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# Environmental crises at the Permian–Triassic mass extinction

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## Key points

- The Permian–Triassic mass extinction (252 Ma) resulted in a substantial reduction of global biodiversity, with the extinction of 81–94% of marine species and 70% of terrestrial vertebrate families.
- Sedimentary, palaeontological and geochemical records during the mass extinction indicate that a cascade of environmental changes caused the extinction.
- The environmental changes can be linked (and attributed to) the effects of volcanic emissions (for example CO<sub>2</sub>, SO<sub>2</sub>, and metals) during the eruption of the Siberian Traps large igneous province.
- Inferred volcanically driven environmental perturbations include global warming, oceanic anoxia, oceanic acidification, and (potentially) ozone reduction, acid rain, and metal poisoning.
- The crisis on land likely started ~60–370 kyrs before that in the ocean, indicating different response times of terrestrial and marine ecosystems to Siberian eruptions.

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- The causes of marine extinctions are inferred from geochemical and sedimentary evidence, but the reasons for the earlier terrestrial ecological crises remain poorly understood, but likely include rapid atmospheric change.

## 34 **Abstract**

35 The link between the Permian–Triassic mass extinction (PTME; 252 Ma) and the emplacement of the  
36 Siberian Traps Large Igneous Province (STLIP) was first proposed over 30 years ago. However, the  
37 complex cascade of volcanic-driven environmental and biological events that led to the largest known  
38 extinction in life’s history is still difficult to reconstruct. In this Review, we critically evaluate the  
39 geologic evidence and discuss the current hypotheses surrounding PTME kill mechanisms. Data  
40 indicate that the initial STLIP extrusive/pyroclastic volcanism was coeval with widespread crisis of  
41 terrestrial biota and marine animal species stress at high northern latitudes. The following onset of  
42 extensive magmatic intrusions is linked with the rapid (~60 kyr) extinction of 81–94% of marine  
43 species. The terrestrial to deep water extinctions are thought to have been caused by a combination of  
44 global environmental perturbations driven by the emissions from STLIP. Nevertheless, it remains  
45 difficult to understand the ultimate reason for the exceptional severity of the PTME. Future research  
46 needs improved geochronology of STLIP and sedimentary sequences (especially terrestrial) to better  
47 resolve the timing of volcanic phases and extinctions. Further ecological and physiological studies are  
48 needed to understand temporal and spatial extinction patterns. Improved modelling is necessary to  
49 reconstruct the causal relations between volcanism, environmental perturbations and ecosystem  
50 collapse.

51

## 52 **Introduction**

53 Many mass extinction [G] events punctuated the history of life and changed evolutionary trajectories  
54 <sup>1</sup>. Most of past biological crises are coeval with the emplacement of Large Igneous Provinces (LIPs)  
55 [G], which drove widespread environmental perturbations. LIP emissions of CO<sub>2</sub> and other gasses are  
56 comparable to current anthropogenic emissions, and future climate projections predict a scenario  
57 similar to the major Phanerozoic extinctions. Hence, understanding past events will help define the  
58 tipping points that lead to a major biological crisis <sup>2</sup>.

59 The Permian–Triassic mass extinction (PTME; 252 Ma) was the most severe biological crisis of the  
60 Phanerozoic (Fig. 1). It almost completely eliminated Palaeozoic fauna and flora, setting the stage for  
61 the evolution of modern ecosystems. Across the Permian–Triassic boundary (PTB), 81–94% of  
62 marine species went extinct <sup>3–5</sup> (Fig. 2 and 3). On land, 89% of tetrapod genera and 49% of families  
63 disappeared <sup>6</sup> (Fig. 4). Recovery began in the Early Triassic <sup>7–9</sup>, but became significant only in the  
64 Middle Triassic, five million years later <sup>10–12</sup>.

65 Data from the fossil, sedimentary, and geochemical record of the PTME suggest there were major  
66 environmental changes in marine and terrestrial settings<sup>13–15</sup> (Fig. 2 and 3). The global crisis is  
67 coeval with the emplacement of the Siberian Traps Large Igneous Province (STLIP)<sup>16–18</sup> (Fig. 5),  
68 that saw a relatively rapid (<1 Ma) eruption of 2–7 million km<sup>3</sup><sup>19–22</sup> of basalt, together with volcanic  
69 emissions of CO<sub>2</sub>, SO<sub>2</sub>, halogens and metals that were capable of causing global climate and  
70 environmental catastrophe.

71 Detailed timing of events has improved remarkably in recent years thanks to advances in high-  
72 precision radioisotope dating [G], and high-resolution biostratigraphy [G] and chemostratigraphy [G]  
73 studies (especially C-isotope and Hg stratigraphy; BOX 1 and 2). Analysis of events from 252 million  
74 years ago at a high temporal resolution allowed identification of distinct phases of STLIP eruptions  
75<sup>18,23</sup> and separate pulses of extinction among marine animals<sup>4,24,25</sup>. Particularly interesting  
76 developments include the increasing evidence that the terrestrial crisis was very likely underway  
77 several tens to hundreds of thousands of years before the marine extinction<sup>26–28</sup>, clearly indicating  
78 that the PTME was not a single, instantaneous catastrophic event. Whilst these findings are expanding  
79 knowledge of STLIP volcanism, environmental changes, and extinction patterns, linking them  
80 remains difficult. The geological record tells a complex and partly obscure story of multiple, co-  
81 occurring phenomena, all playing a role in perturbing the ecosystems, and all probably interlinked in a  
82 cascade of environmental disasters.

83 In this Review we discuss the PTME pattern in the ocean and on land, the age and volcanic style of  
84 the STLIP, the evidence of a link between STLIP phases and the PTME, and the environmental crises  
85 triggered by the volcanic emissions and their role in the extinction and observed selectivity. We  
86 discuss the apparent diachrony between some recorded environmental changes and extinctions. We  
87 then construct a likely chronology of the events based on the current evidence, propose a working  
88 hypothesis for future research, and highlight the open problems.

89

## 90 **Pattern of the PTME**

91 The exact temporal relationship between the marine and terrestrial extinctions is still debated.  
92 However, there is increasing evidence for an earlier onset of the terrestrial crisis and marine stress at  
93 high northern latitudes. The age and pattern of the marine PTME at low latitudes are very well  
94 constrained, and these provide a stratigraphic framework that allows the level of terrestrial crisis to be  
95 pinpointed. Here we examine the marine crisis first.

96 **Marine extinction.** Across the PTB, the Palaeozoic evolutionary fauna [G] was devastated at all  
97 ecological levels, resulting in the largest marine extinction of the entire Phanerozoic (Fig. 1a and  
98 Supplementary Information). It has been estimated that 81–94% of marine species went extinct<sup>3–5</sup>.

99 The PTME appears to have been selective (Fig. 3). Some groups completely disappeared, such as  
100 trilobites, rugose and tabulate corals, fusulinid foraminifers, and blastoid echinoderms<sup>4,29–31</sup>; others,  
101 such as rhynchonelliforms (articulate brachiopods), crinoids, stenolaemate bryozoans, calcisponges,  
102 radiolarians, ammonoids, and ostracods, came close to annihilation with only a handful of surviving  
103 species<sup>4,32</sup>; whilst a few groups, including bivalves, gastropods, conodonts, and fishes, experienced  
104 “only” severe to moderate extinction rates<sup>4,33–35</sup> (Fig. 2). Extinction selectivity is not only evident in  
105 the taxonomic composition of the marine fauna, but also in ecological and physiological traits. Body-  
106 size selectivity is seen in foraminifers, conodonts brachiopods, and bivalves<sup>36–39</sup>, with larger bodied  
107 organisms showing higher extinction rates, but this factor is less obvious in other groups<sup>34,36,40</sup> (Fig.  
108 3).

109 It has been shown that physiologically buffered taxa that can regulate intracellular chemistry and  
110 counterbalance environmental chemical changes, like molluscs, ostracods, arthropods, and fish,  
111 experienced lower extinction rates than unbuffered taxa such as brachiopods and echinoderms<sup>41–44</sup>  
112 (Fig. 3). Moreover, non-motile taxa could in general be affected more by changing environmental  
113 conditions than motile animals, especially swimming animals<sup>12</sup>: Fish were relatively little affected  
114 compared to other groups<sup>44</sup>. However, statistical analysis shows that selectivity between these two  
115 groups was not significant (Fig. 3).

116 Taxa with limited geographic distribution are generally more prone to extinction than widely  
117 distributed groups because they are more dependent on local environmental conditions. However, this  
118 phenomenon is not so strong during the PTME<sup>43,45,46</sup> (Fig. 3), suggesting harsh marine environments  
119 were global in extent; there was no escape even for cosmopolitan species. Indeed, weak geographic  
120 range selectivity appears to be a general pattern with the major mass extinctions, being observed also  
121 at the end-Triassic and the end-Cretaceous<sup>45</sup> (Fig. 1a).

122 The pace of the PTME extinction pattern is long debated<sup>32</sup>, with contrasting hypotheses of gradual vs  
123 abrupt extinction, and single vs discrete extinction pulses. The gradual disappearance of marine  
124 species observed in several PTB successions below the main extinction horizon<sup>3,47</sup> could be  
125 attributed, for most groups, to the Signor-Lipps effect [G] in the fossil record whereby rarer species  
126 are last recorded some time before their final demise<sup>3,48,49</sup>. The one exception is the ammonoid

127 extinction pattern observed in the succession of Iran where, considering the age confidence interval of  
128 each species, ammonoid diversity indeed shows a gradual decline before the PTME<sup>47</sup>.

129 The marine extinction was a geologically brief event in the latest Permian–earliest Triassic<sup>50</sup>. Well-  
130 studied sections from South China, such as Meishan GSSP [G], show enormous losses at the base of  
131 the latest Permian *Clarkina meishanensis* zone<sup>3,51</sup>. Abrupt extinction in the latest Permian has also  
132 been documented in Italian foraminifera and Iranian brachiopods, foraminifera, and algae<sup>48,52</sup>. Thus,  
133 the crisis is often referred to as the end-Permian mass extinction, implying a single, geologically  
134 instantaneous (~30 kyr) event at the end of the Permian, just before the stratigraphic PTB<sup>3,51</sup> (Fig. 2).  
135 However, a significant diversity of Permian taxa, including brachiopods, foraminifers and ostracods  
136 survived beyond this level to become extinct either in the final part of the Permian or in the earliest  
137 Triassic<sup>53–55</sup>. Combining data from sections encompassing a spectrum of water depths shows that  
138 there was an especially intense final extinction phase in South China at the base of the *Isarcicella*  
139 *isarcica* Zone<sup>4</sup>. It is noteworthy that the second extinction pulse was proportionally intense but not as  
140 large in magnitude in terms of species loss.

141 Multi-phase extinction pattern has also been reported in the Dolomites, Italy<sup>24,25</sup>. Here, the main/first  
142 phase (which correlates to the first extinction pulse in South China), witnessed the loss of calcareous  
143 algae, foraminifera, and large-sized brachiopods and molluscs, with a genus extinction rate of 64%<sup>25</sup>  
144 (Fig. 2). 68% of survivors and newcomers subsequently went extinct in the interval ranging from the  
145 upper *H. changxingensis* to lower *H. parvus* zones<sup>25</sup>, with a second extinction pulse that is somewhat  
146 slightly earlier than the second pulse in South China<sup>4</sup> (Fig. 2).

147 Adequate sampling obviously play an important role in the assessment of the extinction pattern. When  
148 fossil occurrences are rare, statistical confidence in the precise timing and number of pulses of  
149 extinction declines. Moreover, the importance of examining extinction patterns in different  
150 environments is highlighted by the record of foraminifer which shows a single extinction pulse in  
151 shallow platform facies but two episodes of extinction in deep slope facies<sup>56</sup>. In contrast, brachiopods  
152 suffered two episodic extinctions in shallow platform<sup>57</sup> and deep slope<sup>3</sup> and basin facies<sup>58</sup>.

153 The latest U-Pb zircon ages from Meishan show that the two pulses of extinction happened at 251.941  
154 and 251.880 Ma, respectively, separated by an interval of ~60 kyrs<sup>59</sup> (Fig. 2). It is unclear if the  
155 intervening interval should be considered a time of high stress or if the two pulses of extinction  
156 represent discrete events. The interlude was certainly an intriguing time, it saw the proliferation of  
157 microbialites and oolitic strata in low latitudes<sup>60,61</sup>, whilst origination rates [G] increased<sup>4</sup>, pointing

158 to a temporary improvement in environmental conditions either within the extinction interval, or  
159 between the two main extinction pulses (Fig. 2).

160 **Terrestrial extinction.** The PTME was the Phanerozoic's largest and most severe extinction of  
161 terrestrial plants and animals, at all latitudes and trophic levels (Fig. 4). Terrestrial floras suffered a  
162 worldwide catastrophic die-off of many plant groups in different geographical and climate zones  
163 during the PTME, which reset plant evolutionary history and was followed by an Early–Middle  
164 Triassic “coal gap”: an interval in which peat-forming communities disappeared<sup>10,26,62–67</sup>. Some have  
165 argued that plant losses were much more moderate compared to animals<sup>68,69</sup>, but the unprecedented  
166 abrupt shutdown of peat formation is a clear signal for major loss of terrestrial biomass across the  
167 PTB.

168 Plant fossil records from South China show that diversity and abundance of the tropical rainforest-  
169 type *Gigantopteris* flora experienced a sharp decrease with a loss of 95% of species and 50% of  
170 genera<sup>70,71</sup>. The Permian gymnosperm-dominated floras of North China and Russia experienced  
171 similar catastrophic losses at the same time<sup>72</sup>. In the southern hemisphere (Gondwana), the coal-  
172 forming *Glossopteris* flora went extinct (and coals disappeared) to be replaced by seed-fern shrubs  
173 (*Dicroidium*)<sup>10,67,73</sup>, a stratigraphically long-ranging genus that survived the PTME and migrated  
174 polewards from low-latitudes<sup>74</sup>. The subsequent earliest Triassic floras throughout Eurasia and the  
175 southern continents were dominated by lycopods, especially *Pleuromeia*.

176 During the crisis, palynological data show widespread spore abundance spikes, accompanied by high  
177 abundances of spore tetrads and teratological [G] pollen, evidencing stressed conditions<sup>67,75–83</sup> (Fig.  
178 4). Peak abundances of *Reduviasporonites* have been noted as marking fungal or algal bloom events.  
179 The former attribution would indicate proliferation of fungal saprotrophs during terrestrial ecosystem  
180 collapse<sup>67,84–86</sup>, but the affinity of *Reduviasporonites* and its ecological significance remain  
181 controversial<sup>87,88</sup>.

182 Major changes at the base of the terrestrial food-web, for example in the structure of floral  
183 communities from luxurious forests to less productive lycophyte-dominated floras, triggered a  
184 cascade of extinction in terrestrial ecosystems at all higher trophic levels<sup>81,89</sup>. It is therefore  
185 noteworthy, but perhaps not surprising, that the mass extinction was the only one to severely affect  
186 insects, with losses of 30% of orders and 50% of families<sup>90–92</sup>.

187 Tetrapods were also severely impacted by the PTME with numerous families lost. Complex latest  
188 Permian ecosystems, dominated by herbivorous pareiasaurs, dicynodonts and carnivorous  
189 gorgonopsians, were replaced by ones with archosaurs and synsids<sup>93,94</sup>. Global tetrapod generic



190 data suggest there was an 89% generic loss of tetrapods near the PTB <sup>6</sup>. Such losses within tetrapods  
191 could have happened during a “sustained extinction interval” of up to ~1 Myr, as seen in the fossil  
192 record from the Karoo Basin (South Africa) <sup>95</sup> (Fig. 4), although it is difficult to determine rates in the  
193 low quality tetrapod record. Many niches disappeared with studies showing the loss of all small fish-  
194 and insect-eaters, medium and large herbivores and large carnivores in Russia <sup>94,96,97</sup>. Coupled to the  
195 terrestrial extinction and vegetation loss, fluvial style changed across the PTME from meandering to  
196 braided rivers and aeolian systems, as observed in the successions of the Karoo Basin, Russia,  
197 Australia and North China (for example ref. <sup>98</sup>).

198 The timing of terrestrial ecosystem crisis relative to extinctions in the oceans is debated. Some studies  
199 argued that the terrestrial extinction was coeval with that in the oceans based on radioisotopic dating,  
200 chemostratigraphy and terrestrial information recorded in marine deposits <sup>71,99,100</sup>. However, recent  
201 high-resolution studies show that the terrestrial ecosystems were already stressed before the marine  
202 PTME (Fig. 4). Evidence of an earlier terrestrial crisis is based on improved stratigraphic frameworks  
203 including C-isotope stratigraphy (BOX 1), Hg (and Ni) spikes (BOX 2), magnetostratigraphy, and  
204 high-precision dating methods <sup>26–28,95,101–103</sup> that supersede previous lower resolution studies. This  
205 earlier crisis is seen in palaeofloras from the high-latitude Sydney Basin <sup>26</sup>, in the tropical peatland  
206 ecosystems in equatorial South China <sup>27</sup>, in the flora and fauna of North China <sup>102</sup>, and in the tetrapod  
207 losses in the high-latitude Karoo Basin <sup>28,95</sup> (Fig. 4). Recurrent wildfire and abnormal pollen in the  
208 latest Permian also indicate that terrestrial ecosystems were under great stress before their collapse  
209 and prior to the subsequent marine extinction <sup>26,27,78,101,102,104</sup>.

210 It is important to note that the terrestrial fossil record primarily derives from lowland settings,  
211 especially lacustrine and riparian environments where much sediment accumulates. This is especially  
212 the case for the plant record which is dominated by plants from wetlands, due to their good  
213 preservational conditions in such settings <sup>105</sup>. Much less is known about plants from drier and upland  
214 habitats which rarely fossilize, although evidence of upland vegetation loss during the PTME has been  
215 inferred from changing sedimentary facies in the Karoo Basin and Russia <sup>106</sup>. Wetland extinctions,  
216 that eliminated the *Glossopteris* and *Gigantopteris* mire communities, were not mirrored by equally  
217 severe losses in drier habitats dominated by conifers and pteridosperms <sup>107,108</sup>. This pattern may partly  
218 explain why the palynological record, which includes data of widely dispersed pollen and spores from  
219 drier and upland habitats mixed with those of lowland floras, often shows a much more muted  
220 extinction intensity during the PTME <sup>107,108</sup>.

## 222 **The trigger**

223 The two main agents suggested to be responsible for the environmental changes that led to the  
224 PTME—which will be discussed in the next section—are extraterrestrial impact or large-scale  
225 volcanism.

226 Extraterrestrial impact as the trigger of the PTME was proposed on the basis of geochemical ( $\text{He}^3$  in  
227 fullerenes) and sedimentological (for example, the finding of chondritic meteorite fragments in the  
228 sedimentary record) data, and of the interpretation of a large structure found in the Indian ocean, the  
229 Bedout High, as a purported impact crater of supposed PTME age<sup>109,110</sup>. However, the  
230 extraterrestrial impact hypothesis has been largely rejected because data have been proven to be  
231 difficult to reproduce, and the age and interpretation of the impact structure and geochemical changes  
232 have been questioned<sup>111,112</sup>. Most scientists now agree that there is negligible evidence to support  
233 extraterrestrial impact as the cause of the PTME.

234 In contrast, overwhelming data support that the PTME was triggered by the eruption of the STLIP.  
235 The STLIP was emplaced during the Permian–Triassic transition in the continental Tunguska Basin  
236<sup>18</sup>, the adjacent West Siberian Basin<sup>113</sup> and Taimyr Peninsula<sup>21,114</sup>, with a poorly-constrained,  
237 original volume between 2 and 7 million  $\text{km}^3$ <sup>19,21,22</sup> (Fig. 5). Changes in geochemistry and mode of  
238 emplacement of the STLIP magmas during its history, as seen in the most accessible lava pile sections  
239 (Norilsk, Putorana and Maymecha-Kotui) and in outcrops and boreholes from the Tunguska, Taimyr  
240 and West Siberian basins<sup>18,115–119</sup>, reveal three phases of magmatic activity<sup>23</sup>.

241 The oldest lava flows and pyroclastic [G] deposits were alkaline [G], mafic to ultramafic, and high in  
242  $\text{TiO}_2$  (>2 wt%)<sup>117</sup>. These magmas have a deep, pyroxenitic mantle source [G], and were rich in  
243 magmatic Cl<sup>119–122</sup>. The gases released by this high-volume, initial phase of magmatism were  
244 probably dominantly mantle-derived, products of recycled oceanic crust entrained by the mantle  
245 plume<sup>119,122</sup>, although additional crustal sources are also likely<sup>120,121,123</sup>. This first phase of  
246 magmatism started just before  $252.27 \pm 0.1$  Ma, with extensive effusive activity taking place over the  
247 ~300 kyr preceding the marine PTME<sup>18,23</sup>. Intriguingly these early eruptions did not produce global  
248 changes in the  $\delta^{13}\text{C}$  record nor in Hg concentrations (Fig. 5). However, northern latitude marine  
249 records downwind of the eruption site show pre-extinction shifts in the  $\delta^{13}\text{C}$  and Hg records<sup>124–126</sup>,  
250 suggesting limited atmospheric mixing of volatiles released in this early eruption phase. This first  
251 STLIP phase appears to have been coeval with widespread terrestrial crisis<sup>26,27</sup> (Fig. 5).

252 The second, tholeiitic [G] phase consisting of sills [G] and intrusions in the Tunguska Basin and  
253 Taimyr Peninsula began at  $251.907 \pm 0.067$  Ma, and is coeval with the onset of the marine PTME (Fig.

254 5). The apparent absence of effusive and/or explosive activity during this phase is debated and may  
255 reflect a lack of sampling in the region <sup>114,127–131</sup>. The tholeiitic phase magmas were derived from a  
256 shallow mantle pyroxenitic-peridotitic source <sup>119,132</sup>, that underwent widespread interaction with the  
257 crust <sup>132–136</sup>, and is poor in juvenile volatiles [G] <sup>137</sup>. During this subvolcanic phase the STLIP  
258 intruded a succession of coal, shales, sandstones, evaporites and carbonates in the Tunguska Basin  
259 <sup>125,129,130</sup> and their baking may have liberated a large amount of both greenhouse gases and  
260 halocarbons <sup>123,129,130,132,138,139</sup>. Explosive basalt pipes and breccia diatremes are widespread in the  
261 Tunguska Basin and are interpreted to have been the result of this gas generation and violent escape to  
262 the atmosphere <sup>128,129,140,141</sup> (although at least some may have erupted later in the Triassic <sup>131</sup>).  
263 Contact metamorphism of organic-carbon rich sediments around large-scaled sill intrusions in Taimyr  
264 and the Tunguska Basin (Siberia) likely produced large quantities of isotopically light CO<sub>2</sub> and CH<sub>4</sub>  
265 capable of changing the C-isotope signature of the atmosphere and ocean <sup>21,125,129,138</sup>. Indeed, the  
266 onset of intrusive magmatism, given analytical uncertainty, coincides with the start of the negative  
267 shift in δ<sup>13</sup>C in the *C. yini* Zone (251.999 ± 0.039 Ma; Fig. 2 and 5) <sup>59</sup>, providing indirect support for  
268 this notion.

269 The third and last STLIP phase started at 251.483 ± 0.088 Ma with renewed lava extrusion (alkaline),  
270 and ongoing intrusive activity (alkaline and tholeiitic), in the Maymecha-Kotui 118 and Taimyr  
271 regions <sup>21</sup>. These magmas are interpreted as extremely deep and hot products of a volatile-rich source  
272 <sup>142</sup>, and were likely enriched in mantle-derived CO<sub>2</sub> <sup>121</sup>. A maximum age for the end of this phase,  
273 and STLIP activity overall, is placed at 250.2 ± 0.3 Ma <sup>18</sup>. A gradual recovery of the δ<sup>13</sup>C curve (BOX  
274 1) towards pre-extinction levels is observed in the sedimentary record during the third phase (Fig. 5).

275

## 276 **Environmental crises**

277 The consequences of the volcanic emissions from the STLIP are considered in this section, including  
278 the emissions produced by contact metamorphism caused by magmatic intrusions in the host rocks,  
279 mainly CO<sub>2</sub> and CH<sub>4</sub>, SO<sub>2</sub>, halogens (for example, Cl, F, Br and halocarbons) and metals (for  
280 example, Hg, Cu). The multiple effects of these emissions are considered separately and are likely to  
281 have operated at different stages in the history of the PTME crisis (Fig. 6). Inferred environmental  
282 crises include global warming, oceanic anoxia, oceanic acidification, and (potentially) ozone  
283 reduction, acid rain, and metal poisoning.

284 **Global warming.** Among the gases released by volcanism, SO<sub>2</sub> has the potential to trigger short-term  
285 cooling episodes over a duration only a little longer than the eruptive interval <sup>143,144</sup>. This is too short

286 an interval to be detectable, given temporal resolution possible in deep time. Furthermore, it is a moot  
287 point whether such brief cooling intervals are capable of causing appreciable environmental stress,  
288 although episodic cooling events set in a context of longer-term warming could have damaged the  
289 ecosystems<sup>144</sup>.

290 Instead, global warming, due to CO<sub>2</sub> and CH<sub>4</sub> emissions is the clearest signal to emerge from the  
291 eruption of LIPs. Temperatures across the PTB have been reconstructed using oxygen isotopes ( $\delta^{18}\text{O}$ )  
292 in conodont apatite and brachiopod calcite. Conodont  $\delta^{18}\text{O}$  data from low latitude sections from Iran  
293<sup>145,146</sup>, Armenia<sup>147</sup> and South China<sup>148–152</sup>, all indicate significant low-latitude warming of 8–10°  
294 C from the latest Permian to Early Triassic (Fig. 2 and 4). Despite differences between the analysed  
295 localities due to different palaeolatitude or depositional settings, calculated sea surface temperatures  
296 (SST) indicate pre-extinction (*C. nodosa*/*C. yini* Zone) SSTs of ~24–30°C that rapidly increased  
297 across the PTB and into the earliest Triassic SSTs (*C. isarcica* Zone), ultimately peaking at ~35–39°C  
298<sup>147</sup>. Conodont  $\delta^{18}\text{O}$  records indicate that temperatures increased over an interval of ~39 kyrs<sup>147</sup>,  
299 although curiously the warming slightly postdates the initial shift in carbonate  $\delta^{13}\text{C}$ <sup>147,151</sup> (Fig. 2).

300 Warming of 8–10° C likely resulted in a loss of performance of many marine organisms. High  
301 ambient temperatures increase metabolic activity and enhance oxygen demand, causing limited  
302 functional capacity of oxygen supply culminating in hypoxemia, anaerobic metabolism and loss of  
303 protein function<sup>153</sup>. Thermal tolerance of marine organisms is also linked with an organisms' level of  
304 metabolic activity, deoxygenation and also oceanic acidification<sup>154,155</sup>. Thus, warming may have  
305 been a major agent of the mass extinction. However, the first phase of the PTME occurred at the onset  
306 of warming when conditions may still have been relatively amenable (Fig. 2), and warming may have  
307 had a stronger role in the second extinction pulse in the earliest Triassic<sup>4</sup>. Lethally hot temperature  
308 may have induced selective extinction of marine animals and poleward migration<sup>148,156,157</sup>.

309 However, two opposite patterns of selective extinction across latitudes had been reported<sup>156,157</sup> one  
310 showing the highest extinction rate in the high latitudes<sup>157</sup>, the other documenting the highest rate in  
311 the tropics<sup>156</sup>. This discrepancy is likely due to the different statistical schemes used. Whilst higher  
312 polar extinction has been inferred, the study only considered the end-Permian extinction pulse<sup>157</sup>  
313 whilst higher tropical extinction is calculated considering two pulses (end-Permian and earliest  
314 Triassic)<sup>156</sup>. Likewise, in the marine fossil record of South China<sup>4</sup>, the calculated extinction rate is  
315 57% if only the first pulse is taken into account, and 93% including both pulses.

316 Poleward migration of about 10–15° is also observed in tetrapods<sup>148,158</sup>. In plants, elevated  
317 temperatures and droughts can inhibit photosynthesis, increase photooxidative stress due to higher

318 irradiance, burn leaves, and limit plants' growth and yield, and ultimately cause their death <sup>159</sup>.  
319 Warming could have also increased the prevalence of wildfire by increasing seasonality and drought  
320 (Fig. 3), for example as proposed for the records of South China where high charcoal abundance is  
321 found in strata recording the ~60 kyrs initial decline of  $\delta^{13}\text{C}$ , up to the onset of the marine crisis  
322 <sup>27,104,160</sup> (Fig. 2). Elevated fire activity would have aided post-fire run-off and erosion <sup>104</sup>.

323 However, the terrestrial extinction appears to have started before the warming trend inferred from the  
324  $\delta^{18}\text{O}$  of conodont apatite (Fig. 2 and 4). In South China, declining  $\delta^{13}\text{C}$  values coincide with high  
325 charcoal abundance <sup>27</sup> (Fig. 3) suggesting atmospheric  $p\text{CO}_2$  was increasing during the interval of  
326 higher wildfire activity. Also, along the northwestern margin of Pangea marine environmental stress  
327 began prior to the main extinction event, suggesting that higher latitude oceans were deteriorating as  
328 the terrestrial extinction initiated <sup>125,161,162</sup>. Curiously, these changes occurred prior to the warming  
329 trend recorded by conodont  $\delta^{18}\text{O}$  data.

330 **Oceanic anoxia.** The PTB coincides with a eustatic sea-level rise and the development of an oceanic  
331 anoxic event (OAE) [G] that has been directly implicated as a cause of the crisis <sup>163</sup>. However, marine  
332 anoxia during transgression is often encountered in the geological record, raising the question of why  
333 these conditions caused such a severe extinction crisis? There are likely to have been three reasons:  
334 the anoxia extended in some regions into extremely shallow waters <sup>164</sup>, although oxic refugia  
335 remained <sup>165</sup>; the Panthalassa superocean also become anoxic throughout much of the water column  
336 <sup>111,166</sup>; the OAE persisted, with varying intensities, for several million years into the Middle Triassic,  
337 prolonging the stressful conditions for marine life <sup>167-169</sup>. Thus, both the extent and duration of anoxia  
338 were exceptional by Phanerozoic standards.

339 Evidence for anoxia is diverse and found in a broad range of environments. Organic-rich, pyritic,  
340 black shales, the typical manifestation of anoxic deposition, are best developed in the deep ocean  
341 sections now found in the accreted terranes in Japan and New Zealand <sup>111,166,170</sup>. Black shales are less  
342 common in shelf and epicontinental seaways, especially in tropical settings, perhaps due to high  
343 organic matter remineralization rates in hot sea water. In the low-latitude carbonate setting of Tethys,  
344 anoxic facies are usually developed as laminated, pyritic micrites such as in northern Italy <sup>50</sup>. In  
345 northern Boreal shelf seas, anoxic facies include finely-laminated, argillaceous strata and pyritic  
346 sandstones with abundant framboidal pyrite [G] <sup>161,164</sup>.

347 Intensity of marine anoxia and its extent are inferred from geochemical data. The uranium isotope  
348 ratio of  $^{238}\text{U}/^{235}\text{U}$  recorded in limestones shows a shift to lower values immediately prior to the first  
349 phase of mass extinction (Fig. 2): a change attributed to the accelerated removal of  $^{238}\text{U}$  in anoxic

350 bottom waters<sup>171</sup>. The degree of anoxia driven metal drawdown was such that the oceans become  
351 depleted in trace metals<sup>172</sup>. The scale of anoxia also affected the ocean's sulphate budget.  
352 Increasingly heavy sulphate-sulphur isotope values in the Early Triassic, relates to removal of  
353 isotopically light pyrite sulphur, suggesting reduced seawater sulphate concentrations<sup>173</sup>. Biomarkers  
354 also provide evidence for oxygen-poor conditions including the presence of isorenieratane, an  
355 indicator that anoxic conditions extended into the photic zone<sup>174</sup>.

356 The development of intensive anoxia profoundly altered the oceans' nutrient structure. Phosphorus  
357 recycling enhances under anoxic conditions<sup>175</sup> and, when combined with higher continental runoff,  
358 this leads to high phosphorus availability in the water column. However, nitrogen rather than  
359 phosphorus was more likely the limiting nutrient in the anoxic oceans of the time<sup>176,177</sup>. Thus,  
360 nitrogen isotope ratios show a significant decrease, from values up to ~10‰ to ~0‰, in most of the  
361 basins across the PTB<sup>177,178</sup>. This suggests strong denitrification accompanied the onset of global  
362 anoxia, likely due to a fundamental shift from a nitrate-dominated to an ammonium-dominated  
363 nutrient supply which would normally favour nitrogen-fixing diazotrophs. However, diazotrophs  
364 require molybdenum and iron for nitrogen fixation and yet these are efficiently removed from anoxic  
365 waters, thereby causing a decrease in the ocean's total fixed-nitrogen and low levels of productivity  
366<sup>176</sup>. Some alternative scenarios favour productivity increase during the extinction interval, driven by  
367 enhanced nutrient run-off<sup>179</sup>, but these fail to account for the micronutrient limitations of diazotrophs  
368 in euxinic waters, as well as the absence of organic-rich shales in the Early Triassic<sup>180</sup>.

369 The ultimate cause of the Permian–Triassic OAE has long been attributed to the effects of STLIP with  
370 warming and more sluggish ocean circulation usually invoked<sup>111,163</sup>. The Community Earth System  
371 Model with its embedded biogeochemical cycles, shows that an 11°C sea-surface temperature rise (a  
372 realistic value supported by  $\delta^{18}\text{O}$  evidence<sup>148</sup>; Fig. 2 and 5), combined with increased freshwater  
373 runoff into high latitude seas, greatly increases ocean stratification and decreases meridional overturn  
374 circulation<sup>157</sup>. The result is a dramatic decrease in seafloor oxygenation. The model also successfully  
375 replicates regional variations with the best ventilated area shown to be the Perigondwanan margin of  
376 southern Tethys<sup>157</sup>, a finding that closely matches field evidence from this region<sup>54</sup>.

377 **Oceanic acidification.** Another potentially harmful effect of massive CO<sub>2</sub> injection into the  
378 atmosphere–ocean system is oceanic acidification (Fig. 6). Huge amounts of CO<sub>2</sub> entering the oceans  
379 acidifies water and decreases carbonate saturation. Evidence for oceanic acidification at the PTB  
380 comes from boron isotope ( $\delta^{11}\text{B}$ ) and calcium isotope ( $\delta^{44/40}\text{Ca}$ ) records<sup>43,181,182</sup> (Fig. 2), and the  
381 sediment record<sup>43,162,183</sup>. However, data from  $\delta^{11}\text{B}$  of bulk carbonates, used to signify acidification  
382 during the second phase of the PTME during the *I. isarcica* Zone<sup>184</sup>, are now generally considered

383 not to actually reflect marine pH<sup>185</sup>. Instead, a composite  $\delta^{11}\text{B}$  record from pristine brachiopod shells  
384 from the Southern Alps (Italy) and South China shows a decline in  $\delta^{11}\text{B}$  values, which suggests  
385 lowering of seawater pH, between the onset of the negative C-isotope excursion and the base of the  
386 *parvus* Zone, just above the PTB<sup>182</sup> (Fig. 2). This composite  $\delta^{11}\text{B}$  record needs, however, further  
387 validation in other sections and improvement of temporal resolution. Ooidal limestones are  
388 widespread during the inferred lower pH interval<sup>25</sup>, indicating saturated conditions, and the analysed  
389 brachiopods come from interbedded levels of microbialites<sup>182</sup>. The prevailing carbonates suggest that  
390 under saturation was not achieved. Acidification could have happened in very brief pulses, which are  
391 not recorded by low-resolution datasets, rather as a relatively longer event between the onset of the  
392 marine extinction and the earliest Triassic<sup>182</sup>.

393 A negative  $\delta^{44/40}\text{Ca}$  shift during the PTME interval has been linked to the injection of  $\text{CO}_2$  from the  
394 STLIP activity on the basis of its stratigraphic correlation with the negative  $\delta^{13}\text{C}$  excursion<sup>186</sup>.  
395 Instead of solely indicating oceanic acidification, Ca-isotope data modelling suggests that a complex  
396 scenario controlled seawater  $\delta^{44/40}\text{Ca}$  changes, involving  $\text{CO}_2$  release, acidification, reduced skeletal  
397 carbonate sink, enhanced weathering of shelf carbonates, changes in carbonate mineralogy and  
398 changes in seawater saturation state<sup>187,188</sup>. In detail though, the negative  $\delta^{13}\text{C}$  excursion (in bed 24 at  
399 Meishan) predates the negative  $\delta^{44/40}\text{Ca}$  shift (which occurs above bed 25<sup>186</sup>; Fig. 2), complicating the  
400 interpretation of the relationships between the Ca- and C-isotope records. Similar negative  $\delta^{44/40}\text{Ca}$   
401 excursions, recorded by both conodont apatite and bulk carbonate, are seen at the same stratigraphic  
402 interval in other localities<sup>188–191</sup>.

403 More indirect evidence for oceanic acidification comes from the fossil record which shows that the  
404 crisis saw the preferential extinction of physiologically unbuffered taxa, with low metabolisms and  
405 high energy demand for the production of calcium carbonate skeletons (for example corals,  
406 brachiopods, calcareous sponges, and foraminifera), whilst well-buffered taxa (for example bivalves,  
407 gastropods, ammonoids and conodonts) could have survived the crisis relatively better<sup>4,43,192</sup>.

408 Analysis of the microstructure of brachiopod shells provides evidence to suggest a role for  
409 acidification in brachiopod extinction losses. All brachiopod groups suffered severe losses with the  
410 diverse Strophomenata going extinct. The Rhynchonellata fared somewhat better and it has been  
411 suggested that their higher shell organic content enabled them to better survive acidified conditions  
412<sup>183</sup>. However, at lower taxonomic order the Rhynchonellata suffered severe losses and their story  
413 during the PTME could also be described as a successful re-radiation of the survivors in the earliest  
414 Triassic that saw some genera become widespread<sup>193</sup>. In addition, the preferential extinction of



415 coarsely ornamented ammonoids supports the pressure of oceanic acidification on shell-building costs  
416 for shelled animals <sup>194</sup>.

417 Along the north western margin of Pangea there is also a gradual loss of carbonate producers through  
418 the late Permian creating an empty ecologic niche that was filled by siliceous sponges expanding from  
419 deep environments to become the dominant organism in late Permian shallow shelves <sup>161,162</sup>,  
420 suggesting decreasing pH prior to the extinction.

421 **Ozone disruption.** High abundance of teratological sporomorphs during the PTME (Fig. 4) has been  
422 attributed to increased UV-B radiation due to disruption of the ozone layer <sup>76,78,81,195</sup>. Experiments on  
423 living *Pinus mugo* showed increasing exposure of plants to UV-B radiation induced malformation on  
424 pollen grains similar to those observed at the PTME and, although all trees survived, their fertility  
425 markedly decreased <sup>81</sup>. Therefore, higher UV-B radiation and lower plant fertility may have triggered  
426 a collapse of the whole terrestrial ecosystem by shutting down most primary productivity.

427 Ozone depletion could have been driven by the release of halogens and halocarbon compounds from  
428 volcanic activity and the combustion of coals and evaporites intruded by STLIP <sup>196–198</sup> (Fig. 5).  
429 However, the first explosive phase of STLIP activity appears to be coincident with the early terrestrial  
430 decline of plants and the first occurrences of teratological sporomorphs (Fig. 4), whilst the release of  
431 halocarbons (for example CH<sub>3</sub>Cl) from contact metamorphism (intrusive phase) is thought to have the  
432 strongest impact on the ozone layer <sup>197,198</sup>. Teratological sporomorphs are found throughout the  
433 PTME (Fig. 4), but ozone is quickly (~10 yrs) restored in the atmosphere, hence making a long-term  
434 disruption of the global ozone unlikely <sup>198</sup>.

435 **Acid rain.** Teratological sporomorphs (Fig. 4) alone are not a direct evidence of UV-B radiation, as  
436 they could be the result of other stresses such as acid rain <sup>81,198</sup> and metal poisoning <sup>82</sup>. Acid  
437 deposition can potentially kill plants, phytoplankton, vertebrates and invertebrates in terrestrial  
438 aquatic ecosystems, and acidification of non-calcareous soil results in leaching of important nutrients  
439 (Ca, Mg and K), with the effect of weakening plants and increasing their mortality rate <sup>199</sup>.

440 Magmatic degassing of SO<sub>2</sub> and halogens from STLIP could have driven acid rain <sup>198</sup>. Earth system  
441 modelling shows that, alongside the previously discussed ozone damage, S injected into the  
442 stratosphere during STLIP pyroclastic activity (Fig. 5) could have triggered extensive acid rains at the  
443 PTB, although these were only severe (pH = 2) in the Northern Hemisphere <sup>198</sup>.

444 Possible direct evidence of acid rain comes from one section in northern Italy, where the abundance of  
445 vanillin—a product of pH-dependent enzymatic decomposition of organic matter in soil—could



446 suggest pulses of soil acidification<sup>200</sup>. Vanillin peaks occur before the marine extinction interval  
447 (latest Permian)<sup>25</sup>. Hence, acid rains may have affected terrestrial ecosystems already before the  
448 onset of the marine extinction (Fig. 5). Significantly, PTB palaeosols in Antarctica show high  
449 chemical weathering but no indication of acid conditions; there was no leaching of Ca and Mg<sup>201</sup>.

450 Other geochemical evidence for acid rain comes from sulfur isotope and concentration records in the  
451 Karoo Basin (South Africa), where higher accumulation of sulfide was interpreted as the effect of  
452 high sulfate supply to the freshwater environment from acid rain<sup>202</sup>. However, the terrestrial  
453 extinction in the Karoo Basin began before the S geochemical changes, making their significance  
454 moot. Currently, except for these local datasets, there is no conclusive evidence that widespread acid  
455 rain triggered the terrestrial collapse in the latest Permian, especially not in the southern hemisphere.

456 ***Metal poisoning.*** Potentially, metal poisoning may have occurred in marine environments, where an  
457 increase of concentration of toxic metals (Hg, Cr, As, and Co) is observed<sup>125,126,161</sup>. High  
458 concentrations of Hg, the most toxic metal, may have been reached after the marine extinction, when  
459 the reduction of bioproductivity could have led to a decrease of Hg drawdown by organic matter and  
460 its potential build-up in marine environments to toxic levels, before it was removed by sulphide  
461 deposition<sup>126</sup>.

462 A coincidence between a peak of teratological lycophte spore tetrads [G] and high Hg and Cu  
463 concentrations has been found a short distance above the terrestrial extinction level in South China,  
464 indicating that the survivor plants might have experienced stress caused by higher metal  
465 concentrations in the environment<sup>82</sup> (Fig. 4). Reduced plant transpiration, changes to the hydrological  
466 cycle and climatic drying following terrestrial vegetation loss may have resulted in reduced water  
467 availability in freshwater ecosystems leading to such metal concentrations increase. Hg is generally  
468 thought to derive from volcanic activity<sup>203</sup>, but Hg isotopes and modelling of Hg cycling indicate  
469 that, superimposed on a general increase of volcanic Hg deposition across the PTME, further Hg  
470 could have been released into the environment due to massive oxidation of terrestrial organic matter  
471 and soil following the collapse of land ecosystems<sup>204</sup> (BOX 2). Similar behaviour could have sourced  
472 Cu<sup>82</sup>. Hence, the increase of metal loading in South China during the PTME might actually be the  
473 consequence of the demise of the *Gigantopteris* rainforests and wetland species<sup>204</sup>.

474

475 **Linking kill mechanisms and extinction patterns**

476 The latest high-resolution chronology of the PTME (Fig. 6) suggests that the terrestrial ecological  
477 disturbance could have started 60–370 kyr before the marine extinction<sup>26–28,95,101–103</sup>. This was  
478 coincidental with the initial, mostly explosive phase of STLIP. However, the temporal resolution of  
479 the terrestrial extinctions remains more poorly known than that of the marine extinctions and may  
480 have been spread over ~1 Myr<sup>95</sup>.

481 The terrestrial extinction mechanism is not clear, and mainly inferred by indirect, often local, and  
482 mainly palaeontological proxies (Fig. 6). Increased seasonality during the initial stage of the negative  
483  $\delta^{13}\text{C}$  (Fig. 6) could have led to increase of wildfires<sup>27</sup>. Declining  $\delta^{13}\text{C}$  values coeval with higher  
484 charcoal abundance suggest addition of isotopically light  $\text{CO}_2$  to the ocean–atmosphere system and  
485 that warming may have played a role. However, the available temperature proxy from marine settings  
486 (conodont  $\delta^{18}\text{O}$ ) suggests temperatures did not begin to increase until after the terrestrial crisis had  
487 begun (Fig. 2 and 5).

488 Temporal decoupling of terrestrial extinctions predating marine extinctions is intriguing and suggests  
489 spatial heterogeneity in the extinction patterns and potentially mechanisms. Delayed onset of marine  
490 extinctions may be partially related to thermal inertia of the oceans and their higher thermal capacity  
491 compared to land that heats and cools quicker<sup>205</sup>, but ocean turnover times occur in the order of 1000  
492 years<sup>206</sup> so are unlikely to have operated at a 60–370 kyrs time scale.

493 Terrestrial stress may have come from emissions of  $\text{SO}_2$  and halogens and their consequent acid rains  
494<sup>202</sup>, and disrupted ozone shield<sup>76,81</sup>. Increasing UV-B radiation on Earth's surface and acid  
495 depositions could have had lethal effects on terrestrial ecosystems, causing stress to the vegetation,  
496 lowering plants' fertility and eventually leading to their death, with repercussions at all higher trophic  
497 levels. However, long-term disruption of the global ozone during the PTME is unlikely<sup>198</sup>.

498 It is not clear what was the effect on marine ecosystems of the first phase of the STLIP activity (Fig.  
499 6). Beds of coal ash and associated Hg spikes are observed in northwest Pangea prior to the main  
500 negative  $\delta^{13}\text{C}$  excursion as well as Ni isotope anomalies that may record this initial phase of eruptions  
501 impacting the terrestrial environment<sup>125</sup>. This region also shows early marine stress<sup>161,162</sup>, while  
502 more equatorial records show no marine impacts.

503 The marine extinction interval has a clear, temporal link with the second mostly intrusive phase of the  
504 STLIP and gas emissions, and persisted for <100 kyrs straddling the PTB. There were two pulses of  
505 extinction intensity at the beginning and end of this interval although significant losses were also  
506 occurring in the interlude interval too.

507 Taxonomic, morphologic, and ecologic selectivity (Fig. 3) and the magnitude of marine extinction  
508 suggest that a combination of global warming, anoxia, and oceanic acidification best explains the  
509 marine PTME (Fig. 6). Groups intolerant to hypoxia and high temperature were preferentially  
510 eliminated during the PTME, suggesting that these stressors played an important role in the extinction  
511 of marine animals<sup>157,207</sup> (Fig. 3). Physiologically buffered taxa experienced lower extinction rates  
512 than unbuffered taxa<sup>42–44</sup> (Fig. 3). Oceanic acidification could have been an important stressor for  
513 shelled animals<sup>43</sup>, as also supported by the preferential extinction of coarsely ornamented ammonoids  
514<sup>194</sup> (Fig. 3). Survival animals migrated to higher latitudes or deep seawaters, possibly to escape the  
515 hot temperature in equatorial regions or surface seawaters<sup>56,148,156</sup> (Fig. 6).

516

### 517 **Summary and future directions**

518 The link between the PTME and the eruption of the STLIP has been well established since the late  
519 1990s<sup>17</sup>. Dramatically improved absolute dating has strengthened the link to the point where  
520 scenarios involving distinct stages of the emplacement history can be linked with consequent  
521 environmental changes (Fig. 6). The effects of the eruptions were likely experienced first in terrestrial  
522 settings, where plant productivity crashed and coal ceased to form, and in high-latitudes marine  
523 settings in the northern hemisphere. The initial explosive phase of the STLIP emplacement may have  
524 driven this crisis, including increased seasonality, ozone depletion, with higher UV-B radiation, and  
525 acid rain.

526 The marine mass extinction is coeval with the mainly intrusive phase of the STLIP. Increasing fossil  
527 and geochemical data resolution indicates that the marine mass extinction could have happened either  
528 in two distinct pulses or gradually within an interval straddling the PTB. The thermogenic gases  
529 produced by the interaction of magma with the intruded sediments introduced into the PTB  
530 atmosphere–ocean system triggered a rapid temperature rise, a decline in ocean ventilation, and ocean  
531 acidification, which led to the mass extinction. However, despite the large amount of available data  
532 and significantly improved geochronology, the reconstruction of the complex co-occurring phenomena  
533 interlinked in the fatal cascade that drove the PTME remains difficult.

534 Future research direction should aim at improving the spatial and temporal resolution of datasets from  
535 PTME terrestrial records. High-precision U-Pb dating of ash beds and detrital zircons, together with  
536 magnetostratigraphy and chemostratigraphy, will increase the chronological constraints of the  
537 terrestrial crisis, clarifying the delay between the beginning of the extinction on land and in the ocean.

538 Improved spatial coverage of high-precision stratigraphic syntheses will further evaluate extinction  
539 pattern heterogeneity.

540 Detailed evaluation of PTME palynological assemblages will give a more comprehensive picture of  
541 through-ranging taxa to understand dynamics and composition of upland “refugial” or survivor floras.  
542 The occurrence of teratologies in sporomorphs must be studied in different plants groups, at different  
543 latitudes and throughout the PTME, to identify their ultimate cause and understand whether it  
544 interested worldwide flora, and at which stages of the event. Further S-isotope and biomarker analysis  
545 of PTME terrestrial successions could strengthen the evidence of acid rains during the terrestrial  
546 extinction interval.

547 The temporal relationship between warming and extinction, both on land and on the ocean, remains  
548 problematic, and further studies, including modelling, should try to understand the apparent lags  
549 between the C-isotope, O-isotope, and fossil records. Future high-resolution studies ( $\delta^{18}\text{O}$  from  
550 conodont apatite or brachiopod shells) will be pivotal in detecting brief temperature changes on the  
551 already manifest long-term  $\text{CO}_2$ -driven warming trend. However, the current limitation is not the  
552 precision of  $\delta^{18}\text{O}$  analysis but sample availability. Higher resolution can only be achieved by  
553 decreasing the size of conodont samples taken in the field followed by SIMS analyses of individual  
554 conodont elements.

555 Further ecological and physiological studies are required to link environmental changes and extinction  
556 patterns. Quantitative predictions for extinction selectivity under different changing environmental  
557 conditions are needed to distinguish among potential killing stressors. More consistent geochemical  
558 ( $\delta^{11}\text{B}$ ) and palaeontological records of ocean saturation are necessary to properly investigate the role  
559 of ocean acidification.

560 Furthermore, future endeavours from the geochronology community should be focused on shedding  
561 more light on the temporal correlations between the intrusive and effusive realms of the STLIP, which  
562 are still weak. Moreover, since most of the STLIP deposits are covered, it is difficult to fully assess  
563 the true nature of the eruption history. Drilling programs could significantly expand the knowledge on  
564 the history of the STLIP emplacement. The voluminous tephra deposits and the explosive pipes are  
565 tangible proof of explosive activity of the STLIP and of gas discharge to the atmosphere. Clarifying  
566 the origin and timing of emplacement of these products and structures would contribute greatly to  
567 understanding the link between STLIP emplacement stages and global environmental changes.

568 Perhaps the most overriding question from the study of mass extinctions driven by volcanic  
569 emissions, of which the PTME is the key example, is what can it tells us about future climate trends.  
570 Clearly, extreme global warming can lead to severe consequences for the life but if these effects lie

571 tens of thousands of years in the future, then they are of no geopolitical concern. If changes occur  
572 over decades or centuries then their significance increases. Despite the great advances in resolving the  
573 details of the PTME, future studies of the crisis should attempt to decipher rates of change on 100–  
574 1000 year scale.

575

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577

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## 1195 AUTHOR CONTRIBUTIONS

1196 JDC coordinated the developing of the article. All authors contributed to the writing of the manuscript  
1197 and building of the figures.

## 1198 COMPETING INTERESTS

1199 The authors declare no competing interests.

1200 **DATA AVAILABILITY STATEMENT**

1201 Data from the Paleobiology Database used for the new calculation of the marine extinction rate are  
1202 available in the Supplementary Materials.

1203 **FIGURE CAPTIONS**

1204 **Figure 1. The Permian–Triassic mass extinction and its world.** The PTME, also known as the  
1205 “Great Dying”, is the largest extinction of the entire Phanerozoic, with severe losses both in marine  
1206 and terrestrial ecosystems. The PTME world consisted in one single continent (Pangea) surrounded by  
1207 a vast ocean (Panthalassa), and a giant gulf (Palaeo- and Neo-Thetys). The Siberian Traps Large  
1208 Igneous Province erupted 2–7 million km<sup>3</sup> of basalt in the northern hemisphere during the PTME. The  
1209 biological crisis was the result of the environmental changes triggered by the volcanic emissions from  
1210 the Siberian Traps, including the emissions produced by contact metamorphism caused by magmatic  
1211 intrusions in the host rocks, such as CO<sub>2</sub>, CH<sub>4</sub>, SO<sub>2</sub>, halogens and metals, into the Permo–Triassic  
1212 atmosphere–ocean system. **a)** Newly calculated Gap-filler (GF) extinction rates<sup>208</sup> (Supplementary  
1213 Note 1) for marine animals show the PTME stands out as the most severe extinction event compared to  
1214 other intervals. Along with the PTME, the Ordovician–Silurian, Frasnian–Famennian, end-Triassic,  
1215 end-Cretaceous mass extinctions are usually regarded as the largest extinction events of the  
1216 Phanerozoic, also known as the “Big 5”. **b)** Palaeogeographic reconstruction of Earth during the  
1217 Permo–Triassic transition. Palaeogeography is from ref.<sup>209</sup>. GSSP = Global Stratotype Section and  
1218 Point.

1219 **Figure 2. Marine mass extinction.** Pattern of the extinction in marine settings and major recorded  
1220 geochemical changes. High-resolution geochemical data coupled to species richness of different  
1221 marine groups. Palaeontological data show two extinction pulses spanning the Permian–Triassic  
1222 boundary (PTB). While the first pulse appears to be synchronous in different areas, the second major  
1223 pulse of extinction may have been diachronous. Geochemical changes mark the marine extinction  
1224 interval (the interval between the two pulses), and testify for major environmental changes coeval to  
1225 the biological crisis, as global warming ( $\delta^{18}\text{O}$ ), oceanic anoxia (Uranium-isotope,  $\delta^{238}\text{U}$ , and sulfur-  
1226 isotope of carbonate-associated sulphate,  $\delta^{34}\text{S}_{\text{CAS}}$ ), and ocean acidification (Boron-isotope,  $\delta^{11}\text{B}$ ,  
1227 calcium-isotope,  $\delta^{44/40}\text{Ca}$ ). Carbon-isotope ( $\delta^{13}\text{C}$ ) data come from the most updated compilations of  
1228 ref.<sup>210,211</sup>. Oxygen-isotope ( $\delta^{18}\text{O}$ ) data from conodont apatite are from StabisoDB (Stable Isotope  
1229 Database for Earth System Research)<sup>212</sup>.  $\delta^{18}\text{O}$  data measured with SIMS (Secondary Ion Mass  
1230 Spectrometer) have been corrected by a factor of -0.6‰ according to estimates by ref.<sup>213</sup> of the offset  
1231 between conodont *in-situ* SIMS and bulk IRMS (Isotope Ratio Mass Spectrometer) analyses.  
1232 Uranium-isotope ( $\delta^{238}\text{U}$ ) data are from ref.<sup>210</sup>.  $\delta^{34}\text{S}_{\text{CAS}}$  data are from ref.<sup>173,179,214</sup>.  $\delta^{11}\text{B}$  data from  
1233 brachiopod calcite are from ref.<sup>182</sup>.  $\delta^{44/40}\text{Ca}$  data are from ref.<sup>186</sup>. Species richness from numerous  
1234 PTB sections in South China is from ref.<sup>4</sup>. Genera richness from the Dolomites (Southern Alps, Italy)  
1235 is from refs.<sup>24,25</sup>.

1236 **Fig. 3. Extinction selectivity during the Permian–Triassic mass extinction.** The pattern of the  
1237 PTME suggests statistically significant extinction selectivity between different ecological groups,  
1238 shedding lights on the causes of the marine mass extinction. However, even if selectivity clearly  
1239 played a role, high extinction rates are recorded for all marine ecological groups. **a)** Summary of  
1240 extinction selectivity trends observed in marine animals: Based on refs. <sup>4,37,38,41–44,183,194</sup>. **b)** Extinction  
1241 magnitude among different ecological groups in South China <sup>4</sup>. There are significant differences  
1242 (Mann Whitney test,  $p < 0.05$ ) between extinction severity among different ecologic groups, i.e.,  
1243 nekton *vs* benthos, buffered *vs* unbuffered, bivalve *vs* brachiopod. Selectivity between motile and non-  
1244 motile animals appears to have been less significant ( $p = 0.05$ ). Bars represent 95% confidence  
1245 intervals. **c)** Ecological selectivity of global extinctions during the PTME <sup>43</sup>. A zero log-odds value  
1246 means there is no association between the ecological traits and extinction. The unbuffered and  
1247 carbonate-shell genera were preferentially killed ( $p < 0.05$ ). Selectivity between narrow-geographic-  
1248 and cosmopolitan-range genera is weaker. Selectivity among genera with calcite shell, infaunal, and  
1249 lower abundance of individuals is not significant ( $p > 0.05$ ).

1250 **Figure 4. Terrestrial mass extinction.** Pattern of the extinction in terrestrial settings and major  
1251 recorded geochemical changes. Organic C-isotope ( $\delta^{13}\text{C}_{\text{TOC}}$ ), Hg and Hg/TOC, and main biological  
1252 events from reference sections of the terrestrial PTME in Northwestern China <sup>102,215–217</sup>, South China  
1253 <sup>27,71,82</sup>, Sydney Basin <sup>26,67</sup> and Karoo Basin <sup>28,95</sup>, and correlation with the marine  $\delta^{13}\text{C}_{\text{carbonate}}$  and  
1254  $\delta^{13}\text{C}_{\text{TOC}}$  (Meishan only) records <sup>217</sup>. The  $\delta^{13}\text{C}_{\text{TOC}}$  record from Meishan has been used as a  
1255 chemostratigraphic tool to correlate the marine GSSP to the terrestrial sections of Northwestern China  
1256 <sup>217</sup>. Data from the terrestrial PTME records with high-resolution chemostratigraphic data and/or  
1257 redioisotopic ages, which allow correlation with the marine PTME, indicate that the terrestrial crisis  
1258 started before the marine mass extinction. *Gigantopteris* and *Glossopteris* forests collapsed 60 kyrs  
1259 (South China) <sup>27,204</sup> to 370 kyrs (Sydney Basin) <sup>26,67</sup> before the marine extinction. Wildfire activity  
1260 widespreadly increased <sup>27,67</sup>. Tetrapods experienced high extinction rates, probably over a relatively  
1261 long interval of up to  $\sim 1$  Myr <sup>95</sup>. Existing data strongly support that the terrestrial crisis started before  
1262 the global marine mass extinction. Evidence of also an earlier marine crisis come from high-latitude  
1263 northwestern margin of Pangea.

1264 **Figure 5. Link between Siberian Traps, extinction, C-cycle changes and global warming.**  
1265 Radiometric ages of the volcanic products (lava, tuff, and sills) of the Siberian Traps Large Igneous  
1266 Province (STLIP) and sedimentary Hg geochemistry (BOX 2) indicate this LIP was active during the  
1267 PTME, and was linked to injection of isotopically-light carbon into the Permian–Triassic atmosphere–  
1268 ocean system, as inferred by the C-isotopes ( $\delta^{13}\text{C}$ ) record (BOX 1), which raised  $p\text{CO}_2$  and increased  
1269 global temperature, as shown by O-isotopes ( $\delta^{18}\text{O}$ ) of conodont apatite. Different volcanic phases can

1270 be defined: a first mainly pyroclastic phase (lava and tuff), a second mainly intrusive phase (sills), and  
1271 a final extrusive phase. **a)** Schematic map of the STLIP (adapted from refs. <sup>119,129</sup>) showing the  
1272 predominance of lava, pyroclastic and subvolcanic magmatic products over cratonic and non-cratonic  
1273 regions of this vast province. M-K stands for Maymecha-Kotuy. **b)** Geochemical data linking the  
1274 STLIP to extinction and environmental changes. Dating U/Pb ages of intrusive and extrusive rocks of  
1275 the Siberian Traps are from ref. <sup>18,21</sup>. Hg and Hg/TOC data are from ref. <sup>218,219</sup>. Only Hg/TOC data  
1276 with TOC>0.2% have been plotted following the approach of ref. <sup>203</sup>. Source of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data as  
1277 in Fig. 2. Time span of marine and terrestrial extinction intervals are as defined in Fig. 2. The eruption  
1278 of STLIP was very likely the trigger of the Permian–Triassic mass extinction.

1279 **Figure 6. Extinction mechanisms.** Summary of the volcanically-triggered extinction mechanism  
1280 inferred from the geochemical, sedimentary and palaeontological record of the PTME and their  
1281 recorded effects on biota. The initial mainly extrusive–pyroclastic volcanic phase is coeval to the  
1282 initial terrestrial crisis, whilst the onset of intrusive volcanism is coeval with the marine extinction  
1283 interval. The different volcanic styles and linked injection of greenhouse gases, halogens and metals  
1284 (only the most relevant volcanic/volcanogenic gases are represented in the figure) in the end Permian–  
1285 earliest Triassic atmosphere–land–ocean system, triggered a cascade of environmental disturbances,  
1286 as summarized in the figure, which firstly affected terrestrial ecosystems and high-latitude marine  
1287 environments, and then marine biota. The effects of the environmental changes on the physiology and  
1288 ecology of terrestrial and marine biota were multiple, showing that a fatal combination of factors,  
1289 sustained for a relatively long interval and each having selective effects on biota, led to the most  
1290 severe extinction of the Phanerozoic.

1291

## 1292 **BOX 1: The Permian–Triassic boundary C-isotope record**

1293 Carbon isotopes ( $\delta^{13}\text{C}$ ) are used as a chemostratigraphic tool to correlate marine and terrestrial  
1294 successions around the world. Many high resolution  $\delta^{13}\text{C}$  records have been collected across the PTB  
1295 and they provide a powerful correlation tool, which helps identifying the PTME interval and link  
1296 biological and environmental phenomena recorded in different locations. Major  $\delta^{13}\text{C}$  shifts in  
1297 carbonate ( $\delta^{13}\text{C}_{\text{carbonate}}$ )<sup>220–223</sup>, and marine and terrestrial total organic carbon ( $\delta^{13}\text{C}_{\text{TOC}}$ )<sup>221,224,225</sup>, are  
1298 documented during the PTME (Figs. 2 and 3). A 3–6‰ negative  $\delta^{13}\text{C}_{\text{carbonate}}$  excursion begins  
1299 gradually in the lower *C. yini* Zone (*C. bachmanni* Zone) ~60 kyrs below the onset of the marine  
1300 crisis<sup>59,221</sup>, before accelerating to reach a minimum values in the earliest Triassic (*H. parvus* to early *I.*  
1301 *isostichia* Zone). Similar shifts are recorded by  $\delta^{13}\text{C}$  values from total organic matter, wood and  
1302 leaves, allowing correlation of non-marine to marine records (for example refs.<sup>217,225–228</sup>; Fig. 2 and  
1303 3). However, because  $\delta^{13}\text{C}_{\text{TOC}}$  is dependent on variable contributions of algal vs. bacterial and marine  
1304 vs. terrigenous organic matter, some records display non-parallel trends in  $\delta^{13}\text{C}_{\text{carbonate}}$  and  $\delta^{13}\text{C}_{\text{TOC}}$ , as  
1305 documented, for example, at Meishan GSSP section<sup>225</sup>. A variety of mechanisms were suggested to  
1306 explain the negative  $\delta^{13}\text{C}$  shifts by the addition of isotopically light carbon to the exogenic carbon-  
1307 cycle reservoirs. Besides soil erosion, reduced primary productivity and destabilization of gas  
1308 hydrates, Siberian Traps volcanism and related processes were favoured as the ultimate cause.  
1309 Identification of the source of the isotopically light carbon and its  $\delta^{13}\text{C}$  signature is critical to estimate  
1310 the amount of carbon transferred into the PTB atmosphere–ocean system, and to model atmospheric  
1311  $p\text{CO}_2$  increase, temperature rise and seawater pH decline.

1312

1313

1314

1315 **BOX 2: Tracing Siberian Traps activity in the sedimentary record**

1316 Significant increases in mercury (Hg) concentrations above background occur at marine and terrestrial  
1317 PTME boundaries globally, and have been attributed to Hg emissions from the Siberian Traps Large  
1318 Igneous Province (STLIP)<sup>27,126,203</sup>. If correct, Hg serves as a ‘fingerprint’ of STLIP in the  
1319 sedimentary record, allowing temporal correlation between the eruption and the extinction with  
1320 resolution on a millennial time scale<sup>229</sup>. As a volatile gas Hg has sufficient atmospheric residence  
1321 time for inter-hemispheric mixing, until eventually being transferred through wet or dry deposition to  
1322 the marine and terrestrial environment, and after going through various biogeochemical cycling,  
1323 eventual geologic sequestration in sediments<sup>203,229</sup>. In theory then, enhanced Hg emissions related to  
1324 the STLIP should be recorded as an Hg spike in sediments<sup>229</sup>. This is not definitive though as  
1325 concurrent changes in sequestration pathways, such as enhanced bioproductivity and consequent  
1326 increased organic matter drawdown, could also create Hg spikes. Careful analyses of Hg data and  
1327 sequestration pathways is required before a linkage with STLIP is possible. Stable isotope data (Fig.  
1328 3), particularly mass independent fractionation (MIF), support Hg anomalies in offshore marine  
1329 deposits being largely derived from a volcanic source<sup>203</sup>. However, these same data show nuances in  
1330 the Hg cycle. Nearshore deposits have Hg spikes with a MIF signature of terrestrial vegetation<sup>203</sup>,  
1331 likely related to devastation of forest and swamp ecosystems at that time<sup>203,204</sup>. Whether Hg  
1332 anomalies are directly from volcanos, or indirectly from terrestrial reservoirs released through STLIP  
1333 induced global warming, they both serve as a fingerprint (or LIP mark) of STLIP. Resolving the  
1334 relative Hg pathways requires further work, along with understanding of how terrestrial and marine  
1335 Hg records can be used to resolve the apparent diachronous extinction. Figure is adapted from ref.<sup>203</sup>

1336

1337 **GLOSSARY (in alphabetic order)**

1338

1339 ALKALINE

1340 Any rock of a magmatic series presenting a high content of alkali ( $\text{Na}_2\text{O}$  and  $\text{K}_2\text{O}$ ) relative to silica  
1341 ( $\text{SiO}_2$ ).

1342

1343 BIOSTRATIGRAPHY

1344 Technique to determine the relative age of sedimentary rocks using their fossil content.

1345

1346 CHEMOSTRATIGRAPHY

1347 The study of geochemical variations in sedimentary rocks; Globally-recorded chemostratigraphic  
1348 changes are used to correlate sedimentary sequences.

1349

1350 CONODONT

1351 The hard part of an extinct jawless vertebrates, similar to an eel.

1352

1353 EVOLUTIONARY FAUNA

1354 A fauna type that typically shows an increase in biodiversity following a logistic curve, i.e., Cambrian  
1355 fauna, Paleozoic fauna, and Modern fauna.

1356

1357 FRAMBOIDAL PYRITE

1358 Aggregates of pyrite (sulfide mineral,  $\text{FeS}_2$ ) with a “raspberry” (“la framboise” in french) aspect. It is  
1359 used as a palaeo-redox proxy.

1360

1361 GSSP

1362 Global Stratotype Section and Point. Reference stratigraphic section and level where boundaries  
1363 between geological stages, for example between the Permian and the Triassic, are defined.

1364

1365 JUVENILE VOLATILE

1366 A gas species that is dissolved in, or exsolved from, a magma, and is thus newly introduced to the  
1367 atmosphere when the magma reaches the Earth's surface.

1368

1369 LARGE IGNEOUS PROVINCE

1370 Rapidly emplaced (<1–5 Myrs) volcanic provinces with areal extents  $>0.1$  million  $\text{km}^2$  and volumes  
1371  $>0.1$  million  $\text{km}^3$ .

1372

1373 MASS EXTINCTION

1374 Global biological events of greatly elevated extinction rates.

1375

1376 OCEANIC ANOXIC EVENT

1377 Interval of severely reduced dissolved oxygen content in the ocean.

1378

1379 ORIGINATION RATES

1380 The ratio of the number of newly occurring species/genera to the total number over a given geological  
1381 period.

1382

1383 PYROCLASTIC

1384 Volcanic rock composed by fragmented pieces of lava. Coarser pyroclastic fragments accumulate in  
1385 proximity to the erupting vent, while finer particles can travel hundreds of kilometres.

1386

1387 PYROXENITIC MANTLE SOURCE

1388 A mantle source dominated by the presence of pyroxene and by paucity or lack of olivine. They  
1389 represent enriched and very fertile mantle lithologies.

1390

1391 RADIOISOTOPE DATING

1392 Technique to determine the absolute age of rocks using radioactive decay.

1393

1394 SIGNOR-LIPPS EFFECT



1395 A paleontological principle which states that the fossil record of organisms is never complete.  
1396  
1397 SILL  
1398 A tabular subvolcanic magma-body, emplaced roughly concordant or to the general bedding  
1399 (stratification or layering) of its host-rocks.  
1400  
1401 SPORE TETRAD  
1402 Four connected immature spore grains in tetrahedral or tetragonal fashion produced by meiotic  
1403 microsporogenesis.  
1404  
1405 TERATOLOGICAL SPOROMORPHS  
1406 Pollen and spores that present congenital abnormalities, such as lack of full development and  
1407 malformations in their structure.  
1408  
1409 THOLEIITIC  
1410 Sub-alkaline series of magmatic rocks, which undergo iron enrichment during differentiation due to  
1411 their poorly oxidised state. Tholeiites are the products of extensive melting of the mantle.  
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