1 **Geographic range did not confer resilience to extinction in**

2 **terrestrial vertebrates at the end-Triassic crisis**

3 Alexander M. Dunhill[1,2] and Matthew A. Wills[1]

4 [1]Milner Centre for Evolution, University of Bath, Claverton Down, Bath, BA2 7AY, UK

5 [2]School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK,

6 a.dunhill@leeds.ac.uk

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8 **Rates of extinction vary greatly through geological time, with losses particularly**

9 **concentrated in mass extinctions. Species duration at other times varies greatly, but the**

10 **reasons for this are unclear. Geographical range correlates with lineage duration**

11 **amongst marine invertebrates, but it is less clear how far this generality extends to other**

12 **groups in other habitats. It is also unclear whether a wide geographical distribution**

13 **makes groups more likely to survive mass extinctions. Here, we test for extinction**

14 **selectivity amongst terrestrial vertebrates across the end-Triassic event. We**

15 **demonstrate that terrestrial vertebrate clades with larger geographical ranges were**

16 **more resilient to extinction than those with smaller ranges throughout the Triassic and**

17 **Jurassic. However, this relationship weakened with increasing proximity to the end-**

18 **Triassic mass extinction, breaking down altogether across the event itself. We**

19 **demonstrate that these findings are not a function of sampling biases; a perennial issue**

20 **in studies of this kind.**

21

22 Is it possible to make generalisations about which clades and higher taxa are most likely to go

23 extinct on geological timescales? Geographic range is often claimed to be a determinant of

24 extinction vulnerability[1-6]. Groups with restricted ranges are widely believed to suffer

25 extinction more frequently than those with broader ranges[1] because the latter are thought to

26 be afforded some resilience to regional environmental perturbations[7,8]. During global biotic

27 crises, by contrast, there is reasoned to be no such selectivity[2,6] since widespread

28 environmental disturbances simultaneously affect both wide and narrow ranging taxa on

29 global scales[1,3,6]. Surprisingly, the effect of geographic range on extinction risk has not been

30 tested comprehensively for the terrestrial fossil record, with a striking paucity of studies on

31 vertebrates of any kind. Most published studies focus on marine invertebrates[3-6,8-10], and

32 despite geographic range being used as a major criterion for assessing the extinction risk of

33 modern terrestrial species[11], it is unclear that the findings from these fossil taxa can be

34 extended to all groups in all major habitats. Moreover, little is known about the difference

35 between intervals with background levels of extinction and those characterised as mass

36 extinctions[3]. The only way to answer such questions is to utilise fossil evidence of past

37 organismal distributions[5,12].

38     The Triassic to Jurassic is a critically important period in terrestrial vertebrate

39 evolution[13,14]. In particular, it follows the largest of all mass extinctions, the Permo-Triassic

40 (P/T) 'great dying' [13-15]. Many terrestrial vertebrate lineages originated in the aftermath of the

41 P/T event, but were subsequently subjected to major changes in terrestrial ecosystems

42 throughout the ensuing Triassic and Jurassic. These changes included the gradual aridification

43 of Pangaea[16], as well as its initial rifting and fragmentation[17] allied to the eruption of the

44 Central Atlantic Magmatic Province (CAMP)[18,19]. This culminated in the end-Triassic mass

45 extinction event[16,20], which saw the demise of numerous amphibian and reptile groups prior

46 to the subsequent rise to dominance of the dinosaurs[13,16,21-23].

47     The significant vertebrate faunal turnover throughout the Triassic and Jurassic (lying

48 either side of the end Triassic mass extinction) make this an ideal period in which to study

49 extinction selectivity. We therefore collated palaeobiogeographical and stratigraphic

50 distributional data[24] for Triassic and Jurassic terrestrial vertebrate clades in order to ask three

51   questions. 1. Is there is a relationship between palaeobiogeographical distribution and the risk

52   of extinction during 'normal' times? 2. Does any such relationship disappear across the end-

53   Triassic mass extinction? 3. Can any of these findings be attributed to sampling biases?

54        We find that wider geographical range conferred greater resilience to extinction in

55   terrestrial vertebrate groups throughout most of the Triassic and Jurassic. However, this

56   insurance weakened towards the end-Triassic mass extinction, and was imperceptible across

57   the event itself. Major sampling biases were discounted as the cause of these patterns.

58

59   **Results and Discussion**

60   **Geographic range and diversification rates are correlated.** Diversification rates and

61   changes in geographic range at the clade level are positively and strongly correlated across all

62   time bins (Figs. 1 and 2 and Supplementary Table 1), with weaker (but still mostly

63   significant) correlations when the data are subdivided into Epochs (Fig. 2 and Supplementary

64   Table 1). The strong correlation between changes in geographic range and diversification rate

65   across all time intervals (and at Epoch level and within stage-level time bins) confirms that

66   increasing range size coincides with increasing diversity, whilst range size reductions

67   typically attend diversity reductions. Taxa with larger geographic ranges are therefore more

68   likely to exhibit increasing diversity and lower extinction rates than those with smaller

69   ranges. Greater rates of origination might also be expected to result from more extensive

70   ranges; firstly because large ranges are more likely to be fragmented into peripheral isolates,

71   secondly because larger ranges encompass a greater diversity of environments and selective

72   forces[25,26]. This pattern is the opposite of that proposed for the marine invertebrate fauna,

73   where taxa with narrow ranges show higher origination rates[6,27]. The results from our

74   geographic range data sets, both raw convex hull and standardized mean great circle distances

75  (Fig. 1), are similar, demonstrating that our findings are not contingent upon the precise

76  methodology used.

77

78  **This relationship breaks down across the mass extinction.** Strikingly, rates of geographic

79  range change and diversification are not significantly correlated immediately before the end-

80  Triassic extinction (during the Rhaetian), whereas this correlation is significant even in the

81  Carnian and Norian stages that immediately precede it (Fig. 2 and Supplementary Table 1).

82  Hence, diversification rate becomes decoupled from range size change rate across the

83  extinction boundary and the insurance against extinction offered by larger geographic ranges

84  at other times disappears. During the end-Triassic mass extinction event, relatively

85  widespread groups are as likely to suffer high levels of extinction as groups with narrower

86  geographic ranges. For example, Phytosauria and Theropoda have similar, geographic ranges

87  in the Rhaetian (Fig. 3). However, phytosaurs suffer complete extinction at the end-Triassic,

88  whereas theropod diversity remains stable across the boundary and into the Hettangian, even

89  whilst undergoing significant range expansion (Fig. 3). Of the time intervals that do not show

90  significant correlation between diversification rate and geographic range change rate, all have

91  very small sample sizes apart from the Rhaetian. The standardised mean great circle distance

92  (GCD) range metrics show less correlation with diversification rate than the raw convex hull

93  metric (Supplementary Table 1). This is unsurprising since a reduced sample size leads to a

94  reduction in statistical power. However, many of these non-significant correlations still have

95  relatively high correlation coefficients and are approaching significance, whereas the

96  Rhaetian results are clearly different (with negative coefficients that are far from significant)

97  (Supplementary Table 1).   Our temporal divisions are very much longer (2.0 to 18.9

98  Myrs)[28,29] than the extinction event[20], which occurred in pulses over a period of less than 1.0

99  Myr[19]. Effects are therefore time averaged, meaning that the breakdown of the relationship

4

100    between diversification rate and the rate of geographic range change in the very end Triassic

101    (an interval known to contain a major biotic crisis) is even more striking.

102

103    **Sampling biases have little effect on our results.** We observed several significant bivariate

104    correlations between diversification rate, geographic range change rate and various putative

105    sampling proxies detrended using first differences (Supplementary Tables 2-3). However,

106    multiple regression models identified the changes in geographic range rate as the dominant

107    variable influencing diversification rate (Table 1 and Supplementary Tables 4-9).

108         Although certain parts of the Triassic-Jurassic are reputed to have a poor terrestrial

109    fossil record (i.e. Ladinian, Toarcian-Mid Jurassic)[13,20,30-32], the Late Triassic possesses one of

110    the best[23,32] (Fig. 4). We see positive correlations between land area and geographic range and

111    a negative correlation between sea level and range in the GCD data, but also positive

112    correlations between sea level and geographic range and between sea level and diversification

113    rate in the convex hull data. This suggests that greater land area and lower sea levels may

114    result in greater geographic ranges amongst terrestrial organisms. However, the negative

115    correlation between standardised range and sea level (and the lack of correlation between

116    diversification rate and land area) suggests that while expanding landmasses might be

117    expected to induce the expansion of terrestrial ranges and increase diversification, climatic

118    and other effects complicate this relationship. Indeed, the typically harsh environments in

119    deep continental interiors may constrain many ranges. Specifically, lethally hot temperatures,

120    particularly in the Early Triassic, may have limited or even excluded diversity in equatorial

121    regions[33]. Individual lineage ranges correlate with total ranges across time bins, and both

122    appear to reflect the same underlying pattern.  The considerable variation between individual

123    lineage ranges within each bin (coupled with the fact that the standardised range metrics still

124    show some correlation with total range, albeit weaker than the raw range metrics) indicates

125   that range estimates are not governed straightforwardly by sampling intensity (Figs. 1 and 3).

126   Moreover, the absence of terrestrial vertebrates from equatorial regions is entirely plausible

127   during the climatic greenhouse of the Early Triassic[33]. Groups with broader geographical

128   distributions are likely to be subject to a wider range of selective pressures and the peripheral

129   isolation of sub groups; both factors favouring speciation and increasing diversity[25,26].

130   However, the weak correlation observed between changes in fossil abundance and both

131   diversification rate and geographic range change may be representative of sampling bias. It is

132   also possible that a greater investment of research effort in more abundant fossil groups may

133   have resulted in increased taxonomic splitting[34].

134        We also observed significant pairwise correlations between both raw and

135   standardised geographic range change and diversification rate on one hand, and changes in

136   numbers of formations on the other. Although formation counts are regarded as effective

137   sampling proxies for terrestrial data sets[35], redundancy between sampling proxies and

138   diversity metrics (arising from the probable non-independence of formation and fossil

139   content) remains problematic[36-38]. In practice, the level of this redundancy is likely to be

140   minimised by the use of all terrestrial vertebrate-bearing formations[39,40], rather than by

141   adopting a stricter count of only those formations containing a particular group of terrestrial

142   vertebrate fossils[31,41-43]. However, standardisation of geographic range data results in the

143   removal of significant correlations between range size and fossil abundance, coupled with a

144   weakening of the correlation between range size and total range size (i.e. standardising

145   geographic range calculations to a constant sample size across all lineages in each time bin

146   appears to remove putative sampling effects). By contrast, standardising range data does not

147   affect the correlation between range size and formation counts. This last relationship may

148   therefore arise from redundancy[36], rather than being a temporal bias resulting from variation

6

149    in the amount of preserved sedimentary rock (and concomitant intensity of sampling) through

150    geological time.

151        The multiple regression models show that geographic range change is the dominant

152    driver of diversification rate through the Triassic-Jurassic, to the exclusion of all the sampling

153    proxies in the model using convex hulls, but with total range and sea level showing some

154    influence in the standardised mean great circle distance models. This suggests that, although

155    sampling biases are a perennial issue in fossil data sets, the link between changes in

156    geographic range and diversification rate appear robust, despite the patchy nature of the

157    vertebrate fossil record.

158

159    **Implications for extinction studies.** We demonstrate that broad geographic range conferred

160    insurance against extinction on major clades of terrestrial vertebrates during periods with

161    background levels of extinction. In line with marine invertebrate studies across the same

162    biotic crisis[6] and at other times in the Phanerozoic[3], this insurance disappeared during the

163    end-Triassic mass extinction. However, these results are in marked contrast to patterns

164    reported for marine invertebrates at the Cretaceous-Paleogene extinction[9,44] (where groups

165    with larger geographic ranges retain increased resilience to extinction across the crisis than

166    those with smaller ranges). It is reasonably common to observe discrete macroevolutionary

167    patterns in different higher taxa or across different major habitats. Notable examples include

168    the incongruence between terrestrial and marine Phanerozoic diversity curves[45-47], variations

169    in the apparent force of Cope's rule *sensu lato* in different higher taxa[48-50], and variations in

170    the relationships between body size, population density and fecundity across clades[51,52].

171    However, the differences between patterns observed at major extinction events may result

172    from differences between the particular driving forces of the crises themselves. These

173    differences highlight the need for greater numbers of large-scale, comparative studies before

174    attempting to make macroevolutionary generalisations. Fortunately, the expansion and

175    refinement of resources such as the Paleobiology Database, coupled with quantitative tools

176    such as GIS, have great potential for testing temporal and spatial macroevolutionary patterns.

177    Equally, palaeontological data provides a broader perspective on the current biodiversity

178    crisis. Specifically, it enables deep time tests of the purported relationships between present

179    day extinction susceptibility and geographical range size[53,54], latitudinal distribution[55], nîche

180    breadth[56] and body size[57,58].

181

182    **Methods**

183    **Fossil occurrence data.** Stage level occurrence data for Triassic-Jurassic terrestrial

184    vertebrates    were    initially    downloaded    from    the    Paleobiology    Databse[24]

185    (https://paleobiodb.org) on 4th February, 2013 (last accessed 20th April, 2015) and, after pre-

186    processing, consisted of 3507 occurrences of 857 genera (see Supplementary Note 1 for

187    Paleobiology Database download specifications). Terrestrial vertebrate occurrences from

188    marine deposits were not included as they would not give a true representation of geographic

189    range. Ichnogenera and other form taxa where then removed from the data set as they could

190    not be assigned accurately to parent genera. Marine tetrapod taxa recorded in terrestrial

191    formations were also removed. Generic indeterminate taxa and taxa with uncertain generic

192    assignments (i.e. *aff.*, *cf.*, *ex gr.*, *sensu lato*, *?*) were also excluded. Although these exclusions

193    inevitably resulted in an underestimation of the geographic range of higher taxonomic

194    groups, it would be inappropriate to compare ranges constructed from taxa of uncertain

195    affiliation with rates of generic extinction, origination, and diversification, which cannot

196    include these indeterminate occurrences.

197         Fossil occurrences were vetted for synonymy and outdated taxonomy and sorted into

198    higher taxonomic groups according to phylogenetic and ecological relationships within the

199   constraints of reasonable sample sizes (see Supplementary Note 1 for detailed classification

200   of taxa). As with all higher taxonomic classification, groups were not directly comparable.

201   This is an unavoidable problem unless working at the species or, to a lesser extent, the

202   generic level. Two datasets were compiled: $data_1$ and $data_2$ (Supplementary Fig. 1). $Data_1$

203   (Supplementary Data 1) contained a number of paraphyletic assemblages where basal taxa of

204   particular lineages were grouped together to form a paraphyletic 'stem' assemblage (e.g.

205   Archosauriformes, basal Cynodontia, Dinosauromorpha) (Supplementary Fig. 1). Since the

206   inclusion of paraphyletic groups is arguably problematic (they do not represent 'true'

207   evolutionary groups), a second dataset excluding all parapyla was also prepared. In $data_2$, the

208   paraphyletic assemblages were collapsed into smaller, monophyletic family-level groups

209   wherever possible (Supplementary Fig. 1). The two data sets correlated very closely in terms

210   of both geographic range change rate and diversification rate. All analyses in the manuscript

211   therefore refer exclusively to $data_1$.

212       Fossil occurrences were binned at the stratigraphic stage level. Any occurrences not

213   assigned to a stage were attached to the stage, or range of stages, corresponding to the

214   formation from which they were recovered. Fossil occurrences that were assigned to more

215   than one stage were randomly assigned to a single stage within their given range, a process

216   that was repeated 1,000 times to obtain a mean value. This method avoided either the

217   artificial inflation or deflation of taxonomic richness in any given stage compared to

218   maximum or minimum diversity values.

219

220   **Sampling and environmental proxy data.** *Non-marine area*[59]: A mean estimate of the

221   continental landmass for each Stage. It was anticipated that geographic range would correlate

222   positively with land area as the area of terrestrial habitat creates an upper limit for the

223   geographic range of terrestrial organisms. These measurements were derived from an

9

224      independent source[59], and were subject to different definitions of Stage-level boundaries than

225      the fossil occurrence data set, which used the Geological Time Scale 2012[60].

226      *Sea level[61]*: A mean estimate of relative sea level for each Stage. It was expected that

227      geographic range would correlate inversely with mean sea level, as higher sea level would

228      result in less terrestrial landmass for terrestrial organisms to inhabit. As with the non-marine

229      area measurements, the sea level averages were obtained from an independent source[61] and

230      are subject to different definitions of Stage-level boundaries from the fossil occurrence data

231      set[60].

232      *Terrestrial formations[24]*: Formation counts are widely regarded as effective sampling proxies

233      for the terrestrial fossil record[31,35,42,62]. It is still unclear if this is true, as formation counts

234      probably share a common signal with fossil occurrence data (i.e. formations are not

235      independent from their fossil content[36,37]). However, given the lack of comprehensive data on

236      global sedimentary rock outcrop area, formation counts offer the only possible metric of

237      global rock availability. In this analysis, redundancy was minimised by using a total count of

238      terrestrial tetrapod bearing formations, rather than a strict count of group-specific bearing

239      formations. There is also an argument for redundancy between formation counts and

240      geographic range, as a taxon that is genuinely wide ranging is more likely to be present in

241      more formations across the globe than a taxon with a small geographic range. Such

242      possibilities were explored using multiple regression models.

243      *Fossil abundance[24]*: Fossil abundance per time period serves as a proxy for human sampling

244      and collecting effort. However, there is danger of circularity, as palaeontologists will be more

245      likely to collect from formations yielding a higher number of fossils[38,63]. Therefore, fossil

246      abundance may be more representative of preservational factors or true biological abundance,

247      rather than a measure of human sampling effort.

248    *Total geographic range*: It is reasonable to assume that vertebrates were not genuinely absent

249    from large areas of the globe through parts of the Triassic-Jurassic. Therefore, if total

250    geographic range (i.e. the total geographic range of all tetrapod occurrences per time bin)

251    were to correlate strongly with the geographic ranges of individual fossil groups, it would

252    indicate that the pattern of geographic range through the study period is controlled by spatial

253    sampling rather than reflecting a biological pattern.

254

255    **Analysis.** Palaeogeographic ranges were constructed by converting modern fossil occurrence

256    coordinates to palaeocoordinates using *PointTracker[64]*. Palaeogeographic ranges were

257    constructed using two methods: (i) in *ArcGIS v10.1* using convex hulls around the

258    palaeogeographic occurrences for each group[65,66]; and (ii) using mean great circle distances

259    (GCD) between palaeogeographic occurrences with sample sizes standardised to 5 and 10

260    occurrences per lineage per time bin and replicated 1,000 times to obtain a mean value. GCD

261    distances were calculated using the spherical law of cosines (as an acceptable approximation

262    of the Haversine formula for terrestrial calculations.

263        Per lineage origination ($O_r$) and extinction ($E_r$) rates were calculated using the

264    methodology of Foote[67] and modified by Foote[68]:

265        (1)    $O_r = -\ln\frac{N_{bt}}{N_{ft}+N_{bt}}$

266        (2)    $E_r = -\ln\frac{N_{bt}}{N_{bL}+N_{bt}}$

267    Where $N_{bt}$ = number of range-through taxa, $N_{ft}$ = number of taxa that originate within time

268    bin and cross top boundary of time bin, $N_{bL}$ = number of taxa that cross bottom boundary of

269    time bin but make their last appearance in time bin. Rates were not expressed relative to time

270    bin duration; although this may cause underestimation of rates in shorter time bins relative to

271   longer time bins, Foote[69] demonstrated that both extinction and origination are pulsed rather

272   than spread throughout time intervals. All analyses were carried out at the generic level.

273       No significant correlations were detected between geographic range change and

274   extinction rate or between geographic range change and origination rate (Supplementary

275   Table 10). The absence of significant correlations between origination/extinction rates and

276   change in geographic range could be regarded as somewhat surprising, but this result is a

277   function of the paucity of data for the rate calculations. However, the extinction and

278   origination rate calculations rely on taxa that range-through three consecutive time bins[67],

279   which are scarce in this data set because of the patchiness of the terrestrial fossil record and

280   the long durations of the time bins. Therefore, it was judged that a metric of diversification

281   calculated from generic range data offered a more robust picture of biotic change.

282   Diversification rate ($D_r$) and geographic change rate ($R_r$) were calculated using a metric

283   modified from Rode and Lieberman[70]:

$$(3) \quad D_r \; = \; (\ln D_1 \; - \; \ln D_0)$$

$$(4) \quad R_r \; = \; (\ln R_1 \; - \; \ln R_0)$$

286   where $D_1$ = ranged-through diversity calculated from first and last appearances for current

287   time interval, $D_0$ = ranged-through diversity calculated from first and last appearances for the

288   previous time interval, $R_1$ = geographic range in time interval, $R_0$ = geographic range in

289   previous time interval.

290       Relationships between geographic range change and generic diversification rates

291   within clades were tested using pairwise Spearman's rank-order correlation tests. Putative

292   sampling biases were investigated using both pairwise correlation and multiple regression

293   models, with diversification rate as the dependent variable and geographic range and various

294   sampling proxies as independent variables. First differencing was used to detrend the

295 sampling proxy data prior to comparison with the biotic rate data. All statistical analyses

296 were carried out in *R* 3.1.1.

297

298 **References**

299 1    Barnosky, A. D. *et al.* Has the Earth's sixth mass extinction already arrived? *Nature*

300      **471**, 51-57, doi:10.1038/nature09678 (2011).

301 2    Jablonski, D. Mass extinctions and macroevolution. *Paleobiology* **31**, 192-210 (2005).

302 3    Payne, J. L. & Finnegan, S. The effect of geographic range on extinction risk during

303      background and mass extinction. *Proceedings of the National Academy of Sciences of*

304      *the United States of America* **104**, 10506-10511, doi:10.1073/pnas.0701257104

305      (2007).

306 4    Powell, M. G. Geographic range and genus longevity of late Paleozoic brachiopods.

307      *Paleobiology* **33**, 530-546, doi:10.1666/07011.1 (2007).

308 5    Rode, A. L. & Lieberman, B. S. Using GIS to unlock the interactions between

309      biogeography, environment, and evolution in Middle and Late Devonian brachiopods

310      and bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* **211**, 345-359,

311      doi:10.1016/j.palaeo.2004.05.013 (2004).

312 6    Kiessling, W. & Aberhan, M. Geographical distribution and extinction risk: lessons

313      from Triassic-Jurassic marine benthic organisms. *Journal of Biogeography* **34**, 1473-

314      1489, doi:10.1111/j.1365-2699.2007.01709.x (2007).

315 7    Foote, M., Crampton, J. S., Beu, A. G. & Cooper, R. A. On the bidirectional

316      relationship between geographic range and taxonomic duration. *Paleobiology* **34**,

317      421-433, doi:10.1666/08023.1 (2008).

318   8     Nürnberg, S. & Aberhan, M. Habitat breadth and geographic range predict diversity

319         dynamics in marine Mesozoic bivalves. *Paleobiology* **39**, 360-372, doi:10.1666/12047

320         (2013).

321   9     Jablonski, D. Extinction and the spatial dynamics of biodiversity. *Proceedings of the*

322         *National Academy of Sciences of the United States of America* **105**, 11528-11535,

323         doi:10.1073/pnas.0801919105 (2008).

324   10    Jablonski, D. & Roy, K. Geographical range and speciation in fossil and living

325         molluscs. *Proceedings of the Royal Society B* **270**, 401-406 (2003).

326   11    Mace, G. M. *et al.* Quantification of Extinction Risk: IUCN's System for Classifying

327         Threatened SpeciesCuantificación del Riesgo de Extinción: Sistema de la UICN para

328         la Clasificación de Especies Amenazadas. *Conservation Biology* **22**, 1424-1442,

329         doi:10.1111/j.1523-1739.2008.01044.x (2008).

330   12    Valentine, J. W., Jablonski, D., Krug, A. Z. & Berke, S. K. The sampling and

331         estimation of marine paleodiversity patterns: implications of a Pliocene model.

332         *Paleobiology* **39**, 1-20, doi:10.1666/0094-8373-39.1.1 (2013).

333   13    Brusatte, S. L., Benton, M. J., Desojo, J. B. & Langer, M. C. The higher-level

334         phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic*

335         *Palaeontology* **8**, 3-47, doi:10.1080/14772010903537732 (2010).

336   14    Ezcurra, M. D. Biogeography of Triassic tetrapods: evidence for provincialism and

337         driven sympatric cladogenesis in the early evolution of modern tetrapod lineages.

338         *Proceedings of the Royal Society B: Biological Sciences* **277**, 2547-2552,

339         doi:10.1098/rspb.2010.0508 (2010).

340    15    Ruta, M., Botha-Brink, J., Mitchell, S. A. & Benton, M. J. The radiation of cynodonts

341         and the ground plan of mammalian morphological diversity. *Proceedings of the Royal*

342         *Society B: Biological Sciences* **280**, doi:10.1098/rspb.2013.1865 (2013).

343    16    Tanner, L. H., Lucas, S. G. & Chapman, M. G. Assessing the record and causes of

344         Late Triassic extinctions. *Earth-Science Reviews* **65**, 103-139 (2004).

345    17    Whiteside, J. H., Grogan, D. S., Olsen, P. E. & Kent, D. V. Climatically driven

346         biogeographic provinces of Late Triassic tropical Pangea. *Proceedings of the National*

347         *Academy of Sciences* **108**, 8972-8977, doi:10.1073/pnas.1102473108 (2011).

348    18    Whiteside, J., Olsen, P. E., Eglinton, T., Brookfield, M. E. & Sambrotto, R. N.

349         Compound-specific carbon isotopes from Earth's largest flood basalt eruptions

350         directly linked to the end-Triassic mass extinction. *PNAS* **107**, 6721-6725 (2010).

351    19    Blackburn, T. J. *et al.* Zircon U-Pb Geochronology Links the End-Triassic Extinction

352         with the Central Atlantic Magmatic Province. *Science* **340**, 941-945,

353         doi:10.1126/science.1234204 (2013).

354    20    Toljagić, O. & Butler, R. J. Triassic–Jurassic mass extinction as trigger for the

355         Mesozoic radiation of crocodylomorphs. *Biology Letters* **9**,

356         doi:10.1098/rsbl.2013.0095 (2013).

357    21    Benton, M. J. in *The Fossil Record, vol. 2* Vol. 2 (ed M. J. Benton) 681-715

358         (Chapman and Hall, 1993).

359    22    Brusatte, S. L. *et al.* The origin and early radiation of dinosaurs. *Earth-Science*

360         *Reviews* **101**, 68-100 (2010).

361    23    Langer, M. C., Ezcurra, M. D., Bittencourt, J. S. & Novas, F. E. The origin and early

362         evolution of dinosaurs. *Biol. Rev.* **85**, 55-110, doi:10.1111/j.1469-185X.2009.00094.x

363         (2010).

364  24  Carrano, M. T. & Butler, R. J.   Taxonomic occurrences of Triassic to Jurassic

365      Tetrapoda. Paleobiology Database (http://paleobiodb.org, 2013-2015).

366  25  Roy, K. Effects of the Mesozoic Marine Revolution on the Taxonomic, Morphologic,

367      and Biogeographic Evolution of a Group: Aporrhaid Gastropods During the

368      Mesozoic. *Paleobiology* **20**, 274-296, doi:10.2307/2401004 (1994).

369  26  Budd, A. F. & Coates, A. G. Nonprogressive evolution in a clade of Cretaceous

370      *Montastraea*-like corals. *Paleobiology* **18**, 425-446 (1992).

371  27  Jablonski, D. Larval ecology and macroevolution in marine invertebrates. *Bulletin of*

372      *Marine Science* **39**, 565-587 (1986).

373  28  Foote, M. Pulsed origination and extinction in the marine realm. *Paleobiology* **31**, 6-

374      20, doi:10.1666/0094-8373(2005)031<0006:poaeit>2.0.co;2 (2005).

375  29  Bambach, R. K. Phanerozoic biodiversity and mass extinctions. *Annual Review of*

376      *Earth and Planetary Sciences* **34**, 127-155 (2006).

377  30  Stubbs, T. L., Pierce, S. E., Rayfield, E. J. & Anderson, P. S. L. Morphological and

378      biomechanical disparity of crocodile-line archosaurs following the end-Triassic

379      extinction. *Proceedings of the Royal Society B: Biological Sciences* **280**,

380      doi:10.1098/rspb.2013.1940 (2013).

381  31  Upchurch, P., Mannion, P. D., Benson, R. B. J., Butler, R. J. & Carrano, M. T.

382      Geological and anthropogenic controls on the sampling of the terrestrial fossil record:

383      a case study from the Dinosauria. *Geological Society, London, Special Publications*

384      **358**, 209-240, doi:10.1144/sp358.14 (2011).

385  32  Wang, S. C. & Dodson, P. Estimating the diversity of dinosaurs. *PNAS* **103**, 13601-

386      13605 (2006).

387  33  Sun, Y. D. *et al.* Lethally Hot Temperatures During the Early Triassic Greenhouse.

388      *Science* **338**, 366-370, doi:10.1126/science.1224126 (2012).

389    34    Lloyd, G. T., Young, J. R. & Smith, A. B. Taxonomic structure of the fossil record is

390         shaped by sampling bias. *Systematic Biology* **61**, 80-89 (2012).

391    35    Benson, R. B. J. & Upchurch, P. Diversity trends in the establishment of terrestrial

392         vertebrate ecosystems: Interactions between spatial and temporal sampling biases.

393         *Geology* **41**, 43-46, doi:10.1130/g33543.1 (2013).

394    36    Dunhill, A. M., Hannisdal, B. & Benton, M. J. Disentangling geological megabias and

395         common-cause from redundancy in the British fossil record. *Nature Communications*

396         **5**, 4818, doi:10.1038/ncomms5818 (2014).

397    37    Benton, M. J., Dunhill, A. M., Lloyd, G. T. & Marx, F. G. Assessing the quality of the

398         fossil record: insights from vertebrates. *Geological Society, London, Special*

399         *Publications* **358**, 63-94, doi:10.1144/sp358.6 (2011).

400    38    Dunhill, A. M., Benton, M. J., Twitchett, R. J. & Newell, A. J. Testing the fossil

401         record: sampling proxies and scaling in the British Triassic-Jurassic.

402         *Palaeogeography Palaeoclimatology Palaeoecology* **404**, 1-11,

403         doi:http://dx.doi.org/10.1016/j.palaeo.2014.03.026 (2014).

404    39    Benson, R. B. J. & Butler, R. J. Uncovering the diversification history of marine

405         tetrapods: ecology influences the effect of geological sampling biases. *Geological*

406         *Society, London, Special Publications* **358**, 191-208, doi:10.1144/sp358.13 (2011).

407    40    Benson, R. B. J., Butler, R. J., Lindgren, J. & Smith, A. S. Mesozoic marine tetrapod

408         diversity: mass extinctions and temporal heterogeneity in geological megabiases

409         affecting vertebrates. *Proceedings of the Royal Society B* **277**, 829-834 (2010).

410    41    Fröbisch, J. Global taxonomic diversity of Anomodonts (Tetropoda, Therapsida) and

411         the terrestrial rock record across the Permian-Triassic boundary. *PLoS ONE* **3**, e3733,

412         doi:10.1371/journal.pone.0003733 (2008).

413    42    Barrett, P. M., McGowan, A. J. & Page, V. Dinosaur diversity and the rock record.

414          *Proceedings of the Royal Society B* **276**, 2667-2674 (2009).

415    43    Butler, R. J., Barrett, P. M., Nowbath, S. & Upchurch, P. Estimating the effects of the

416          rock record on pterosaur diversity patterns: implications for hypotheses of

417          bird/pterosaur competitive replacement. *Paleobiology* **35**, 432-446 (2009).

418    44    Jablonski, D. Scale and hierarchy in macroevolution. *Palaeontology* **50**, 87-109,

419          doi:10.1111/j.1475-4983.2006.00615.x (2007).

420    45    Benton, M. J. The origins of modern biodiversity on land. *Phil. Trans. R. Soc. Lond.B*

421          **365**, 3667-3679 (2010).

422    46    Alroy, J. The shifting balance of diversity among major marine animal groups.

423          *Science* **329**, 1191-1194 (2010).

424    47    Sepkoski, J. J., Bambach, R. K., Raup, D. M. & Valentine, J. W. Phanerozoic marine

425          diversity and the fossil record. *Nature* **293**, 435-437 (1981).

426    48    Jablonski, D. Body-size evolution in Cretaceous molluscs and the status of Cope's

427          rule. *Nature* **385**, 250-252, doi:10.1038/385250a0 (1997).

428    49    Benson, R. B. J., Frigot, R. A., Goswami, A., Andres, B. & Butler, R. J. Competition

429          and constraint drove Cope's rule in the evolution of giant flying reptiles. *Nature*

430          *Communications* **5**, 3567, doi:10.1038/ncomms4567 (2014).

431    50    Raia, P., Carotenuto, F., Passaro, F., Fulgione, D. & Fortelius, M. Ecological

432          specialization in fossil mammals explains Cope's Rule. *American Naturalist* **179**, 328-

433          337 (2012).

434    51    Van M. Savage,    James F. Gillooly,    James H. Brown,    Geoffrey B. West    &

435          Eric L. Charnov. Effects of Body Size and Temperature on Population Growth. *The*

436          *American Naturalist* **163**, 429-441, doi:10.1086/381872 (2004).

437    52    Don, R. L. Influence of Body Size and Population Density on Fertilization Success

438          and Reproductive Output in a Free-Spawning Invertebrate. *Biological Bulletin* **181**,

439          261-268, doi:10.2307/1542097 (1991).

440    53    Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. Macroecology and extinction risk

441          correlates of frogs. *Glob. Ecol. Biogeogr.* **17**, 211-221, doi:10.1111/j.1466-

442          8238.2007.00355.x (2008).

443    54    Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction,

444          distribution, and protection. *Science* **344**, doi:10.1126/science.1246752 (2014).

445    55    Cardillo, M. *et al.* The predictability of extinction: biological and external correlates

446          of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences* **275**,

447          1441-1448, doi:10.1098/rspb.2008.0179 (2008).

448    56    Slatyer, R. A., Hirst, M. & Sexton, J. P. Niche breadth predicts geographical range

449          size: a general ecological pattern. *Ecology Letters* **16**, 1104-1114,

450          doi:10.1111/ele.12140 (2013).

451    57    McCain, C. M. & King, S. R. B. Body size and activity times mediate mammalian

452          responses to climate change. *Global Change Biology* **20**, 1760-1769,

453          doi:10.1111/gcb.12499 (2014).

454    58    Exploring macroevolution using modern and fossil data. *Proceedings of the Royal*

455          *Society B, Biological Sciences* **282**, 20150569, doi:10.1098/rspb.2015.0569 (2015).

456    59    Smith, A. G., Smith, D. G. & Funnell, B. M. *Atlas of Mesozoic and Cenozoic*

457          *coastlines*.  99 (Cambridge University Press, 1994).

458    60    Gradstein, F. M., Ogg, J. G., Schmitz, M. D. & Ogg, G. M. *The Geologic Time Scale*

459          *2012*. Vol. 2 1144 (Elsevier, 2012).

460    61    Haq, B. U., Hardenbol, J. & Vail, P. R. Chronology of fluctuating sea levels since the

461          Triassic. *Science* **235**, 1156-1167 (1987).

462   62      Butler, R. J., Benson, R. B. J., Carrano, M. T., Mannion, P. D. & Upchurch, P. Sea

463           level, dinosaur diversity and sampling biases: investigating the 'common cause'

464           hypothesis in the terrestrial realm. *Proc. R. Soc. Lond. B* **278**, 1107-1113 (2011).

465   63      Raup, D. M. Systematists follow the fossils. *Paleobiology* **3**, 328-329 (1977).

466   64      PALEOMAP Project - PointTracker v. 7h (2010).

467   65      Myers, C. E. & Lieberman, B. S. Sharks that pass in the night: using Geographical

468           Information Systems to investigate competition in the Cretaceous Western Interior

469           Seaway. *Proceedings of the Royal Society B: Biological Sciences* **278**, 681 (2010).

470   66      Myers, C. E., MacKenzie, R. A. & Lieberman, B. S. Greenhouse biogeography: the

471           relationship of geographic range to invasion and extinction in the Cretaceous Western

472           Interior Seaway. *Paleobiology* **39**, 135-148, doi:10.1666/0094-8373-39.1.135 (2013).

473   67      Foote, M. Origination and Extinction Components of Taxonomic Diversity: general

474           problems. *Paleobiology* **26** (supplement), 74-102, doi:10.2307/2666101 (2000).

475   68      Foote, M. Origination and extinction through the Phanerozoic: a new approach. *The*

476           *Journal of Geology* **111**, 125-148 (2003).

477   69      Foote, M. Pulsed origination and extinction in the marine realm. *Paleobiology* **31**, 6-

478           20 (2005).

479   70      Rode, A. L. & Lieberman, B. S. Integrating evolution and biogeography: A case study

480           involving Devonian crustaceans. *Journal of Paleontology* **79**, 267-276 (2005).

481

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489

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491    A.M.D. designed the project and compiled the data. M.A.W. wrote scripts. A.M.D. and

492    M.A.W. analysed the data and wrote the manuscript.

493

494    **Additional Information**

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**Figure Legends**

**Figure 1| Mean rates of change in geographic range size and diversification rates for terrestrial vertebrates, partitioned by time bin**. Rate of change in geographic range size (ΔGeographic range) as represented by (**a**) convex hulls around raw palaeogeographic occurrences and (**b**) mean great circle distance (GCD) between palaeogeographic occurrences standardised to 5 and 10 samples; and (**c**) mean vertebrate diversification rates of ranged-through diversity data (ΔDiversification). The fossil records of the Ladinian[12], Toarcian[19], and much of the Middle Jurassic[28-30,] are of lower quality than the rest of Mesozoic, and this may contribute to some of the negative diversity changes therein. The drop in diversity observed through the Rhaetian could also be regarded as a sampling artefact as the Rhaetian is not as well sampled as the preceding Norian. However, the upper Triassic represents one of the highest quality terrestrial fossil records[22,30]. Alternating grey and white bars correspond to Triassic-Jurassic epochs..

**Figure 2| Scatter plots of diversification rates against per lineage rates of change in geographic range size.** (**a-c**) Rate of geographic range size change (ΔGeographic range) as calculated using convex hulls around raw occurrence data for (**a**) all time bins; (**b**) Late Triassic; (**c**) Rhaetian. (**d-f**) Rate of geographic range size change calculated as mean great circle distances between occurrences standardised to samples of 5 and 10 occurrences for (**d**) all time bins; (**e**) Late Triassic; and (**f**) Rhaetian. Spearman rank correlation coefficients *significant at $p < 0.05$, **significant at $p < 0.01$, ***significant at $p < 0.001$..

**Figure 3| Geographic range maps before and after the end-Triassic mass extinction.** Convex hull geographic range maps and mean generic diversity of six terrestrial vertebrate groups during the (**a**) Rhaetian and (**b**) Hettangian. The Aetosauria, Cynognathia and Phytosauria became extinct during the biotic crisis, despite the widespread distribution of

528    Cynognathia and Phytosauria in the Rhaetian. The Probainognathia, Sauropodomorpha and

529    Theropoda all survived the biotic crisis and expanded their ranges in the Hettangian, albeit

530    with different diversification trajectories. The diversity of Sauropodomorpha increased, the

531    diversity of Theropoda was stationary, and that of Probainognathia decreased across the

532    boundary.

533

534    **Figure 4| Sampling and environmental proxy data.** (**a**) non-marine area[58]; (**b**) average

535    sea level[60]; (**c**) terrestrial formation count[24]; (**d**) fossil abundance[24]; (**e**) total geographic

536    range of all taxa. Alternating grey and white bars correspond to Triassic-Jurassic epochs.

537

**Table 1**| Summary of multiple regression models of diversity change (dependent variable) in terms of geographic range change and sampling and environmental proxies.

| Model | Dependent | Independents | adj $R^2$ | $p$ | AIC |
|---|---|---|---|---|---|
| Convex full | Diversity change | Range change + land area + sea level + formations + abundance + total range | 0.53 | < 0.001 | -98.59 |
| Convex best | Diversity change | Range change | 0.64 | < 0.001 | -100.53 |
| GCD5 full | Diversity change | Range change + land area + sea level + formations + abundance + total range | 0.22 | < 0.001 | -65.5 |
| GCD5 best | Diversity change | Range change + total range + sea level | 0.23 | < 0.001 | -68.95 |
| GCD10 full | Diversity change | Range change + land area + sea level + formations + abundance + total range | 0.32 | < 0.001 | -63.66 |
| GCD10 best | Diversity change | Range change + total range + sea level | 0.35 | < 0.001 | -68.97 |

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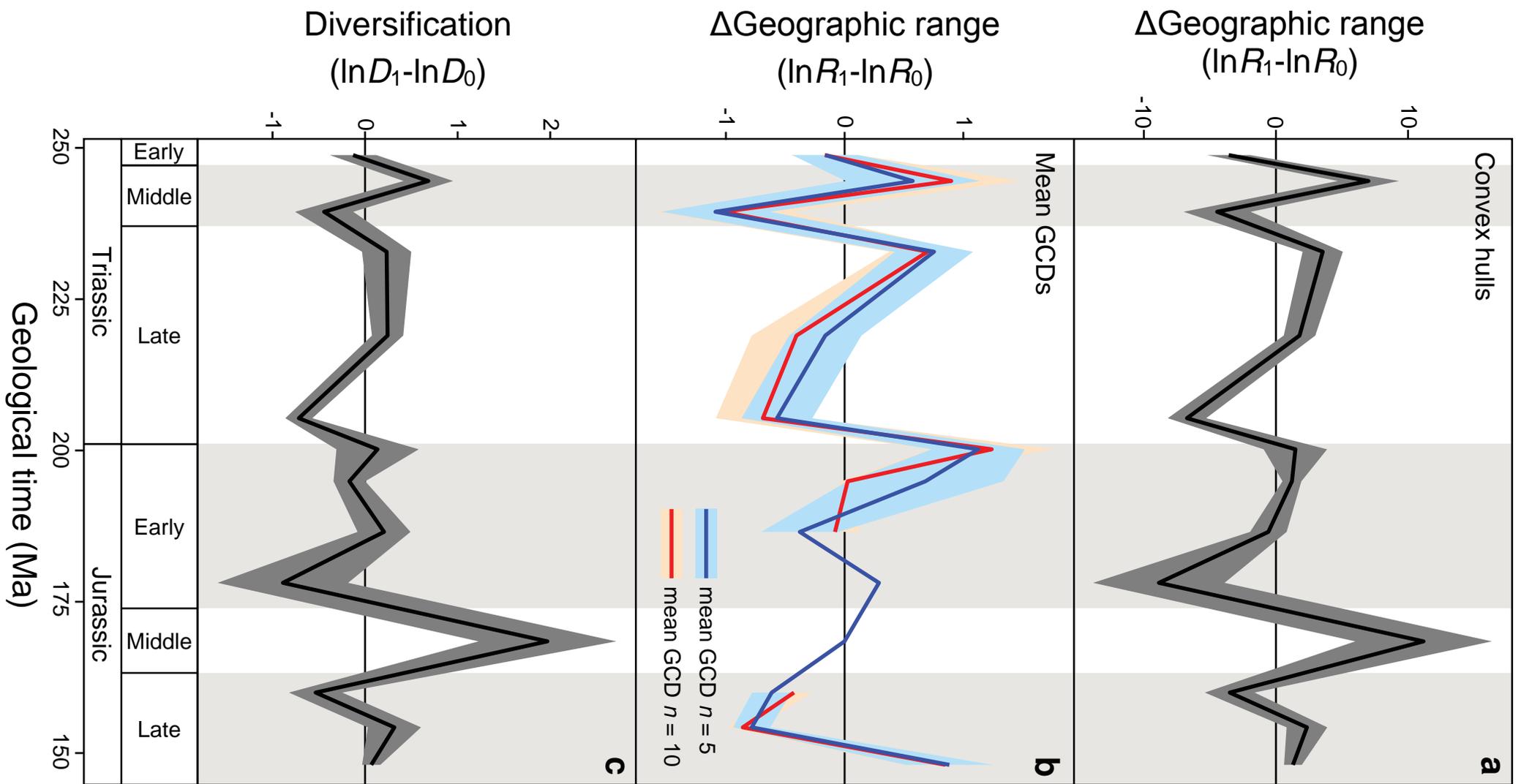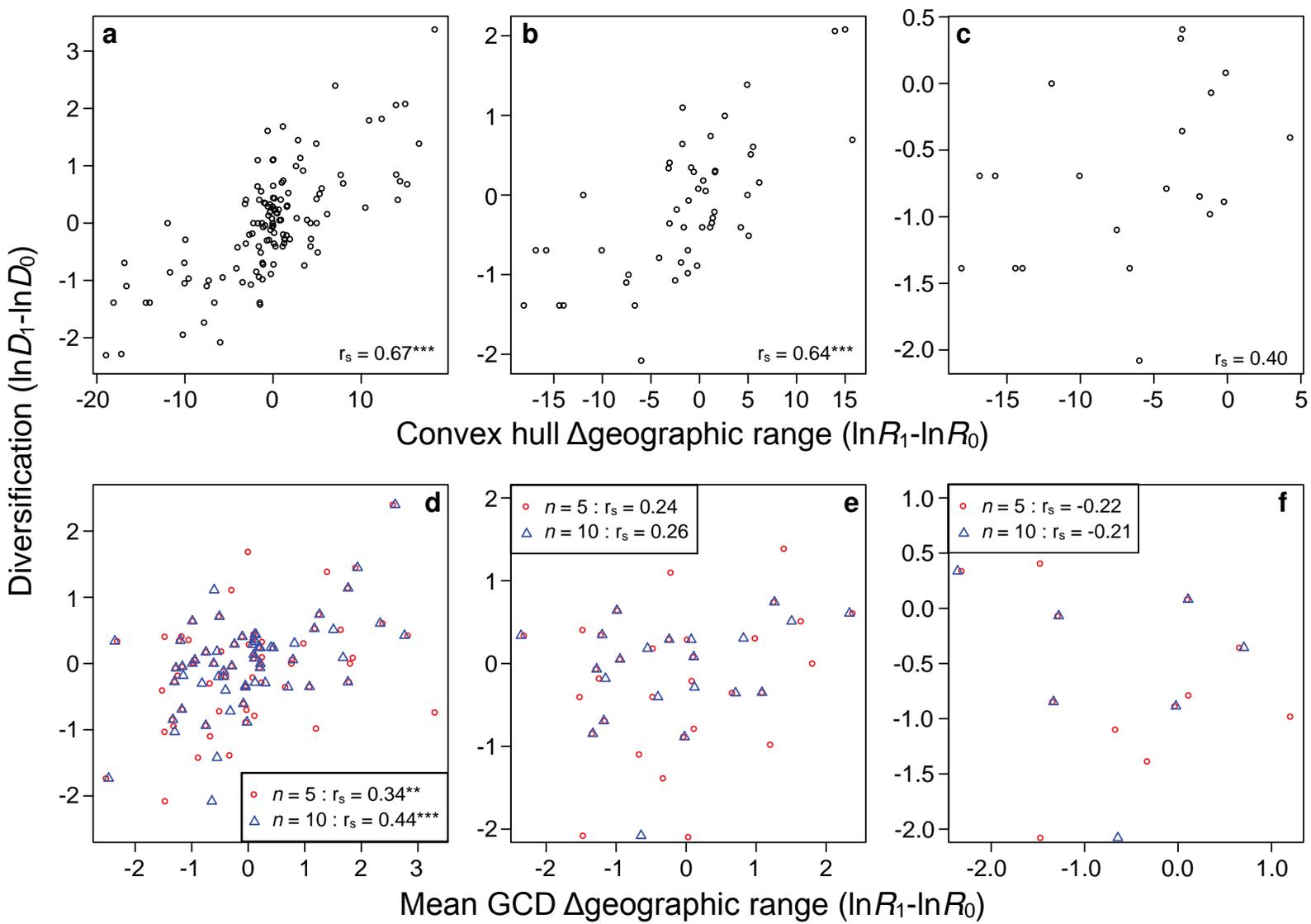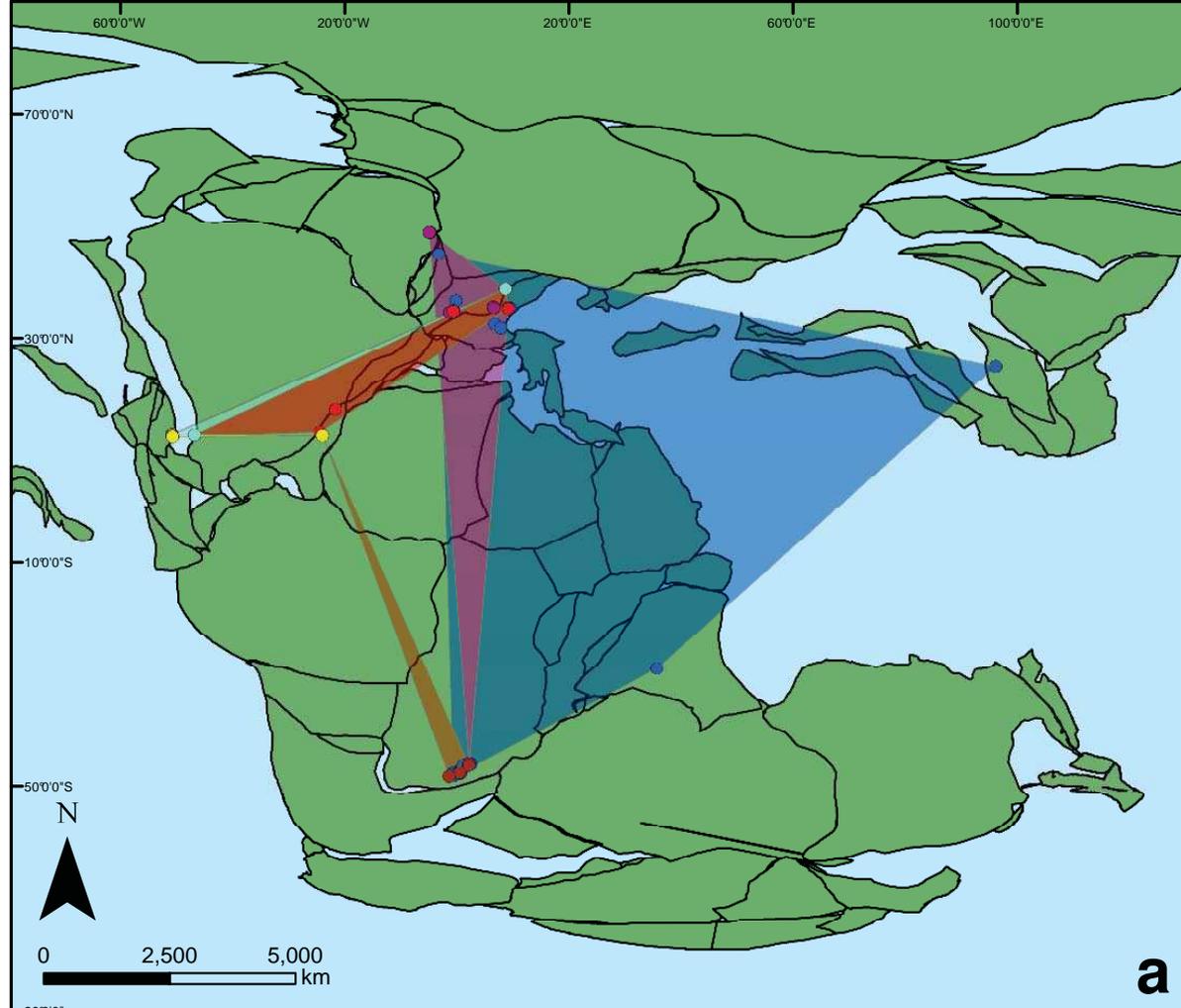
**Aetosauria**
Rhaetian: 1.832
Hettangian: †

**Cynognathia**
Rhaetian: 1.337
Hettangian: †

**Phytosauria**
Rhaetian: 6.967
Hettangian: †
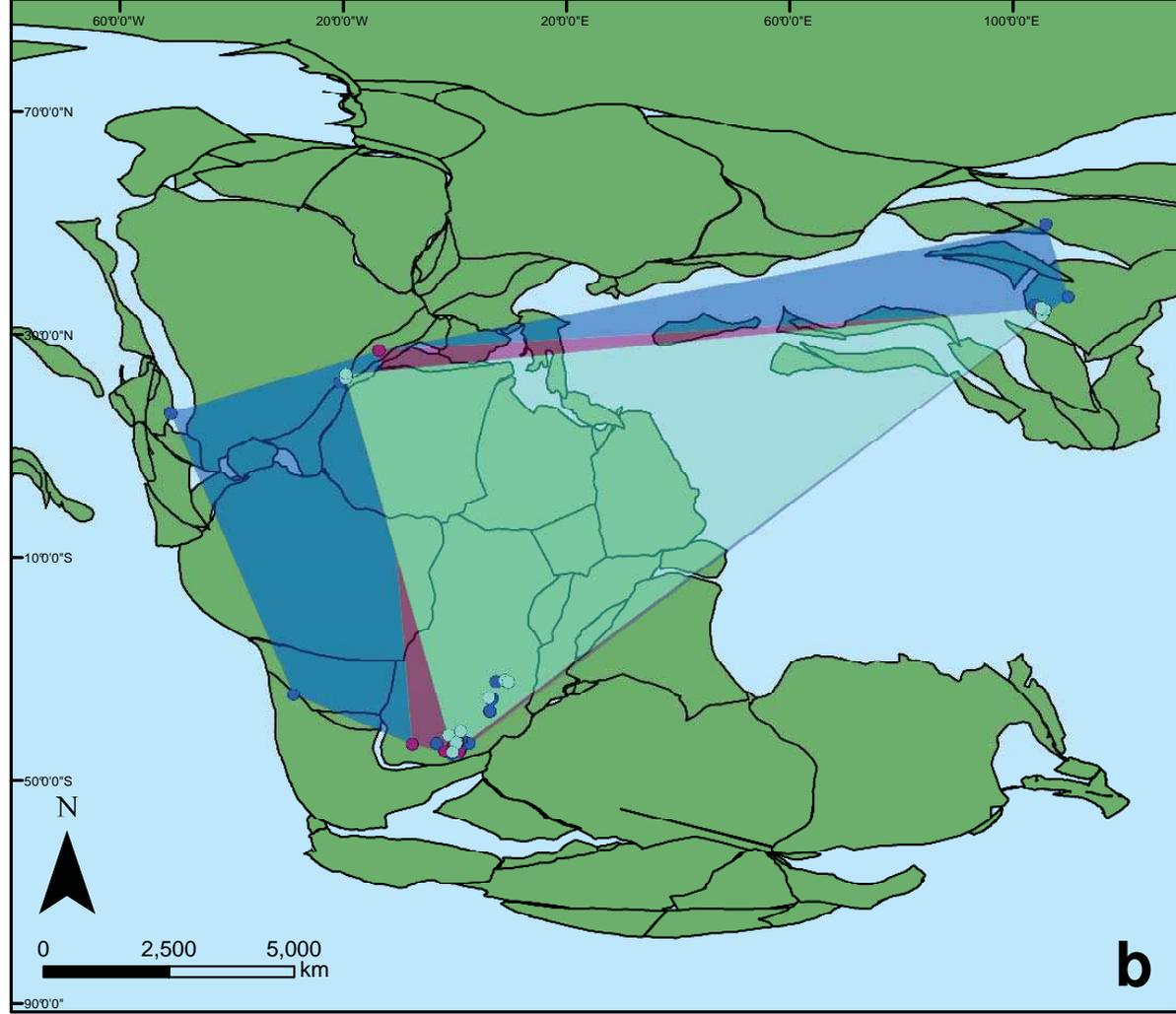
**Probainognathia**
Rhaetian: 13.23
Hettangian: 10

**Sauropodomorpha**
Rhaetian: 12.503
Hettangian: 15.935

**Theropoda**
Rhaetian: 5
Hettangian: 5