

2019-07-01

# Jurassic shift from abiotic to biotic control on marine ecological success

Eichenseer, K

<http://hdl.handle.net/10026.1/14472>

---

10.1038/s41561-019-0392-9

Nature Geoscience

Nature Research

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

This is the author's accepted manuscript. The final published version of this work is published by in *Nature Geoscience* available at: DOI 10.1038/s41561-019-0392-9. This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

accepted on the 22<sup>nd</sup> of May 2019

# **Jurassic shift from abiotic to biotic control on marine ecological success**

Kilian Eichenseer<sup>1</sup>, Uwe Balthasar<sup>1</sup>, Christopher W. Smart<sup>1</sup>, Julian Stander<sup>2</sup>, Kristian A. Haaga<sup>3,4,5</sup>, Wolfgang Kiessling<sup>6</sup>

<sup>1</sup> School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

<sup>2</sup> School of Computing, Electronics and Mathematics, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

<sup>3</sup> Department of Earth Science, University of Bergen, N-5020 Bergen, Norway

<sup>4</sup> Bjerknes Centre for Climate Research, PO Box 7803, NO-5020 Bergen, Norway

<sup>5</sup> K.G. Jebsen Centre for Deep Sea Research, P.O. Box 7803, N-5020, Bergen, Norway

<sup>6</sup> GeoZentrum Nordbayern, Department of Geography and Geosciences, Universität Erlangen-Nürnberg, Loewenichstraße 28, 91054 Erlangen, Germany

1 **Environmental change and biotic interactions both govern the evolution of the biosphere,**  
2 **but the relative importance of these drivers over geological time remains largely unknown.**  
3 **Previous work suggests that, unlike environmental parameters, diversity dynamics differ**  
4 **profoundly between the Palaeozoic and post-Palaeozoic eras. Here we use the fossil record**  
5 **to test the hypothesis that the influence of ocean chemistry and climate on the ecological**  
6 **success of marine calcifiers decreased throughout the Phanerozoic eon. Marine calcifiers**  
7 **build skeletons of calcite or aragonite, and the precipitation of these calcium carbonate**  
8 **polymorphs is governed by the magnesium-to-calcium ratio and temperature in abiotic**  
9 **systems. We developed an environmental forcing model based on secular changes of ocean**  
10 **chemistry and temperature and assessed how well the model predicts the proliferation of**  
11 **skeletal taxa with respect to calcium carbonate polymorphs. Abiotic forcing governs the**  
12 **ecological success of aragonitic calcifiers from the Ordovician to the Middle Jurassic, but**  
13 **not thereafter. This regime shift coincides with the proliferation of calcareous plankton in**  
14 **the mid-Mesozoic. The deposition of biomineralizing plankton on the ocean floor buffers**  
15 **CO<sub>2</sub> excursions and stabilizes Earth's biochemical cycle, and thus mitigates the evolutionary**  
16 **impact of environmental change on the marine biota.**

17 Dramatic shifts in the success of dominant animal groups in Earth history abound in the fossil  
18 record<sup>1</sup> and there are numerous Phanerozoic-scale macroevolutionary trends. Traits such as  
19 body size, the metabolic rate of dominant taxonomic groups, and physiological buffering  
20 capacity have increased over the course of the Phanerozoic<sup>2-5</sup>. As a consequence, biotic  
21 interactions may have increased as well<sup>6-9</sup>. In contrast, climate and seawater composition  
22 show a cyclical behaviour rather than Phanerozoic-scale trends<sup>10,11</sup>. The biosphere has  
23 evolved to cushion some environmental variability: for example, the buffering of ocean

24 chemistry has increased due to the mid-Mesozoic ascent of calcifying plankton<sup>12</sup>.  
25 Perturbations of the carbon cycle have fallen in amplitude, particularly since the mid-  
26 Mesozoic<sup>13</sup> (Fig. 1d), and extinction rates have decreased towards the present<sup>14</sup> (Fig. 1e).  
27 Accordingly, we hypothesize that the evolutionary importance of the abiotic environment,  
28 relative to intrinsic, biotic factors, has declined through geological time.

29 We tested this hypothesis using the vast fossil record of marine calcifiers. In the inorganic  
30 formation of calcium carbonate ( $\text{CaCO}_3$ ), high Mg/Ca ratios and high temperatures have been  
31 shown to favour the precipitation of aragonite over calcite, and *vice versa*<sup>15</sup>. Across the  
32 Phanerozoic, tectonically driven changes in sea water chemistry and climate have caused  
33 aragonite and calcite favouring conditions to alternate, giving rise to episodes of “aragonite  
34 seas” and “calcite seas”<sup>10,16</sup> (Fig. 1b). The skeletal mineralogy of calcifying organisms is  
35 strongly tied to phylogenetic history, but the *de novo* acquisition of biominerals, skeletal  
36 composition, skeletal production, and growth rates of many marine calcifiers are affected by  
37 the Mg/Ca ratio and temperature of the surrounding sea water<sup>17-21</sup>, analogous to inorganic  
38  $\text{CaCO}_3$  formation. If aragonite and calcite seas were influential in the evolution of marine  
39 calcifiers, we expect a correspondence of aragonite sea conditions with greater success of  
40 aragonitic taxa.

#### 41 **Aragonite - calcite seas and the success of marine calcifiers**

42 We combine a model of past Mg/Ca ratios<sup>22</sup> (Fig. 1b) with  $\delta^{18}\text{O}$  temperature  
43 reconstructions<sup>23</sup> (Fig. 1c) to quantify *aragonite sea intensity* (*ASI*) in 85 post-Cambrian stages.  
44 The *ASI* is parametrized from experimental data<sup>15</sup> via multiple regression. We contrast *ASI*  
45 with a measure of the environmental occupancy, or success, of aragonitic genera relative to  
46 all calcifying genera ( $SCOR_{ara}$ ), calculated with the Summed Common species Occurrence Rate

47 (SCOR)<sup>24</sup>. Given that novel acquisitions of calcium carbonate skeletons are rare and that  
48 switches in skeletal mineralogy are largely restricted to a few clades<sup>20,21,25</sup>, changes in *SCOR<sub>ara</sub>*  
49 reflect predominantly the differential success of aragonitic taxa, rather than changing  
50 mineralogies within calcifying clades (Supplementary Materials S6). Although the lower  
51 preservation potential of aragonitic taxa may lead to underestimate the abundance of  
52 aragonitic taxa<sup>26</sup>, we find that the completeness of the record of aragonitic and calcitic genera  
53 is not significantly different (Wilcoxon signed-rank test:  $p = 0.28$ , Supplementary Materials  
54 S3). The strength of abiotic controls on marine calcifiers is assessed by estimating linear  
55 models of *SCOR<sub>ara</sub>* against *ASI* using generalised least squares (GLS) to account for temporal  
56 autocorrelation, and by convergent cross mapping (CCM) to detect causal coupling<sup>27</sup>  
57 (*Methods*).

58 Visual inspection of the *SCOR<sub>ara</sub>* and *ASI* time series suggests an association in the Ordovician  
59 – Carboniferous and again in the early Mesozoic, but not for most of the Mesozoic and  
60 Cenozoic (Fig. 1a). A linear model of *SCOR<sub>ara</sub>* against *ASI* is significant in the Palaeozoic  
61 ( $R^2 = 0.15$ ,  $p = 0.017$ , Table 1), and not in the Mesozoic – Cenozoic ( $R^2 < 0.01$ ,  $p = 0.68$ ),  
62 suggesting a decreasing dependence of ecological success on relevant environmental  
63 conditions in the Mesozoic. In the entire Ordovician – Pleistocene data, the linear relationship  
64 is not significant ( $R^2 < 0.01$ ,  $p = 0.70$ ), however the sharp rise of *SCOR<sub>ara</sub>* across the Permian-  
65 Triassic makes estimating linear models across this boundary problematic.

66 We used a Bayesian approach to identify the timing of the changes in the relationship  
67 between *SCOR<sub>ara</sub>* and *ASI* (see *Methods*). This analysis identifies the Permian-Triassic  
68 boundary as the strongest change point of the entire Phanerozoic time series (supported by  
69 100 % posterior probability; Fig. 2a, purple bar). When evaluating only the Palaeozoic time

70 series, the Carboniferous – Permian boundary shows the strongest change (73% probability;  
71 Fig. 2a, red bars), whereas no unambiguous single change point is found for the Mesozoic –  
72 Cenozoic time series (all probabilities <25%; Fig. 2a, green bars).

73 To evaluate the possibility of a gradual change, we fitted linear models of  $SCOR_{ara}$  against  $ASI$   
74 from the Triassic onwards, adding successively more stages towards the present, and  
75 repeated the same process with the Palaeozoic data, separately. The relationship of  $SCOR_{ara}$   
76 and  $ASI$  is consistently strong in the Palaeozoic, with a weakening around the Carboniferous  
77 – Permian boundary (Figure 2b). In the Mesozoic, a positive linear relationship persists up to  
78 the Middle Jurassic, although with lower statistical support. No relationship is supported from  
79 the Late Jurassic onwards. The relationship of  $SCOR_{ara}$  and  $ASI$  evolves in a similar way when  
80  $SCOR_{ara}$  is calculated only in the subset of organisms which are considered especially  
81 responsive to physiochemical changes in the environment (Supplementary Fig. S7)<sup>2,25,28</sup>.

82 These results are reinforced by using CCM, a technique developed to detect causal coupling  
83 between time series by quantifying the extent to which a putative response time series can  
84 be used to predict a driver time series<sup>27</sup> (see *Methods*). If this prediction is successful beyond  
85 some appropriate null hypothesis (*Methods*), we take it as evidence of dynamical coupling.  
86 Applying CCM in expanding time windows, we find a significant dynamical influence of  $ASI$  on  
87  $SCOR_{ara}$  in the Ordovician - Jurassic (Fig. 2c), implying a causal link between aragonite-calcite  
88 sea conditions and  $SCOR_{ara}$  in this part of the record. Following a maximum in the early  
89 Jurassic (Sinemurian), the CCM prediction skill decreases gradually until the Early Cretaceous  
90 and remains low thereafter. This decline indicates a weakening influence of  $ASI$  on the success  
91 of marine calcifiers towards the present.

92 Our findings corroborate the hypothesis of a decreasing environmental influence on marine  
93 calcifiers' success. The correlation of aragonite-calcite seas and the success of aragonitic  
94 calcifiers decreased chiefly in two episodes: Around the Carboniferous-Permian boundary,  
95 and in a second episode centred in the Middle Jurassic (Fig 2). Permian seawater had an  
96 unusually high  $\text{CaCO}_3$  saturation<sup>12,29</sup>. All else being equal, higher  $\text{CaCO}_3$  saturation facilitates  
97 calcification<sup>30</sup> and tends to shift the  $\text{CaCO}_3$  polymorph balance in favour of calcite<sup>31</sup>.  
98 Consequently, calcifiers with a calcitic skeleton performed better than predicted by *ASI* when  
99 the  $\text{CaCO}_3$  saturation state rose in the Permian. Calcitic taxa, particularly brachiopods,  
100 became more successful across the Carboniferous – Permian boundary (Supplementary  
101 Fig. S8, a detailed discussion of the relative success of the major taxonomic groups of marine  
102 calcifiers is provided in the Supplementary Materials). The influence of *ASI* on  $SCOR_{ara}$   
103 decreased but their correlation remained positive within the Permian (Fig. 2b, Table 1).  
104 Although  $\text{CaCO}_3$  saturation state probably remained high during the Triassic<sup>32</sup>, *ASI* continued  
105 to affect  $SCOR_{ara}$  in the early Mesozoic, but not thereafter.

## 106 **The role of calcifying plankton**

107 In the mid-Mesozoic, the Earth-Life system was revolutionised by the rise of calcifying  
108 plankton<sup>12</sup>. Before the widespread occurrence of planktonic calcifiers,  $\text{CaCO}_3$  precipitation  
109 was largely confined to the continental shelves and linked to the success of benthic calcifiers  
110 such as corals and brachiopods. The evolutionary success of calcifying plankton, especially of  
111 coccolithophores<sup>33</sup>, shifted the carbonate factory from the shelves to the open ocean.  
112 Calcareous tests sink to the ocean floor and either dissolve or accumulate, depending on the  
113 local  $\text{CaCO}_3$  saturation state. Since the proliferation of planktonic calcifiers, changes in the  
114 atmospheric and oceanic  $\text{CO}_2$  content have been compensated on geologically short time

115 scales by increased CaCO<sub>3</sub> deposition or dissolution in the deep sea<sup>34</sup>. The evolutionary impact  
116 of episodes of severe climatic change with associated ocean acidification such as the  
117 Palaeocene-Eocene Thermal Maximum has been less severe than comparable events in the  
118 Palaeozoic and early Mesozoic<sup>35,36</sup>, possibly a consequence of the increased ocean  
119 buffering<sup>12,37</sup>

120 Producing a skeleton out of *sync* with aragonite-calcite sea conditions may be costly especially  
121 when CaCO<sub>3</sub> secretion is impeded by ocean acidification. Enhanced ocean buffering after the  
122 proliferation of calcifying plankton can explain the diminished response of marine calcifiers  
123 to changing aragonite-calcite sea conditions after the mid-Jurassic. Several key events in the  
124 evolution of calcifying plankton fall into the Middle – Late Jurassic. Planktonic foraminifera  
125 first appear in the fossil record during the Lower Jurassic, but the first known deep water  
126 carbonate oozes composed of planktonic foraminifera date back to the Middle Jurassic<sup>38,39</sup>.  
127 The thick-walled coccolithophore genus *Watznaueria* diversified in the early Middle Jurassic,  
128 resulting in an increase of coccolith flux to the sediment by two orders of magnitude<sup>40</sup>.  
129 Nannofossil deposits from the Tethys ocean show that coccolithophores colonised the open  
130 ocean during the Late Jurassic and became abundant enough to affect the marine carbonate  
131 system<sup>41</sup>.

## 132 **A new evolutionary regime**

133 Beyond skeletal mineralogy, there is evidence for a wider regulatory change of evolutionary  
134 patterns and environmental state shifts in the mid-Phanerozoic. Devastating extinctions in  
135 the Late Permian – early Mesozoic overturned the taxonomic composition of marine  
136 calcifiers<sup>36,42</sup> and favoured the survival of active and physiologically buffered animals<sup>28,43</sup>. As  
137 a consequence, the dominant, modern marine biota are less vulnerable to abiotic stressors

138 than their Palaeozoic counterparts<sup>43</sup>, and individual energy budgets of bivalves and  
139 gastropods increased throughout the early Mesozoic<sup>3,5</sup>. This rise in available metabolic energy  
140 may have helped absorb the cost of secreting a shell out of *sync* with aragonite-calcite sea  
141 conditions.

142 The Mesozoic rise of plankton such as foraminifera<sup>38</sup>, coccolithophores, and dinoflagellates<sup>44</sup>  
143 had an additional effect on the bio-geosphere: tests of phytoplankton act as ballast,  
144 increasing its sinking velocity and increasing the depth at which organic carbon is oxidised,  
145 which in turn can explain the much lower prevalence of anoxia on Mesozoic and Cenozoic  
146 shelves<sup>45</sup>. Increasing oxygenation of shallow ocean water is indicated from the Jurassic  
147 onwards by iodine-to-calcium ratios<sup>46</sup> (Fig. 1f). Well-oxygenated shelves stabilise the carbon  
148 cycle by reducing the impact of sea level changes on the burial capacity of organic carbon<sup>13</sup>,  
149 thus decreasing the potential for catastrophic environmental change. Increasing oxygen  
150 availability also allows for higher metabolic rates and more active modes of life in the shelf  
151 biota, as has been inferred for the mid-Mesozoic<sup>47</sup> and may have increased the pace of  
152 escalation in evolution<sup>48</sup>. The onset of a persistent diversity rise in the Middle Jurassic agrees  
153 with this interpretation (Fig. 1g).

154 Our results specify the long-held notion that “the evolutionary milieu in which taxa find  
155 themselves changed substantially” from the Palaeozoic to the modern world<sup>49</sup>: We found a  
156 prominent decrease in environmental influence on the ecological success of marine calcifiers,  
157 although some 80 million years after the end of the Palaeozoic. This regime shift was caused  
158 by a number of abiotic and biotic revolutions in the Earth-Life system. Of all the factors  
159 contributing to this pattern, the onset of the modern carbon cycle via deep-sea CaCO<sub>3</sub>  
160 sedimentation was likely the most consequential for marine calcifying organisms. The high-

161 level taxonomic composition of marine life changed towards a “modern” biota after the end-  
162 Permian catastrophe<sup>1</sup>, but the Palaeozoic evolutionary regime may have persisted well into  
163 the Mesozoic.

## 164 **References**

- 165 1 Alroy, J. The shifting balance of diversity among major marine animal groups. *Science*  
166 **329**, 1191-1194 (2010).
- 167 2 Bambach, R. K., Knoll, A. H. & Sepkoski, J. J. Anatomical and ecological constraints on  
168 Phanerozoic animal diversity in the marine realm. *Proceedings of the National*  
169 *Academy of Sciences* **99**, 6854-6859 (2002).
- 170 3 Finnegan, S., McClain, C. M., Kosnik, M. A. & Payne, J. L. Escargots through time: an  
171 energetic comparison of marine gastropod assemblages before and after the  
172 Mesozoic Marine Revolution. *Paleobiology* **37**, 252-269 (2011).
- 173 4 Heim, N. A., Knope, M. L., Schaal, E. K., Wang, S. C. & Payne, J. L. Cope’s rule in the  
174 evolution of marine animals. *Science* **347**, 867-870 (2015).
- 175 5 Payne, J. L., Heim, N. A., Knope, M. L. & McClain, C. R. Metabolic dominance of bivalves  
176 predates brachiopod diversity decline by more than 150 million years. *Proc. R. Soc. B*  
177 **281**, 20133122 (2014).
- 178 6 Ausich, W. I. & Bottjer, D. J. Tiering in Suspension-Feeding Communities on Soft  
179 Substrata throughout the Phanerozoic. *Science* **216**, 9 (1982).
- 180 7 Vermeij, G. J. The Mesozoic marine revolution: evidence from snails, predators and  
181 grazers. *Paleobiology* **3**, 245-258 (1977).
- 182 8 Vermeij, G. J. *Evolution and escalation: an ecological history of life*. (Princeton  
183 University Press, 1987).

- 184 9 Aberhan, M., Kiessling, W. & Fürsich, F. T. Testing the role of biological interactions in  
185 the evolution of mid-Mesozoic marine benthic ecosystems. *Paleobiology* **32**, 259-277  
186 (2006).
- 187 10 Sandberg, P. A. An oscillating trend in Phanerozoic non-skeletal carbonate mineralogy.  
188 *Nature* **305**, 19-22 (1983).
- 189 11 Veizer, J., Godderis, Y. & François, L. M. Evidence for decoupling of atmospheric CO<sub>2</sub>  
190 and global climate during the Phanerozoic eon. *Nature* **408**, 698-701 (2000).
- 191 12 Ridgwell, A. A Mid Mesozoic Revolution in the regulation of ocean chemistry. *Marine*  
192 *Geology* **217**, 339-357 (2005).
- 193 13 Bachan, A. *et al.* A model for the decrease in amplitude of carbon isotope excursions  
194 across the Phanerozoic. *American Journal of Science* **317**, 641-676 (2017).
- 195 14 Alroy, J. Accurate and precise estimates of origination and extinction rates.  
196 *Paleobiology* **40**, 374-397 (2014).
- 197 15 Balthasar, U. & Cusack, M. Aragonite-calcite seas—Quantifying the gray area. *Geology*  
198 **43**, 99-102 (2015).
- 199 16 Hardie, L. A. Secular variation in seawater chemistry: An explanation for the coupled  
200 secular variation in the mineralogies of marine limestones and potash evaporites over  
201 the past 600 my. *Geology* **24**, 279-283 (1996).
- 202 17 Higuchi, T., Shirai, K., Mezaki, T. & Yuyama, I. Temperature dependence of aragonite  
203 and calcite skeleton formation by a scleractinian coral in low mMg/Ca seawater.  
204 *Geology* **45**, 1087-1090 (2017).

- 205 18 Ramajo, L., Rodríguez-Navarro, A. B., Duarte, C. M., Lardies, M. A. & Lagos, N. A. Shifts  
206 in shell mineralogy and metabolism of *Concholepas concholepas* juveniles along the  
207 Chilean coast. *Marine and Freshwater Research* **66**, 1147-1157 (2015).
- 208 19 Ries, J. Review: geological and experimental evidence for secular variation in seawater  
209 Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification.  
210 *Biogeosciences* **7**, 2795 (2010).
- 211 20 Harper, E. M., Palmer, T. J. & Alphey, J. Evolutionary response by bivalves to changing  
212 Phanerozoic sea-water chemistry. *Geological Magazine* **134**, 403-407 (1997).
- 213 21 Porter, S. Calcite and aragonite seas and the *de novo* acquisition of carbonate  
214 skeletons. *Geobiology* **8**, 256-277 (2010).
- 215 22 Demicco, R. V., Lowenstein, T. K., Hardie, L. A. & Spencer, R. J. Model of seawater  
216 composition for the Phanerozoic. *Geology* **33**, 877-880 (2005).
- 217 23 Veizer, J. & Prokoph, A. Temperatures and oxygen isotopic composition of  
218 Phanerozoic oceans. *Earth-Science Reviews* **146**, 92-104 (2015).
- 219 24 Hannisdal, B., Henderiks, J. & Liow, L. H. Long-term evolutionary and ecological  
220 responses of calcifying phytoplankton to changes in atmospheric CO<sub>2</sub>. *Global Change*  
221 *Biology* **18**, 3504-3516 (2012).
- 222 25 Kiessling, W., Aberhan, M. & Villier, L. Phanerozoic trends in skeletal mineralogy driven  
223 by mass extinctions. *Nature Geoscience* **1**, 527-530 (2008).
- 224 26 Foote, M., Crampton, J. S., Beu, A. G. & Nelson, C. S. Aragonite bias, and lack of bias,  
225 in the fossil record: lithological, environmental, and ecological controls. *Paleobiology*  
226 **41**, 245-265 (2015).
- 227 27 Sugihara, G. *et al.* Detecting causality in complex ecosystems. *science*, 1227079 (2012).

228 28 Knoll, A. H., Bambach, R. K., Payne, J. L., Pruss, S. & Fischer, W. W. Paleophysiology  
229 and end-Permian mass extinction. *Earth and Planetary Science Letters* **256**, 295-313  
230 (2007).

231 29 Grotzinger, J. P. & Knoll, A. H. Anomalous carbonate precipitates: is the Precambrian  
232 the key to the Permian? *Palaios*, 578-596 (1995).

233 30 Langdon, C. *et al.* Effect of calcium carbonate saturation state on the calcification rate  
234 of an experimental coral reef. *Global Biogeochemical Cycles* **14**, 639-654 (2000).

235 31 De Choudens-Sanchez, V. & Gonzalez, L. A. Calcite and aragonite precipitation under  
236 controlled instantaneous supersaturation: elucidating the role of CaCO<sub>3</sub> saturation  
237 state and Mg/Ca ratio on calcium carbonate polymorphism. *Journal of Sedimentary*  
238 *Research* **79**, 363-376 (2009).

239 32 Webb, G. E. Was Phanerozoic reef history controlled by the distribution of non-  
240 enzymatically secreted reef carbonates (microbial carbonate and biologically induced  
241 cement)? *Sedimentology* **43**, 947-971 (1996).

242 33 Bown, P. R., Lees, J. A. & Young, J. R. in *Coccolithophores* 481-508 (Springer, 2004).

243 34 Ridgwell, A. & Zeebe, R. E. The role of the global carbonate cycle in the regulation and  
244 evolution of the Earth system. *Earth and Planetary Science Letters* **234**, 299-315  
245 (2005).

246 35 Clapham, M. E. & Renne, P. R. Flood Basalts and Mass Extinctions. *Annual Review of*  
247 *Earth and Planetary Sciences* **47** (2019).

248 36 Wignall, P. B. *The Worst of Times: How Life on Earth Survived Eighty Million Years of*  
249 *Extinctions*. (Princeton University Press, 2015).

250 37 Zeebe, R. E. & Westbroek, P. A simple model for the CaCO<sub>3</sub> saturation state of the  
251 ocean: The “Strangelove,” the “Neritan,” and the “Cretan” Ocean. *Geochemistry,*  
252 *Geophysics, Geosystems* **4** (2003).

253 38 Hudson, W., Hart, M. B. & Smart, C. W. Palaeobiogeography of early planktonic  
254 foraminifera. *Bulletin de la Société géologique de France* **180**, 27-38 (2009).

255 39 Hart, M. B., Hudson, W., Smart, C. W. & Tyszka, J. A reassessment of ‘Globigerina  
256 bathoniana’Pazdrowa, 1969 and the palaeoceanographic significance of Jurassic  
257 planktic foraminifera from southern Poland. *Journal of Micropalaeontology* **31**, 97-109  
258 (2012).

259 40 Suchéras-Marx, B. *et al.* Impact of the Middle Jurassic diversification of Watznaueria  
260 (coccolith-bearing algae) on the carbon cycle and  $\delta^{13}\text{C}$  of bulk marine carbonates.  
261 *Global and Planetary Change* **86**, 92-100 (2012).

262 41 Roth, P. H. Mesozoic palaeoceanography of the North Atlantic and Tethys oceans.  
263 *Geological Society, London, Special Publications* **21**, 299-320 (1986).

264 42 Alroy, J. Dynamics of origination and extinction in the marine fossil record.  
265 *Proceedings of the National Academy of Sciences* **105**, 11536-11542 (2008).

266 43 Clapham, M. E. Organism activity levels predict marine invertebrate survival during  
267 ancient global change extinctions. *Global change biology* **23**, 1477-1485 (2017).

268 44 Falkowski, P. G. *et al.* The evolution of modern eukaryotic phytoplankton. *Science* **305**,  
269 354-360 (2004).

270 45 Meyer, K., Ridgwell, A. & Payne, J. The influence of the biological pump on ocean  
271 chemistry: implications for long-term trends in marine redox chemistry, the global  
272 carbon cycle, and marine animal ecosystems. *Geobiology* **14**, 207-219 (2016).

273 46 Lu, W. *et al.* Late inception of a resiliently oxygenated upper ocean. *Science* **361**, 174-  
274 177, (2018).

275 47 Vermeij, G. J. Escalation and its role in Jurassic biotic history. *Palaeogeography,*  
276 *Palaeoclimatology, Palaeoecology* **263**, 3-8 (2008).

277 48 Vermeij, G. J. On escalation. *Annual Review of Earth and Planetary Sciences* **41**, 1-19  
278 (2013).

279 49 Foote, M. Origination and extinction components of taxonomic diversity: Paleozoic  
280 and post-Paleozoic dynamics. *Paleobiology* **26**, 578-605 (2000).

281

## 282 **Corresponding author**

283 Correspondence and requests for materials should be addressed to Kilian Eichenseer  
284 (kilian.eichenseer@plymouth.ac.uk).

285

## 286 **Acknowledgements**

287 This project was supported by the University of Plymouth (K.E., U.B., C.W.S. and J.S.) , by the  
288 Trond Mohn Foundation (funding to K.A.H.) and by the Deutsche Forschungsgemeinschaft (KI  
289 806/16-1, funding to W.K.). We thank all contributors to the Paleobiology Database, and  
290 David Diego for discussions on pullback attractor formalism and CCM interpretations. We are  
291 grateful to James Crampton, Ashleigh Hood for their comments on an earlier version of this  
292 manuscript. This is Paleobiology Database publication no. 344.

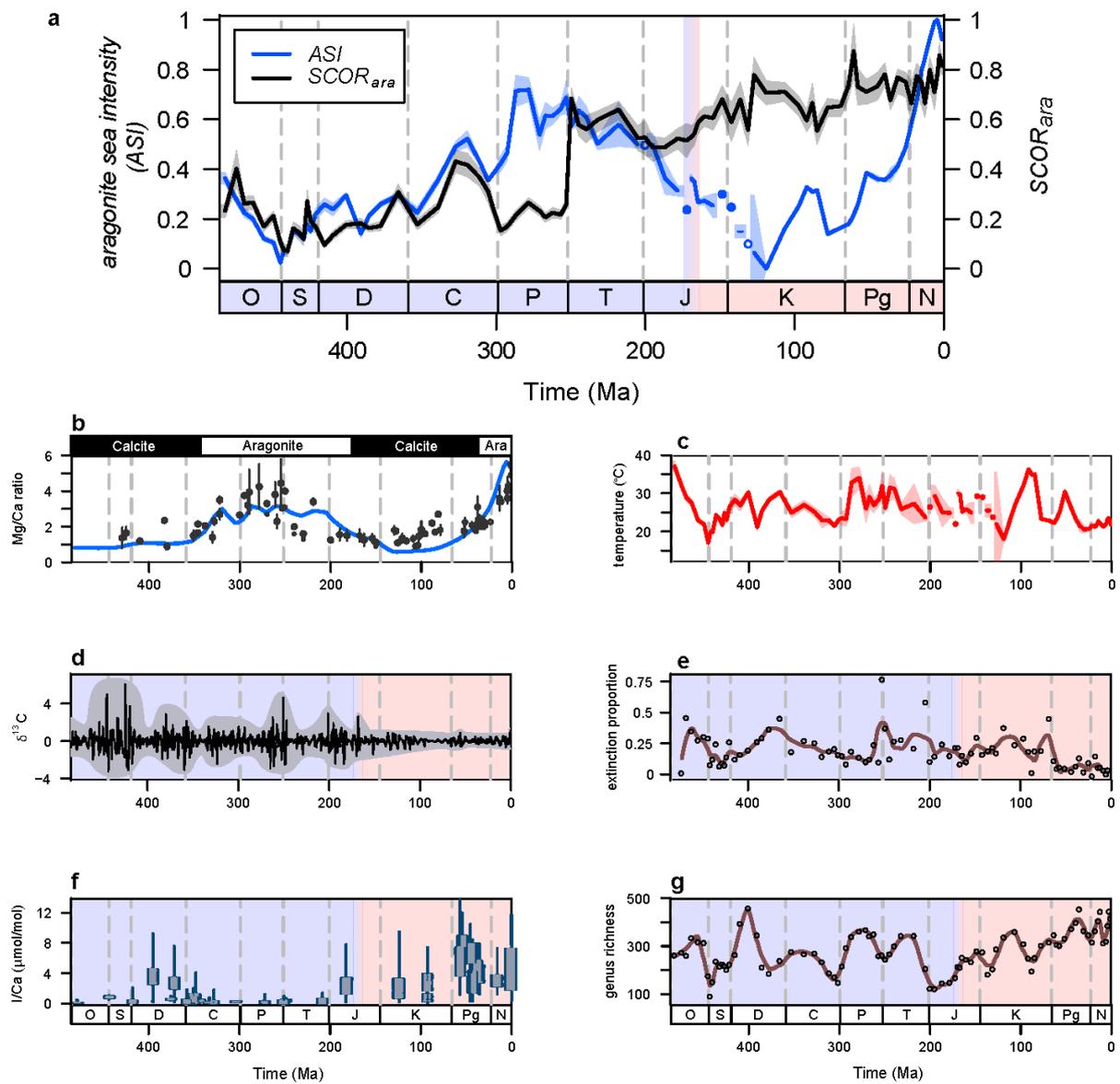
293 **Author contributions**

294 K.E., U.B., W.K. and C.W.S. designed the study. J.S. developed and implemented the Bayesian  
295 changepoint regression analysis. K.A.H. performed the convergent cross mapping analysis.  
296 K.E. carried out all other data analysis and wrote the initial manuscript draft, and all authors  
297 contributed substantially to its improvement.

298 **Competing interests**

299 The authors declare no competing interests.

**Figure 1**



301

302 **Figure 1: Environmental and biotic changes across the Ordovician – Neogene**

303 (a) *ASI* (aragonite sea intensity, blue) and *SCOR<sub>ara</sub>* (relative Summed Common species  
 304 Occurrence Rate of aragonitic genera, black), in 85 Ordovician – Pleistocene stages.  
 305 Shaded areas represent 2 standard errors around the mean with  
 306 the *ASI* error envelope being based on the temperature component (*Methods*). Stages

307 with only one measurement are drawn as solid dots, stages without observations  
308 (circles) have been averaged from the neighboring stages.

309 Legend: O = Ordovician, S = Silurian, D = Devonian, C = Carboniferous, P = Permian, T  
310 = Triassic, J = Jurassic, K = Cretaceous, Pg = Palaeogene, N = Neogene and Quaternary,  
311 Ma = Million years ago. The blue – red transitions and the vertical bar mark the time  
312 when the relationship between *ASI* and *SCOR<sub>ara</sub>* decreased most strongly (See Fig. 2b,  
313 c).

314 (b) Modelled Mg/Ca ratio from ref. 22 (blue line) and a compilation of Mg/Ca proxy data  
315 (black dots, see Supplementary Materials S1). The bar at the top delineates calcite and  
316 aragonite sea intervals as predicted by ref. 16.

317 (c) Mean stage-level tropical shallow water temperatures calculated from oxygen isotope  
318 measurements compiled in ref. 23. Stages with only one measurement are drawn as  
319 solid dots, stages without observations have been averaged from the neighbouring  
320 stages and are shown as circles. Shaded areas represent 2 standard errors around the  
321 mean.

322 (d) Periodic changes in the envelope of third-order  $\delta^{13}\text{C}$  variations, reprinted from ref. 13  
323 with permission of the American Journal of Science. The grey area highlights the  
324 variability.

325 (e) Genus-level, sampling-standardised extinction proportions (circles, see *Methods*) with  
326 long-term trend line (brown; LOESS regression with a smoothing span of 0.1).

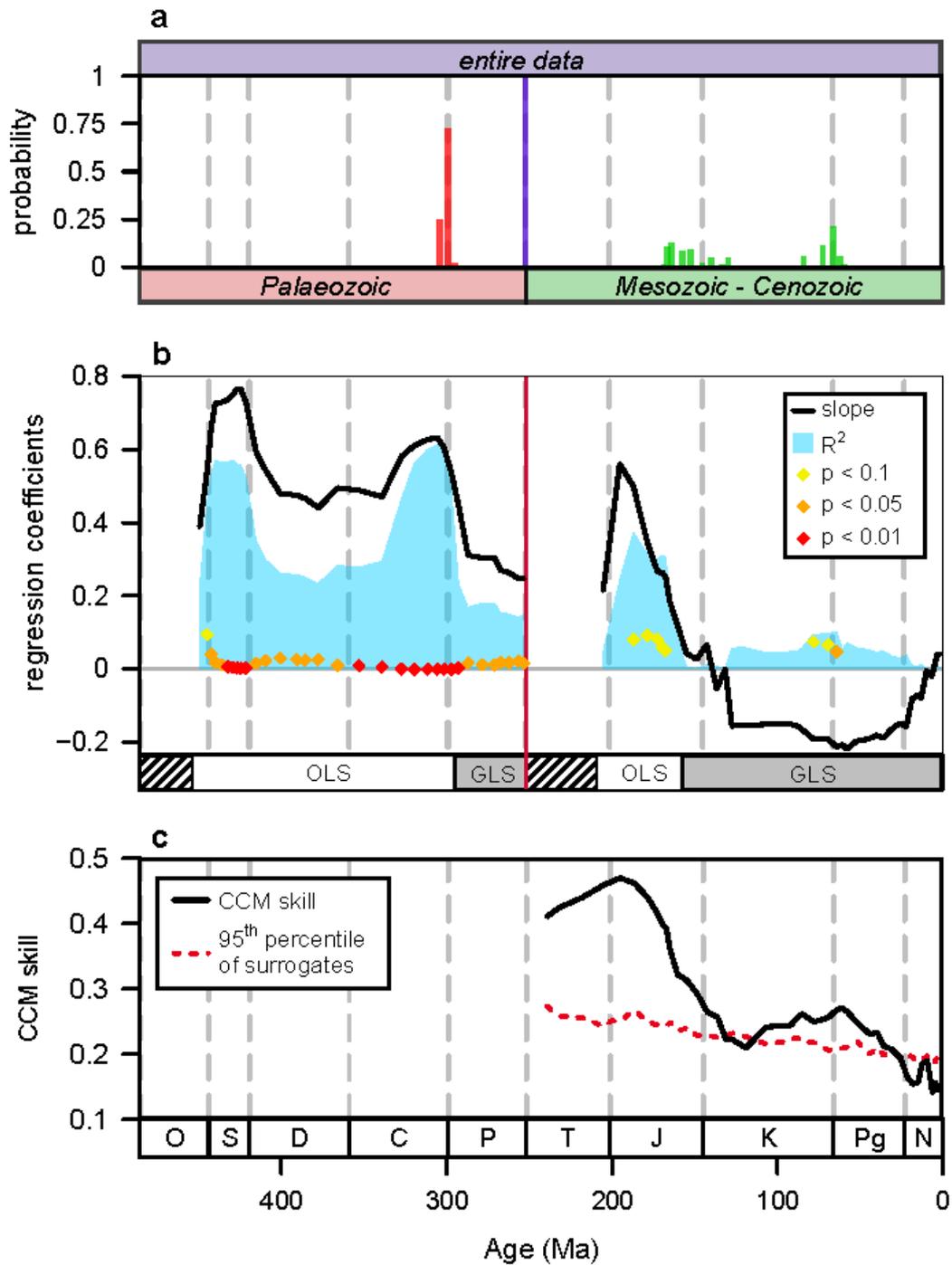
327 (f) Box plots showing the variability of iodine-to-calcium (I/Ca) ratios from shallow water  
328 carbonates within sampling localities, reprinted from ref. 46 with permission from

329 AAAS. I/Ca ratios are considered a proxy for oxygenation, with higher I/Ca ratios  
330 indicating better oxygenation.

331 (g) Sampling-standardised marine genus-level diversity (circles, see *Methods*) with long-  
332 term trend line (brown; LOESS regression with a smoothing span of 0.1).

333

Figure 2



334

335 **Figure 2: Changing relationship of  $SCOR_{ara}$  and  $ASI$ .**

336 (a) Bayesian posterior probabilities for changes in the linear regression of  $SCOR_{ara}$  against  $ASI$

337 for the entire time series (purple bar), the Palaeozoic (red) and the Triassic – Pleistocene

338 (green). The strength of correlation between  $SCOR_{ara}$  and  $ASI$  changed around the  
339 Carboniferous – Permian boundary and at the Permian – Triassic boundary, whereas no  
340 distinct point of change is found in the Mesozoic – Cenozoic time series.

341 (b) Linear models of  $SCOR_{ara}$  against  $ASI$  in windows of increasing length for the Palaeozoic  
342 and for the Mesozoic – Cenozoic. Expanding windows start with the first six stages and all  
343 data are plotted at the last stage of the respective window. Black line = slope; blue  
344 area =  $R^2$ ; diamonds = p-values; only p-values < 0.1 are shown. The boxes at the bottom  
345 of the graph indicate the gap for the first five stages (hatched pattern), and whether linear  
346 models were generated using ordinary least squares (OLS), or generalised least squares  
347 (GLS, *see Methods*). These results demonstrate a strong positive correlation between  
348  $SCOR_{ara}$  and  $ASI$  for the Palaeozoic time series, and a strong, although less robust positive  
349 correlation in the early Mesozoic that weakens with the inclusion of data from the Middle  
350 Jurassic onwards-

351 (c) Predicting  $ASI$  from  $SCOR_{ara}$  with convergent cross mapping (CCM) for expanding time  
352 series. All included time series start with the first Ordovician stage and all data are plotted  
353 at the last stage of their respective window. The CCM prediction skills (solid black line)  
354 can be interpreted as the strength of dynamical influence of  $ASI$  on  $SCOR_{ara}$ . The dashed  
355 red line shows the 95<sup>th</sup> percentile of 500 random surrogate time series, which we take as  
356 a significance criterion. Time windows shorter than the Ordovician – Middle Triassic did  
357 not pass the CCM convergence test and were not included (*see Methods*). The CCM skill  
358 shows a sustained drop when Jurassic – Early Cretaceous stages are added, which implies  
359 a continuously weakening dynamical influence of  $ASI$  on  $SCOR_{ara}$ .

360 **Tables****Table 1: Linear models with GLS**

(d) Generalised least squares linear models of  $SCOR_{ara}$  against  $ASI$  in the entire data set and in temporal subsets.  $N$  denotes the number of observations,  $\epsilon$  denotes the error term of the regression, with AR indicating autoregressive errors and *ind.* indicating independent errors.  $\phi$  denotes the autocorrelation of the error at lag = 1. In models with autocorrelated error terms,  $R^2$  is calculated from the log-likelihoods of the model and the corresponding null model (*Methods*). Models with independent errors are equivalent to an ordinary least squares linear model.

	<b>N</b>	<b><math>\epsilon</math></b>	<b><math>\phi</math></b>	<b>Intercept</b>	<b>Slope</b>	<b><math>R^2</math></b>	<b><math>p</math></b>
entire data set	85	AR	0.93	0.45	0.05	0.00	0.70
Palaeozoic	38	AR	0.57	0.13	0.25	0.15	<b>0.017</b>
Ordovician - Carboniferous	29	<i>ind.</i>	-	0.07	0.60	0.59	<b>&lt; 0.001</b>
Permian	9	<i>ind.</i>	-	0.05	0.28	0.68	<b>0.006</b>
Mesozoic - Cenozoic	47	AR	0.68	0.65	0.04	0.00	0.68

361

362

## 363 **Methods**

364 Fossil and palaeoenvironmental data were grouped into 85 Ordovician to Pleistocene geological  
365 stages. To achieve more uniform stage durations, we combined stages shorter than 1 million years  
366 (myr) with neighbouring stages (Table S4). Consequently, the two Early Triassic stages were combined,  
367 as were the four Pleistocene stages. All analyses were carried out in R, version 3.4.1<sup>50</sup>

368 **Fossil data.** We used the Paleobiology Database (PBDB, <https://paleobiodb.org/>) to assess the global  
369 fossil record of marine calcifiers. The PBDB records occurrences of fossil organisms and the geological  
370 setting in which they were preserved. For our analysis, we relied on internal PBDB information on  
371 stratigraphy, taxonomy, mineralogy, life habits, preservation, lithification, and palaeocoordinates  
372 (Table S3). All Phanerozoic occurrence data were downloaded on 24 January 2017 with standard  
373 settings. Cambrian occurrences were later omitted as *ASI* could only be calculated in the Ordovician –  
374 Pleistocene due to the insufficient Cambrian palaeotemperature record. We also excluded  
375 occurrences from non-marine settings and occurrences that could not be assigned with confidence to  
376 a geological stage. We only included occurrences that were identified to genus level and that could be  
377 reliably assigned to an invertebrate animal phylum, Foraminifera, Chlorophyta, Rhodophyta, or  
378 calcifying “Problematica”. Occurrences of plankton (coccolithophores, planktonic foraminifera,  
379 planktonic gastropods or planktonic tentaculites) were omitted. We followed the classification of  
380 skeletal mineralogy in the PBDB and considered calcifiers as “aragonitic” if their dominant mineralogy  
381 was aragonite and no secondary mineral was listed. The skeletal mineralogies recorded in the PBDB  
382 are based on the protocol described in ref. 25, from which we deviated in few exceptions – labechiid  
383 and Palaeozoic chaetetid sponges were classified as possessing a high Mg calcite skeleton (Balthasar  
384 *et al.*, unpublished).

385 As aragonite is thermodynamically unstable at Earth surface conditions and eventually dissolves or  
386 recrystallizes to calcite, aragonite has a lower preservation potential than calcite<sup>26,51</sup>. Most  
387 occurrences of aragonite preservation are therefore concentrated in the youngest stages. We

388 minimized this time-dependant bias by excluding all occurrences from collections with aragonite  
389 preservation and unlithified sediments, but kept the 19 % of data which had no information on their  
390 preservation recorded to avoid excessive loss of fossil data (see Supplementary Text S3). Barring some  
391 potential undeclared occurrences of aragonite preservation, the record of aragonitic taxa used herein  
392 thus consists of specimens that have been recrystallized to the stable calcite polymorph or that have  
393 been preserved in another way, e.g. by silicification.

394 **Aragonite sea intensity (ASI).** We developed a proxy for the degree to which aragonite precipitation  
395 is favoured relative to calcite precipitation in the non-biogenic environment based on the joint  
396 influence of temperature ( $T$ ) and the Mg/Ca ratio on  $\text{CaCO}_3$  formation in experiments<sup>52</sup>. We conducted  
397 a multiple linear regression of the mole percent of aragonite present in every experiment against the  
398 temperature and Mg/Ca ratio under which the experiments were conducted (see figure 1 in ref. 15).  
399 We only used experiments that produced > 1 % calcite and > 1 % aragonite. This yields the equation

400

$$401 \quad (1) \text{ ASI} = -119.61 + 46.57 \times \frac{\text{Mg}}{\text{Ca}} + 4.30 \times T$$

402 To infer past *ASI* for the Ordovician – Pleistocene, palaeotemperatures were calculated from a  
403 Phanerozoic  $\delta^{18}\text{O}$  compilation<sup>23</sup>, including only measurements from fossil brachiopods, bivalves and  
404 planktonic foraminifera from 35° south to 35° north, because measurements from higher latitudes are  
405 unavailable for most of the Phanerozoic. For the  $\delta^{18}\text{O}$  (‰ PDB) to  $T$ (°C) transfer function, we calculated  
406 palaeotemperatures assuming a Phanerozoic trend of increasing  $\delta^{18}\text{O}$  as in equation (2) from ref. 23.  
407 The Mg/Ca ratio ratios were taken from a Phanerozoic model of seawater composition and digitised  
408 from fig. 2.A of ref. 22 in steps of 2 million years using the R package *digitize*. For the Mg/Ca data, the  
409 mean from all observations falling into a geological stage was taken. *ASI* was calculated with average  
410 Mg/Ca data and with every individual temperature observation using equation (1). Mean and standard  
411 error of all *ASI* were calculated for each stage, and the resulting *ASI* was normalised to values between  
412 0 and 1. No temperature data was available for the Hettangian and for the Hauterivian stage. We

413 calculated *ASI* for these stages with the mean temperature of the two neighbouring stages,  
414 respectively.

415 **SCOR<sub>ara</sub>**. Evolutionary success is widely assessed by diversity. Although species diversity and  
416 abundance of higher taxonomic ranks or ecological groups are tightly coupled<sup>53</sup>, we prefer a direct  
417 measure of occupancy to assess the ecological success of individual genera. We apply the Summed  
418 Common species Occurrence Rate (SCOR), which is driven by the most widespread and common  
419 taxa<sup>24</sup>. SCOR reflects the actual abundance of a group of taxa with good accuracy<sup>54</sup>. The cumulative  
420 SCOR of a set of  $m$  genera is calculated as

$$421 \quad (2) \text{ SCOR} = \sum_{i=1}^m -\ln\left(1 - \frac{y_i}{k}\right)$$

422 where genus  $i$  is present in  $y_i$  subsets out of a total of  $k$  occupied localities. We defined a locality as a  
423 cell in a global penta-hexagonal grid with 6240 hexagonal and 12 pentagonal grid cells, with an area  
424 of ca. 40,800 km<sup>2</sup>. The grid was generated using the hexagrid() function in the icoso package<sup>55</sup>. The  
425 contribution of a genus to SCOR thus depends solely on the number of cells it was sampled in.  
426 Repeated sampling within a cell does not increase SCOR. *SCOR<sub>ara</sub>* reflects the ecological occupancy of  
427 aragonitic taxa, relative to all calcifiers occurring at  $k_{all}$  localities. *SCOR<sub>ara</sub>* is generated by dividing the  
428 SCOR of aragonitic taxa with  $k = k_{all}$  by the SCOR of all calcifying genera, again with  $k = k_{all}$ . To get the  
429 relative success of major taxonomic groups, we divided the group SCOR by the SCOR of all calcifiers.  
430 For every stage, we calculated SCOR using all genera recorded in the PBDB fossil data recorded in that  
431 respective stage.

432 We calculated the variance of any SCOR metric with the delta method<sup>24,56</sup>

$$433 \quad (3) \text{ Var(SCOR)} = \sum_{i=1}^m \frac{\frac{y_i}{k}}{\left(1 - \frac{y_i}{k}\right)^{*k}}$$

434 and can approximate the variance of *SCOR<sub>ara</sub>* using the means and variance of aragonitic SCOR and the  
435 SCOR of all calcifiers, assuming they are independent:

436 (4)  $\text{Var}(\text{SCOR}_{ara}) = \left(\frac{\text{aragonitic SCOR}}{\text{all calcifier SCOR}}\right)^2 \times \left(\frac{\text{Var}(\text{aragonitic SCOR})}{\text{aragonitic SCOR}} + \frac{\text{Var}(\text{all calcifier SCOR})}{\text{all calcifier SCOR}}\right).$

437 **Bayesian change point regression analysis.** The relationship of *ASI* and  $\text{SCOR}_{ara}$  changed through time.

438 We developed statistical methodology to identify change points. In particular, we performed

439 inference in the Bayesian framework about the unknown parameters of the model  $y_i \sim N(\mu_i, \sigma_i^2),$

440  $i = 1, \dots, n,$  independently, in which  $n$  is the overall sample size and

441 (5) 
$$\mu_i = \begin{cases} \alpha_1 + \beta_1 x_i & i = 1, \dots, n_1 \\ \sum_{j=1}^2 \alpha_j + \sum_{j=1}^2 \beta_j x_i & i = n_1 + 1, \dots, n \end{cases}$$

442 This model allows a distinct linear relationship between  $y_i$  and the covariate  $x_i$  in a first and second

443 part of the time series. The parameter  $\alpha_2$  and  $\beta_2$  represent the additional intercept and slope in the

444 second part, added to  $\alpha_1$  and  $\beta_1$  of the first part.  $\log \sigma_i$  is defined in a similar way, allowing for a

445 different relationship between the standard deviation  $\sigma_i$  and the covariate  $x_i$  in each time series part.

446 In the Bayesian framework, it is necessary to specify prior distributions for all unknown parameters.

447 We adopted normal priors with very high variances for all intercept and slope parameters. For the

448 change point  $n_1,$  we adopted a discrete uniform prior across integer values from 5 to  $n - 5,$  implying

449 that the change point divides the time series into two sections with at least five data points each. This

450 prior distribution expresses considerable uncertainty about the position of the change point before

451 seeing the data. As it is impossible to handle the posterior distribution of all these parameters

452 analytically, we followed the standard approach of sampling from this distribution using a Markov

453 chain Monte Carlo (MCMC) algorithm<sup>57</sup>. To do this we used the jags program<sup>58</sup>, accessed in R through

454 the R2jags package<sup>59</sup>. Our posterior inference is based on 100,000 iterations of the MCMC algorithm,

455 half of which were discarded as burn-in.

456 After inferring a first change point at the Permian-Triassic boundary, we split the data set into a

457 Palaeozoic part and a Mesozoic – Cenozoic part. In each of the two parts, we estimated additional

458 change points with the method described above.

459 **Generalised least squares.** Linear regression with ordinary least squares (OLS) of the form

460 
$$(6) \quad y = \alpha + \beta x + \varepsilon$$

461 assumes that the errors  $\varepsilon$  are independent between observations. For our data, the residuals of an  
462 OLS linear model of  $SCOR_{ara}$  against  $ASI$  are autocorrelated, which suggests that this assumption of  
463 independent errors does not hold. Generalised least square regression (GLS) can incorporate  
464 autoregressive errors and thus allows us to test for linear relationships between autocorrelated time  
465 series<sup>60</sup>. Autocorrelated errors  $\varepsilon$  of order  $p$  can be modelled as

466 
$$(7) \quad \varepsilon_i = \sum_{j=1}^p \phi_j \varepsilon_{i-j} + \delta_i$$

467 with  $\delta_i \sim N(0, \sigma^2)$  independently, in which  $\sigma$  is the standard deviation. We created linear models with  
468 independent and with autocorrelated error terms of the first order using the `gls()` function of the nlme  
469 R package<sup>61</sup>, performing maximum likelihood estimation by specifying `gls(..., method = "ML")`. For  
470 model selection we compared pairs of models with and without autoregressive errors using a  
471 likelihood ratio test<sup>62</sup>, implemented using the `anova.gls()` function. We selected the more complicated  
472 model only if the associated p-value was  $< 0.05$  and the likelihood ratio was  $> 1$ . In a few instances,  
473 models with autocorrelated errors estimated  $\phi < 0$ , which we attributed to model overfitting. In these  
474 cases, we chose the model without autocorrelation.

475 As a goodness-of-fit measure for GLS models, we calculated the likelihood ratio test  $R^2$  as

476 
$$(8) \quad R^2 = 1 - \exp\left(-\frac{2}{m}(\log L_M - \log L_0)\right)^{63,64},$$

477 with  $m$  being the number of observations,  $\log L_M$  being the log-likelihood of the model, and  $\log L_0$  being  
478 the log-likelihood of the null model of the form  $y = 1 + \varepsilon$ , with  $\varepsilon$  being the error as in equation (7).

479 We take 0.05 as the alpha level for the statistical significance of linear regressions.

480 **Regression in expanding windows.** We assessed the changing strength of a relationship between  $ASI$   
481 and  $SCOR_{ara}$  through time by calculating linear models in windows of expanding length. Due to the

482 severe increase of  $SCOR_{ara}$  across the Permian-Triassic boundary, calculating the linear relationship  
483 across the entire data set may be misleading. Instead, linear models were formulated separately in  
484 the Palaeozoic and Mesozoic-Cenozoic. In both cases, the shortest window considered comprised the  
485 first six data points, while the longest window had 38 points in the Palaeozoic and 47 points in the  
486 Mesozoic – Cenozoic. In every window, an OLS and a GLS model was fitted, with autoregressive errors  
487 of the first order incorporated into the GLS model. GLS models were used from the first window  
488 onwards in which  $\phi$  was positive and a likelihood ratio test comparing the OLS and the GLS model  
489 produced a  $p$ -value  $< 0.05$ .

490 **Convergent cross mapping.** The success of marine calcifiers may be influenced by environmental  
491 parameters other than climate and ocean chemistry, as well as biotic interactions and chance. It is  
492 therefore possible that a causal connection between ASI and  $SCOR_{ara}$  exists even when no linear  
493 relationship is detected. We test for this possibility using CCM, a model-free time series analysis  
494 method based in dynamical systems theory that can detect causal coupling in nonlinear and even  
495 chaotic systems<sup>27</sup>. It asserts that if two processes are causally linked, then information about the  
496 driver variable can be recovered from the response variable<sup>27</sup>. CCM indirectly measures the dynamical  
497 influence of the driver variable on the response variable by quantifying the extent to which a state  
498 space reconstruction (time delay embedding) of the response variable can be used to predict the  
499 driver time series. A description of the algorithm can be found in the Supplementary Materials (S2).

500 To test for a temporally variable influence of ASI on  $SCOR_{ara}$ , we performed CCM analysis on expanding  
501 time windows on the stage level data, under the assumption that these coarse-grained data  
502 contain sufficient dynamical information about Phanerozoic Earth system dynamics (see  
503 Supplementary Materials S2). We used the rEDM R package<sup>65</sup> to perform CCM analyses for the main  
504 paper. Because of the limited number of time series points, we used embedding dimension 2 and  
505 embedding lag 1, with zero temporal exclusion radius in the predictions due to the coarse temporal  
506 resolution of the data. For a given time window, the CCM analysis is convergent if prediction skill

507 increases with increasing library size (Supplementary Materials S2). If convergence is achieved, for  
508 each time window of length  $L$ , we report the median CCM skill for 500 bootstrapped samples at a  
509 library size  $L$ . In addition, to assess the significance of the results, we used surrogate testing with  
510 randomly shuffled surrogates<sup>66</sup>. The analysis for a given time window was considered significant if the  
511 median prediction skill at the largest library size exceeded the 95th percentile of the median  
512 prediction skills obtained for an ensemble of 500 surrogate CCM analyses (dashed, red line in Fig. 2c),  
513 where each surrogate realization, the driver time series is replaced by a randomly shuffled version of  
514 itself.

515 **Diversity dynamics.** We calculated second-for-third extinction proportions<sup>67</sup> using classical  
516 rarefaction<sup>14,68</sup> with a sampling quota of 500 occurrences per stage and took the mean extinction  
517 proportions over 100 subsampling trials. A sampling-standardised diversity curve was generated with  
518 shareholder-quorum subsampling<sup>1</sup> by taking the mean of 100 subsampling iterations, each with a  
519 quorum of 0.7. Following the recommendations in ref. 1, we relied on the reference-based singleton  
520 count, excluded the dominant genus from frequency calculations, and excluded the largest collection  
521 from the single-publication occurrence count. To control for short-term sampling variation, we used  
522 the corrected sampled-in-bin richness metric<sup>69</sup>, except for the first and the last stage, in which no  
523 sampling correction could be made. A locally estimated scatterplot smoothing (LOESS) regression<sup>70</sup>  
524 has been calculated from these results using a smoothing span of 0.1. Extinction and diversity  
525 computations were performed using the divDyn R package<sup>71</sup>.

## 526 **Data availability**

527 The data used to calculate  $SCOR_{ara}$  are available from the Paleobiology Database at  
528 <https://paleobiodb.org/>. The data used to calculate aragonite sea intensity were taken from ref. 15,  
529 22, and 23.

530 **Code availability**

531 The code used to generate the results can be accessed at  
532 [https://figshare.com/articles/R\\_scripts\\_and\\_protocols/7199561](https://figshare.com/articles/R_scripts_and_protocols/7199561).

533

534 **Methods only References**

535 50 R Core Team. R: A Language and Environment for Statistical Computing.  
536 <https://www.R-project.org/> (2017).

537 51 Cherns, L. & Wright, V. P. Quantifying the impacts of early diagenetic aragonite  
538 dissolution on the fossil record. *Palaios* **24**, 756-771 (2009).

539 52 Balthasar, U. *et al.* Relic aragonite from Ordovician–Silurian brachiopods: Implications  
540 for the evolution of calcification. *Geology* **39**, 967-970 (2011).

541 53 Madin, J. S. *et al.* Statistical independence of escalatory ecological trends in  
542 Phanerozoic marine invertebrates. *Science* **312**, 897-900 (2006).

543 54 Hannisdal, B., Haaga, K. A., Reitan, T., Diego, D. & Liow, L. H. Common species link  
544 global ecosystems to climate change: dynamical evidence in the planktonic fossil  
545 record. *Proc. R. Soc. B* **284**, 20170722 (2017).

546 55 Kocsis, Á. T. The R package icoso: Coarse resolution global triangular and penta-  
547 hexagonal grids based on tessellated icosahedra. R package version 0.9.81.  
548 <https://CRAN.R-project.org/package=icoso> (2017).

549 56 Casella, G. & Berger, R. L. *Statistical inference*. Vol. 2 (Duxbury Pacific Grove, CA, 2002).

550 57 Brooks, S., Gelman, A., Jones, G. & Meng, X.-L. *Handbook of markov chain monte carlo*.  
551 (CRC press, 2011).

552 58 Plummer, M. JAGS Version 3.3. 0 user manual. *International Agency for Research on*  
553 *Cancer, Lyon, France* (2012).

554 59 Su, Y. & Yajima, M. R2jags: Using R to run 'JAGS'. R package version 0.5–7.  
555 <https://CRAN.R-project.org/package=R2jags> (2015).

556 60 Faraway, J. J. *Linear models with R*. (CRC press, 2014).

557 61 Pinheiro, J. *et al.* nlme: Linear and Nonlinear Mixed Effects Models. R package version  
558 3.1-131. <https://CRAN.R-project.org/package=nlme> (2017).

559 62 Davison, A. C. *Statistical models*. Vol. 11 (Cambridge University Press, 2003).

560 63 Kramer, M. R 2 statistics for mixed models. *Presented at the 17th Annual Kansas State*  
561 *University Conference on Applied Statistics in Agriculture, Manhattan, Kansas, 24–26*  
562 *April* (2005).

563 64 Magee, L. R 2 measures based on Wald and likelihood ratio joint significance tests. *The*  
564 *American Statistician* **44**, 250-253 (1990).

565 65 Ye, H., Clark, A., Deyle, E., Keyes, O. & Sugihara, G. *rEDM: Applications of empirical*  
566 *dynamic modeling from time series*. R Package Version 0.5 7. [https://CRAN.R-](https://CRAN.R-project.org/package=rEDM)  
567 [project.org/package=rEDM](https://CRAN.R-project.org/package=rEDM) (2017).

568 66 Theiler, J., Eubank, S., Longtin, A., Galdrikian, B. & Farmer, J. D. Testing for nonlinearity  
569 in time series: the method of surrogate data. *Physica D* **58**, 77–94 (1992).

570 67 Alroy, J. A more precise speciation and extinction rate estimator. *Paleobiology* **41**, 633-  
571 639 (2015).

572 68 Sanders, H. L. Marine benthic diversity: a comparative study. *The American Naturalist*  
573 **102**, 243-282 (1968).

574 69 Alroy, J. *et al.* Phanerozoic trends in the global diversity of marine invertebrates.  
575 *Science* **321**, 97-100 (2008).

576 70 Cleveland, W. S., Grosse, E., Shyu, W. M., Chambers, J. M. & Hastie, T. Statistical  
577 models in S. *Local regression models*, Chapter 8 (1992).

578 71 Kocsis, Á. T., Reddin, C. J., Alroy, J. & Kiessling, W. The r package divDyn for quantifying  
579 diversity dynamics using fossil sampling data. *Methods in Ecology and Evolution* **10**,  
580 735-743 (2019).