

2019-07-01

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Eichenseer, K

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

10.1038/s41561-019-0392-9

Nature Geoscience

Nature Research

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accepted on the 22nd of May 2019

Jurassic shift from abiotic to biotic control on marine ecological success

Kilian Eichenseer¹, Uwe Balthasar¹, Christopher W. Smart¹, Julian Stander², Kristian A. Haaga^{3,4,5}, Wolfgang Kiessling⁶

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

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

³ Department of Earth Science, University of Bergen, N-5020 Bergen, Norway

⁴ Bjerknes Centre for Climate Research, PO Box 7803, NO-5020 Bergen, Norway

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

⁶ 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 **CO₂ 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 record¹ 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 Phanerozoic²⁻⁵. As a consequence, biotic
21 interactions may have increased as well⁶⁻⁹. In contrast, climate and seawater composition
22 show a cyclical behaviour rather than Phanerozoic-scale trends^{10,11}. 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 plankton¹².
25 Perturbations of the carbon cycle have fallen in amplitude, particularly since the mid-
26 Mesozoic¹³ (Fig. 1d), and extinction rates have decreased towards the present¹⁴ (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 (CaCO₃), high Mg/Ca ratios and high temperatures have been
31 shown to favour the precipitation of aragonite over calcite, and *vice versa*¹⁵. 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”^{10,16} (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 water¹⁷⁻²¹, analogous to inorganic
38 CaCO₃ 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 ratios²² (Fig. 1b) with $\delta^{18}\text{O}$ temperature
43 reconstructions²³ (Fig. 1c) to quantify *aragonite sea intensity* (*ASI*) in 85 post-Cambrian stages.
44 The *ASI* is parametrized from experimental data¹⁵ 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)²⁴. Given that novel acquisitions of calcium carbonate skeletons are rare and that
48 switches in skeletal mineralogy are largely restricted to a few clades^{20,21,25}, changes in *SCOR_{ara}*
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 taxa²⁶, 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_{ara}* against *ASI* using generalised least squares (GLS) to account for temporal
56 autocorrelation, and by convergent cross mapping (CCM) to detect causal coupling²⁷
57 (*Methods*).

58 Visual inspection of the *SCOR_{ara}* 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_{ara}* 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_{ara}* 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_{ara}* 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)^{2,25,28}.

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 series²⁷ (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 CaCO_3 saturation^{12,29}. All else being equal, higher CaCO_3 saturation facilitates
97 calcification³⁰ and tends to shift the CaCO_3 polymorph balance in favour of calcite³¹.
98 Consequently, calcifiers with a calcitic skeleton performed better than predicted by *ASI* when
99 the 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 CaCO_3 saturation state probably remained high during the Triassic³², *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 plankton¹². Before the widespread occurrence of planktonic calcifiers, 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 coccolithophores³³, 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 CaCO_3 saturation state. Since the proliferation of planktonic calcifiers, changes in the
114 atmospheric and oceanic CO_2 content have been compensated on geologically short time

115 scales by increased CaCO₃ deposition or dissolution in the deep sea³⁴. 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^{35,36}, possibly a consequence of the increased ocean
119 buffering^{12,37}

120 Producing a skeleton out of *sync* with aragonite-calcite sea conditions may be costly especially
121 when CaCO₃ 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^{38,39}.
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 magnitude⁴⁰.
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 system⁴¹.

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^{36,42} and favoured the survival of active and physiologically buffered animals^{28,43}. As
137 a consequence, the dominant, modern marine biota are less vulnerable to abiotic stressors

138 than their Palaeozoic counterparts⁴³, and individual energy budgets of bivalves and
139 gastropods increased throughout the early Mesozoic^{3,5}. 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 foraminifera³⁸, coccolithophores, and dinoflagellates⁴⁴
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 shelves⁴⁵. Increasing oxygenation of shallow ocean water is indicated from the Jurassic
147 onwards by iodine-to-calcium ratios⁴⁶ (Fig. 1f). Well-oxygenated shelves stabilise the carbon
148 cycle by reducing the impact of sea level changes on the burial capacity of organic carbon¹³,
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-Mesozoic⁴⁷ and may have increased the pace of
152 escalation in evolution⁴⁸. 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 world⁴⁹: 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 CaCO₃
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 catastrophe¹, but the Palaeozoic evolutionary regime may have persisted well into
163 the Mesozoic.

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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.

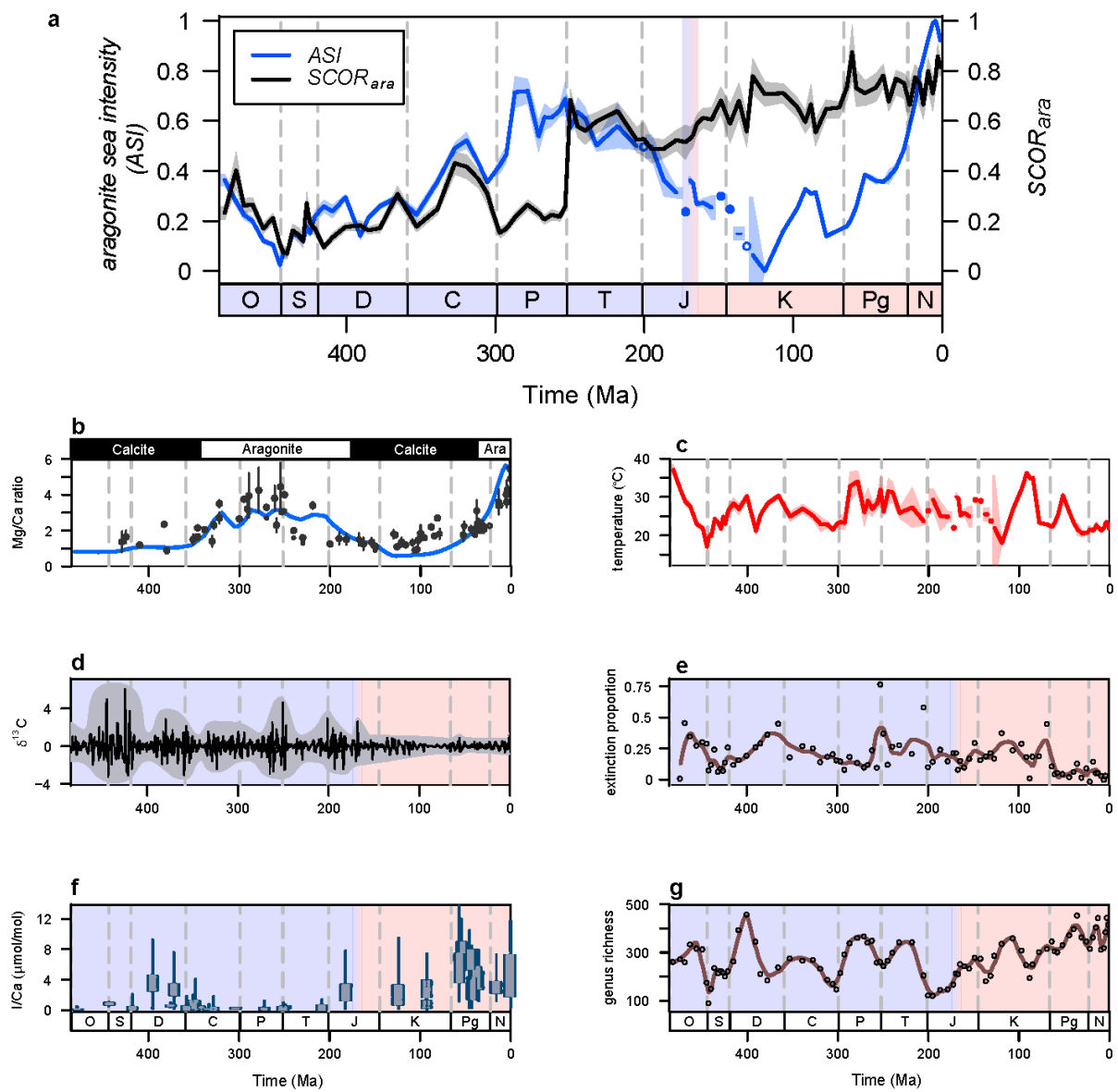
293 **Author contributions**

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 $SCOR_{ara}$ (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_{ara}* 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).

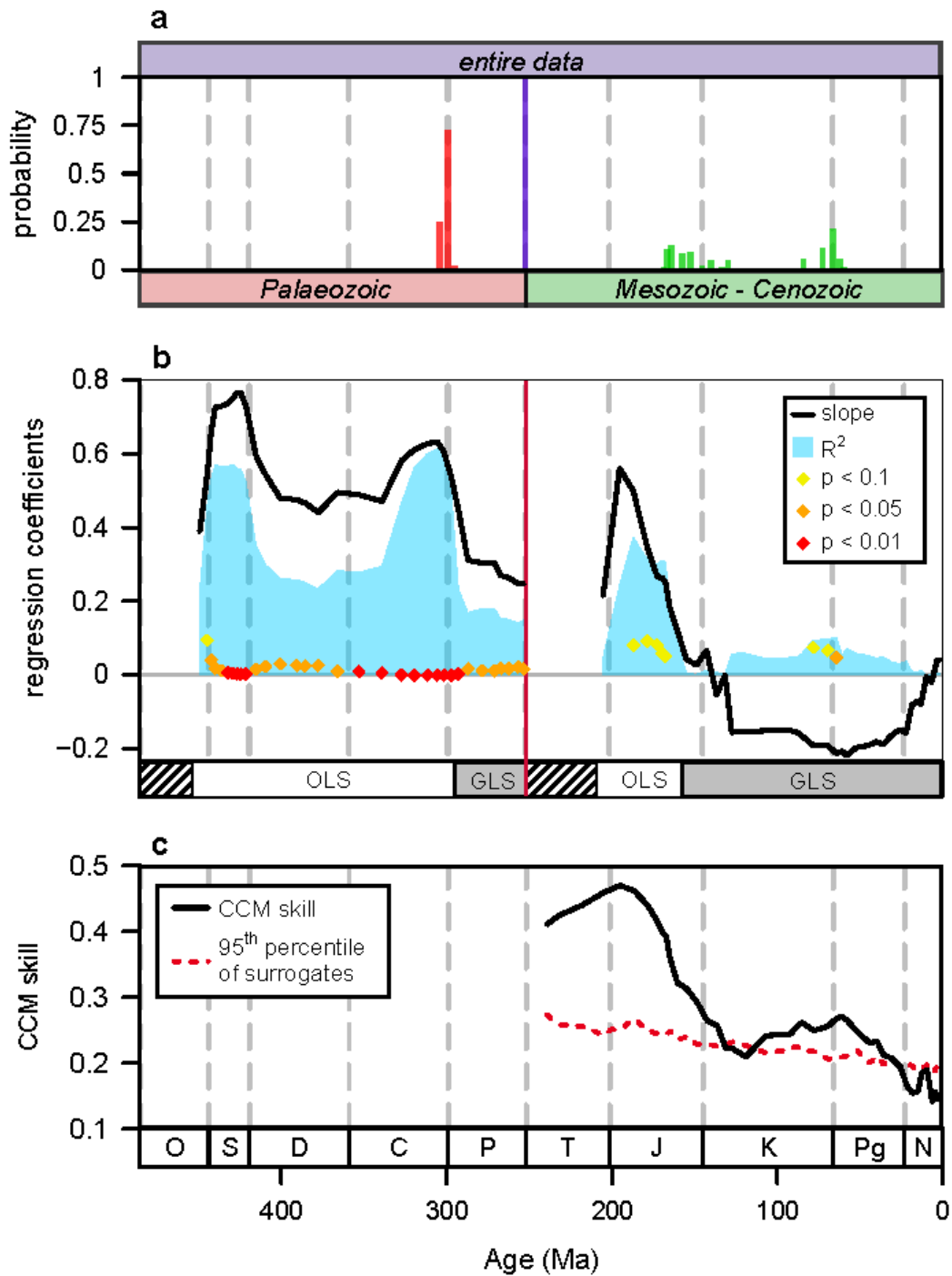
327 (f) Box plots showing the variability of iodine-to-calcium (I/Ca) ratios from shallow water
328 carbonates within sampling localities, reprinted from ref. 46 with permission from

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 95th 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, ϵ denotes the error term of the regression, with AR indicating autoregressive errors and *ind.* indicating independent errors. ϕ 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.

	N	ϵ	ϕ	Intercept	Slope	R^2	p
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	0.017
Ordovician - Carboniferous	29	<i>ind.</i>	-	0.07	0.60	0.59	< 0.001
Permian	9	<i>ind.</i>	-	0.05	0.28	0.68	0.006
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 3.4.1⁵⁰

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^{26,51}. 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 CaCO_3 formation in experiments⁵². 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 $\delta^{18}\text{O}$ compilation²³, 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_{ara}**. Evolutionary success is widely assessed by diversity. Although species diversity and
416 abundance of higher taxonomic ranks or ecological groups are tightly coupled⁵³, 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 taxa²⁴. SCOR reflects the actual abundance of a group of taxa with good accuracy⁵⁴. 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 km². The grid was generated using the hexagrid() function in the icoso package⁵⁵. 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_{ara}* reflects the ecological occupancy of
427 aragonitic taxa, relative to all calcifiers occurring at k_{all} localities. *SCOR_{ara}* 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^{24,56}

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

434 and can approximate the variance of *SCOR_{ara}* 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 *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 α_2 and β_2 represent the additional intercept and slope in the

444 second part, added to α_1 and β_1 of the first part. $\log \sigma_i$ is defined in a similar way, allowing for a

445 different relationship between the standard deviation σ_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) algorithm⁵⁷. To do this we used the jags program⁵⁸, accessed in R through

454 the R2jags package⁵⁹. 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 ε 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 series⁶⁰. Autocorrelated errors ε 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 σ 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 package⁶¹, 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 test⁶², 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 ε 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 ϕ 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 systems²⁷. It asserts that if two processes are causally linked, then information about the
496 driver variable can be recovered from the response variable²⁷. 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 package⁶⁵ 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 surrogates⁶⁶. 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 proportions⁶⁷ using classical
516 rarefaction^{14,68} 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 subsampling¹ 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 metric⁶⁹, except for the first and the last stage, in which no
523 sampling correction could be made. A locally estimated scatterplot smoothing (LOESS) regression⁷⁰
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 package⁷¹.

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.

533

534 **Methods only References**

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