invertebrates promise deep insights into both the diversity and general concepts of stem cell biology beyond the classical model organisms.

DECLARATION OF INTERESTS
The authors declare no competing interests.

REFERENCES


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Palaeoecology: Rapid succession during mass extinction

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The mass extinction at the end of the Permian period was a time of considerable ecological upheaval. A new study shows that in Southern Africa top predators replaced each other in succession across the end-Permian interval, suggesting that ecological crisis preceded the mass extinction.

There is a conundrum with mass extinctions: it is sometimes easier to reconstruct the physical aspects of an environmental crisis than its biological aspects. We read about impact craters, global darkness, volcanic eruptions, carbon isotopes or ocean acidification; and yet, the reason we care about mass extinctions is because of their dire effects on life. Direct of all was the Permian-Triassic mass extinction (PTME) 252 million years ago, which wiped out about 95% of species1–3. Did everything die at once, or were there a series of crises over months, years or thousands of years? As ecosystems collapsed, which species went first, top predators or primary consumers? Did the crisis proceed equally across the world, from equator to poles? Life came so close to complete annihilation during the PTME that we
require detailed information on ecosystem collapse. Frustratingly, such information on terrestrial ecosystems has been sparse, limited mainly to localities in South Africa, Russia and China, which are hard to date. Despite this, individual faunas may be well documented, represented by hundreds or thousands of specimens.

As an example, the Vyatkian community from the latest Permian of European Russia\(^4\)\(^5\) has yielded dozens of skeletons of a wide variety of tetrapods and fishes, allowing a reasonable reconstruction of one of the last ecosystems before the PTME (Figure 1). The anatomy and adaptations of each of the species have been studied in detail, and food webs can be constructed and tested, but the conundrum is how to link this to the next such fauna and infer what occurred between these snapshots of ancient life. Work on the Permian and Triassic rock sequences in the Karoo Basin of South Africa, however, is beginning to address these problems. In a new study, in this issue of Current Biology, Christian Kammerer, Jennifer Botha and colleagues\(^6\) identify a large sabre-toothed predator from South Africa as *Inostrancevia*, a genus well known already from the terminal Permian of Russia, providing a strong link across the world.

That an animal known from Russia should crop up in South Africa is an unexpected finding because in those times, South Africa lay far south, as it does today, and Russia in the northern hemisphere, but there were substantial arid zones and mountains across the equatorial belt that inhibited biotic interchange between both areas. *Inostrancevia* is particularly interesting, because it was a large, sabre-toothed predator, belonging to the clade Gorgonopsia, at the top of the food chains in both territories. In Russia, *Inostrancevia* has been known for a long time from the terminal Permian faunas (Figure 1), preying upon the one-tonne pareiasaurs, such as *Scutosaurus*.

Figure 1. The latest Permian Vyatkian fauna from Russia. At the back, the gorgonopsian *Inostrancevia* looks speculatively at the one-tonne, plant-eating pareiasaur *Scutosaurus*. A dicynodont stands at the water’s edge, while the flesh-eating therocephalian *Annatherapsidus* sits on a log, with the cynodont *Dvinia* below. The temnospondyl *Chroniosuchus* sits on a sand bank, with the reptiliomorph *Kotlassia* in the water. In the foreground, the little procolophonid *Microphon* is to the left, and the temnospondyl *Raphanodon* to the right (artwork: © John Sibbick, reproduced with permission).

The second key aspect of the new paper by Kammerer and colleagues\(^6\) is that they identify a four-step replacement process among the top predators, from rubidgeine gorgonopsians to *Inostrancevia*, then to therocephalians, and, following the mass extinction, proterosuchids. These four taxa represent a close-up view of the turmoil of those crisis days, and a major switch from synapsids — the large tetrapod group that led to mammals (gorgonopsians, therocephalians) — to archosauromorphs, which led to birds.
and crocodilians (proteosuchid). All the gorgonopians were large predators, mostly armed with sabre teeth, and yet victims in the end of the PTME. Their replacements, the proteosuchids, were long-snouted, faintly crocodilian-like reptiles that may have been partly aquatic, hunting fish and smaller tetrapod prey.

Kammerer and colleagues note that their new discovery, not only that there are two surprising aspects about their new discovery, not only that there was a Russian interloper, but also that faunal turnovers began well before the PTME itself. This suggests that some perturbation of environments may have occurred before the crisis, and that top predators were turning over and the functional guild continued into the Triassic, whereas ecological theory might suggest that top predators would have disappeared entirely during the crisis. Admittedly though, the earliest Triassic predator, the proteosuchid, might have fed on fish or at best Lystrosaurus, rather than being a sabre-toothed predator on 1-tonne prey, so it could be debated whether the top predator guild was untouched or not. This whole relay of top predators Figure 2A spans an interval of 3–4 million years; still not the kind of time scale ecologists would like, but a massive improvement on what was possible.

This relay replacement of top predators can be related to wider research on ecological dynamics. Even though the exact position of the Permian–Triassic boundary in the Karoo beds is debated Figure 2B,C), the large collections of fossils have enabled a tracking of speciation dynamics. Extinction rates remained high over an interval of up to one million years, beginning some time before the Permian-Triassic boundary and continuing high into the earliest Triassic. At this point, origination rates of tetrapods increased, corresponding to a time of rapid faunal turnover immediately after the peak of extinction. Measures of faunal evenness and dominance were relatively constant through the Permian, but dropped through the PTME, reflecting perturbation and loss of ecosystem stability.

There were several ‘disaster taxa’ in the immediate aftermath of the PTME, species that evolved fast and went extinct fast. The one-metre long herbivorous synapsid Lystrosaurus was famously one of these (Figure 2C), present in South Africa in the latest Permian, surviving the crisis and diversifying worldwide in the earliest Triassic. It was successful for a while but disappeared without contributing descendants to the subsequent Triassic faunas.

How long life took to recover after the PTME has been much debated: there is evidence for a long process, as well as for an early recovery of ecosystems, even within one million years after the crisis. Certainly, physical environments were hugely perturbed by repeated heating crises, and conditions did not return to normal until six million years after the extinction crisis. It was hard for plant and animal species to become established and for ecosystems to rebuild.
and stabilise. The debate on the timing of recovery is resolved by accepting that both sides are right; life could recover fast and quite complex ecosystems became established, but these were hit hard by the next heating crisis. The fast-evolving species of foraminifera, ammonoids, conodonts, fishes and reptiles crashed to extinction, then the ecosystem was rebuilt and crashed again. But can these early-recovery ecosystems be regarded as stable or merely transient and part of the disaster aftermath?

In fact, extinct ecosystems can be assessed for stability just as modern examples. Computational network analyses can be applied, especially a method called ‘cascading extinction on graphs’ (CEG)\(^1\). The CEG is based on the observation that if one species is knocked out of a food web, there is a cascade effect on other species up and down the food chain. In normal situations, that local species extinction or removal might be only temporary, and neighbouring species expand their functions, or a new species emerges to plug the gap. By species expand their functions, or a new species emerges to plug the gap. By species expand their functions, or a new

The new work by Kammerer and colleagues\(^2\) on succession of top predators adds detail to our understanding of ecosystem collapse and rebuilding through the greatest of all mass extinctions. Palaeontologists are concerned to document their data carefully, in terms of the taxonomy and phylogeny, and functional and ecological inferences about fossil taxa, as well as their exact temporal and spatial occurrences. Importantly, the new work, and other studies mentioned here, are beginning to allow us a view of the impacts on life of these past environmental crises, but with some levels of confidence. Because of heterogeneity in the fossil record, the comparative methods have been chosen to work with the strengths of the fossil record and avoid the weaknesses.

**DECLARATION OF INTERESTS**

The author declares no competing interests.

**REFERENCES**

Social conflict: Illuminating the great resignation

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Social conflict between con specifics results in the establishment of a hierarchy composed of a winner and loser. A recent study elucidates the molecular mechanism that may underlie the behavioral switch between winner and loser states.

The establishment of hierarchies by social conflict in con specifics is deemed necessary to create a stable environment. The idea that higher levels of aggression correlate with dominance is widely accepted as evidenced by the ubiquitous use of the expression ‘alpha male’ or ‘pecking order’ to describe dominance in humans. As such, studies have identified various factors that regulate aggression levels including hormones (glucocorticoids, testosterone), neurotransmitters (serotonin) and brain regions, including the ventromedial hypothalamus and the brain area that is responsible for this switch in behavior.

As in many fish species, when two adult male zebrafish are placed in a confined tank, they resort to circling and biting attacks until one surrenders and displays a fleeing behavior, at which point the conflict is resolved. The biting fish is referred to as the winner and the fleeing fish as the loser. A previous study by Okamoto’s lab identified a key role for an neurotransmitter glutamate: the lateral habenula-interpeduncular nucleus (LHb-IPN) pathway, in regulating the outcome of the social conflict paradigm. The LHb-IPN pathway consists of two distinct circuits that co-release different neurotransmitters in addition to the neuromodulator glutamate: the lateral subnucleus (dHbL) contains peptidergic ( Substance P) neurons that project to the lateral/intermediate IPN (d/iIPN) and the medial subnucleus (dHbM) contains cholinergic (acetylcholine) neurons projecting to the intermediate/ventral IPN (i/vIPN). Fish with silenced dHbL or dHbM outputs exhibit a decreased or increased probability to win in the social conflict paradigm, respectively. Furthermore, the experience of losing results in the potentiation of the dHbL-i/vIPN circuit as the loser circuit.

Neuronal potentiation refers to a long-term change in synaptic plasticity leading to learning and memory. The mechanisms that drive neuronal potentiation are not fully understood. One emerging idea is that neuromodulators recruit specific glutamatergic AMPA receptors in the postsynaptic neurons leading to the strengthening of the synaptic weight. In the new study by Kinoshita and Okamoto, they first elucidated the neuromodulator and corresponding receptor type that promotes the potentiation of the loser circuit. As this circuit contains neurons that co-release the neuromodulator acetylcholine, it was the primary candidate for circuit potentiation.

Nicotinic acetylcholine receptors (nAChRs), named due to their high affinity to the compound, represent a main receptor class for acetylcholine. They are composed of homomeric or heteromeric combinations of 12 different subunits in...