolution — whether the key driver is the physical environment or biotic interactions^{6,9,20,98}. The ‘Red Queen’ model, the idea that large-scale evolution is driven mainly by ecosystem-scale biotic interaction, contrasts with the ‘Court Jester’ model, in which macroevolution is driven by unpredictable perturbations in the physical environment⁹⁸. The balance between the Red Queen and Court Jester, as exemplified in the Triassic recovery of life from near annihilation, may be core to a comprehensive theory of evolution.

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Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience.