Impacts of global warming on Permo-Triassic terrestrial ecosystems

Michael J. Benton a,⁎, Andrew J. Newell b

a School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK
b British Geological Survey, Maclean Building, Wallingford OX10 8BB, UK

Abstract

Geologists and palaeontologists have expressed mixed views about the effects of the end-Permian mass extinction on continental habitats and on terrestrial life. Current work suggests that the effects on land were substantial, with massive erosion following the stripping of vegetation, associated with long-term aridification and short-term bursts of warming and acid rain. Wildfires at the Permo-Triassic boundary contributed to the removal of forests and the prolonged absence of forests from the Earth’s surface for up to 10 Myr. These physical crises on land impinged on the oceans, suggesting tight interlocking of terrestrial and marine crises. Levels of extinction on land may well have been as high as in the sea, and this is certainly the case for tetrapods. The mass extinction seems to have been less profound for plants and insects, but it is hard at present to disentangle issues of data quality from reductions in abundance and diversity. Several killing agents have been proposed, and of these tetrapods may have succumbed primarily to acid rain, mass wasting, and aridification. Plants may have been more affected by the sudden effects of heating and wildfires, and the crisis for insects has yet to be explored.

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1. Introduction

Most work on the end-Permian mass extinction (EPME) has focused on marine rather than terrestrial organisms. Killing agents in the oceans have generally been linked to increased CO₂ concentrations and global anoxia, associated with euxinia (anoxic and sulphidic conditions), hypercapnia (CO₂ poisoning), and ocean acidification, although the relative importance of each aspect of this cocktail is debated (Wignall and Twitchett, 1996; Kump et al., 2005; Knoll et al., 2007; Riccardi et al., 2007; Algeo et al., 2011). For life on land, many killing mechanisms have been proposed, but dominant among these have been long-term and short-term changes in atmospheres and oceans, including global warming and reduction in the oxygen content of the atmosphere. Global warming could clearly have had an important role in killing land animals and plants, and the severity of the effects would depend on the amount and speed of the temperature rise, but perhaps more importantly on related mass wasting and aridity. For oxygen reduction, only animals would obviously be affected, and scenarios for selective extinction through hypoxia have been proposed for tetrapods at least (e.g. Huey and Ward, 2005).

Much of the evidence for a long-term rise in mean temperature and fall in mean oxygen content of the atmosphere through the Permian Period, have come from global models, notably the Geocarlsburg model of Berner (2006, 2009). Further, the sharp increase in temperature and the drop in oxygen across the Permo-Triassic boundary (PTB) have been based on evidence from stable isotopes, palaeosols, leaf stomata, and charcoal distribution (Glasspool and Scott, 2010; Retallack, 2012). There are still many questions about the nature of the long-term and short-term warming and oxygen reduction processes, and the evidence for both.

The killing models for land plants and animals are also open to discussion. First is the difficulty of establishing just how severe were the effects of the EPME crisis on key terrestrial organisms such as plants, insects, and vertebrates. Some have stated that there was no extinction in each of these major groups, others have indicated a major crisis, and yet others point to more subtle effects of limits on origination and changes in dominant ecosystems. Second, having determined what may have happened to life, the explanations have sometimes been incomplete, and do not necessarily provide a convincing killing model for all the terrestrial life that disappeared at the time.

Recovery from the EPME has also been extensively discussed (reviewed, Chen and Benton, 2012), with debate focusing on whether the post-PTB world suffered a series of climate crises over some 5 Myr or not, the causes of such crises, and their potential effects on the timing of the recovery of terrestrial life, whether rapid or delayed.

The purpose of this review is to consider the evidence both for the physical aspects of climate and atmospheric change on land, and the potential killing consequences of such long-term and short-term changes.

2. The end-Permian mass extinction and loss of life on land

The model for causation of the EPME has become focused on the consequences of the Siberian Trap volcanic eruptions. The most widely accepted model today (Wignall, 2001; Benton, 2003; Benton and Twitchett, 2003; Erwin, 2006; Knoll et al., 2007; Algeo et al., 2011; S.-z. Shen et al., 2011; Payne and Clapham, 2012; Retallack, 2012) identifies consequences of the eruption of the Siberian flood basalts (Reichow et al., 2009) which over a peak eruptive period of around 600 kyr generated large volumes of sulphate aerosols and carbon dioxide (Fig. 1). Methane was probably a major contributor towards a runaway greenhouse effect through its release from destabilised isotopically light hydrate reservoirs (Berner, 2002) and the thermal metamorphism of Siberian coal measures and organic-rich shales (Retallack et al., 2006; Grasby et al., 2011).

Decreases in the δ¹⁸O ratio of shallow marine biogenic carbonate suggest that seawater temperature during the extinction event may have risen by 6–10 °C (Kearsey et al., 2009). Joachimski et al. (2012) suggest low-latitude surface water warming of 8 °C based on oxygen isotope records in south China, and these values are confirmed by palaeosol studies (Retallack, 2012). Temperatures at the Equator are estimated at 32–35° in the earliest Triassic (Joachimski et al., 2012), and up to 40° at the Smithian–Spathian boundary (Sun et al., 2012).

EPME killing models (Fig. 1) are based on the massive volumes of CO₂ that were suddenly pumped into the atmosphere, and led to global warming and the short-term production of acid rain. The acid rain killed plants on land, and this led to massive erosion as regolith was released, which is indicated by a shift from fine-grained sediments deposited in lakes and meandering rivers to conglomeratic braided fluvial facies, in Russia, South Africa, Europe, and some other locations (Newell et al., 1999; Ward et al., 2000; Arche and López-Gómez, 2005). The massive erosion was associated with wildfires, perhaps triggered during the unusually arid conditions (S.-z. Shen et al., 2011; W. Shen et al., 2011). Sedimentation rates in terrestrial successions increased (Retallack, 1999) and there was an abrupt, increased influx of terrigenous siliciclastics to the oceans (Algeo and Twitchett, 2010; Algeo et al., 2011) associated with soil-derived biomarkers (Wang and Visscher, 2007). Edie Taylor, in review, noted a criticism of this scenario, that the sedimentary conditions themselves in the earliest Triassic, namely high-energy sandstones, are not conducive to preservation of plant fossils, and so their absence could be more apparent than real. Indeed, it would seem unlikely that all
woody plants disappeared, even though there was a substantial turnover in plants worldwide at the PTB (see Section 8).

The timing of the crisis is relatively well established. High-resolution U–Pb dating at Meishan and other PTB sections in south China show that the extinction peak occurred just before 252.28 Ma, had a duration of less than 200 kyr and coincided with a δ13C excursion of −5‰ that is estimated to have lasted for around 20 kyr (S.-z. Shen et al., 2011). It had been suggested that the terrestrial PTB might be slightly younger than the marine PTB (e.g. Yin et al., 2003; Peng and Shi, 2009), but this is not substantiated by recent stratigraphic work, which shows that the PTB in South China at least is coincident on land and in the sea (S.-z. Shen et al., 2011). Further, this has been the assumption for the terrestrial successions in South Africa (Smith and Ward, 2001) and Russia (Taylor et al., 2009), based on biostratigraphy and magnetostratigraphy in the Russian sections. Further work on dating the PTB and the EPME crisis interval outside the South China basins is still required, and this is especially true of the terrestrial redbed successions.

The magnitude of the EPME has been debated, and data from global and regional sources have been brought under consideration. Global databases cannot represent extinction and recovery at the species level because it would be impossible to ensure all groups had a uniform and updated species-level taxonomy, and further, sampling issues would be especially prominent at such low taxonomic level (Raup, 1979). Generic- and family-level data bases for marine animals have had been suggested that species globally suffered extinction levels of 96% (McKinney, 1995), the differences reflecting especially among relatively understudied groups such as insects. Estimates of extinction rates and patterns for plants, insects, and vertebrates are considered in more detail below (Sections 8–10).

3. The first 10 million years of the Triassic

Attention has generally focused on the EPME itself, but conditions continued to be challenging to life for some time into the Triassic (Fig. 2). Poor environmental conditions in the Early Triassic are indicated by unusual bio sedimentary features in marine sediments, including abundant microbialites, wrinkle structures, and seafloor carbonate precipitates, which reflect the absence of metazoans that had been devastated by the EPME, combined with episodes of low oxygen and high chemical precipitation (Algeo et al., 2011). These unusual conditions are matched in the sea by the ‘coral gap’, when there were no reefs built by colonial metazoans in shallow water (Flügel, 2002) and on land by the ‘coal gap’ (Veevers et al., 1994; Retallack et al., 1996, 2011; Rees, 2002; Retallack, 2012), during which forests, and hence coal deposits, are absent. The loss of reefs and trees was more than just the loss of a large number of species, but rather the loss of entire ecosystems, that left large holes in world marine and terrestrial communities until they had rebuilt themselves from different constituent species.

This evidence for continuing poor environmental conditions in the first 5 Myr of the Triassic is confirmed by four negative excursions in carbon isotope ratios, suggesting repeated greenhouse crises (Payne et al., 2004; Retallack et al., 2011). These carbon isotope shifts (Fig. 2) are as large as that at the PTB, and so, if they are worldwide phenomena, they might have been associated with similarly
devastating physical environmental consequences. Apart from the debate over their timing, magnitude, and effects on recovering life of the time, it is still uncertain how such repeated light-carbon excursions could have been generated so frequently. One spike could represent an episode during which the global reserves of methane stored in deep ocean gas hydrates were exhausted. Either the methane reserves could recharge faster than had been assumed, or large volumes of CO2 were repeatedly released from coal beds (Retallack et al., 2011) or from frequent volcanic eruptions (Payne and Kump, 2007).

The pattern and rate of recovery of life in the Triassic is debated (Chen and Benton, 2012), whether it is possible to refer to ‘early’ recovery, within the first 1–3 Myr after the EPME, or ‘delayed’ recovery, some 7–10 Myr into the Triassic. Examples of marine taxa that began to recover quickly include ammonoids (Brayard et al., 2009) and conodonts (Orchard, 2007; Stanley, 2009), which diversified in the first 2 Myr of the Early Triassic, reaching apparently stable local diversities. Likewise, foraminifera in the South China sections show that recovery began 1 Myr into the Triassic, and was not much affected by Early Triassic crises at the end of the Smithian and Spathian (Payne et al., 2004, 2011b; Galfetti et al., 2007; Orchard, 2007). Ecosystems had apparently recovered substantially in the sea in the middle to late Anisian, 8–10 Myr after the crisis (Hallam and Wignall, 1997; Payne et al., 2004, 2011b; Stanley, 2009; Algeo et al., 2011; Hu et al., 2011; Chen and Benton, 2012). The recovery of life on land shares some of these patterns (see below, Sections 8–10).

The stepwise recovery of life in the Triassic (Fig. 2) could have been delayed either by biotic drivers (complex multispecies interactions; Solé et al., 2010) or physical perturbations, or a combination of both. Certainly, if the repeated carbon isotope spikes and sedimentary evidence for unusual and poor environmental conditions through the first 5 Myr of the Triassic are confirmed, it would seem reasonable to assume that these were a key cause of the prolonged recovery, epitomised by the 10 Myr it took for coral reefs and 15 Myr for forests to re-establish themselves.

4. Reconstructing ancient climates

4.1. Sedimentological evidence for ancient climates

In understanding the Late Permian and Early Triassic on land, accurate reconstruction of palaeoclimates is crucial, and sedimentary rocks are the key. The formation of many sedimentary rocks is directly influenced by climate and so they are key indicators of palaeoclimatic variables such as wind direction and strength, rainfall, and atmospheric or oceanic temperature. An understanding of palaeoclimate proxies and their reliability is important for understanding the cause and effect of major events such as the EPME, as input data and control in numerical palaeoclimatic models (Roscher et al., 2011) and, through the recognition of rain-shadow effects, estimating the palaeorelief of mountain belts (Fluteau et al., 2001).

Coals, evaporites, aeolian dunes, glacial deposits and fossil plants are some of the most widely applied palaeoclimatic indicators. Coals indicate former peatlands and lush vegetation growth and are generally taken as proxies for an ever-wet (humid to perhumid) climate, although they also have a strong dependence on basin subsidence and high regional water tables (Falcon-Lang and DiMichele, 2010). Evaporites are generated under specific climatic conditions of high mean annual temperature and low precipitation and today form mostly within narrow (25–40°) latitudinal belts. However, they can occur at lower latitudes where topography creates local rain shadows. Like coals, their distribution is strongly controlled by structural geology with isolated rift basins and continental sags forming preferential sites for evaporative water bodies (Warren, 2010). Aeolian dune
deposits indicate arid climates, but their formation and preservation also require an abundant supply of mobile (dry and unvegetated) sand and basin subsidence. The presence or absence of permanent ice is the primary feature of icehouse and greenhouse global climates. Polar ice sheets moving across lowland basins and marine shelves leave behind a distinctive suite of ice-contact facies with high preservation potential. However, glaciers in long-eroded mountain belts leave no direct evidence in the geological record and their former presence is remarkably difficult to establish from linked basin deposits such as fluvial outwash (Smith et al., 1998). Plant fossils can be used for climate reconstruction either through an understanding of their ecology based on living relatives or through the leaf stomatal index, which varies inversely with the partial pressure of carbon dioxide (Retallack et al., 2011). This is important because atmospheric carbon dioxide levels are closely linked to global climate (Royer et al., 2004).

Clay minerals provide additional crucial data on palaeoclimates. They form by chemical weathering so that the types of clay mineral and their relative abundance in a geological unit are often closely related to climate. Kaolinite, for example, is created by intense chemical weathering in warm, humid climates where silica is leached out, leaving soils enriched in alumina. However, climatic interpretations should always consider additional controls, such as source rock composition, which may include clay-rich soils and formations deposited under a different climatic regime, sorting during transport, and later diagenetic alteration (Yakimenko et al., 2000). The framework mineralogy of sandstones may also record palaeoclimatic signals (Suttner and Dutta, 1986), with similar caveats on their interpretation to clays.

Red beds have long been interpreted as desert deposits, but it is now acknowledged that well drained conditions are probably a more important control on the red colouration than specific palaeoclimatic conditions (Sheldon, 2005). Many red beds appear to have formed under warm, humid conditions, sometimes with evidence for strong seasonality.

Changes in river channel style or palaeohydraulics calculated from cross-bed or point bar thickness may be an indicator of climate change, although it is important to eliminate alternative external controls such as tectonics and autecologyspheric (events responsible for the accumulation of sediments that are part of the sedimentary system itself, such as the size and configuration of a river channel). Moreover, while it is relatively straightforward to estimate channel size, it is much more difficult to determine the duration of peak flows within palaeochannels, a requirement for estimates of long-term discharge and precipitation within the catchment. Fluvial systems in semi-arid settings tend to scale toward the largest flood event, even if these are infrequent. Thus an increase in channel size may not equate to increased climatic humidity (Newell et al., 1999).

The relationship between climatic zones and broad belts of similar soils has long been appreciated, and this inspired the zonal concept of soils. This relationship has been extended to the geological record through the use of palaeosols as proxies for precipitation, temperature, and climate seasonality (Retallack, 1999, 2012; Sheldon and Tabor, 2009; Retallack et al., 2011). Reliable interpretations require an appreciation of how relief, parent material, and vegetation can locally override climate as a primary control on soil type. Carbonates precipitated within soil profiles have played an important role in charting atmospheric δ13C changes through geological time in terrestrial sequences (Royer et al., 2004), and often produce results with remarkable similarity to the marine record (Korte and Kozur, 2010), providing that factors such as soil drainage (Tabor et al., 2007), microbial activity, and root respiration are taken into account.

The time resolution offered by terrestrial deposits is an important consideration in their use as climate proxies. Climate change can occur over short time scales, but some terrestrial geological deposits accrete very slowly and will not capture a record of each climate change event. For example, many palaeosols appear to show the overprint of more than one climate type (Yakimenko et al., 2000). Some climate change events may be represented only by non-deposition or erosion. For example, fluvial systems may respond to climate change by switching between aggradational and degradational regimes as the balance between sediment supply and stream power shifts (Bull, 1990). Aeolian dune systems may become inactive during wet phases so that humid climates are represented only by cryptic stabilisation surfaces (Newell, 2001).

4.2. Palaeogeography and climate in the Permo-Triassic

Around the PTB, all continents were merged into the supercontinent Pangaea, centred more or less on the equator and stretching almost from pole to pole (Fig. 3). Pangaea was surrounded by the Panthalassa Ocean and a deep oceanic gulf, Tethys, which was latitudinally confined to the tropical–subtropical belt, and contained several Asian landmasses (Roscher et al., 2011). The impact on climate of this peculiar plate configuration has been investigated by modelling (Kutzbach and Gallimore, 1989; Kiehl and Shields, 2005). The concentration of exposed land at low and mid-latitudes, and the presence of a warm sea-way would have maximised summer heating in the circum-Tethyan part of the continent and created a strong monsoonal regime (Kutzbach and Gallimore, 1989). Furthermore, extreme continentality, with hot summers and relatively cold winters, is expected (Kutzbach and Gallimore, 1989). Polar regions were ice-free, and their latest Permian deposits contain coals, plants and soils typical of cool temperate latitudes (Retallack et al., 2006). The polar regions were temperate, not only because of elevated CO2 levels (Royer et al., 2004), but also from the unrestricted ocean transport of heat toward the poles and a reduced albedo arising from the lack of permanent land ice (Kiehl and Shields, 2005).

The harsh hot-house climatic conditions that characterised the Late Permian were probably maintained (Preto et al., 2010) or exacerbated during the Early Triassic with, for example, the northward and southward expansion of low-latitude arid belts into the vast, formerly humid basins of European Russia and the Karoo (Chumakov and Zharkov, 2003; Royer et al., 2004).

4.3. Numerical climate models

The peculiar plate configuration of Pangaea around the PTB attracted some early and pioneering work on energy balance models (Crowley et al., 1989) and atmospheric general circulation models (Kutzbach and Gallimore, 1989). These models demonstrated the likelihood of extreme seasonal temperature variation within the large continental interiors of Pangaea and the probability of arid conditions on the western side of Gondwana and Laurussia. The early models were also successful in reproducing the expected high precipitation and strong monsoonal circulation of the Tethys coast. However, there appeared to be discrepancies in polar and high-latitude regions where the models generally predicted much colder conditions than suggested by the presence of coal forests in the Antarctic (Retallack et al., 2007).

More recent models (Kiehl and Shields, 2005), which include coupling of atmospheric and oceanic circulation, have had greater success at reproducing cool temperate polar regions by allowing a flow of warm water into high latitudes, which, because of the configuration of Pangaea, was relatively unrestricted in high latitudes. Models are now being turned toward understanding climate change events across the EPME. The climate models of Roscher et al. (2011) show that an episode of global cooling around the PTB was more effective at producing the observed changes in climate belts than global warming.

Coupled climate–carbon cycle models by Winguth and Winguth (2012) have been used to explore oceanic anoxia. These authors found it hard to generate complete anoxia, but that the oxygen minimum zone expanded considerably, while the deep Panthalassa remained ventilated. Further, these models suggested that upwelling of toxic water was probably not a global phenomenon, and so
probably not a major player in the EPME. The effects of increased weathering and enhanced nutrient input into the oceans was felt only in the Early Triassic, according to the models, and so probably contributed to the delayed recovery of life.

5. Sedimentology of the terrestrial Permo-Triassic boundary interval

5.1. Location and setting of key sections

PTB sections in terrestrial deposits are distributed across five modern continents, with key sections located in Russia, western Europe, China, South Africa, Australia and the Antarctic. Relative to the palaeogeography of the Pangaean supercontinent these terrestrial sections occupy a range of palaeolatitudes and pre-extinction palaeoclimatic zones (Figs. 3 and 4), including the high latitude cool-temperate deposits of Australia, Antarctica, and Siberia, the sub-tropical, semi-humid to semi-arid basins of Western Europe, the Russian Platform and South Africa, and the ever-wet tropical coastal zone of India and south China (Table 1). The terrestrial boundary sections were deposited within a broad range of structural settings including major foreland basins (Russia, South Africa), intracratonic sags (Paraná), narrow extensional rifts (Spain), and pull-apart basins (India). Each structural setting creates a unique combination of relief, sediment source, local climate, and scale. The range of pre-extinction terrestrial depositional systems is equally broad, ranging from small semi-arid alluvial fans to vast channel–floodplain systems with peat-forming swamps (Table 1). The wide range of pre-extinction scenarios in terms of palaeoclimate, structural setting and depositional system is both interesting and useful in that it provides an opportunity to examine how different environments responded to the effects of PTr climate change.

Over the past decade much time and effort has been expended on the EPME, with the result that detailed stratigraphical and sedimentological descriptions are now available for many of the terrestrial sections across the world; however, there is still much to do in all locations. Moreover, with the emergence of Earth Systems Science and ongoing efforts to understand the possible environmental outcomes of modern global warming (IPCC, 2007) the information to make informed interpretations of observed changes in the stratigraphic record of the PTB are now increasingly available. Modelling studies in particular highlight the complex interactions and feedbacks that can occur between the lithosphere, atmosphere, and hydrosphere during global warming events. It should of course be remembered that studies investigating anthropogenic global warming do not consider the vast magmatic eruptions that accompanied events at the PTB. The configuration of the continents was also very different in the Late Permian (see Section 4.2), and global warming started from a much higher initial temperature in a world that was free from permanent ice sheets (Roscher et al., 2011).

5.2. General character of PTB terrestrial sections

The distinctive negative $\delta^{13}$C excursions that occur around the PTB in marine sections have now been recognised in many non-marine PTB successions around the world, including South Africa, Australia, Antarctica, and Germany (Fig. 4; Retallack et al., 2006; Korte and Kozur, 2010). Concerns about how continental bulk carbon isotope values could readily deviate from coexisting atmospheric values (Tabor et al., 2007; Korte and Kozur, 2010) have been largely alleviated by the use of independent dating methods on excursion events (Taylor et al., 2009). The presence of age-verified isotope excursions in many sections greatly increases confidence that continental facies, with their considerable potential for stratigraphic gaps, can capture a record of events at the PTB. Given the apparent completeness of the stratigraphic record in many terrestrial PTB sections and the magnitude of events surrounding the EPME, it is surprising, and somewhat disappointing, that discrete ‘event beds’ are generally not identified (Gastaldo et al., 2009). More usually, the PTB is marked by a shift in...
depositional environment (which may be either gradational or abrupt) that extends upwards to include much of the Early Triassic (see Sections 6.2 and 6.4).

The most obvious environmental changes generally occur in high-latitude, cool temperate settings (Australia, Antarctica, Siberia) and in the ever-wet coastal tropics (e.g., south China, India) where peat-forming swamps disappear abruptly at the end of the Permian. This ‘coal gap’ extends across much of the Early and Middle Triassic (Veevers et al., 1994; Retallack et al., 1996). In tropical, semi-humid basins such as the Karoo (Smith, 1995) or the south Urals (Newell et al., 1999), brown overbank mudstones with plant remains in the Late Permian are replaced by highly oxidised red mudstones in the Early Triassic, often reworked into coarse braided river deposits. In the semi-arid rift basins of the Iberian Peninsula, Late Permian fluvial strata with plant remains are replaced in the Early Triassic by mixed aeolian–fluvial deposits (Arche and López-Gómez, 2005). These shifts in sedimentary style were the first clues towards developing a new model for the EPME on land, and for important drivers of extinction in the sea arising from these perturbations on land (Newell et al., 1999; Algeo et al., 2011). Mass wasting of the landscape following aridification and acid rain supplied bursts of nutrient rich soil and siliciclastic debris to shallow seas, expanding the oxygen minimum zone (OMZ) and boosting surface productivity. Anoxia and euxinia combined to drive marine extinctions, while terrestrial extinctions presumably resulted from aridity, acid rain, loss of soils, and perhaps short-term effects of wildfires and damage to the ozone layer.

Regardless of palaeolatitude or basin setting, most terrestrial PTB sections appear to record a shift towards warmer and drier conditions at the time of the EPME (Smith, 1995; Newell et al., 1999; Erwin et al., 2002; Chumakov and Zharkov, 2003).

However, to view PTr climate change as a unidirectional shift towards hotter and more arid conditions is probably an oversimplification. Much modelling work on modern global warming has concluded that more extreme climates with intense droughts and floods are a likely consequence of global warming (IPCC, 2007). As discussed below, a range of sedimentary evidence supports this view, including changes in fluvial style (Newell et al., 1999), enlargements of drainage networks (Newell et al., 2010), variations in pedogenic carbonate (Pace et al., 2009), mixed aeolian–fluvial sedimentation (Arche and López-Gómez, 2005), and shifts in the maturity of sandstone composition (Ghosh and Sarkar, 2010).

Conceptual and numerical models of PTr climate change are still at an early stage of development. For example, it is still uncertain whether the extension of the environmental crisis in the Early Triassic is a consequence of repeated environmental disturbances or the result of complex feedbacks resulting from the initial disruption to the carbon cycle. More detailed information is required on how terrestrial processes such as wildfires, weathering, and erosion were affected by the EPME, so that the complex feedbacks of these processes on climate can be incorporated into models of increasing sophistication. Our understanding of how a number of earth surface processes may have been altered by PTr global warming is considered below.
### Table 1

<table>
<thead>
<tr>
<th>Basin</th>
<th>Palaeolatitude</th>
<th>Pre PTB Climate</th>
<th>Pre PTB deposystem</th>
<th>Reference</th>
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<tr>
<td>Paraná Basin</td>
<td>Continental sag</td>
<td>20–30°S</td>
<td>Arid, rain shadow</td>
<td>Delorenzo et al. (2008)</td>
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<tr>
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<td>Pull apart</td>
<td>60–80°S</td>
<td>Tropical, semihumid</td>
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<td>60–80°S</td>
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<td>Bowen Basin, Australia</td>
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<td>40–60°S</td>
<td>Tropical, ever wet</td>
<td>Reallack et al. (2016)</td>
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<tr>
<td>South China</td>
<td>Pull apart</td>
<td>40–60°S</td>
<td>Tropical, ever wet</td>
<td>Davies et al. (2010)</td>
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<td>South Urals/Russian Platform</td>
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<td>Bacia</td>
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<td>20–30°N</td>
<td>Tropical, semihumid</td>
<td>Neill et al. (2010)</td>
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### 6. Impact of PTB global warming on geomorphic processes

#### 6.1. Weathering

Chemical weathering is the term used to describe the transformation of minerals formed at particular pressure and temperature conditions within the Earth into more stable secondary minerals and solute species through interaction with dilute waters close to the Earth’s surface. Silicate weathering is an important control on atmospheric CO<sub>2</sub> because mineral dissolution and subsequent precipitation results in a net loss of CO<sub>2</sub> from the Earth’s surface (Berner et al., 1983). This makes estimates of weathering rates and processes in the PTB interval an important element in understanding Early Triassic climatic instability.

The strontium isotope record in marine limestones is one of the most widely applied proxy indicators of continental weathering intensity (Martin and MacDougall, 1995; Huang et al., 2008). Temporal variations in the isotopic ratio of 87 Sr/86 Sr reflect changes in the fluvial (continental) input relative to hydrothermal inputs to the ocean, controlled by the rate of seafloor spreading. Martin and MacDougall (1995) recognised a major excursion in 87 Sr/86 Sr ratios at the PTB which was characteristic of a greatly increased flux of riverine 87 Sr, and may indicate enhanced rates of chemical weathering at the PTB, possibly related to global warming and increased humidity. Influxes of soil-derived biomarkers at the EPME into shallow marine deposits have been similarly interpreted as indicators of enhanced weathering (Algeo et al., 2011). Further, virtually all marine sections at the PTB show a shift toward greater clay content in the immediate aftermath of the EPME, which suggests generally greater chemical weathering intensity in continental areas and enhanced production of pedogenic clay minerals (Algeo and Twitchett, 2010).

Palaeosols are weathering profiles formed during pauses in deposition within terrestrial sedimentary basins. Within a palaeosol, the relative proportion of immobile elements such as aluminium to mobile elements such as magnesium may provide information on contemporaneous weathering rates (Sheldon and Tabor, 2009). This approach has been used at a number of PTB locations. At the Graphite Peak section in Antarctica, earliest Triassic palaeosols show enrichment of barium relative to strontium, which was interpreted as a result of greater leaching relative to underlying coal-measure palaeosols of the latest Permian (Sheldon, 2006). Comparable increases in chemical weathering were reported from PTB palaeosols in the Sydney Basin (Retallack et al., 2011). At the Chahe terrestrial PTB section in SW China, an increase of aluminium relative to magnesium in the so called ‘geochemo-anomal layer’ was interpreted as an escalation of weathering around the EPME (Yu et al., 2007).

The interpretation of weathering rates from palaeosols clearly requires the elimination of local factors that may enhance leaching, such as improved soil drainage and any changes in palaeosol geochemistry that are related to changes in source material rather than weathering processes. Palaeosols only provide a record of weathering patterns in depositional basins and not in eroding source areas, which globally may account for a higher proportion of weathering products.

The framework mineralogy of sandstones provides an alternative source of information on weathering intensity, which may be representative of eroding source areas (Suttner and Dutta, 1986). Mature sands and sandstones that have a high ratio of quartz relative to feldspar and rock fragments are often derived from highly weathered sources, on the assumption that other factors such as multiple cycles of reworking, time-dependent or tectonically-controlled changes in source rock, source area relief, and unstable-grain destruction by transport and burial diagenesis have been eliminated. Michaelsen (2002) observed that in the Bowen Basin of Australia the Early Triassic Sagittarius Sandstone showed a significant enrichment of quartz and a decrease in feldspar relative to the underlying Late Permian Rangal Coal Measures. He interpreted this as an indicator of increased temperature-driven
weathering rates in the Early Triassic. Interestingly, a reverse situation was observed in the Precaspian Basin of Kazakhstan where core from the Saigak-2 borehole showed that potassium feldspar was very rare in Late Permian deposits but occurs in the Early Triassic (Barde et al., 2002). This was interpreted as a shift from relatively wet conditions in the Late Permian to relatively dry in the Early Triassic, reasonable since there is evidence that chemical weathering is driven much more by water availability than temperature rise (Goddéris et al., 2009). In the Raniganj Basin in India, Sutten and Dutta (1986) found no marked change in sandstone composition and weathering regime at the PTB, the lowermost 295 m of the Early Triassic Panchet Formation having similar framework mineralogy to the Late Permian Raniganj Formation. However, above 295 m, the Early Triassic Panchet Formation showed an abrupt increase in sandstone maturity, which was interpreted as a shift from warm semiarid conditions to warm humid conditions.

Strontium isotopes, biomarkers, palaeosols, and sandstone mineralogy, while not in total agreement, point to increased weathering rates at the EPME. While increased temperature around the PTB is commonly implicated as the primary cause of enhanced weathering, and high temperatures can speed up weathering by a factor of 3 or more (Drever and Zobrist, 1992), there is evidence to suggest that the availability of undersaturated soil waters is actually a more important control on silicate mineral dissolution rate (Kump et al., 2000). A direct link between temperature and weathering is difficult to obtain, even in modern catchments, because of the complex linkages among temperature, rainfall, plant growth, elevation, and other factors (Drever and Zobrist, 1992; Kump et al., 2000); but the temperature rise of 8–10 °C at the PTB (see above) might then itself have doubled or trebled normal weathering rates on land.

Land plant cover is a particularly neglected variable in discussions of EPME weathering rates, given the evidence for major changes in vegetation type and the possible importance of wildfire around the PTB (W. Shen et al., 2011). Land plant cover has an important impact on weathering rates by increasing the residence time of water in soil systems and the concentrations of acid species such as CO₂ and organic acids. Removal of land plants causes an increase in soil drainage, primarily because of a decrease in evapotranspiration, an effect particularly marked in tropical environments because of the dense plant cover (Goddéris et al., 2009). Modelling studies indicate a vast increase in the flux of chemical weathering products when land plants are removed (e.g. by wildfire) without the need for elevated temperatures or increased precipitation (Goddéris et al., 2009).

The complex relationships between rates of erosion and weathering is a further factor that should be taken into account. If erosion rates are low, thick soils depleted in cations are developed, and these may yield little in the way of solute load (Goudie and Viles, 2012). Increase in the erosion rate, as would occur if binding vegetation were removed by wildfire, creates thin soils with greater contact between soil waters and fresh mineral surfaces. Chemical weathering then proceeds at a fast rate, limited only by the rate of mineral dissolution, and the solute load is high.

Finally the importance of lichens, fungi and bacteria in accelerating chemical weathering processes (Burford et al., 2003) provides an interesting and unexplored link between evidence for enhanced weathering at the PTB and the fungal spike. Their fossil records are poor, but these taxa all include species with profound abilities to survive drought (see Section 11.5).

6.2. Erosion rates in the PTB interval

Increased rates of erosion are widely reported consequences of PTB global warming. It is also important to understand the links between global warming and erosion rates because erosion makes a major contribution to carbon cycle feedbacks in a changing climate (Goudie and Viles, 2012). The best record of changes in terrestrial erosion is likely to be found in the marine stratigraphic record, particularly in nearshore deltaic and estuarine settings that receive a large input of land-derived sediment. A number of studies have now recognised increases or changes in soil-derived biomarkers in shallow marine sequences at the EPME, and these have been used as evidence for enhanced rates of weathering and erosion (Sephton et al., 2005; Xie et al., 2005, 2007). Increases in the bulk sediment accumulation rate around the PTB have also been used as evidence for higher terrestrial sediment fluxes to marine depositional systems (Algeo and Twitchett, 2010).

There may have been a major change in the nature of mass wasting during the Early Triassic (Algeo and Twitchett, 2010; Algeo et al., 2011), with a switch from massive soil erosion at the time of the EPME to bedrock erosion. The immediate biological indicators of massive terrestrial erosion at the EPME are soil-derived biomarkers (Sephton et al., 2005; Xie et al., 2005, 2007; Wang and Visscher, 2007) and nutrient-stimulated algal blooms (Kozur, 1998; Afonin et al., 2001). These phenomena occur just below the EPME horizon, so linking these events to the marine extinctions (Sephton et al., 2005). However, soil biomarkers are not recorded later in the marine Lower Triassic successions, and this was interpreted by Algeo and Twitchett (2010) as evidence for a brief soil erosion crisis during the EPME episode, with later increases in the influx of siliciclastics to the oceans resulting from bedrock erosion. Further work on the basin sedimentology of Early Triassic river-dominated deltas may further test this idea. Evidence of Early Triassic deltaic progradation against a background of eustatic sea-level rise (Hallam and Wignall, 1999) could result from high rates of terrestrial sediment delivery. For example, seismic sections in Early Triassic deltaic strata of the Northern Barents Sea show a remarkable series of large clinoform beds formed by huge prograding delta systems (Hey and Lundschen, 2011).

There is also a range of evidence from terrestrial settings for increased rates of erosion. PTB sections in Antarctica developed in muddy palaeosols show thin (15 cm) beds of reworked soil fragments (peds) suggesting unusually voluminous and short-lived episodes of soil erosion around the PTB (Retallack, 2005). Comparable features have been observed in Australia and South Africa (Sheldon, 2006). Many fluvial sequences which cross the PTB, for example in the Karoo, India, and the south Urals, show a marked increase in grain size across the boundary, often towards coarse pebbly material (Newell et al., 1999; Ward et al., 2000; Chakraborty and Sarkar, 2005). In the absence of evidence for tectonic uplift or changes in source, this grain-size shift could indicate the rapid erosion of coarse debris that was formerly locked in hillslope reservoirs by vegetation cover (Newell et al., 1999). Removal of vegetation lowers erosion thresholds and increases runoff rates, which both promote the transport of coarse-grained bedload (Svivitskii and Kettner, 2011).

As discussed below (see Sections 6.3 and 8), the extent of Early Triassic land-cover change is difficult to evaluate. Beyond the disappearance of the cool-adapted Glossopteris flora of Gondwana, it is difficult to determine extinction patterns among plants, and they do not appear to show clear-cut losses of major clades at the PTB (McElwain and Punyasena, 2007; Xiong and Wang, 2011). Wildfire may have played a more important role in land-cover related erosion than plant loss by taxon extinction. More detailed work is required on how changes in plant communities may have influenced sediment yield through changes in root density/depth and leaf canopy. Vegetation change may in fact have played a minor role relative to changes in precipitation pattern. As postulated by Newell et al. (1999) an increase in the grade of sediment across the PTB could be related to intense rainfall and high-magnitude discharge events, which, even if these were of low frequency, would have moved a much higher volume of coarse sediment.

Considering Pangaea as a whole, it is probable that large areas of the land surface were predisposed to the risk of increased erosion.
following a shift toward a hotter climate at the PTB. Increases in erosion and sediment yield are particularly marked where landscapes shift from sub-humid to semi-arid regimes, reflecting an optimum balance between a reduction in vegetation cover and sufficient precipitation to generate runoff and move sediment (Fig. 6). In the Late Permian, Pangaea was characterised by vast continental interiors and unusually wide sub-humid climate belts (Chumakov and Zharkov, 2003).

**Fig. 5.** Interpretative reconstructions of changes in terrestrial–marine systems during the PTB crisis. Early stage Siberian Traps volcanism with minimal environmental effects during the Late Permian (A). Main stage eruptions with attendant environmental effects during the latest Permian (B). Late stage eruptions with lessening environmental effects during the first part (Induan Stage) of the Early Triassic (C). Post-eruption recovery of terrestrial and marine ecosystems by the Middle Triassic (D). Modified from Algeo et al. (2011).
6.3. Wildfire

Wildfires were common throughout the Permian, and to the end of the Changhsingian at the PTB, and there was then a long gap through the Early Triassic and much of the Middle Triassic that corresponded to the 'coal gap' (Veevers et al., 1994; Retallack et al., 1996). Abundant charcoal, black carbon and carbon spherules have been described at the EPME from the Meishan section in south China (W. Shen et al., 2011) and are interpreted as evidence for extensive wildfire associated with the mass extinction. Evidence for wildfires is important because they are well known catalysts for erosion and increased sediment yield in small basins (Meyer et al., 1992), although the potential contribution of climate-driven increases in wildfire activity to the sediment production in large river basins has not been well quantified. Moreover trace gas and particle emissions associated with wildfires have a major impact on atmospheric composition and chemistry and on climate itself (S.P. Harrison et al., 2010). The record of wildfires through the Permian and Triassic is also now used as key evidence in determining likely changes in atmospheric oxygen levels (see Section 7.3).

Climate change is known to have a strong influence on all aspects of the wildfire regime from the seasonal timing of lightning ignitions, through temperature and humidity control of fuel drying to wind-driven fire spread (S.P. Harrison et al., 2010). Other major climate change events in the geological record such as the PETM are characterised by major increases in biomass burning (Collinson et al., 2007).

6.4. Changes in fluvial style

Changes in the style of river channels are marked in many terrestrial PTB sections (Figs. 4 and 7). Currently, most of these changes in fluvial style or grain size at the PTB have been interpreted as results of changing climate or vegetation cover. Such interpretations are actually remarkably rare in pre-Quaternary fluvial sequences, where tectonics or sea level is often favoured as the dominant control on fluvial stratigraphy. Many of the documented changes show remarkable similarities.

In the Karoo Basin, South Africa sediments below the PTB comprise drab greenish grey mudrocks with a few thick laterally accreted sandstone bodies. Above a boundary transition zone of around 20 m these strata change to reddish brown mudrocks with calcic palaeosols and numerous ribbon sandstone bodies and more continuous sheet sandstones. Smith (1995) interpreted the facies transition as a change in fluvial style from meandering to low sinuosity channels with general drying of the floodplain habitats (Fig. 7). He postulated a structural control, but the alteration in river morphology was later interpreted as the result of a rapid and major die off of rooted plant life producing a marked increase in sediment yield (Ward et al., 2000).

In the south Urals, the PTB is marked by a dramatic shift from metre-thick sandstone-dominated channel fills in the Late Permian to major, multi-storey gravelly, braided channels in the Early Triassic (Fig. 8; Newell et al., 1999). An apparent increase in channel size is also accompanied by a large increase in the length of the drainage system. In central parts of the Russian Platform, the PTB is marked by the abrupt progradation of sandy fluvial systems into former muddy lacustrine floodbasins which lie up to 900 km from source areas in the Urals (Newell et al., 2010).

In the northern Bowen Basin of Australia, the PTB is expressed as an abrupt and sharp change in fluvial regime at the contact between the Rangel Coal Measures and the Sagittarius Sandstone (Michaelensen, 2002). The Late Permian fluvial style is characterised by large-scale, sandstone-dominated, low-sinuosity trunk river channel deposits flanked by extensive crevasse-splay systems. The fluvial architecture of the Sagittarius Sandstone is characterised by sheet-like elements suggesting deposition in broad shallow channels in a deforested braid-plain setting with flashy runoff regime (Michaelensen, 2002).

Sandy braided river systems also make an appearance at the PTB in the rift basins of the Iberian Ranges (Arche and López-Gómez, 2005), the pull-apart Sapatura Basin in India (Chakraborty and Sarkar, 2005), and the giant intracratonic Kuzevsk Basin of Siberia (Davies et al., 2010). Only in the terrestrial PTB sections of western Guizhou and eastern Yunnan has such a major shift in grain size across the boundary not been observed (Yu et al., 2007), although a concentration of brecciated volcanic materials occurs at the PTB in all South China sections, associated with a colour shift from the olive, grey or multicoloured sandstones and mudstones of the coal-bearing uppermost Permian to maroon and purple interbedded sandstones and mudstones of the Early Triassic (S.-z. Shen et al., 2011). These earliest Triassic sediments are frequently associated with scours, poorly sorted pyroclastic breccia and calcareous siltstone nodules, all of which suggest a dramatic collapse of soil systems near the PTB in South China.

The wide palaeogeographic distribution of basins, synchronicity, wide range of tectonic settings, and close temporal association with mass extinctions, vegetation turnover, and carbon isotope excursions is strong evidence that there is a link between the changes in fluvial style and climate. The similarity of the changes in fluvial style is remarkable given the many different configurations of drainage basins in terms of bedrock, elevation, vegetation cover, palaeolatitude, and other factors. Some differences, such as those observed in western Guizhou and eastern Yunnan (Yu et al., 2007; S.-z. Shen et al., 2011) would actually be expected.

The most common explanation for the change in fluvial style is as a result of vegetation dieback, which would have increased sediment delivery, created flow variability, and decreased bank stability, all factors that are known to promote a multichannel, braided river pattern. Newell et al. (1999) also stress the probable importance of a switch toward low frequency, but high-magnitude flood events, which can

![Fig. 6. Conceptual plot of sediment yield relative to precipitation and vegetation cover. The largest increases in sediment yield are likely to occur when climate changes from temperate to semi-climate, which represent the optimum combination of reduced vegetation cover with sufficient precipitation and runoff to facilitate sediment erosion. Many of the large Late Permian basins (e.g. Karoo, Russian Platform) appear to have changed from relatively humid to semiarid conditions across the PTB, which would account for large global increases in sediment yield. Modified from Goode et al. (2012).](image-url)
drive increases in the grain size of the sediment load and enlargement of drainage systems. In dryland environments, channels and drainage systems typically scale towards the largest flood event rather than the average (Newell et al., 1999).

6.5. Changes to lacustrine systems

Long-lived, deep lacustrine basins are probably the terrestrial settings with greatest potential to capture a high-resolution record of climate change events. It is unfortunate then that thick sequences of laminated, perennial lake deposits crossing the PTB have not been found. Despite the presence of suitable tectonic settings for deep perennial lakes (e.g. linear rift basins), most Late Permian and Early Triassic lacustrine deposits are shallow, ephemeral, and evaporative, probably reflecting the high global temperatures and rates of evaporation relative to water input.

Late Permian perennial lake successions have been recognised in the rapidly subsiding Satpura Gondwana pull-apart basin of central India (Chakraborty and Sarkar, 2005), but these do not persist beyond the PTB because they were overrun by Early Triassic sandy braided river deposits. Comparable disruption to lacustrine environments has been recorded elsewhere; for example, Late Permian playa lacustrine deposits of the Moscow Basin are also replaced by sandy braided river deposits around the PTB (Newell et al., 2010). The abrupt switch in environment could reflect increased sediment supply coupled with an enlargement of fluvial distributary networks to cope with low frequency but high magnitude flood events.

The North German Basin is one of the few locations where lacustrine environments persist across the PTB. Hiete et al (2006) documented the

Fig. 7. Changing river styles across the PTB. Summary sedimentological log of the PTB sequence compiled from the study sections in the Bethulie District, Karoo Basin, South Africa, with interpreted palaeolandscape reconstructions. Vertical scale in metres. Modified from Smith and Botha (2005).
boundary succession in great detail using core from the Wulften-1 borehole just south of the Harz Mountains. In the Wulften-1 borehole, the PTB, as determined by palynology, is located close to the so-called Graubankbereich towards the base of the Calvörde Formation in the Lower Buntsandstein (Hiete et al., 2006). This is stratigraphically above the major basin-wide change from sabkha to playa lacustrine facies that occurs in the upper part of the Zechstein. The Graubankbereich is a distinctive 8–9 m thick grey mudstone, which probably represents a phase of perennial lacustrine deposition that was greatly extended relative to that seen elsewhere in the Calvörde Formation. The grey colouration and abundance of pyrite indicates synsedimentary or syndiagenetic anoxic conditions (Hiete et al., 2006). This is comparable to the Moscow Basin around Vyazniki (Newell et al., 2010), where a distinctive bed of dark grey, laminated lacustrine mudstone (c. 1 m thick) occurs close to the PTB. The bed contains a rich fossil assemblage and is sandwiched between more typical Late Permian strongly oxidised/evaporitic playa lacustrine mudstones and a thick succession of latest Permian to Early Triassic fluvial sands (Newell et al., 2010, 2012).

These examples from Germany and Russia provide evidence that in two northern hemisphere basins the PTB is marked by a temporary positive shift in the water balance of latest Permian lakes. This could result from either increased precipitation/water inflow to the lakes or because of decreased evaporation. The timing of these anomalous perennial lacustrine deposits relative to the Siberian flood basalt is uncertain, but it has been suggested that sulphur emissions from the eruptions would have created short-term climate cooling (and reduced evaporation), which, given the high latitude of the eruptions, may have had most impact on the northern hemisphere (Black et al., 2012). However, laminated shales coincident with the PTB are also known from the southern hemisphere Karoo Basin, which were interpreted by Smith (1995) and Ward et al. (2000) as evidence for an episode of extensive playa lakes in an otherwise fluvially-dominated succession. On the other hand, Gastaldo et al. (2009) have questioned the uniqueness and environmental significance of the PTB event bed in the Karoo Basin, but their interpretation has been rejected by Ward et al. (2012).

Early Triassic fluvial lacustrine deposits of the North German Basin are also notable because they contain common oolitic and microbial carbonates, particularly in the Dienerian to Smithian Bemburg Formation, which overlies the Calvörde Formation discussed above (Paul and Peryt, 2000). The Bemburg Formation is generally accepted as a non-marine deposit, but the microbial carbonates mirror the appearance of this anachronistic facies in Early Triassic shallow marine settings (Wignall, 2008). In these marine deposits, it has been suggested that such microbialites may record carbonate supersaturation from the widespread development of bicarbonate-rich, oxic waters (Woods et al., 1999). Accepting similar controls on non-marine microbial carbonates, an increased flux of bicarbonate to lakes could have resulted from enhanced weathering of silicate minerals or an increase in soil water fluxes following land cover change (Raymond et al., 2008).

There were major changes in the importance of evaporites between the Late Permian and the Early Triassic (Warren, 2006). Late Permian evaporites include major deposits in the Zechstein Basin in northwest Europe and in west Texas, which together define a broad band of equatorial aridity extending from about 50°N to 30°S palaeolatitude (Chumakov and Zharkov, 2003). However, Warren (2006) notes a broadening and intensification of evaporite deposits in the Early Triassic, with huge deposits associated with continental redbeds in southeast and western USA, western Canada, northwest Africa, western and southeast Europe, central South America, and east Greenland. Interestingly, Warren (2006) does not consider that the increase in salt volume reflects increased aridity in the Early Triassic, but is a result of increased tectonic activity and the creation of many isolated, low-latitude rift basins and intracratonic sags that formed suitable sites for salt accumulation.

6.6. Desertification and aeolian activity

In the Late Permian, Pangaea was characterised by high average temperatures and vast continental interiors with unusually wide semi-arid to subhumid climate belts (Chumakov and Zharkov, 2003). Large areas of the land surface were thus at risk from desertification should global mean temperature rise higher.

The geological record of large Late Permian deserts is relatively limited, with extensive areas of aeolian dune sandstones best known from the Paraná Basin of eastern South America (Preto et al., 2010). This basin was located in the arid western sector of Pangaea and was probably strongly influenced by a rain shadow effect. At the PTB there appears to have been a geographic expansion in the area of aeolian activity, with ergs developing in a number of new locations including the rift basins of Iberia (Soria et al., 2011; López-Gómez et al., 2012), the central Urals (Tverdokhlebov et al., 2003), and central Europe (Uličný, 2004) in what were formerly relatively humid environments in the Late Permian.

7. Evidence for atmospheric change

7.1. Carbon dioxide

Variation in the carbon-isotope stratigraphy across at the EPME has been widely explored because it is recorded in both marine and
The pronounced negative carbon isotopic excursion at the PTB has long been known and is key evidence in many extinction scenarios. A causal link between major changes in the global carbon cycle in the oceans and the atmosphere and the synchronous eruption of the Siberian flood basalts seems likely (Korte and Kozur, 2010), but the magnitude of the negative excursion requires additional inputs of isotopically light carbon from sources such as methane hydrate release or thermal metamorphism of coal and organic-rich shale (Wignall, 2007; Grasby et al., 2011).

Using the stomatal leaf index, Retallack (2012) compiled estimates of atmospheric CO₂ through the Permian and Triassic: he noted peaks in the mid-Capitanian, at the PTB, and six further peaks through the Early and Middle Triassic. The highest calculated level of CO₂ was at the EPME horizon, a remarkable 7832 ±1676 ppm, which is 28 times the postglacial–preindustrial CO₂ levels of 280 ppm, and 20 times the current, industrial value of 394 ppm. The broad magnitudes of these estimates have been confirmed from carbon isotopic measurements on palaeosol carbonates (Retallack, 2012).

The elevated levels of carbon dioxide and methane in the atmosphere drove a runaway greenhouse effect (Wignall, 2008). The EPME carbon isotope shift was not an isolated event: a second major negative excursion occurred shortly after the first (Xie et al., 2007), and a series of high-magnitude fluctuations continued throughout much of the Early Triassic (Payne et al., 2004; Retallack et al., 2011). It is still uncertain whether the carbon isotope fluctuations that followed the EPME are the result of external drivers such as further volcanism or the result of internal feedbacks from a disrupted global carbon cycle.

7.2. Oxygen

Low atmospheric oxygen levels around the PTB are based primarily on the isotope mass balance model of Berner (2005), which predicted a continuous drop in O₂ concentration from ~30% to ~13% over a 20 Myr period from the Middle Permian to Middle Triassic. In the stratigraphic record, undisputed supporting evidence for low atmospheric oxygen levels has yet to be found; conclusions based on palaeosol mineralogy (Huggett and Hesselbo, 2003; Sheldon and Retallack, 2003) and the palaeobiology of Lystrosaurus (Retallack et al., 2003) have both proved to be controversial. Glasspool and Scott (2010) reconstructed an oxygen curve from charcoal and wildfire data, with a highest value of 29% in the Early Permian, matching the Berner (2005) model value, and a low of 18.5% in the Middle Triassic, but with uncertainty over Early Triassic values because of the coal gap. Charcoal is rare to absent after the EPME, re-appearing sporadically in the Spathian–Anisian, and achieving pre-crisis values in the Anisian (Mangerud and Remul, 1991; Uhl and Montenari, 2011; Abu Hamad et al., 2012).

The charcoal gap in the Early Triassic has been used as evidence for excessively low atmospheric oxygen levels in the Triassic as a whole, and the Early and Middle Triassic in particular. This is based on the assumption that relatively high oxygen levels are required for spontaneous fires to occur (A.C. Scott, 2000), and the suggestion of excessively low (<12%) levels of oxygen in the entire Triassic (Berner, 2005). However, high oxygen levels are not essential for spontaneous wildfires (Belcher and McElwain, 2008), and the absence of records of wildfires in the Induan or early Olenekian (see Section 6.3) is probably more directly explained by the absence of forests and the ‘coal gap’ (Uhl and Montenari, 2011; Abu Hamad et al., 2012). All the indicators of wildfires, namely fossil charcoal, inertiinites, and pyrogenic polycyclic aromatic hydrocarbons, increased in frequency through the Triassic, from very low levels in the Early Triassic, to Permian levels. This could indicate a collecting bias, or that it took much of the Triassic for sufficient woody material to become available following the re-emergence of forests at the end of the ‘coal gap’ (Abu Hamad et al., 2012). These differences between modelled (low of 13–16%) and charcoal-based (low of 18.5%) atmospheric oxygen compositions in the Early and Middle Triassic are profound in their implications for life, and whether hypoxia had a key role as a killing agent, and they require further exploration.

7.3. Sulphur, chlorine, and fluorine

Degassing of the Siberian Traps would have released a range of other volatiles into the atmosphere, such as sulphur, chlorine, and fluorine. Measurements of these volatiles in melt inclusions from the Siberian Traps show concentrations that are anomalously high relative to other continental flood basalts (Black et al., 2012). Contact metamorphism of evaporites and coals during the volcanic eruptions would have been a second source of volatile gas release (Svensen et al., 2009).

Kump et al. (2005) suggested that anoxia may have become sufficiently severe in the oceans at the EPME that hydrogen sulphide leaked into the atmosphere, with the combined effect of reaching toxic levels, destroying the ozone shield, and raising methane levels. The injection of sulphur, chlorine, and fluorine into the upper atmosphere could have had a range of other effects including direct toxicity, acid rain, and temperature change. Volcanic SO₂ reacts with water in the atmosphere to form sulphate aerosols, which increase the optical depth of the atmosphere and may result in a short (possibly a maximum of 10 years) episode of global cooling (Black et al., 2012).

7.4. Destruction of the ozone layer (?)

Destruction of the ozone layer has become increasingly popular as a postulated mechanism for EPME extinction on land, especially as an agent that killed plants (e.g. Kump et al., 2005; Collinson et al., 2006; Beerling, 2007; Beerling et al., 2007), and yet evidence is currently limited (Wignall, 2007).

The evidence for destruction of the ozone layer is the appearance of mutated spores and pollen at the EPME (Vischer et al., 2004), interpreted as a result of increased UV-B radiation which would have disrupted normal meiotic (cell division) processes. Beerling et al. (2007), however, note a measure of uncertainty about the environmental agent that caused such mutations. They cite work that shows such mutations of pollen in modern soybean caused by elevated UV-B radiation, but they note further work that shows mutated pollen and spores in modern gymnosperms can be induced by high levels of sulphur dioxide in polluted areas. If this is the case, then the primary evidence for destruction of the ozone layer at the time of the EPME is shaly.

In modelling how the ozone layer might have been destroyed, Kump et al. (2005) emphasised the role of massive sulphide release in the oceans. They argued that hydrogen sulphide reacts with oxygen in the stratosphere, oxygen levels then fall, and, because oxygen is an essential reactant in the production of ozone, the loss of stratospheric oxygen leads to the destruction of the ozone layer. Lamarque et al. (2006), on the other hand, argued that the ozone layer could have been damaged by levels of methane some 5000 times preindustrial values. In a third system, Visscher et al. (2004) argued that the ozone layer was destroyed by the production of large quantities of organohalogens that arose from the heating of organic-rich rocks and hydrothermal fluids during the eruption of the Siberian Traps. Halogen emissions can destroy atmospheric ozone. Beerling et al. (2007) estimated the effects of releases of both HCl from the volcanic eruption itself, and organohalogens such as chloromethane arising from the passage of molten lava through the rich coal deposits around the Siberian Traps. They found that, at high levels of injection of those gases into the stratosphere, the ozone layer would be penetrated at high latitudes, but not around the Equator because of its ‘self-healing’ properties.
Only the last of these three models has survived scrutiny (Wignall, 2007; Harfoot et al., 2008). The postulated volumes of hydrogen sulphide and methane required to destroy the ozone shield are far beyond anything possible, so leaving the third, halogen, model as the only viable explanation. But was the ozone shield breached at the time of the EPME? The only evidence is from the mutated spores and pollen, which could have arisen from other drivers. However, estimated volumes of halogens ejected from the Siberian Trap eruptions are unusually high (Black et al., 2012), as was the explosive nature of the eruptions, which might have propelled these halogens into the stratosphere, so the suggestion of enhanced UV radiation as a potential killer at the EPME has not been rejected.

8. Plant evolution through the Permo-Triassic crises

The timing of extinction patterns among plants at the PTB has been debated, and patterns differ in the northern and southern hemispheres (McLoughlin et al., 1997; McElwain and Punyasena, 2007; Xiong and Wang, 2011). Certainly, the cool-adapted Glossopteris flora of Gondwana disappeared (Retallack, 1995), but the wider debate may have been partly obscured by the use of a distinct terminology and methodology (DiMichele et al., 2008). In particular, palaeobotanists generally described the evolution of floras through the Permian and Triassic in terms of the long term replacement of so-called Paleophytic floras, dominated by broad-leaved pteridosperms, cordaites, and pecopterid ferns, by Mesophytic floras largely of conifers (Knoll, 1984; Knoll and Niklas, 1987; Traverse, 1988). This transition began well before the PTB, and lasted essentially from the end of the Early Permian to the Middle Triassic, and it did not seem that the PTB was a focus for enhanced extinction, or that plant life in any sense had to disappear (Retallack, 1995), but the wider debate may have been at odds with the evidence that acid rain and massive erosion may have affected the land surface of large parts of the world at the time of the PTB (Newell et al., 1999; Ward et al., 2000; Algeo and Twitchett, 2010), and that the first 15 Myr of the Triassic are notable for the ‘coal gap’ (Retallack et al., 1996, 2011), a time during which trees were rare to absent, and coals, plentiful in the latest Permian, did not recur until well into the Middle Triassic.

Indeed, DiMichele et al. (2008) suggest that use of the ‘Paleophytic’ and ‘Mesophytic’ concepts has been misleading, and they recommend abandonment of the terms. They report that there is no evidence for global ‘Paleophytic’ and ‘Mesophytic’ floras. Instead, they argue that Permo-Triassic plants are best thought of as occurring in a complex of biome-scale species pools that reflected climate at many spatio-temporal scales. Therefore, they recommend that vegetation changes in the late Paleozoic and early Mesozoic will be best understood in terms of responses of such species pools to global climate changes, at local and regional scales. This is a more complex approach, requiring intense study of palaeobotany and sedimentology of individual basins, but it highlights the problem hitherto of confounding floristic successions that reflect changes in palaeogeography, climate, and topographic location with temporal or evolutionary changes. Some terrestrial settings, such as low-lying basins, preserve floras better than others, such as mountains, and stratigraphic successions that document changing floras may simply be sampling changing environmental conditions rather than evolution. As temperature and rainfall change through time, so too may the assemblages of plants, characterised as distinct biomes or species pools by DiMichele et al. (2008, p. 161), ‘assemblages of plants tied to different kinds and ranges of environmental conditions, and strongly reflective of the naturally sharp environmental discontinuities that characterise terrestrial Earth.’

Detailed studies in Antarctica, and generalised across Gondwana (McLoughlin et al., 1997) show that the PTB was marked by the extinction of glossopterid and cordaitalean gymnosperms, and by the disappearance or extreme decline of a range of gymnospermous and pteridospermatous trees. Earliest Triassic macrofloras and pteridophytic palynomorph groups in Antarctica were dominated by peltasperms and lycophytes; coniferids, and ferns become increasingly common elements of assemblages through the Lower Triassic part of the formation and dominate floras of the Upper Triassic strata.

In a numerical study of land–plant diversity through the Permo-Triassic of South China, Xiong and Wang (2011) found that total diversity declined steadily from the early Late Permian (Wuchiapingian) to the early Middle Triassic (Anisian), a span from 260 to 237 Myr ago, based on macroplant fossils (Fig. 9). Microfossils (pollen and spores), on the other hand, showed only a small fluctuation across the PTB and this was in fact a diversity rise. The long-assumed relative stability of plants through the PTB crisis is confirmed in this study, although rates of generic extinction were acutely high (91%) in the Induan (earliest Triassic), at a time when origination rates were also at their lowest level (18%) for the sampled time interval. Importantly, however, Xiong and Wang (2011) identify that land plants in South China underwent sustained high extinction rates (>60%) throughout the entire Late Permian to early Middle Triassic interval, a span of 23 Myr, compared to estimated durations of heightened extinction among marine faunas of some 3–11 Myr (Payne et al., 2004, 2011b; Chen and Benton, 2012). Considered in a broader context, these times of enhanced extinction were part of continued fluctuations in generic turnover through the entire Permian and Triassic time span, perhaps related to the major changes in temperature and aridity through this interval. Xiong and Wang (2011, p. 157) conclude that ‘More stable diversity and turnover rate as well as longer extinction duration suggest that plant families near the PTB of South China may have been involved in a gradual floral reorganisation and evolutionary replacement rather than a mass extinction like those in the coeval marine faunas.’

The moderate to high rates of extinction of plant species and genera were not reflected in the loss of major clades other than Glossopteridales, and this appears to be a difference from animal extinctions (Wing, 2004; McElwain and Punyasena, 2007). If this is the case, longer-term changes among plants, and the apparent absence of a sharp, single event, paints a picture of broader-scale floral biome evolution and turnover, with species and genera being replaced over long time spans. Plants differ from most animals in being autotrophic primary producers, limited by temperature, rainfall, and topography, but perhaps less liable to sudden extinction by environmental shock. It may indeed be true that plants have more survival strategies than many animals, and can survive certain kinds of environmental crisis by local extinction or by the loss of only certain species and genera within higher taxa (Traverse, 1988; Valentine et al., 1991).

In a global-scale study of fossil plant families, Cascales-Miñana and Cleal (2012) found that the EPME did stand out as a major extinction event. The extinction affected some non-seed-plant families, especially those of palaetropical wetlands (e.g. Bowmanitaceae, Lepidocarpaceae, Arsterothecaceae), but the most severe effects were on seed-plant families, particularly conifers. This may seem a surprising result because conifers are known to be well adapted to survive in stressed conditions, especially shortage of water, and increased aridity was one of the features of the Late Permian and the EPME (see Section 6). However, many of the conifer families that died out were monogeneric. Survivors among the non-seed plants were mostly small in habit, such as the Lycopodiaceae, Selaginellaceae, Isoetaeaceae, Equisitaceae, and Gleicheniaceae, all of which survive to the present day. Fewer seed plants survived, and these include Cycadaceae, which are also alive today, and perhaps their slow growth and reproductive strategy helped them at the time of the EPME, and through subsequent crises.

The replacement of stable gymnosperm-dominated Permian floras by rapidly growing, early successional communities dominated by lycopods and ferns in the earliest Triassic of the northern hemisphere (Grauvogel-Stamm and Ash, 2005; Galletti et al., 2007; Hermann et al.
1996), resulted in reduced sequestration of organic matter in terrestrial facies during the Early Triassic 'coal gap' (Veevers et al., 1994; Retallack et al., 1996, 2011). The changeover in floras is marked also by the well known 'spore spike' at or close to the PTB, which is marked by high abundance of the enigmatic palynomorph Reduviaporites. This is identified by some authors as a fungal spore (Eshet et al., 1995; Visscher, et al., 1996) and by others as an algal spore (Foster et al., 2002). Whether a 'fungal event' or an 'algae event', the spore spike reflects the massive dieback of plants of the latest Permian gymnosperm-dominated ecosystems prior to the radiation of lycopods.

Earliest Triassic floras throughout Eurasia and the southern continents were dominated by dense stands of the succulent lycopod Pleuromeia, which reached a height of 2 m at most. This genus would appear to be a classic 'disaster taxon', which emerged suddenly into the post-extinction world, and did so worldwide — cosmopolitanism following the loss of endemic floras and faunas is a key feature of the initial post-crisis recovery. Pleuromeia was unusually abundant, with its spores (Densoisporites) dominating palynological assemblages to levels over 90% (Looy et al., 1999), so floras were spectacularly uneven, or unbalanced, and all other plant taxa were rare. Pleuromeia dominated terrestrial floras to the end of the Early Triassic, a span of 4–5 Myr, and was then replaced wholesale in the earliest Middle Triassic by floras dominated by the conifer Voltzia (Looy et al., 1999; Hermann et al., 2011). Floras dominated by Dicroidium in Gondwana did not attain Permian levels of diversity and provinciality until the Middle Triassic (Retallack, 1995; McLoughlin et al., 1997). A further spore spike occurred in the middle Smithian (Hermann et al., 1997), 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 (Gaffetti et al., 2007; Hermann et al., 2011).

The 'coal gap', lasting through the Early and early Middle Triassic corresponds then to a time of overall impoverishment of terrestrial floras. Plants had declined substantially in diversity through the EPME, and they diversified again in the Smithian, but did not return to pre-extinction levels until the Late Triassic (Retallack et al., 2011). During the recovery phase, some long-lasting clades that survive today appeared, including many fern families, but especially a substantial diversification of seed plants, including conifers, seed ferns, ginkgophytes, and cycads.

9. Insect evolution through the Permo-Triassic crises

The fossil record of insects through the Permian and Triassic has not provided a clear picture of their evolution in response to possible environmental stresses, nor of their response to the EPME, and many noted palaeontologists are not convinced that there was a crisis: Ponomarenko (2006), for example, argues rather that there was nothing other than a long-term decline. Labandeira and Sepkoski (1993) and Béthoux et al. (2005) accept that there was a mass extinction event, but they note the problems of a temporally and geographically incomplete fossil record, the lack of extensive study of many entomo-faunas, and the absence of an agreed phylogenetic system.

An enduring problem for understanding the response of insects to the EPME is that there is a largely unsampled temporal gap, spanning the Late Permian and Early Triassic, and insect faunas can only be compared at either end. This gap was estimated at 15 Myr by Béthoux et al. (2005), but Shcherbakov (2008b) pruned that to less than 5 Myr. The latter author noted that there are several very good insect faunas from the latest Permian of the Sydney and Karoo basins, as well as five or six fossil insect sites in the Early Triassic of Russia and Mongolia, including the Bajiy Kamen' site in the Kuznetsk Basin, which has yielded representatives of more than 15 insect families.

In their global-scale study, Labandeira and Sepkoski (1993) documented that 8 out of 27 orders of insects (30%) disappeared in the Late Permian to Early Triassic interval, and a further three that survived into the Triassic at reduced diversity became extinct during that period. The extinction rate through the Late Permian at familial level was about 50%, on a par with vertebrates and with marine organisms as a whole (Sepkoski, 1984; Benton, 1995). On the other hand, it should be noted that insects evolve slowly when compared to tetrapods: for example, looking back from the present day to the KT boundary 65 Myr ago, nearly 100% of contemporary insect families still had representatives, whereas this is true for only 20% of tetrapod families (Labandeira and Sepkoski, 1993) — such comparisons of course depend on the assumption of equivalence of families of insects and tetrapods. In an overview focusing on Russian sites, Shcherbakov (2008a) notes a loss of 40% of insect families through the latest Permian to Induan interval, but he notes also that there were high extinction peaks in the Middle Permian (Kazanian) and...
Middle Triassic (Ladinian). It is hard to establish the true nature of extinction and origination of insects through this episode, and whether these apparent extinction peaks are real or not.

Detailed studies of two large clades, the Archaeoorthoptera and Odonatoptera, reveal common trends (Béthoux et al., 2005). Several lineages became extinct at or close to the PTB, and other clades either expanded or appeared in the Middle Triassic. There were important radiations of Diptera (flies) and Coleoptera (beetles) in the Triassic, which confirms the role of the EPME in stimulating a major turnover in insect faunas, and in setting some of the groundwork of modern insect ecosystems.

The Late Permian to Middle Triassic turnover in entomofaunas was marked also by major changes in ecology, as the late Mississippian to Permian fauna of herbivorous arthropods (mites and apterygote and basal pterygote insects feeding on pteridophytes and basal gymnosperms) gave way to the modern phase (Triassic to Recent) comprising mites, orthopteroids, hemipteroids, and basal holometabolans feeding on pteridophytes and gymnosperms (Labandeira, 2006). The latter assemblage persisted of course when additional novel arthropod groups began feeding on angiosperms from the Cretaceous to Recent. It is frustrating, in light of the crucial importance of the Late Permian to Early Triassic interval in witnessing one of the four key diversifications in insect evolution, that this episode cannot be investigated in more detail; palaeontologists can only hope for new discoveries of rich insect-bearing fossil deposits in the latest Permian and Early Triassic terrestrial deposits, perhaps in Russia, China, and South Africa.

10. Vertebrate evolution through the Permo-Triassic crises

10.1. Changing opinions

Just as with plants and insects, many palaeontologists did not see compelling evidence for a mass extinction among vertebrates at the end of the Permian. For example in the standard textbook in the field, Carroll (1988) wrote: The most dramatic extinction in the marine environment occurred at the end of the Permian, wiping out 95% of the non-vertebrate species and more than half the families. Surprisingly, there was not a correspondingly large extinction of either terrestrial or aquatic tetrapods. Carroll (1988) was echoing conclusions reached earlier by Pitrat (1973) and Thomson (1977), and accepted by Erwin (1990) and others at the time as evidence that the end-Permian mass extinction was largely a marine affair that had little effect on terrestrial life.

Viewpoints have changed substantially since 1990, not only for plants and insects, but importantly for vertebrates, whose record through the Permian and Triassic has now been studied in considerable detail. There are still of course all the serious problems of an incomplete and highly sporadic fossil record, which must be recognised and mitigated if possible (Benton et al., 2004, in press; Smith, 2007; Irmis and Whiteside, 2012). However, since 1990, three practical improvements have occurred that enable such studies:

(1) Stratigraphic reference sections have been established for the Permian and Triassic, and the new standard Permian time scale (Gradstein et al., 2004; Ogg et al., 2008) has hugely changed and stabilised understanding. This is especially true for the Permian, where the switch from the Russian continental time divisions (Ufimian, Kazanian, Tatarian) to North American and Chinese marine systems (Guadalupian, Lopingian) for the Middle and Upper Permian, respectively, has made an enormous difference to assumptions about correlation and relative timings of key tetrapod-bearing successions (e.g. Rubidge et al., 2010; Benton, 2012).

(2) Palaeontologists have been able to move freely between the West, Russia, and China to compare sections in the field and specimens in museums, and this has clarified many aspects of basic geology and alpha taxonomy.

(3) The cladistic revolution has meant that every group of Permo-Triassic tetrapods has been revised thoroughly and in a cladistic context, and this provides reasonable phylogenetic trees, which in turn allow meaningful phylogenetic correction of diversity estimates, and the possibility of palaeobiogeographic and functional-morphometric studies.

10.2. Scaling the vertebrate extinctions

So far, most attention has focused on tetrapods rather than fishes. Pitrat (1973) found that marine fishes declined in diversity sharply at the end of the Permian, just like other marine animals, but that freshwater and euryhaline fishes experienced their main extinctions earlier in the Permian. Thomson (1977, p. 401) also concluded that ‘there is little evidence among fishes for a Permo-Triassic mass extinction’. Benton (1989b), on the other hand, identified an extinction rate of 44% for all families of fishes through the Late Permian, but with most of the losses occurring in the Kazanian, the stage that then preceded the terminal-Permian Tatarian. Such a ‘Kazanian’ event would now equate to Roadian in the Middle Permian, but the dating of Permian fish-bearing units against the global standard time scale has changed substantially since 1989, and the ‘Kazanian event’ is likely to disappear. Meaningful regional and global-scale studies of fish diversity and disparity across the PTB are still required.

In narrative terms, the EPME had a notable impact on tetrapod evolution. Complex latest Permian ecosystems dominated by herbivorous pareiasaurs and dicynodonts and carnivorous gorgonopsians, were replaced by new clades of archosaurs (crurotarsans, dinosauromorphs) and synapsids (cynodonts) (Benton, 1983, 1995; Ward et al., 2000; Benton and Twitchett, 2003; Benton et al., 2004; Brusatte et al., 2008, 2010, 2011; Sookias et al., 2012). The difficulties arise when this broad narrative is explored in closer, numerical detail.

In an early compilation of family-level data, Benton (1985, 1987) found an extinction rate of 49% through the Tatarian to Scythian interval. Benton (1989a) listed 21 families of amniotes that had died out during the EPME, equivalent to the Kazanian, and stabilised understanding. This is especially true for the Permian, Kazanian, Tatarian) to North American and global-scale studies of fish diversity and disparity across the PTB are still required.

Based on the new ‘Early Tetrapods Database’ (ETD; Benton et al., in press), an updated record of all basalmost tetrapod genera from Devonian to Jurassic (Table 2), four out of 11 families of amphibians (36%) and 17 out of 32 families of amniotes (53%) became extinct at the end of the Changhsingian. This represents an overall loss at family level of 49% of tetrapods through the EPME, equivalent to the figure noted by Benton (1985), but based on substantially revised data. It is important to note that 11 of the 22 familial lineages (50%) that survived through the EPME were extinct by the end of the Induan, evidence of a ‘dead cladewalking’ effect (Jablonski, 2001). There was a high rate of origination of new tetrapod families, especially amniotes, in the Early Triassic, but a high proportion of these died out before the end of the Olenekian (Table 2), and this was especially true for amphibians, which lost 10 out of 15 families (67%), compared to 7 out of 26 families of amniotes (27%), which together equate to a high value for all tetrapods (41%).

The analysis can be continued at generic level, but the gains in taxonomic detail are offset by losses in statistical confidence because of the likely deterioration in completeness of sampling at lower taxonomic levels (Sepkoski, 1984; Robeck et al., 2000). Taken at face value, the ETD data show a rise in tetrapod generic diversity from 94 to 112 from the Changhsingian to Induan stages, crossing the PTB (Fig. 10, arrow 5; Benton et al., in press). This seemingly counter-intuitive result
of a rise in diversity across the largest mass extinction horizon of all time arises because the totals encompass major losses of genera in the Changhsingian, and an even higher rate of origin in the subsequent Changhsingian stage (89% generic loss for tetrapods). The recovery after the EPME is shown by the origin of 102 out of 112 taxa that were present in the Induan (a remarkably high origination rate of 91%).

10.3. Triassic recovery of vertebrates

Problems of selective preservation of fossils and changes in sedimentary facies especially confound the data on tetrapod recovery in the Early and Middle Triassic, and it is hard to know how to correct for such a bias (Benton et al., 2004; Irms and Whiteside, 2012). For example, the raw data for the earliest Triassic (Induan stage) show a remarkable diversity peak for amphibians', with the origin of 50 of 58 genera (86% rise), but followed by a rate of loss that was just as rapid as their rise, as was noted from the familial data (Fig. 10; Table 2). This diversity peak among temnospondyls and other non-amniotes has long been noted (Millers, 1990; Benton et al., 2004; Ruta and Benton, 2008), but has yet to be fully understood. Was this a real burst of radiation following the EPME, in which the primarily aquatic temnospondyls were disaster taxa that were somehow favoured by prevailing climatic conditions, or is this an artefact of a major change in sedimentation across the PTB towards higher-energy systems (Newell et al., 1999; Ward et al., 2000) that show excessive preservation of the detrital remains of water-living animals combined with under-representation of other ecological categories, including terrestrial amniotes?

Numerical palaeoecological studies confirm the unusual nature of these earliest Triassic terrestrial tetrapod communities. Roopnarine et al. (2007) applied a trophic network model to Perminian and Triassic communities of the Karoo Basin, South Africa, and showed that while Perminian communities did not appear to be especially susceptible to extinction, Early Triassic communities were markedly less stable. The instability was reflected in the incomplete trophic webs in the earliest Triassic, in which large herbivores and predators were absent, and in which some taxa such as Lystrosaurus and many of the temnospondyls were seemingly over-represented. It will be important to carry this study forward to explore Olenekian and Middle Triassic tetrapod communities to determine when stability was re-established. The restructuring of Induan tetrapod communities is seen in the loss of browsers and predators and the increase in piscivores (Sahney and Benton, 2008). The loss of browsers could be linked to changes in vegetation, marked by the Early Triassic ‘coal gap’, linked to the major worldwide change in sedimentation regime to high-energy erosion at the PTB (Newell et al., 1999; Ward et al., 2000). Perhaps only when the full diversity of plant types, and more substantial biomass, was achieved in the Middle Triassic tetrapod communities to achieve their pre-extinction diversity and abundance.

Following a late Olenekian peak of 90 tetrapod genera, diversity fell to 76 in the lower Anisian, rose again to 96 in the late Anisian, and then plummeted to 39 in the lower Ladinian (Fig. 10, arrow 6). In earlier works, Benton (1985, 1995) and Maxwell (1992) noted a terminal Early Triassic peak of extinction among tetrapods, but re-dating of redbed units in South Africa (e.g. Cynognathus Assemblage Zone) and elsewhere, has extended many formerly late Olenekian ranges into the Middle Triassic. It is yet to be resolved, however, whether any of these declines are real, and that the turbulence in atmospheric and oceanic conditions that continued through the Olenekian and early Anisian (Payne et al., 2004), or are artefacts of sampling.

10.4. Regional studies on vertebrate extinction and recovery

These kinds of global-scale diversity studies may never yield a detailed narrative of what really happened through the EPME and
The Triassic recovery, because of all the problems of sampling and a patchy fossil record already noted. More fruitful may be regional or basin-scale studies and phylogenetically based analyses of individual basins or regions that explore important questions concerning the rate of the recovery and morphological changes within diversifying clades.

The rate of recovery of tetrapod ecosystems has been debated, whether they became re-established rather slowly, over perhaps 10–15 Myr (Benton et al., 2004) or fast, within 1–2 Myr (Smith and Botha, 2005). Close study of events through the Middle Permian to Middle Triassic in the southern Urals in Russia confirmed the complexity of events (Benton et al., 2004). Late Permian tetrapod communities in Russia consisted of seven families of amphibians and 15 families of reptiles. In the rivers and lakes of each of the six Middle and Late Permian time slices, four to seven genera of small, medium and large aquatic tetrapods (‘amphibians’) fed on the abundant thick-bodied bony fishes and the less common freshwater sharks and lungfishes. On the wooded banks were five to 11 genera of terrestrial tetrapods (‘reptiles’), ranging in size from tiny insect-eaters to rhino-sized plant-eating pareiasaurs and the wolf-to-bearded, sabre-toothed gorgonopsians that preyed on them. Twenty of the 22 Middle and Late Permian families died out at, or before, the PTB, and only two, the small, mainly herbivorous procolophonids and the larger herbivorous dicynodonts, survived through the EPME. Of the 22 families, 11 were present at the end of the Vyatkian, the terminal Permian Russian time unit, and the extinction of nine of these corresponds to a regional family-level extinction rate of 82%.

Earliest Triassic terrestrial ecosystems in Russia were unusual and seemingly ecologically unbalanced. As well as the two surviving reptile families, the procolophonids and dicynodonts, the faunas were dominated by temnospondyls, as noted above. In the basal Triassic (Kopanskaya Svita; Induan), there were only medium-sized and large fish-eaters in the rivers and lakes (Tupilakosaurusidae, Capitosauridae, Bentosuchidae) and medium-sized insect/tetrapod-eaters (Prolacertidae, Proterosuchidae). Dicynodonts must have been present, and indeed Lystrosaurus is known from localities in Siberia. Only one genus, Tupilakosaurus, could be identified as a ‘disaster taxon’, present for a short time immediately after the crisis. Other families present in the Kopanskaya Svita persisted through the Early Triassic. New taxa were added through the 15 Myr of the Early and Mid Triassic; further medium-sized and large fish-eaters in the fresh waters, and further medium-sized herbivores and large carnivores on land. The Middle Triassic faunas of Donguz and Bukobay times still lacked small fish-eaters and small insect-eaters, as well as large herbivores and specialist top carnivores. Middle and Late Triassic faunas from elsewhere in the world show the addition of further taxa that fill these ecological gaps — various amphibians as small fish-eaters, small diapsids as insect-eaters, ever-larger dicynodonts as large herbivores, and rauisuchians as large carnivores.

Statistical study of the Russian data (Benton et al., 2004) showed that the EPME did not simply remove diversity, but it also affected the dynamics of turnover within tetrapod communities. Throughout the Middle and Late Permian, origination and extinction rates followed a dramatically reversing series of peaks and troughs. The Early and Mid Triassic are characterized by the steady addition of taxa, and slow loss of existing families, but origination and extinction rates remained uniformly low until the Ladinian; the sudden rise at this point might be an edge effect. Overall, the data from the South Ural indicate a slow recovery of tetrapod ecosystems, which seemed to remain unbalanced even at the end of the sampling period, some 15 Myr after the mass extinction.

Initial analyses of the South African PTB revealed rather different results. Smith and Botha (2005) reported a 69% generic extinction rate, based on their localised collection of 225 tetrapod specimens. This figure might fall to 54% if ghost ranges, implying collection failure, are taken into account (Botha and Smith, 2006). All the extinctions took place within a single sedimentary facies, and Smith and Ward (2001) estimate the extinction lasted for 50,000 years. Only four genera, Lystrosaurus, Tetracyodon, Moschorhinus and Ictidosuchus, survived the EPME in South Africa, and yet, only 37 m above the PTB in the Karoo succession, Smith and Botha (2005) reported a total of ten genera, compared to 13 just below the PTB. They interpreted this to mean that recovery was relatively fast, really within a few hundred thousand years of the mass extinction event. The key question is whether those ten genera represent a stable ecosystem, with balanced relative abundances of species (no one species dominating in an unnatural fashion) and a full diversity of ecological niches filled, from small to large, and across all dietary options.

A comparative study by Irmis and Whiteside (2012) has suggested a delayed recovery in both Russia and South Africa (Fig. 11). By assessing community evenness, they showed that ecosystem structure was massively perturbed by the EPME in both Russia and South Africa at the same time that overall diversity plunged, confirming the ecological studies of Roopnarine et al. (2007) and Sahney and Benton (2008). Importantly in these studies, Benton et al. (2004) and Irmis and Whiteside (2012) applied a variety of methods to attempt to control for bias, including rarefaction to normalise for differing sample sizes. In addition, Benton et al. (2004, 2011) found no correlations of the diversity data with metrics of sampling such as numbers of localities, numbers of specimens, and mean specimen quality, but this does not rule out the
10.5. Vertebrate clades through the EPME crisis

Further recent studies have concentrated on particular clades, each of which followed its own trajectory. In a study of temnospondyl evolution through the Permian and Triassic, Ruta and Benton (2008) found that the Induan diversity peak was robust to a variety of numerical treatments to control for error (different cladograms, phylogenetically corrected diversity signal, rarefied bin-by-bin samples). Species, genus, and family trajectories consistently revealed a rapid increase in temnospondyl diversity from the latest Permian to earliest Triassic. Ruta et al. (2011) explored patterns of evolution of parareptiles through the PTB, and found, after careful data exploration, little evidence for a sudden decline among pareiasaurs and procolophonoids, but rather a rapid alternation of originations and extinctions in a number of subclades, both before and after the PTB.

Among larger clades that crossed the PTB, anomodonts have been explored in most detail. Anomodonts, including dicynodonts, were important medium-sized to large herbivores in many continental ecosystems, with 128 species in 77 faunal assemblages, spanning the Middle Permian to Late Triassic. A diversity analysis (Fröbisch, 2008, 2009) confirms the importance of an end-Guadalupian mass extinction, as well as the EPME. Both events were driven not simply by enhanced extinction rate, but also by reduced origination rate. By applying a variety of techniques to assess the adequacy of sampling, such as comparing raw anomodont diversity to numbers of formations, localities, and specimens, Fröbisch (2008, 2009) explored the data both with and without sampling correction, and concluded that the EPME remained the key crisis in their history.

Phylogenetic studies show that at least four anomodont lineages survived the EPME, including the genus Lystrosaurus, formerly thought to be uniquely Triassic in age, but they survived at low abundance, and Lystrosaurus radiated explosively in the basal Triassic, as a classic generalist disaster taxon (Irmiis and Whiteside, 2012), superabundant and representing over 90% of finds in large samples from typical communities (Benton, 1983), geologically short-lived, as well as cosmopolitan, being known from South Africa, Antarctica, India, China, and Russia. In the Middle and Late Permian, most anomodont genera had been endemic, known from only a single palearctic geographic region. After 1 Myr or so, Lystrosaurus disappeared, to be replaced by a wider range of anomodont genera later in the Early Triassic, and the clade expanded dramatically in the Middle Triassic, before its long decline through the Late Triassic. In terms of morphological disparity, the anomodonts also show evidence for a classic ‘bottleneck’ effect, whereby a hugely diverse and important group in the Middle and Upper Permian was reduced to a limited species pool by the impact of the EPME crisis, and rebounded slowly to recover almost its pre-extinction species diversity, but the former morphological disparity was not reacquired. In other words, the EPME wiped out so much of anomodont morphological disparity and adaptive/ecological range of forms that the recovering clade could not reacquire this wealth of form, and the re-emerging clade, important as it became again, represented a modest remnant of the pre-extinction morphological range.

The two clades that came to dominate the world after the EPME were the cynodonts, including the progenitors of mammals, and the archosaurs, including the dinosaurs. Cynodonts were a modest group in the Late Permian, but they expanded step-by-step through the Triassic, splitting into two major clades in the Middle Triassic, and further diversifying through the Late Triassic and Early Jurassic, but latterly mainly as small flesh-eaters. A study of diversity, phylogeny, and discrete-character disparity shows a rapid expansion of disparity, as cynodonts filled ecospace emptied by the EPME, and then a rise in diversity considerably later. Disparity rose steadily through the Early Triassic, attained a peak in the Middle Triassic and then stabilised; on the other hand, cynodont diversity rose continuously and substantially through the entire 50 Myr duration of the Triassic, and the Late Triassic origin of mammals, as traditionally defined, was not marked by a major leap in either diversity or disparity.

Archosaurs show similar patterns of radiation through the Triassic, seemingly slow and steady, rather than explosive (Benton, 1983; Brusatte et al., 2008, 2010, 2011; Sookias et al., 2012). Early Triassic archosaurs were predators, perhaps never abundant or diverse, and the clade diversified substantially through the Middle and Late Triassic, giving rise to dinosaurs at least by the early part of the Late Triassic, but perhaps earlier. In both cases, the rise of basal archosaurs, and then of dinosaurs in the Carnian, was a slow affair, showing the classic disparity-first pattern in both cases (Brusatte et al., 2008), with no sign of a massive drive or competitive process whereby they exerted their superior characters over other taxa. Indeed, passive processes of body size change appear to have predominated throughout the Triassic, with archosaurs in general, and dinosaurs in particular, becoming abundant and diverse through opportunistic replacement of synapsids following extinction, both the EPME, and a later series of losses of major herbivore groups in the Late Triassic (Benton, 1983; Sookias et al., 2012). An unusual feature of the rise of the mainly carnivorous basal archosaurs was that these predatory forms were generally larger than their herbivore prey, perhaps because of their innate biological characters in comparison to the contemporary synapsids (Sookias et al., 2012).

11. Killing agents

11.1. Introductory remarks: advocacy or science?

In the post-EPME world, numerous presumed consequences of the environmental crisis might have killed life, either singly or in concert, namely hypoxia, hypercapnia, ocean acidification, warming, aridity, acid rain and mass wasting, wildfires, and ozone layer destruction. These potential killing agents will be considered in turn.

Before proceeding, it is worth considering how arguments about killing agents are constructed: there is a serious methodological problem in determining a proper scientific approach to testing whether a postulated agent had an effect or not. Geologists can certainly seek to determine the evidence for each of the proposed physical environmental changes following the eruption of the Siberian Traps, their extent, and their geographic and temporal distribution. However, it has so far proved difficult to devise a test of a killing agent, and this has been especially acute in the decades-long discussions of the KT event: the impact happened, and the details can be studied, but what actually killed the dinosaurs and ammonites? The normal line of argument is to establish the coincidence of the killing agent and the extinction, to muster evidence from modern experimental biological studies of the effects of the proposed killing agent, and to declare the likelihood of a connection. Sometimes, auxiliary evidence can be sought in terms of predictions of anatomical modifications (such as larger nostrils and nasal turbinates to counter hypoxia; see below). Normally there is no such detectable anatomical consequence. This means that, regrettably, many published arguments are examples of advocacy rather than science. They list pieces of evidence that cumulatively work in favour of a particular view, but provide no means of refutation.

The most impressive approach has been meta-analytical, as employed by Knoll et al. (1996, 2007), Clapham and Payne (2011), and Kiessling and Simpson (2011), in arguing the case for hypercapnia, hypoxia, and ocean acidification as the EPME killers in the oceans. Here, summary data of all marine taxa were divided into
physiological categories (physiologically well or poorly buffered, need for carbonate ions to build skeleton or not), and the predicted levels of extinction and survival of each category were sufficiently statistically distinct to confirm the prediction that physiology was the key. Such an approach is still required for land on this time; but it may fail because of the much wider disparity in physiology between insects, tetrapods, and plants, and the lack of uniformity in terrestrial habitats.

11.2. Hypoxia as the EPME killer

Hypoxia has been advanced as a key killing agency during the EPME by several authors (Retallack et al., 2003, 2006; Huey and Ward, 2005; Berner et al., 2007; Knoll et al., 2007). Oxygen levels in the atmosphere have varied enormously through the last 600 Myr, ranging from 13% to 31%, compared to a modern value of 21% (Berner et al., 2007). Modelled oxygen levels (see Section 7.3) fell from an estimated 28% in the Late Permian to 20% at the PTB, and 16% in the Early Triassic (Berner et al., 2007), but the latter value has been recalculated as 18.5% based on charcoal evidence (Glasspool and Scott, 2010).

Atmospheric oxygen levels have frequently been cited as crucially important in animal evolution, for example in terms of the overall increase in animal body size through time (e.g. Graham et al., 1995; Falkowski et al., 2005; Payne et al., 2009, 2011a), and especially in the unusually large body size of insects and vertebrates during the Carboniferous and Permian, which has been explained by high oxygen levels (Graham et al., 1995; Dudley, 1998; J.F. Harrison et al., 2010). Further, two of the ‘big five’ mass extinctions, those at the end of the Triassic and the EPME, were associated with falling oxygen levels, and this has been interpreted as a contributing factor in the extinctions, especially of vertebrates (e.g. Kump et al., 2005; Ward, 2006).

In marine settings, there is extensive evidence for anoxic conditions nearly worldwide at the PTB (Wignall and Twitchett, 1996), and this has been seen as a major contributor to extinction and size reduction during the EPME and Early Triassic (Wignall and Twitchett, 1996; Knoll et al., 2007). Size reduction has been noted among marine gastropods as a whole, within some bivalve, gastropod, and brachiopod lineages, and in general burrow dimensions, and this too has been explained by oxygen stress (Payne et al., 2005; Twitchett, 2007). Marine extinction and selection against large size during the EPME may relate in part to the reduced oxygen levels, but could also be driven by reduced predation pressure and decreased primary productivity (Payne et al., 2011a), although the last point is disputed by Algeo et al. (2012) who find no evidence, except in South China, for worldwide reduction in marine productivity.

It is well known that major physiological effects occur in both the hypoxic (>21%) and hypoxic (<21%) ranges, and the focus here is on the latter (Harrison, 2011). For example, physiological experiments on flies, cockroaches, and beetles have shown that hypoxia generally decreases body size (Frazier et al., 2001; J.F. Harrison et al., 2010; Payne et al., 2011a; VandenBrooks et al., 2012) by reducing development time, growth rate and fecundity. Further, oxygen concentration is negatively correlated with tracheal diameter in insects of the same body size (Henry and Harrison, 2004; VandenBrooks et al., 2012), causing changes to these and other respiratory organs as part of an adaptive response to the need for greater respiratory efficiency (J.F. Harrison et al., 2010). Atmospheric oxygen levels can set thermal limits to the body size of aquatic insects at least (Verberk and Bilton, 2011).

Hypoxia also has effects on vertebrates. Alligators exhibit reduced growth rates and compensatory changes in lung volume in response to changes in atmospheric oxygen (Owerkowicz et al., 2009), and carp show similar changes in their gill structures (Solé, 2003). Generally, experimental studies confirm that hypoxia is associated with body size reduction in fishes, alligators, snakes, rats, and humans (Payne et al., 2011a).

It is worth noting on the other hand that many organisms display remarkable hypoxia tolerance (Schmitz and Harrison, 2004; Bickler and Buck, 2007). Insects, for example, are much more capable of recovery from anoxia than most vertebrates, but there is also a very wide range of tolerance to hypoxia and anoxia among terrestrial invertebrates. Crustaceans and arachnids are less tolerant to hypoxia than insects and myriapods, and this may relate to the frequency with which these organisms face such stresses (Schmitz and Harrison, 2004). Among vertebrates, fishes, amphibians, and reptiles are much more hypoxia-tolerant than birds or mammals, which relates to the substantial differences in metabolism and oxygen requirement between such ectotherms and endotherms (Bickler and Buck, 2007).
Among modern ectothermic vertebrates, the degrees of tolerance vary considerably. At an extreme are some carp and turtles, which can survive without any oxygen for several weeks or months. But such short-term miracles of survival say nothing about responses to the long-term fall in oxygen levels through the Triassic. Here, it is important to be aware that many or most modern ectotherms that tolerate hypoxia by making long-term physiological adaptations in suppressing their metabolism, being able to tolerate metabolite accumulation, and in establishing free-radical defences during reoxygenation (Bickler and Buck, 2007)

The effects of hypoxia on plants are hard to predict, and likely complex (Payne et al., 2011a). Experiments show that hypoxia generally increases vegetative growth for C3 plants, but not for C4 plants, and it decreases seed growth.

Such observations on the physiology of modern organisms have been applied to the PTB and Early Triassic. The response of many terrestrial animals to PTB hypoxia was presumably extinction combined with range contraction for the survivors. Huey and Ward (2005) note that a reduction of the atmospheric oxygen concentration to 16% is equivalent to changing the atmospheric conditions at sea level to those at an altitude of 2.7 km today: lowland animals would have faced the extremes of high-altitude life; some could adapt, but many presumably went extinct.

In more detail, Retallack et al. (2003, 2006) suggested that many of the differences between Permian and Triassic anomodonts were related to the rapid decline in atmospheric oxygen concentrations. They noted that Lystrosaurus had a massive barrel-like chest, perhaps in part to accommodate expanded lungs, perhaps a muscular diaphragm to force air in and out of the lungs more speedily, and a possible four-chambered heart to improve the efficiency of blood circulation. These claims are hard to test, and it is not clear in any case that postulated PTB oxygen levels were low enough that they would have created a major problem (Engoren, 2004). In addition, it has been noted (Hillenius, 1994) that Late Permian and Triassic synapsids had nasal turbinates, bone laminae within the nasal cavity that substantially increase the area of nasal mucous membranes, either to improve oxygen uptake, or as a countercurrent heat exchanger to limit body temperature changes during breathing, or both. These structures emerged in the Late Permian, and they could relate to the long-term decline in oxygen levels.

A further two anatomical changes in anomodonts have proved equivocal, enlargement of the secondary palate and enlargement of internal nostrils, both suggested to improve oxygen uptake in hypoxic conditions (Retallack et al., 2003, 2006; Ward, 2006). Angielczyk and Walsh (2008) tested whether this was likely, and found mixed results: the raw data certainly showed that Triassic anomodonts had significantly larger secondary palates and internal nostrils than Permian anomodonts. However, these characters are partially related to body size and phylogenetic relationships, and so their changes provide only weak support for the hypoxia scenario.

11.3. Hypercapnia and ocean acidification as the EPME killers

Knoll et al. (1996, 2007) made a strong and convincing case that the main killing agents in the oceans at the PTB were hypercapnia (excess CO2) associated with acidification, hypoxia, and toxic sulphide levels. In particular they noted that marine animals suffered very different levels of extinction depending on their need for carbonate ions to construct their skeletons, and how well physiologically buffered they were, in other words, how well they could control their intracellular pH and maintain respiratory efficiency under elevated CO2 levels. Excess CO2 in seawater causes suppression of metabolism, disrupts acid–base homeostasis, and impairs calcification through reduced mineral saturation (Portner, 2008).

The highest risk group were the poorly buffered forms with a high need for carbonate ions, such as rugose corals, rhychonelliform brachiopods, and crinoids. Next were the well-buffered forms that needed lower amounts of carbonate, such as gastropods, bivalves, nautiloids, ammonoids, ostracods, and echinoids. Finally, the forms that required little or no carbonate were the ctenostome bryozoans, lingulid brachiopods, holothurians, conodonts, and chondrichthians. The generic extinction rates of these three groups were 86%, 54%, and 5%, respectively. These figures highlight the importance of shell mineralogy and the key role of ocean acidification as a major killer of marine life at the EPME (Clapham and Payne, 2011; Kiessling and Simpson, 2011).

Increased atmospheric CO2 concentrations across the PTB would also have had effects in surface waters (Fraiser and Bottjer, 2007). Passive diffusion of atmospheric CO2 into ocean-surface waters would have decreased the pH and CaCO3 saturation state of seawater, causing a physiological and biocalcification crisis for many marine invertebrates. These deleterious effects may have lasted for much of the Early Triassic, and so contributed to the delay in biotic recovery.

As Knoll et al. (2007) say, the terrestrial record of the EPME is incomplete, but that is not the reason that hypercapnia and acidification were unlikely prime killers of life on land. First, it is not clear how oceanic anoxia, acidification, or hypercapnia could be transmitted onto land. Atmospheric O2 and CO2 levels may have changed, but the questions concern physiological correlates in modern organisms. Hypoxia and hypercapnia have severe physiological effects on modern animals, as noted earlier, but plants can generally adapt to low atmospheric O2 and high CO2 levels. Land animals would not be affected by the physiological calcification stresses of marine animals. Hypoxia and hypercapnia could reduce adult body size in terrestrial animals, and extremes would be fatal for many species.

11.4. Global warming as the EPME killer

Temperature is a primary extrinsic driver of the abundance and distribution of species (Gaston, 2003; Hofmann and Todgham, 2010), a key reason for current concerns about the likely current and future effects of global warming on biodiversity. Biogeographic studies show numerous examples of major range shifts among plants and animals that have already occurred thanks to the global temperature rise of some 1 °C in the past century (Root et al., 2003; Parmesan, 2006; Harley, 2011). Environmental temperature changes affect many plants and animals directly because they have narrow physiological tolerance windows within which they function normally; their response is usually local extinction, and migration to a geographic area that retains their favoured life conditions.

The physiological mechanisms underlying temperature-induced migrations remain unclear (Hofmann and Todgham, 2010). Ecosystems are less able than endotherms to adjust to changes in external environmental temperatures, and so have been most studied with these questions in mind. Forecasting whether a plant or animal can survive a particular change in temperature resulting from global climate change depends on both physiology, the ability of an organism to buffer the change physiologically, and behaviour. Fundamental physiological reasons for narrow thermal tolerances in organisms include the thermal stability of proteins essential for bodily function, cellular membrane properties, genomic responses to temperature change, and respiratory efficiency (Hofmann and Todgham, 2010).

Physiological and ecological studies show that the nature and timing of temperature change can be as important as the magnitude of the change. The timing between extreme high temperature events is an important determinant of survival, because organisms that have undergone a thermal challenge require time to recover physiologically. For example, some corals can increase their thermal tolerance by 1–1.5 °C, and this is predicted to reduce their vulnerability to bleaching.
events by some 30–50 years (Donner et al., 2007). However, certain species and growth forms can increase their tolerance more effectively than others, and this can lead to major changes in the coral reef ecosystem that affects all species.

The rate of warming is also crucial, and experiments with marine and terrestrial species show that the upper temperature tolerance limit decreases substantially when the rate of temperature rise is reduced (Chown et al., 2009; Peck et al., 2009). It might seem counter-intuitive that more rapid warming allows survival to a higher temperature, but there are two effects at work, the critical maximum temperature at which cellular and biochemical processes fail, and the maximum temperature to which a species can become acclimatised (Peck et al., 2009). There is a difference between short-term survival during a rapid pulse of heating that is not sustained, and acclimatisation to longer-term higher temperatures. During fast warming, species can survive at higher temperatures before anaerobic end-product accumulation overcomes resistance capacity, a process termed hardening (Hoffmann et al., 2003). At slow rates of warming, over months or years, and where the upper limits are well below the critical oxygen limits, acclimatisation and adaptation effects become important. Long-term thermal limits are significantly lower than medium-term survival values (Peck et al., 2009). This suggests that many organisms might survive a very short, but acute, episode of global warming (days or weeks at most), but would succumb if the elevated temperature was maintained for months or years.

If temperatures persist at high levels, this can simply be lethal for most plants and animals. In C3 plants, photosynthesis replaces photosynthesis at temperatures over 35 °C and few plants can survive above 40 °C (Berry and Bjorkman, 1980; Ellis, 2010). Some animals show rather lower lethal temperatures, but for most temperatures to 35 °C or higher can cause protein damage that can be countered only for short heat shocks by the production of heat-shock proteins (Somero, 1995).

Temperature change has important synergistic effects with other environmental changes. For example, in experimental studies of marine organisms, elevated CO2 can reduce the upper thermal limits for species, and exacerbate the effects of low pH on lowering metabolic rate (Hofmann and Todgham, 2010). Likewise, low pH (= acidification) can affect the ability of organisms to survive elevated temperatures in echinoderm larvae, coralline algae, and corals (Reynaud et al., 2003). Such findings are made also in longer-term ecological studies: for example, Cooper et al. (2008) found that synergistic stressors were linked to a decline in calcification in corals of the Great Barrier Reef in a 16-year field study. These synergistic effects mean that the lethal temperature for most animals is 35 °C (Somero, 1995), because oxygen demand increases with temperature (Pörtner, 2001, 2008). This causes hypoxaemia and the onset of anaerobic mitochondrial metabolism that is only sustainable for short periods.

As for the EPME, a global mean rise of 5–10 °C would clearly have caused severe heat stress for many terrestrial plants and animals, but it is unclear how high the species extinction levels would have been. If ocean surface, and presumably also land surface, temperatures rose to 35° or more (Joachimski et al., 2012; Sun et al., 2012), then this could have proved lethal to many plants and animals. Terrestrial vertebrates at least are largely absent from equatorial latitudes during the Early Triassic (Shishkin and Ochev, 1993; Sun et al., 2012). If equatorial temperatures reached 35°, then most plants and animals would have been unable to survive, and they would have been driven entirely from these regions.

### 11.5. Aridity as the EPME killer

As evidence for the direct effects of aridity at the time of the EPME, Smith and Botha (2005) described drought associations of tetrapod skeletons from the Karoo in South Africa. Sedimentological evidence shows lowering of water tables and the onset of drought conditions at the same time as the disappearance of the Glossopteris flora and the appearance of the new anomodont taxon Lystrosaurus in earliest Triassic sediments. These authors report several ‘bonebeds’ comprising numerous (± 10) jumbled and disarticulated sub-adult Lystrosaurus skeletons, which they interpret as drought-induced aggregations. Animals died in large groups on the periphery of a shrinking waterhole, and subsequent massive rainfall transported the desiccated bones into shallow depressions along with intraformational sediment debris. It should be noted that this is telling, but circumstantial, evidence, and such possible drought-associated accumulations of tetrapods are reported also from the Middle and Late Permian (e.g. Benton et al., 2012), and are not unique to the post-EPME time. Perhaps droughts were merely seasonal, and not year-round.

Aridity can be a physiological stressor either through elevated temperatures (see Section 11.4) or through reductions in water and desiccation of terrestrial habitats. Desiccation stress dramatically affects physiology and ecology of modern plants and animals (Hofmann and Todgham, 2010). Physiological responses to desiccation include mechanisms to retain water or to tolerate dehydration. Further, behaviour can be a crucial defence for animals, which can move to the shade or forage at night.

Some of the most desiccation-tolerant organisms are prokaryotes, including bacteria and cyanobacteria, and the most desiccation-tolerant of all are Gram-positive bacteria (Garcia, 2011). Desiccation tolerance in such simple organisms extends to complete anhydrobiosis, the near-complete removal of water, defined as water content below 0.1 g H2O g-1 dry mass. The ability of some prokaryotes to survive these conditions makes many prokaryotes extremely drought resistant for long periods in natural situations; this ability has been exploited in the pharmaceutical and food industries which dry, store, and distribute prokaryote lines.

Desiccation tolerance in many animals may depend on simple physiological and biochemical mechanisms. Insects have a distinct critical temperature limit above which water loss increases rapidly, presumably related to the biochemistry of their cuticle. Gibbs (2002) proposed a lipid-melting model that links this critical temperature to the lipid phase state and cuticular permeability: at a certain temperature the lipid bonds fail and resistance to water loss is compromised. Birds show a similar strategy, in which cutaneous water loss may be primarily mediated through changes in the lipid composition of the stratum corneum, the outermost layer of the skin (Muñoz-García and Williams, 2008).

For many species, the critical desiccation level is lower than that associated with the lipid failure temperature. Desiccation resistance has a high heritability in some Drosophila species (Hofmann and Todgham, 2010). For example, it has been shown that invasive North American populations of Drosophila subobscura have evolved desiccation resistance within the past 30 years, and the more arid populations have a higher desiccation tolerance. This is not the case, however, for all Drosophila species, many of which are apparently desiccation-intolerant, and so more vulnerable to climate change.

Very few animals are truly tolerant of desiccation. The exceptions are brine shrimp, tardigrades, rotifers, and some insects. The brine shrimp Artemia franciscana can produce larvae or embryonic cysts from its fertilised eggs, and these cysts can survive for 2 years in dry conditions, without oxygen, or even at temperatures below freezing or up to 80 °C (Clegg, 2005). In this species, the outermost envelope of the cyst is essential for its remarkable tolerance to stress. Tardigrades, a phylum related to arthropods, are able to survive in extreme environments, including temperatures close to absolute zero and as high as 151 °C, massive doses of radiation, and spans of up to 10 years without water (Wright, 1989). Tardigrades have even survived the vacuum of outer space for a few days in low earth orbit. Different species of
tardigrades show different degrees of desiccation tolerance, with low lower humidities for initial desiccation ranging from 78 to 53%. Tardigrades resist desiccation by shrinking, infolding their cuticle, and reducing transpiration, forming an inert cyst, or tun. The reduction in transpiration causes a slump in permeability of the cuticle, and so water can be retained despite overall desiccation (Wright, 1989; Guidetti et al., 2011). Rotifers, a phylum of small (<2 mm) aquatic animals, include forms that live in temporary freshwater pools or terrestrial mosses or lichens, and when these habitats dry up, they can alter their morphology and physiology, assuming a compact shape also called a ‘tun’ (dormant stage) and entering a dormant state (Robles-Vargas and Snell, 2010). Rotifers can survive whole annual cycles or drought, and the longest reported survival is 9 years. They then recover in minutes or hours when exposed to water.

Insects do not generally show such extremes of desiccation tolerance, but most taxa have adaptations to avoid water loss, such as an impermeable cuticle with waxy components, tracheae with spiracles that can close, and limiting water excretion. Many of these conditions change in dormant insects, which can combine several adaptations to maintain water balance, including habitat choice, reduction of body water content, decreased cuticular permeability, absorption of water vapour, and tolerance of low body water levels (Dansis, 2000). The chironomid midge Polypedilum vanderplanki is the largest multicellular animal known to tolerate almost complete dehydration without ill effect. Its larvae show extremely high thermal tolerance from –270 °C to +106 °C and can recover soon after prolonged dehydration of up to 17 years. Part of the explanation seems to involve the rapid accumulation of the carbohydrate trehalose and yet that cerebral regulation is not involved (Watanabe et al., 2002).

Plants are often thought to be more tolerant of desiccation than animals (Hoekstra et al., 2001). The ability to survive desiccation is common in seeds or pollen, it occurs in terrestrial microalgae, fungi, and yeasts, and it is widespread among bryophytes, but it is rarely present in the vegetative tissues of other plants. Seeds commonly survive for 5 or 10 years, and there are several credible records of survival for more than 200 years (Daws et al., 2007). Over time, the viability of such long-lived seeds reduces substantially, and the main causes of eventual death relate to water loss. Desiccation tolerance in seeds (Leprince et al., 1993) is enabled by mechanisms that prevent lethal damage to cellular components including membranes, proteins and cytoplasm. There are three main protective systems: the accumulation of non-reducing sugars, which stabilise membranes and proteins in dry conditions and promote the formation of a glass phase in the cytoplasm; the ability to prevent, tolerate, or repair a free radical attack during desiccation; and, protective late embryogenesis abundant proteins that are inducible by abscisic acid.

Extreme survivors of desiccation are bryophytes (mosses and liverworts); as an example, a dried herbarium specimen was reported to have regrown after 23 years of storage in entirely dry conditions (Proctor and Pence, 2002). This remarkable desiccation tolerance by bryophytes (Proctor et al., 2007) depends on their unique physiology, which differs from that of vascular plants: they are smaller, their leafy shoots equilibrate rapidly with the water potential in their surroundings, and the shoots tend to be either fully hydrated or desiccated and metabolically inactive. The length of desiccation affects the time to recover and the degree of that recovery; both also depend on temperature and the intensity of desiccation. The recovery of respiration, photosynthesis and protein synthesis takes place within minutes or hours; recovery of the cell cycle, food transport and the cytoskeleton may take a day or more.

Such feats of survival are extremely rare among pteridophytes and angiosperms, so much so that the 350 or so species that can survive desiccation are set apart as ‘resurrection plants’ (P. Scott, 2000; Proctor and Pence, 2002; Bartels and Hussain, 2011). These include some 300 species of angiosperms that can survive extreme drying through special adaptations of their cell membranes and macromolecules, especially the production of large amounts of desiccation-induced protective proteins. These have different roles in cellular protection, by conserving the structures of macromolecules and membranes, by stabilising membrane structures and proteins, by avoiding mechanical damage from vacuole shrinkage in dehydrating cells, and by minimising oxidative stress from the enhanced production of reactive oxygen. These resurrection plants can survive for months or years without water, and then regrow at full vigour when watered (P. Scott, 2000). Survival for more than a few years however is not possible.

Evidently, drought is a key problem for terrestrial life. As described, a wide range of plants and animals can tolerate complete desiccation. Species in five phyla of animals and four divisions of plants contain desiccation-tolerant adults, juveniles, seeds, or spores, and some of these, as indicated, can survive for years or even decades. Importantly, there may be physiological limits in these drought-tolerant organisms, restricting the ability to small organisms (plants shorter than 3 m; animals shorter than 5 mm), and to animals with rigid skeletons (Alpert, 2005, 2006). Many desiccation-tolerant organisms share biochemical and cellular mechanisms, such as sugars that replace water and form glasses, proteins that stabilise macromolecules and membranes, and anti-oxidants that counter damage by reactive oxygen species (Alpert, 2006). These systems are often triggered by drying, and some of the genes involved may be homologous in microbes, plants, and animals (Leprince and Buïnk, 2010). If desiccation resulting from elevated temperatures were one of the EPME killers on land, the likely survivors and victims could be predicted from the observations just outlined of desiccation tolerance in modern organisms.

11.6. Acid rain and mass wasting as the EPME killers

As argued above (Sections 2, 6.1, 6.2, 6.4 and 7.2), the apparent removal of vegetation from the land surface following acid rain at the EPME probably significantly increased weathering processes and terrestrial nutrient fluxes, and these then had a major impact on marine environmental conditions (Algeo et al., 2011). Widespread loss of plants led to massive erosion on land areas at the time of the EPME, as shown by the shift from fine-grained meandering to conglomeratic braided fluvial facies (Newell et al., 1999; Ward et al., 2000; Michaelsen, 2002; López-Gómez et al., 2005), by transported soil clasts (pedoliths; Retallack, 2005), by increased sedimentation rates in terrestrial successions (Retallack, 1999), and by an abrupt influx of terrigenous siliciclastics to carbonate platforms nearby worldwide (Algeo and Twitchett, 2010). Continuing episodic massive erosion events through the Early Triassic may have further repeated aspects of the EPME crisis (Algeo et al., 2011).

The sudden influxes of sediment may have killed filter-feeding marine organisms by swamping them and reducing their feeding activity, osmoregulation, growth rate, body size, larval recruitment, and development (Algeo and Twitchett, 2010). Grazers could have been affected also if the masses of fine-grained sediment covered their food sources. Algeo et al. (2011) noted that many of the immediate survivors of the EPME in shallow seas, such as the paper pectens, were adapted to living on unstable, soft sediments. Continuing influxes of sediment through the first few Myr of the Triassic may have had a major, previously under-emphasised role in disturbing marine benthic communities (Algeo et al., 2011).

On land, acid rain removed forests and soils, both of which are massive repositories of biodiversity (Lindenmeyer and Franklin, 2002; Nielsen et al., 2011). It is impossible to estimate how important these two broad habitats are, but they likely account for the large majority of life on land, when one considers the remarkable dominance of species inventories by insects today (perhaps 70–
80%), and especially tropical forest insects, coupled with the high diversities of other terrestrial arthropods (spiders, mites) and flowering plants in those habitats (Briggs, 1995). The current very high biodiversity on land compared to the sea is a phenomenon of the past 125 Myr or so, and terrestrial biodiversity in the Permo-Triassic was surely much lower than today (Vermeij and Grosberg, 2010), and yet the loss of forests and soils during the EPME would have removed the habitats of considerably more than 50% of land life.

Acid rain affects both the living plants and the soil, and effects can be long term. From a selection of 13 environmental variables, Dietze and Moorcroft (2011) found that the clearest determinants of forest decline in the eastern and central United States were air pollutants (acid rain, nitrogen deposition, ozone) and stand characteristics (forest size, tree mean age, tree mean size).

These effects are widely studied in modern ecosystems affected by industrial acid rain. For example, in North America, forest soil acidification and depletion of nutrient cations have been reported for several forested regions (Fenn et al., 2006). Continuing inputs of anthropogenic sulphur dioxide, together with ozone and nitrogen oxides (Schulze et al., 1989), lead to leaching of base cations (Ca, Mg, K), increased availability of soil Al, and the accumulation and transmission of acidity from forest soils to streams. More subtle changes in soil acidity affect the ion balance and, in depleted soils, the trees are affected immediately. The key is the balance of Ca and Al ions in forest soils: Ca is an essential plant nutrient, contributing to many cellular structures and physiological processes as well as overall forest function. Al in soil solution can inhibit Ca uptake by plants and disrupt these Ca-dependent metabolic and physiological processes. The ratio of Ca to Al in soil solution can be an important indicator of forest health, especially in acid soils, and Ca loss points to acidification.

Calcium reduction has profound effects on trees. Movement of labile Ca among cellular compartments acts as a signal mediating physiological responses to environmental stresses such as drought, cold, heat, salinity, fungal pathogens, and oxidative and mechanical stresses (Knight, 2000). Ca deficiency may then affect the ability of plants to sense and respond adaptively to their environment. Further, Ca is essential to the photosystem function and carbohydrate metabolism of plants: shortage of Ca reduces the storage of sugars, and reduces the cold tolerance of leaves. Exposure to acid rain reduces red spruce cold tolerance through a reduction in Ca availability, thereby increasing the risk of winter injury and crown deterioration (DeHayes et al., 1999). Further, shortage of Ca impairs the function of the leaf stomata, essential for correct water balance (Borer et al., 2005). In addition, reduced Ca affects seed germination and seedling growth, all combining to confirm that acid rain can cause immediate leaf loss in trees, and ultimately death.

11.7. Wildfires as the EPME killer

The evidence for extensive wildfires in the Late Permian, and a burst of wildfires coincident with the EPME has been described above (Sections 6.1 and 6.3). It is unclear, however, whether wildfire could be considered a major contributor to the species loss experienced at the EPME. The wildfires associated with the EPME, and other mass extinctions, such as that at the end of the Cretaceous, were triggered by the eruptions or impacts. However, wildfires have been common throughout geological time (A.C. Scott, 2000; Bowman et al., 2009), and yet most are not associated with any global extinction. The frequency of fires in Earth history correlates with oxygen levels (Bowman et al., 2009).

Fire is a key ecosystem driver in grasslands, savannas, boreal forests, and heathlands. Historical records, sedimentary successions, and dendrochronology show that wildfires have recurred with frequencies from years to decades. Fire is an important agent for maintaining biodiversity at several different scales, by altering species diversity, landscape diversity and dynamics, and ecosystem function. Fires act as a disturbance, preventing species of late successional stages from excluding those of earlier stages. Individual fires can therefore increase biodiversity by preventing any single species from dominating. However, when fires are too frequent, total biodiversity can be reduced as vulnerable species are removed. Fires may affect biodiversity at larger scales by, for example, creating patchy landscapes, as well as altering nutrient cycling, successional processes, and stand composition.

Large fires can be a normal part of ecosystem functioning. In Australia, perhaps the most fire-affected continent, large proportions of the northern tropical savanna landscapes are burnt (Andersen et al., 2005). Much of the savanna biota is remarkably resilient to fire, even of high intensity. The relative abundances of plants and animals are generally unaffected by fire, except for riverbank plants and animals, and small mammals. The 2-yearly managed burning appears to be too frequent for these species, and small mammals have undergone significant declines. Overall, Andersen et al. (2005) conclude that although individually massively destructive, it is hard to make a case that fires have a substantial long-term effect on biodiversity. In many ecosystems, fire is a vital and natural part of some forest ecosystems, and humans have used fire for thousands of years as a land management tool.

Moretti et al. (2002) obtained similar results in their study of winter forest fires in the southern Alps. They found that overall species richness was significantly higher in plots with repeated fires than in unburnt control sites. The frequency of fires increased the richness of species that live deep within forests and at forest edges, but species of open landscapes, open forests and interior forests were not influenced by fire frequency. A positive effect of fire was found for most subclades of insects and spiders, with negative effects only for isopods and weevils. Further, Moretti et al. (2006) noted that terrestrial arthropods were more resilient to single fires than to repeated events, recovering 6–14 years after a single fire, but only 17–24 years after the last of several fires. Flying arthropods proved to be most resilient to fire, then pollen-feeders and foragers, and with ground-litter scavengers least able to recover following major fires.

12. Death on land during the EPME

Whereas key killing agents of marine life during the EPME were likely hypercapnia, ocean acidification, hypoxia, and high sulphide levels (Knoll et al., 2007), it is unlikely that this cocktail of killers acted so substantially on land life. The immediate burst of wildfires would have killed plants, but whether irrevocably is less clear. The significance of hypoxia is also unclear, in that atmospheric oxygen levels had been falling throughout the Permian, and the Triassic lows may not have been as low as suggested by models (Glasspool and Scott, 2010). Further, although hypoxia and hypercapnia would have had a major impact on vertebrates, some other animal groups might have suffered less, and microbes and plants presumably not at all. At times, the postulated destruction of the ozone layer and enhanced UV-B radiation have been cited as the major cause of extinction on land (Beerling, 2007), but evidence for these dramatic environmental perturbations is currently mixed (see Section 7.4).

There were three scales of potential physical drivers of extinction around the time of the EPME: long-term, short-term, and repeated. One long-term process was continuing aridification through the Late Permian and Early Triassic. Short-term consequences of the initial major eruption of the Siberian Traps may have been flash warming, wildfires, acid rain and mass wasting, and breaching of the ozone layer at high latitudes. Some of these short-term processes may have been repeated during subsequent Early Triassic crises, but this has yet to be established. There is evidence for repeated phases of input of siliciclastic debris into the sea through the Early Triassic, so suggesting repeated episodes of acid rain (Algeo and Twichett, 2010).
Global warming at the time of the EPME presumably increased stress on much of land life, and may have driven many plants and animals from the tropical belt. However, it is currently hard to estimate the global killing effects of such high, even lethal, equatorial temperatures on land because many species could presumably have migrated to cooler climates. The real killers were likely a combination of acid rain, mass wasting of the land surface, and aridity. How much soil was removed following the acid rain generated from volcanic gases is unclear, but the changes in terrestrial sedimentary regimes in many basins, and the magnitude of the influx of terrestrial siliciclastics into the ocean suggest a major loss of soil. Surviving plants and animals were then challenged by aridity and drought.

If acid rain, soil removal, and aridity were the killers of life on land during the EPME, it ought to be possible to distinguish differences in survival rates between those species that were most likely to have been drought-resistant compared to those that were not. In broad terms, insects and bryophytes might then be expected to have shown higher survival than vertebrates and vascular plants. Regrettably, the quality of the data at present is probably insufficient to make such a comparison with confidence.

Acknowledgments

We are very grateful to Zhong Qiang Chen for the invitation to the IGCP572 Symposium 3: Latest Permian Mass Extinction and IGCP572 Symposium 4: Ecosystem Recovery in Triassic, jointly held with the XVII International Congress on the Carboniferous and Permian, from 3 to 8 July, 2011, in Perth, Australia, and for funding for MJB to attend. We are grateful to Thomas Algeo (University of Cincinnati), Zhong Qiang Chen (China University of Geosciences, Wuhan), Randy Iris (University of Utah), Jessica Whiteside (Brown University), Deming Wang (Peking University) and Conghui Xiong (Peking University) for providing their original images on which Figs. 1, 2, 5, 9, and 11 are based. We thank Edie Taylor (University of Kansas) and Thomas Algeo (University of Cincinnati) for very helpful review comments on the MS.

References


Michael J. Benton is a Professor of Vertebrate Palaeontology at the University of Bristol, U.K. He received his undergraduate training at the University of Aberdeen, and his PhD in Geology from the University of Newcastle-upon-Tyne. He had positions at the University of Oxford, and Queen’s University of Belfast, before moving to the University of Bristol in 1989. He has always been interested in the Triassic, and made early contributions to the understanding of the origin of dinosaurs. More recently he has been working on the Permian-Triassic boundary in Russia, and the time of recovery from the end-Permian mass extinction in the marine successions of South China.

Andrew J. Newell is a Senior Geologist at the British Geological Survey. Wallingford, UK. He received his undergraduate training and his PhD in Geology at the Queen’s University of Belfast. His PhD research was on the sedimentology of the Otter Sandstone Formation of Devon, and he has gone on to specialise in clastic sedimentology, stratigraphy, and 3D geological modelling. He has done fieldwork all round the world, including in the classic Permo-Triassic red bed successions in Russia. His particular interests in this field are to understand the successions of sedimentary facies in different redbed basins, their stratigraphy, and the information they provide on ancient palaeoclimates.