

# Mass extinctions drove increased global faunal cosmopolitanism on the supercontinent Pangaea

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1 **Mass extinctions drove increased global faunal cosmopolitanism on the supercontinent**  
2 **Pangaea**

3

4 David J. Button<sup>1,2,3\*</sup>, Graeme T. Lloyd<sup>4</sup>, Martín D. Ezcurra<sup>1,5</sup>, and Richard J. Butler<sup>1\*</sup>

5 <sup>1</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham,  
6 Edgbaston, Birmingham, B15 2TT, United Kingdom.

7 <sup>2</sup>Current address: North Carolina Museum of Natural Sciences, Raleigh, NC 27607, USA;  
8 david.button44@gmail.com

9 <sup>3</sup>Current address: North Carolina State University, Department of Biological Sciences, 3510  
10 Thomas Hall, Campus Box 7614, Raleigh, NC 27695, USA.

11 <sup>4</sup>School of Earth and Environment, Maths/Earth and Environment Building, The University  
12 of Leeds, Leeds, LS2 9JT, United Kingdom.

13 <sup>5</sup>Sección Paleontología de Vertebrados, CONICET–Museo Argentino de Ciencias Naturales  
14 "Bernardino Rivadavia", Avenida Ángel Gallardo 470, Buenos Aires, C1405DJR, Argentina.

15

16 Correspondence and requests for materials should be addressed to D.J.B. (email:  
17 david.button44@gmail.com) or R.J.B. (email: r.butler.1@bham.ac.uk).

18 **Editor’s summary:** Mass extinctions are thought to produce ‘disaster faunas’, communities  
19 dominated by a small number of widespread species. Here, Button and colleagues develop a  
20 phylogenetic network approach to test this hypothesis and find that mass extinctions did  
21 increase faunal cosmopolitanism across the supercontinent Pangaea during the late  
22 Palaeozoic and early Mesozoic.

23 **Abstract:** Mass extinctions have profoundly impacted the evolution of life through not only  
24 reducing taxonomic diversity but also reshaping ecosystems and biogeographic patterns. In  
25 particular, they are considered to have driven increased biogeographic cosmopolitanism, but  
26 quantitative tests of this hypothesis are rare and have not explicitly incorporated information  
27 on evolutionary relationships. Here we quantify faunal cosmopolitanism using a phylogenetic  
28 network approach for 891 terrestrial vertebrate species spanning the late Permian through  
29 Early Jurassic. This key interval witnessed the Permian-Triassic and Triassic-Jurassic mass  
30 extinctions, the onset of fragmentation of the supercontinent Pangaea, and the origins of  
31 dinosaurs and many modern vertebrate groups. Our results recover significant increases in  
32 global faunal cosmopolitanism following both mass extinctions, driven mainly by new,  
33 widespread taxa, leading to homogenous “disaster faunas”. Cosmopolitanism subsequently  
34 declines in post-recovery communities. These shared patterns in both biotic crises suggest  
35 that mass extinctions have predictable influences on animal distribution and may shed light  
36 on biodiversity loss in extant ecosystems.

37

38 Earth history has been punctuated by mass extinction events <sup>1</sup>, biotic crises that  
39 fundamentally alter both biodiversity and biogeographic patterns <sup>1,2</sup>. A common  
40 generalisation is that mass extinctions are followed by periods of increased faunal  
41 cosmopolitanism <sup>1-4</sup>. For example, the Early Triassic aftermath of the Permian-Triassic mass  
42 extinction, the largest extinction event known <sup>5,6</sup>, has been considered as characterized by a  
43 globally homogeneous ‘disaster fauna’ dominated by a small number of widely distributed  
44 and abundant taxa <sup>1,3,6-8</sup>. Similar patterns have been proposed for the aftermath of the mass  
45 extinction at the end of the Triassic <sup>9</sup>. However, explicit quantitative tests of changes in  
46 cosmopolitanism across mass extinctions are rare and have been limited to small  
47 geographical regions <sup>3</sup> or have not incorporated information from evolutionary relationships  
48 (phylogeny) <sup>2,3</sup>.

49 In order to test the impact of mass extinctions on biogeographic patterns, a method for  
50 quantifying relative changes in cosmopolitanism through time is required. Sidor *et al.* <sup>3</sup>  
51 proposed that spatial occurrence data can be modelled as a bipartite taxon-locality network,  
52 specifying the distribution of fossil taxa (e.g., species) within defined localities (e.g.,  
53 geographic areas such as continents or basins). The biogeographic structure of this network  
54 can then be quantified. Faunal heterogeneity (or biogeographic connectedness, BC) can be  
55 measured as the rescaled density of the network – the number of taxa actually shared between  
56 localities relative to the total possible number of taxon links between them<sup>3</sup> (Fig. 1a, b).  
57 Higher values of BC equate to increased cosmopolitanism (i.e., less heterogeneity), whereas  
58 decreases in BC indicate increasing faunal endemism or provinciality (i.e., greater  
59 heterogeneity). This approach has been previously applied to assess regional changes in  
60 cosmopolitanism within southern Gondwana across the Permian-Triassic mass extinction <sup>3</sup>.  
61 Results indicated a decline in BC from the late Permian to the Middle Triassic, indicating that  
62 cosmopolitanism increased following the extinction event. However, this study did not

63 include the critical immediate post-extinction faunas (earliest Triassic), and it is also unclear  
64 whether this regional signal is representative of global biogeographic trends.

65 This network method uses only binary presence-absence data – i.e., information on  
66 whether a given species was present (and sampled) within a given locality or not. It does not  
67 explicitly incorporate information on the supra-specific phylogenetic relationships between  
68 taxa, such as could be used to estimate phylogenetic distance present between different  
69 species present at different localities. As such, it may be difficult or impossible to apply to a  
70 global fossil record dominated by singletons (species occurring at just one locality), as is  
71 common for tetrapods. Moreover, the results are potentially sensitive to systematic variation  
72 in taxonomic practice (i.e., ‘lumping’ versus ‘splitting’) and differential temporal and spatial  
73 sampling. Consequently, it may be useful to consider how closely related sets of species from  
74 pairs of localities are on a continuous scale.

75 Here we present a modification of this network model that addresses these issues by  
76 incorporating phylogenetic information into the calculation of BC. Rather than treating links  
77 between taxa in different geographic regions in a binary fashion, they are instead inversely  
78 weighted in proportion to the phylogenetic distance between them (Fig. 1a, c). These  
79 reweighted links are then used to calculate phylogenetic biogeographic connectedness (pBC).  
80 As with BC, higher levels of pBC equate to more cosmopolitan faunas, with less  
81 phylogenetic distance between sets of species from pairs of localities. By contrast, lower  
82 values of pBC indicate greater endemism, and increased phylogenetic disparity between sets  
83 of species from pairs of localities. This method was applied using an informal supertree  
84 (figure 2a; Supplementary Note 1) and species-level occurrence dataset of terrestrial amniotes  
85 ranging from the late Permian to late Early Jurassic (c. 255–175 Ma; see Supplementary Note  
86 2). A k-means cluster analysis was used to group taxa into ten distinct geographical regions  
87 based on their occurrence palaeocoordinates (figure 2b; Supplementary Information Note 3).

88 The sampled interval includes the Permian-Triassic and Triassic-Jurassic mass extinction  
89 events, and the origins of key terrestrial vertebrate clades such as crocodylomorphs,  
90 dinosaurs, lepidosaurs, mammaliaforms, pterosaurs, and turtles<sup>9</sup>. It is of particular  
91 biogeographic interest due to the presence of the supercontinent Pangaea<sup>10</sup>, which began to  
92 break apart by the Early Jurassic. Although barriers to dispersal might be perceived as sparse  
93 on a supercontinent, numerous studies have suggested faunal provinciality and endemism on  
94 Pangaea, perhaps driven by climatic variation<sup>3,9,11-13</sup>. Our methodological approach allows  
95 patterns of global provincialism to be quantified, and the impact of mass extinctions on  
96 faunal cosmopolitanism tested, within an explicit phylogenetic context. Results demonstrate  
97 the evolution of relatively cosmopolitan ‘disaster faunas’ following both the Permian-Triassic  
98 and Triassic-Jurassic mass extinctions, suggesting that mass extinctions may have common  
99 biogeographical consequences.

100

## 101 **Results**

102 **Global phylogenetic network biogeography results.** A marked and significant increase in  
103 global phylogenetic biogeographic connectedness (pBC) is observed across the Permian-  
104 Triassic mass extinction (Fig. 3). A gentle, non-significant, decrease occurs from the Early  
105 Triassic to the Middle Triassic. This is followed by a strong, significant decrease to minimum  
106 pBC values (and so maximum provincialism) in the Late Triassic. A significant increase in  
107 pBC is then observed after the Triassic-Jurassic mass extinction, in the early Early Jurassic,  
108 although pBC does not reach the levels seen in the Early Triassic. Phylogenetic BC declines  
109 to levels similar to those seen in the Late Triassic by the end of the Early Jurassic. These  
110 results show no correlation with the number of taxa or regions sampled in each time bin

111 (Supplementary Note 4, Supplementary Figs 1, 2, 3) and appear robust to variance in time bin  
112 length (Supplementary Figs 3d, 4).

113 Results for non-phylogenetic network biogeographic connectedness (non-  
114 phylogenetic BC) of the global dataset significantly differ from the phylogenetic results (Fig.  
115 3). An overall decline in non-phylogenetic BC is still observed through the Triassic, but  
116 differences between the Lopingian, Early Triassic, and Middle Triassic time bins are not  
117 significant. In addition, no increase in non-phylogenetic BC is observed over the Triassic-  
118 Jurassic boundary.

119 **Global analysis of taxon subsets.** An increase in global pBC across a mass extinction  
120 boundary may result from preferential survivorship of cosmopolitan lineages<sup>8,14-17</sup>, radiation  
121 of opportunistic ‘disaster taxa’<sup>6</sup>, or both. In order to test which of these processes drove  
122 observed increases in global pBC, we carried out additional analyses on subsets of our data.  
123 The first set of comparisons was restricted to those less inclusive clades that exhibit high  
124 levels of survivorship across each extinction event, thereby removing the influence of  
125 preferential extinction and focusing on patterns for clades established prior to the extinction.  
126 Among these taxa, a significant change in pBC is no longer observed across the Permian-  
127 Triassic boundary (Fig. 4a), although the increase across the Triassic-Jurassic mass extinction  
128 remains significant (Fig. 4b). The second set of comparisons focused on novel, recently-  
129 diverging clades, and demonstrates very high levels of pBC for these taxa in both the Early  
130 Triassic and the earliest Jurassic, significantly greater than total pBC in both these and the  
131 preceding time bins (Fig. 4a, b). Comparison of recently diverging clades in all time bins  
132 recovers the same signal as that from the total dataset (Supplementary Note 5, Supplementary  
133 Fig. 5), indicating that variation in pBC is not a result of differences in average clade age in  
134 each time bin.

135 **Geographically localised analyses.** To compare hemispherical trends in biogeographic  
136 connectedness, pBC was also calculated for Laurasia and Gondwana separately. The signal  
137 from Laurasian occurrences matches very closely with the global pattern (Fig. 5a). By  
138 contrast, patterns in Gondwana diverge markedly from global trends in the latest Triassic,  
139 where pBC abruptly rises, and then gradually declines through the Early Jurassic (Fig. 5a).

140 In addition, pBC analysis was implemented on terrestrial amniote occurrences from  
141 the southern Gondwanan dataset of Sidor *et al.*<sup>3</sup>. This dataset groups taxa at a geological  
142 basin, rather than broader regional, level; as a consequence, this analysis indicates how pBC  
143 differs at geographically smaller scales. Biogeographic connectedness is lower in the Middle  
144 Triassic than in the late Permian under both phylogenetic and non-phylogenetic treatments of  
145 these data (Fig. 5b); however, the result is not significant for phylogenetic BC.

## 146 **Discussion**

147 The Triassic represents an important time in the evolution of vertebrate life on land. It  
148 witnessed a series of turnover events that resulted in a major faunal transition from  
149 Palaeozoic communities, dominated by non-mammalian synapsids and parareptiles, to more  
150 modern faunas including clades such as crocodylomorphs, dinosaurs, lepidosaurs,  
151 mammaliaforms, and turtles<sup>9,18</sup>. Our novel phylogenetic network approach helps to place  
152 these major faunal transitions of the Triassic within a global biogeographical context by  
153 allowing changes in faunal connectivity to be quantified within an explicit evolutionary  
154 framework.

155 Our results demonstrate an overall decrease in pBC from the Lopingian to the Early  
156 Jurassic, but punctuated by significant increases across both the Permian-Triassic and  
157 Triassic-Jurassic mass extinction events. This provides quantitative support for classically  
158 held hypotheses about the presence of a global cosmopolitan fauna in the aftermath of and in



159 response to these events <sup>2,3</sup>. The robustness of these results to sampling variation and variable  
160 time bin length supports their interpretation as real biogeographical signals.

161 Our taxon subset analyses were explicitly aimed at disentangling the impact of  
162 alternative mechanisms that could lead to this pattern of increased post-extinction pBC.  
163 Novel clades, those diverging immediately prior to or immediately after each mass extinction,  
164 were analysed separately and exhibit relatively high levels of pBC (i.e., increased  
165 cosmopolitanism relative to the preceding time bin) in both the Early Triassic and earliest  
166 Jurassic (Fig. 4a, b). By contrast, surviving clades, those well-established prior to the  
167 extinction and extending through it, exhibit no increase across the Permian-Triassic boundary  
168 and only a moderate increase across the Triassic-Jurassic boundary (Fig. 4b). This indicates  
169 that the increases in pBC following each extinction were primarily driven by the  
170 opportunistic radiation of novel taxa to generate cosmopolitan ‘disaster faunas’, rather than  
171 being due to preferential extinction of endemic taxa <sup>19</sup>. Recently-diverging clades in other  
172 time bins do not exhibit elevated pBC (Supplementary Note 5) and there is no correlation  
173 between pBC and average branch length in each time bin (Supplementary Note 6,  
174 Supplementary Fig. 6), indicating that this result is due to abnormal conditions following  
175 each mass extinction as opposed to being a property of clade age.

176 The global biogeographic restructuring of biological communities associated with  
177 these mass extinction events hence provides evidence of the release of biotic constraints <sup>3</sup>,  
178 which would have facilitated the radiation of new or previously marginal groups, such as  
179 archosaurs following the Permian-Triassic mass extinction <sup>3</sup>, and dinosaurs and  
180 mammaliaforms during the Early Jurassic <sup>20,21</sup>. This highlights the importance of historical  
181 contingency in the history of life, where unique events such as mass extinctions have exerted  
182 strong influences on the subsequent macroevolutionary patterns observed in deep time <sup>22-24</sup>.

183           The global pBC pattern recovered here differs from the more geographically focused  
184 and temporally limited non-phylogenetic study of Sidor *et al.*<sup>3</sup>, which found Middle Triassic  
185 levels of BC in southern Pangaea to be lower than those seen in the late Permian. Reanalysis  
186 of the amniote occurrences from the basin-level dataset of Sidor *et al.* demonstrates that pBC  
187 also declines between these time bins, although not significantly (Fig. 5b). Looking more  
188 broadly, pBC trends in Gondwana differ from those seen in Laurasia (Fig. 5a). This is  
189 particularly evident in the Late Triassic and Early Jurassic, in which a significant increase  
190 and decrease in pBC is seen in Laurasia for each time bin, respectively, but not in Gondwana  
191 (Fig. 5a).

192           These results suggest that localised biogeographic patterns within Gondwana may  
193 have been decoupled from those seen elsewhere in the northern hemisphere. This would  
194 corroborate previous work suggesting the evolution of a distinct fauna, that includes  
195 massopodan sauropodomorphs, ornithischians, basal saurischians, and prozostrodonian  
196 cynodonts as relatively common taxa in South America and Africa during the Late Triassic  
197<sup>11</sup>. The occurrences of guaibasaurids<sup>25</sup> and floral similarities<sup>26,27</sup> provide some links between  
198 South American communities and the upper Maleri Formation of India, although the latter  
199 assemblage remains relatively poorly-known and sampled. The Triassic-Jurassic mass  
200 extinction was a global event<sup>19</sup> and it is unclear why decoupling of biogeographic trends  
201 within Gondwana should occur. Sampling within Gondwana during this interval is uneven,  
202 with the bulk of occurrences coming from palaeolatitudes between 30-60°S (see  
203 Supplementary Note 4). During the Late Triassic the 30-60° latitudinal belts were dominated  
204 by subtropical desert<sup>28</sup>. Interestingly, whereas this biome was more fragmented by seasonally  
205 wet conditions through into the Jurassic within Laurasia, it remained relatively stable in  
206 Gondwana<sup>26,28</sup>. It is possible that this stability may have contributed to the evolution of a  
207 distinct fauna in the southern hemisphere. Alternatively, however, this distinct Gondwanan

208 pattern may be a sampling artefact. Although the inclusion of phylogenetic information  
209 allows the approach used here to incorporate more data than previous methods, sampling of  
210 latest Triassic and earliest Jurassic Gondwanan localities is relatively poor and uneven,  
211 leading to the low statistical power of results within these time bins. In the earliest Jurassic, in  
212 particular, over 80% of Gondwanan tetrapod occurrences are from the upper Elliot and  
213 Clarens formations of South Africa. Further evaluation of this possible signal will require  
214 sampling of new Late Triassic and Early Jurassic Gondwanan localities, particularly from  
215 India and Antarctica.

216 Under our non-phylogenetic network analysis of the global dataset, no increase in BC  
217 is observed across the Triassic-Jurassic boundary; indeed, no significant differences are  
218 observed between any consecutive time bins (Fig. 3). This highlights the importance of  
219 including phylogenetic information in global analyses such as that conducted here; without  
220 the incorporation of phylogeny, aspects of biogeographic signal may be obscured. The  
221 decline of pBC to minimal levels towards the end of the Triassic supports hypotheses of  
222 strong faunal provinciality and increased endemism within Pangaea during the early  
223 Mesozoic<sup>3,9,12,13,29</sup>. The distribution of Late Triassic tetrapods varies with latitude<sup>9,11-13</sup>, a  
224 pattern also observed in terrestrial floras<sup>9,27</sup>. This is somewhat unexpected, given that  
225 oceanic barriers to dispersal were scant<sup>30</sup> and the latitudinal temperature gradient was weak  
226<sup>28</sup> in Pangaea during the Late Triassic. Instead, the ‘mega-monsoonal’ climate of Late  
227 Triassic Pangaea<sup>28</sup> would have driven provinciality of faunas through strong latitudinal and  
228 seasonal variation in precipitation<sup>12,13</sup>. Patterns of endemism farther back into the Palaeozoic  
229 are presently unclear because the Lopingian was preceded by a poorly-understood period of  
230 taxonomic turnover during the Guadalupian<sup>31</sup>. Analysis of older Palaeozoic time bins will be  
231 required to elucidate changes in endemism during the earlier history of Pangaea.

232           This background trend of increasing endemism contrasts sharply with the increase in  
233 pBC immediately following each mass extinction. This highlights the unique  
234 macroevolutionary regimes associated with mass extinctions<sup>24,32</sup>, with post-extinction  
235 ‘disaster faunas’ being the result of the abnormal selective conditions operating in the wake  
236 of these crises. An increase in global cosmopolitanism, with a prevalence of ‘disaster taxa’,  
237 has also been observed in marine invertebrates across the Ordovician-Silurian<sup>33,34</sup>, Permian-  
238 Triassic<sup>35,36</sup>, and Cretaceous-Palaeogene<sup>14</sup> mass extinctions, although these studies have not  
239 explicitly incorporated phylogenetic data. Similarly, more generalized insect-plant  
240 associations show higher survivorship across the Cretaceous-Tertiary mass extinction<sup>37</sup> and,  
241 on the smaller scale, Pleistocene-Holocene warming resulted in a greater unevenness of small  
242 mammal faunas in northern California<sup>38</sup>. Our demonstration of a similar signal in terrestrial  
243 communities in the latest Palaeozoic and early Mesozoic suggests that mass extinctions exert  
244 predictable biogeographical influences. However, the Permian-Triassic and Triassic-Jurassic  
245 events may be unique amongst terrestrial mass extinctions due to the presence of Pangaea,  
246 where the perceived reduction in barriers to overland dispersal might have facilitated the  
247 development of high levels of terrestrial cosmopolitanism. Extending the methodology  
248 employed here to other extinction events, such as for terrestrial faunas across the Cretaceous–  
249 Palaeogene boundary, will provide further tests of generalizable biogeographic trends across  
250 different mass extinction events.

251           These common trends observed in the fossil record have the potential to inform  
252 modern conservation efforts, given that the current biodiversity crisis is acknowledged as  
253 representing another mass extinction event<sup>39</sup>. Global homogenisation due to human  
254 activities, such as landscape simplification<sup>40</sup>, ecosystem disruption<sup>40–42</sup>, anthropogenic  
255 climate change<sup>4,38,42</sup>, and introduction of exotic species<sup>42–44</sup>, represents a principal threat to  
256 contemporary biodiversity<sup>43,45</sup>. Ongoing extinction will exacerbate this<sup>42,43</sup> with a shift

257 towards a more generalised ‘disaster’ fauna projected on the basis of current trends<sup>4,46</sup>. The  
258 observation of global collapse in biogeographic structure accompanying previous mass  
259 extinctions, as documented here, corroborates this and is of key importance in forecasting the  
260 biological repercussions of the current biodiversity crisis.

261

## 262 **Methods**

263 **Phylogeny.** An informal supertree of 1046 early amniote species ranging from 315–170 Ma  
264 was constructed from pre-existing phylogenies (Fig. 2a; see Supplementary Note 1,  
265 Supplementary Data 1). We used an informal supertree approach rather than a formal  
266 supertree in order to maximise taxonomic sampling, including species that have not been  
267 included in quantitative phylogenetic analyses. In addition to the taxa included in the  
268 biogeographic connectedness analyses, this sample included some stratigraphically older taxa  
269 in order to more accurately date deeper nodes. In order to account for phylogenetic  
270 uncertainty, 100 time-calibrated trees, with random resolution of polytomies, were produced  
271 from this supertree utilizing the ‘timePaleoPhy’ function of the paleotree package<sup>53</sup> in R  
272 (version 3.2.3; 34). Trees were dated according to first occurrence dates, with a minimum  
273 branch length of 1 Myr.

274

275 **Taxon occurrences and ages.** A global occurrence database of 891 terrestrial amniote  
276 species was assembled, primarily from the Paleobiology Database<sup>47</sup>, with the addition of  
277 some occurrences from the literature (see Supplementary Note 2, Supplementary Data 2).  
278 Taxa were dated at stage level. They were then placed in the following time bins for analysis:  
279 Lopingian, Early Triassic (Induan and Olenekian), Anisian, Ladinian, early Late Triassic  
280 (Carnian–early Norian), late Late Triassic (late Norian–Rhaetian), early Early Jurassic

281 (Hettangian, Sinemurian), and late Early Jurassic (Pliensbachian, Toarcian). The Late  
282 Triassic was not split into its constituent stages due to the disproportionately long Norian  
283 stage<sup>48–51</sup>: rock units from this epoch were instead assigned to either the early Norian or the  
284 late Norian (see Supplementary Tables S1, S2).

285

286 **Geographic areas.** In order to conduct network and many other palaeobiogeographic  
287 analyses it is necessary to identify a series of geographically discrete areas (the localities of  
288 the taxon-locality network in the network methodology). These areas are typically defined  
289 solely on the basis of geography (rather than shared flora or fauna) because the aim is to test  
290 faunal similarity between geographically distinct regions of the world. For example, previous  
291 analyses have commonly used modern continents as input areas<sup>10, 11, 13, 15</sup>. This traditional  
292 approach is potentially problematic on a supercontinent where, for example, eastern North  
293 American and north-western African localities were much closer to each other than to  
294 localities in southwestern North America or southern Africa. Instead, we defined our  
295 geographic areas on the basis of k-means clustering of palaeocoordinate data for 2144  
296 terrestrial fossil occurrences from the relevant time span, obtained mostly from the  
297 Paleobiology Database (see Supplementary Note S3). Importantly, this approach does not  
298 require or use any information on taxonomy or phylogeny – it is solely designed to find  
299 geographically-discrete clusters of fossil localities – and thus it is fully independent from the  
300 subsequent network analyses.

301 Data were binned at epoch level, with each epoch analysed separately to avoid  
302 confusion arising from continental movements. K-means clustering was performed within R,  
303 varying the value of  $k$  from 5–15. For each value of  $k$ , the analysis was repeated with ten  
304 random starts, with 100 replicates). Performance of different analyses was then compared on

305 the basis of the percentage of variance explained, and results were compared with  
306 palaeogeographic reconstructions through this interval <sup>10,52</sup> (Supplementary Table 3; full  
307 results are given as Supplementary Data 3). This resulted in the designation of ten discrete  
308 palaeogeographic regions that each represent localities for the network analyses (Fig. 1b).  
309 Taxa were assigned to one or more regions as appropriate, yielding a taxon-locality matrix  
310 for each time bin (Supplementary Data 4).

311

312

313 **Phylogenetic network biogeography analyses.** Non-phylogenetic biogeographic  
314 connectedness (BC) was previously quantified <sup>3</sup> as the rescaled density of a taxon-locality  
315 matrix, calculated as follows:

$$316 \quad BC = \frac{O-N}{(L*N)-N} \quad [1]$$

317 In this formula,  $O$  = the number of links in the network (the sum of all values in a taxon-  
318 locality matrix, which will equal the number of occurrences in a non-phylogenetic analysis),  
319  $N$  = the number of taxa, and  $L$  = the number of localities. This gives the ratio between the  
320 number of taxa present beyond a single locality and the maximum possible number of  
321 occurrences (i.e., every taxon present at every locality). Aside from whether a taxon is  
322 identical or not, no further phylogenetic information is included using this method – links are  
323 only considered where an individual taxon is shared between different localities, and are all  
324 equally weighted.

325 Herein, this method was modified to include phylogenetic information (phylogenetic  
326 biogeographic connectedness = pBC) by weighting links between taxa as inversely  
327 proportional to the phylogenetic distances between them. Phylogenetic distances between

328 taxa were measured by summing the branch lengths in millions of years representing the  
329 shortest distance between two taxa. This was then scaled against the maximum possible  
330 phylogenetic distance (i.e., the total distance of the summed branch lengths between the two  
331 most distantly related taxa). This scaled value was then subtracted from one to yield the  
332 weight of each link: the values of links between taxa hence vary between one (co-occurrence  
333 of the same species in two separate localities) and zero (when comparing the two most  
334 distantly related taxa in the taxon-locality matrix). The sum of the reweighted taxon-locality  
335 matrix was then substituted for  $O$  in equation 1 to yield a value of phylogenetic  
336 biogeographic connectedness. This method has been made available as the “BC” function  
337 within the R package `dispeRse`<sup>55</sup> (available at [github.com/laurasoul/dispeRse](https://github.com/laurasoul/dispeRse)): example  
338 analysis scripts are given as Supplementary Data 5 and Supplementary Data 6. It should be  
339 noted that a given value of pBC will be a non-unique solution: the same value could  
340 theoretically be generated by many links between distantly-related taxa or by fewer links  
341 between more closely-related species. Disentangling these possibilities is difficult. However,  
342 comparison of results with measured phylogenetic distances and number of taxa in each time  
343 bin indicates that pBC results are not merely driven by differences in the relatedness of  
344 sampled taxa, and instead reflect genuine biogeographical signal (see supplementary  
345 information).

346         Analysis of a simulated null (stochastically generated) dataset indicated a predictable  
347 and systematic pattern of increasing pBC through time. This is due to the increasing distance  
348 from a persistent root to the tips through time, resulting in phylogenetic branch lengths  
349 between nearest relative terminal taxa becoming proportionately shorter. In order to compare  
350 pBC between different time bins, it is therefore necessary to remove this tendency for pBC to  
351 increase in later time bins. We achieved this through the introduction of a constant,  $\mu$ , which  
352 collapses all branches below a fixed “depth” such that root age is equal to  $\mu$  million years



353 before the tips. The introduction of this constant also alleviates problems of temporal  
354 superimposition of biogeographic signals that may otherwise occur. It means that pBC results  
355 reported for each time bin reflect patterns generated by biogeographic processes in the  
356 preceding  $\mu$  million years, preventing these recent biogeographic signals of interest from  
357 being swamped by those from deeper time intervals. A  $\mu$  value of 15 was chosen based on the  
358 results of sensitivity analyses varying the value of  $\mu$  from 5–25 Myr in 1 Myr increments (see  
359 Supplementary Note 7, Supplementary Fig 7).

360 This method was applied to the taxon-region matrix for each time bin, and the 100  
361 time-calibrated supertrees, pruning taxa not present within the bin of interest (effectively  
362 making each tree ultrametric) to calculate pBC. Jackknifing, with 10,000 replicates, was used  
363 to calculate 95% confidence intervals. This analysis was then repeated without phylogenetic  
364 information to gauge the importance of phylogeny on observed patterns.

365

366 **Taxon subset analyses.** In order to investigate the processes giving rise to observed changes  
367 in cosmopolitanism over mass extinction events, analyses were also performed on two  
368 taxonomic subsets. The first reanalysed time bins either side of each mass extinction (the  
369 Lopingian and Early Triassic and late Late Triassic and early Early Jurassic) including only  
370 small clades exhibiting high survivorship (<20 species, with  $\geq 20\%$  of lineages crossing the  
371 extinction boundary). This was intended to minimize the influence of possible preferential  
372 extinction of geographically-restricted taxa.

373 The removal of taxa during mass extinctions opens new vacancies in ecospace,  
374 promoting adaptive radiations in surviving, often previously marginal, clades<sup>56,57</sup>. For  
375 example, the Permian-Triassic mass extinction is seen as a causal factor in the succeeding  
376 radiation of epicynodonts<sup>58</sup> and archosaurs<sup>3,59,60</sup>, and the Triassic—Jurassic radiation as

377 pivotal in the diversification of crocodylomorph<sup>61</sup> and dinosaur clades<sup>20,62</sup>. ‘Disaster faunas’  
378 will hence be expected to be composed of relatively recently diverging clades, as surviving  
379 taxa diversify into broader geographic ranges (e.g.,<sup>59</sup>). To test the significance of this, we  
380 reanalysed the time bins immediately following each mass extinction, including only clades  
381 that branched <2 Myr prior to or after the boundary. In order to ensure that the results of this  
382 analysis reflected differences in the post-extinction bins as opposed to an artefact of clade  
383 age, also performed analyses applying this filter to the other time bins (see Supplementary  
384 Note 6).

385

386 **Geographically localised analyses.** To atomise global pBC signals into hemispheric trends,  
387 pBC was re-calculated for Laurasian and Gondwanan areas separately following an identical  
388 procedure to that for global analyses. Finally, to compare global results obtained from this  
389 new method with the more localised analysis of Sidor *et al.*<sup>3</sup>, another set of analyses was  
390 performed following the taxonomic sampling of the latter. Terrestrial amniote occurrences  
391 from the late Permian and Middle Triassic of the Karoo Basin of South Africa; Luangwa  
392 Basin of Zambia; Chiweta beds of Malawi; Ruhuhu Basin of Tanzania, and the Beacon Basin  
393 of Antarctica were taken from the dataset of Sidor *et al.*<sup>3</sup>. These data and the 100 time-  
394 calibrated trees described above were then used to calculate BC and pBC between these  
395 basins for each of the sampled time bins.

396

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548 wrote new functions as required for these analyses. D.J.B. compiled the data, performed the  
549 analyses and prepared the figures. All authors discussed results and contributed to writing the  
550 manuscript.

551 **Data availability:** All data analysed in this study and example code are available in the  
552 supplementary data files.

553 **Competing financial interests:** The authors declare no competing financial interests.

554 **Figure legends**

555 **Fig. 1: Schematic illustration of network biogeography methods.** a) Simplified phylogeny  
556 of Dicynodontia. b-c) Taxon-locality networks. Localities are indicated by the large, pale  
557 brown circles, taxa are coloured as in a). Taxa are connected by brown lines to the locality at  
558 which they occur. b) Rescaled non-phylogenetic biogeographic connectedness (BC) of Sidor  
559 *et al.*<sup>3</sup>. A single taxon, *Kannemeyeria* (yellow), is present at all three localities, resulting in a  
560 link of value=1 (solid black line) between each locality. c) Phylogenetic biogeographic  
561 connectedness (pBC), as proposed here. Links (grey lines) between taxa from different  
562 localities are weighted inversely to their phylogenetic relatedness. Line thickness and shade is  
563 proportional to the strength of the link (and thus inversely proportional to phylogenetic  
564 distance between the two taxa).

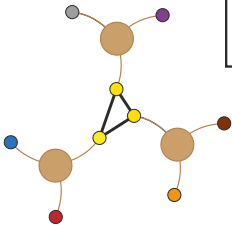
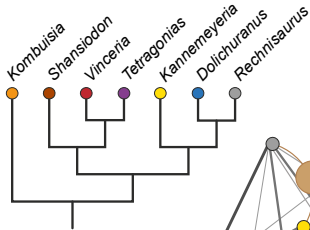
565 **Fig. 2: Phylogenetic framework and biogeographic regions employed in this study.** a)  
566 Informal supertree of amniotes used in the analyse. b) Triassic palaeogeography, redrawn  
567 after<sup>10,30,63</sup>, with the geographic regions used as localities for the network analysis. 1:  
568 Western USA, British Columbia, Mexico, Venezuela; 2: Eastern USA, Eastern Canada,  
569 Morocco, Algeria; 3: Europe, Greenland; 4: Russia; 5: China, Thailand, Kyrgyzstan; 6:  
570 Argentina; 7: Brazil, Uruguay, Namibia; 8: South Africa, Lesotho, Zimbabwe; 9: Tanzania,  
571 Zambia, Madagascar, India, Israel, Saudi Arabia; 10: Antarctica, southeast Australia.

572 **Fig. 3: Results from BC analysis of Lopingian-Early Jurassic terrestrial amniotes.**  
573 Results from both non-phylogenetic (BC, red) and phylogenetic (pBC, blue) analyses of  
574 global biogeographic connectedness are shown. Shaded polygons represent ninety-five  
575 percent confidence intervals (calculated from jackknifing with 10,000 replicates) for both the  
576 BC and pBC analyses. The Permian-Triassic boundary (PTB) and Triassic-Jurassic boundary  
577 (TJB) extinction events are indicated by dotted lines. E. Tr. refers to the Early Triassic.

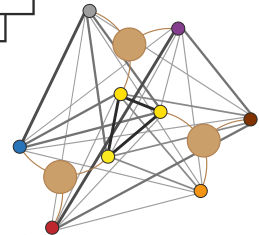
578 **Fig. 4: Results from BC analysis of taxonomic subsets.** Comparison of results for data  
579 subsets across the Permian-Triassic (a) and Triassic-Jurassic (b) mass extinctions. Results for  
580 the entire dataset are in black, those for less inclusive clades showing high survivorship in  
581 red, and those for the most recently diverging taxa in purple. Ninety-five percent confidence  
582 intervals, calculated from jackknifing with 10,000 replicates, are indicated.

583 **Fig. 5: Results from BC analysis of geographically localised areas.** a) Comparison of pBC  
584 trends during the Lopingian-Early Jurassic from Gondwana localities (in green) against those  
585 for Laurasia (in purple). Ninety-five percent confidence intervals are indicated. Abbreviations  
586 as in Fig. 3; E. Jur. refers to Early Jurassic. Ninety-five percent confidence intervals,  
587 calculated from jackknifing with 10,000 replicates, are indicated. b) Results from analysis of  
588 basin-level terrestrial amniote occurrences from the late Permian and Middle Triassic of  
589 southern Pangaea, from the dataset of Sidor *et al.*<sup>3</sup>. Phylogenetic BC results are given in  
590 blue, non-phylogenetic BC in red. Ninety-five percent confidence intervals, calculated from  
591 jackknifing with 1000 replicates, are indicated.

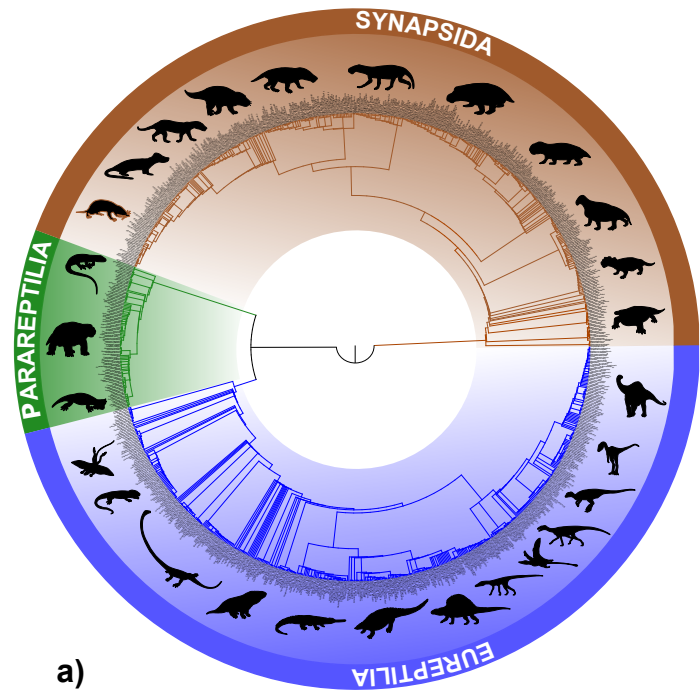
**a)**



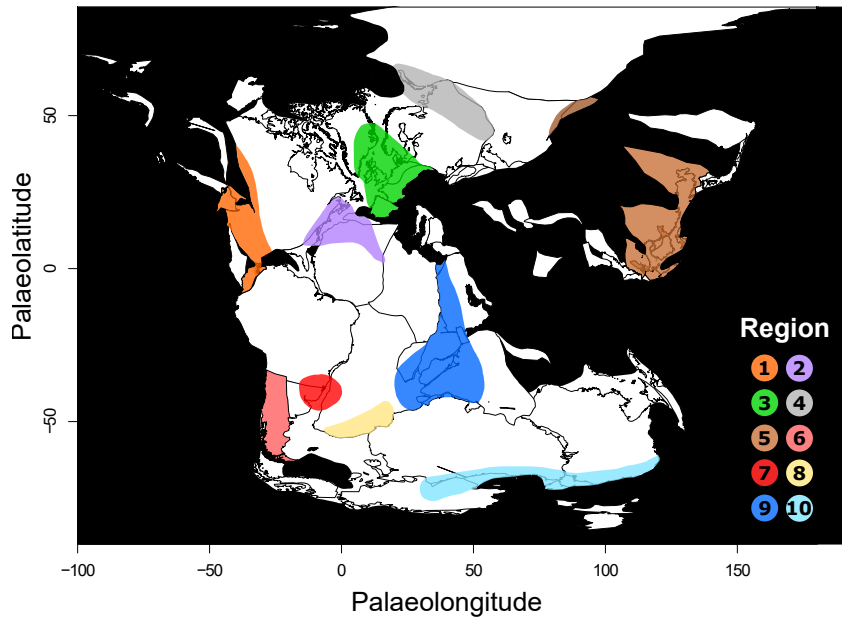
**b)**



**c)**



a)



b)

**Biogeographic connectedness**

