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ABSTRACT

The early evolutionary and much of the extinction history of marine animals, is thought to be driven by changes in dissolved oxygen concentrations ($[O_2]$) in the ocean[1–3]. In turn, $[O_2]$ is widely assumed to be dominated by the geological history of atmospheric oxygen (pO_2)[4,5]. Here, in contrast, we show via a series of Earth system model experiments how continental rearrangement during the Phanerozoic drives profound variations in ocean oxygenation and induces a fundamental decoupling in time between upper-ocean and benthic $[O_2]$. We further identify the presence of state transitions in the global ocean circulation, which lead to extensive deep-ocean anoxia developing in the early Phanerozoic even under modern pO_2. The occurrence of stable kyr-scale oscillations in ocean oxygenation that we find also provides a causal mechanism that might explain elevated rates of metazoan radiation and extinction during the early Paleozoic[6]. The absence, in our modelling, of any simple correlation between global climate and ocean ventilation, and the occurrence of profound variations in ocean oxygenation independent of atmospheric pO_2, presents a challenge to the interpretation of marine redox proxies, but also points to a hitherto unrecognized role for continental configuration in the evolution of the biosphere.

MAIN TEXT

The availability of dissolved oxygen in the ocean exerts a critical control on habitability for marine animals[1,7] and is thought to have dramatically impacted their evolution from the late Neoproterozoic and through the Phanerozoic Eon (541-0 Ma)[1–3]. Indeed, the emergence of the first unambiguous metazoans during the Ediacaran period (635–541 Ma) may have been triggered by the occurrence of ambient $[O_2]$ sufficient to support the metabolism of a large body size[1]. Further increases in ocean oxygenation may have contributed to the Great

Ordovician Biodiversification Event[8] as well as the rise of large predatory fish in the Devonian[9]. Conversely, episodic deoxygenation is considered the primary kill mechanism during many of the major Phanerozoic mass extinction events, including the Late Ordovician[10], Late Devonian[11] and end Permian[7].

The past few decades have seen the development and application of a variety of geochemical redox proxies such as $\delta^{238}U$[12], $\delta^{98}Mo$[9], I/Ca[13] and iron speciation[14], which have provided us with unprecedented insights into the Phanerozoic history of ocean oxygenation[5,13]. In parallel, numerical models have been instrumental in helping interpret the proxy trends and test hypotheses for the underlying driving mechanisms[4,15]. Principal amongst the ideas that have arisen is that changes in atmospheric pO_2 can be inferred from the ocean[4,5,15]. However, for computational reasons, this link between ocean $[O_2]$ and atmospheric pO_2 has invariably been made without considering how ocean circulation may have changed through time[4,5,15]. While the importance of continental configuration for ocean circulation and surface climate has started to be studied systematically[16–18], spatial patterns of ocean geochemistry and redox have only been considered in a limited number of continental configurations (e.g. refs[7,19]) and often analyzed in temporal isolation. Here we explicitly address this gap, employing an Earth System Model of intermediate complexity to quantify how continental configuration can modulate the distribution of $[O_2]$ in the ocean, thereby leading us to a radically different conclusion regarding the inferences that can be drawn from marine redox proxy records.

We base our analysis on a series of past ocean circulation scenarios generated using cGENIE[20], an Earth System Model of intermediate complexity designed to simulate the large-scale biogeochemical cycles and patterns in the ocean, and one that has previously been shown to be capable of simulating regional-scale distributions of $[O_2]$ in the present-day ocean[20] as well as in the geological past[19,21] (see Methods, Extended Data Fig. 1). In these experiments, we consider both the potential role of changing ecological structure in the ocean

(using the size-structured plankton model of ref[22]) as well as the influence of temperature on metabolic rates (following ref[23]) in creating 3D realizations of the potential distribution of $[O_2]$ in the ocean. Based on the continental reconstructions of Scotese and Wright[24], we conducted one simulation every 20 Myrs through the Phanerozoic, for a total of 28 simulated time slices. In order to help isolate the impact of continental configuration from other changes occurring through the Phanerozoic, only the continental configuration[24] (plus physical atmospheric boundary conditions – see Methods) was varied from one time slice to the other. Solar luminosity (1368 W m^{-2}), atmospheric oxygen concentration (20.95 %), and ocean nutrient inventory (2.1 μmol kg^{-1} PO_4) were kept identical in every model run, and in a first series of simulations (#1), we also kept atmospheric pCO_2 fixed (at 2240 ppm, see Methods). We hence are not aiming to reconstruct the Phanerozoic evolution of climate here (see e.g. refs[16,18]), nor necessarily provide a reconstruction of past $[O_2]$ in the ocean or even recover modern distributions with high fidelity, but rather, expose the specific impact of changes in continental configuration on gross ocean oxygenation.

Despite assuming both invariant solar constant and pCO_2, substantive variability in climate through the Phanerozoic occurs in the model (Fig. 1b). This is an expected result of sea-level driven changes in the proportion of absorptive ocean surface vs. more reflective land surface[17,25] as well as of continental latitudinal distribution, and in a principal component analysis conducted across all 28 time slices we find a strong positive correlation between global mean sea-surface temperature (SST) and global ocean surface area (Fig. 1e; $R^2 = 0.585$). Given our assumption of invariant pO_2 (deliberately chosen to expose the role of the continental configuration), we find a relatively straightforward and expected inverse relationship between mean ocean surface $[O_2]$ and SST (Fig. 1b, e) – driven primarily via changes in oxygen solubility and modulated by the latitudinal distribution of ocean surface area. Global mean subsurface (ca. 90–190 m depth in the model) $[O_2]$ exhibits a more

exaggerated temporal evolution (Fig. 1c). Respiration of organic matter exported from the ocean surface now strongly amplifies subsurface oxygen variability (Fig. 1c, e) and introduces new features unconnected to SST changes, such as the ~35 μmol kg^{-1} decrease from 460 to 400 Ma. This is our first hint of the importance of changing continental distribution and hence large-scale pattern of ocean circulation, which in the case of subsurface [O_2] is via changes in the resupply of nutrients to the surface. Even without attempting to simulate a realistic sequence of Phanerozoic climate states (and hence changing ocean surface oxygen solubility), our modelling provides hints as to the timing of Oceanic Anoxic Events (OAEs) during the Phanerozoic (Fig. 2, Extended Data Fig. 2). For instance, seafloor ocean deoxygenation develops in the paleo-Tethys during the Permian-Triassic transition (ca. 260 Ma)[26] and in the central Atlantic during the Early Cretaceous (ca. 120 Ma)[27] and Late Cretaceous (ca. 100 Ma)[28]. That the Late Devonian OAE (380 Ma)[29] and Toarcian OAE (ca. 180 Ma)[30] are not captured by our simulations may be a result of the coarse model grid (for the Tethys Ocean during the Toarcian OAE in particular[30]; Fig. 2, Extended Data Fig. 2). This could also be interpreted as reflecting the need for a strong perturbation (warming and nutrient-driven increase in primary productivity) at that time to trigger an OAE, since the continental configuration itself is not particularly prone to ocean deoxygenation in our model simulations.

Our unexpected discovery from the numerical modelling is how variable global deep-ocean [O_2] (calculated as the mean of all benthic grid points in the model below 1000 m depth) is (Fig. 1d); ranging from 30 μmol kg^{-1} (and near fully anoxic) to 178 μmol kg^{-1} (a little higher than modern). The early Paleozoic (541 to 460 Ma) in particular stands out, and is characterized by anomalously poor deep seafloor oxygenation (generally < 45 μmol kg^{-1}) in the model, with an abrupt rise to 171 μmol kg^{-1} at 440 Ma and thereafter mostly remaining above 100 μmol kg^{-1} (Fig. 1d). The step change in benthic oxygenation simulated between

125 460 Ma and 440 Ma is similarly observed using an alternative set of continental
126 reconstructions[31] (Extended Data Fig. 4). Simulated water age (the mean time since a water
127 parcel was last exposed to the atmosphere) anti-correlates with mean global and benthic [O_2]
128 (Fig. 1d, e), while SST and global water age do not correlate (Fig. 1e; $R^2 = 0.001$), pointing
129 to the dominance of a paleogeographical control on deep-ocean oxygenation.
130 To further simplify the attribution of causes of benthic [O_2] variability through the
131 Phanerozoic and eliminate global climate change and resulting solubility-driven upper-ocean
132 [O_2] variations as explanatory factors, we carried out a second series of model experiments
133 (#2) in which we kept mean global SST and surface oxygenation largely invariant (Fig. 3).
134 Climate detrending was achieved by varying pCO_2 in the model. Variance in mean benthic
135 [O_2] (Fig. 3d) is now if anything, even greater than in #1 (Fig. 1d) and the general trend of a
136 poorly oxygenated early Paleozoic deep ocean still stands. These results confirm that benthic
137 anoxia in the early Paleozoic ocean results from changes in the deep-ocean circulation in the
138 model, rather than temperature-driven variations in upper-ocean [O_2]. Sensitivity tests
139 demonstrate that global mean temporal trends and spatial oxygenation patterns are largely
140 independent of whether a temperature-dependent (Fig. 1) or fixed remineralization profile
141 (Extended Data Fig. 5) is assumed. Similarly, patterns of benthic [O_2] are only weakly
142 impacted by uncertainties in the position of mid-ocean ridges (Extended Data Figs. 6, 7).
143 The role of continental configuration in creating conditions of extreme deep-ocean
144 deoxygenation and weakened ventilation (old water mass ages) during the early Paleozoic
145 (prior to 440 Ma in series #1 (Fig. 1d), and prior to 420 Ma in series #2 (Fig. 3d)), arises from
146 the existence of state transitions in the large-scale circulation of the ocean in the model.
147 Using series #1 as an example, the oldest time slices (540 – 500 Ma) are characterized by a
148 poorly ventilated seafloor with deep waters forming over the South Pole (Figs. 1d and 2,
149 Extended Data Fig. 8a). At 480 and 460 Ma, the ocean circulation oscillates between the

150 previous poorly-ventilated state and a better-ventilated state, the latter state subsequently
151 becoming stabilized at 440 Ma by further tectonic rearrangement (Figs. 1d and 2, Extended
152 Data Fig. 8a). Of course, the differences in the two simulation series illustrate that the climate
153 state also influences the ocean circulation regimes (contrast Figs. 1 and 3; see also Extended
154 Data Figs. 8 and 9). Several lines of evidence suggest that these state transitions are a robust
155 characteristic of the early Paleozoic, at least in the cGENIE model. Indeed, additional
156 simulations conducted using idealized land-sea masks reveal that these state transitions may
157 be a characteristic feature of continental configurations with one pole free of land (Extended
158 Data Fig. 10; Methods), such as the one of the early Paleozoic (Fig. 2), and a similar
159 reorganization of the global ocean circulation has previously been shown to best explain the
160 expansion of seafloor anoxia during Late Ordovician glaciation (Extended Data Fig. 10 and
161 ref.[21]).

162 The occurrence of climate-driven state transitions in ocean circulation and oxygenation
163 is well established in the context of changes in Atlantic and Pacific basin meridional
164 overturning since the last glacial maximum (21 ka)[32,33]. In contrast, the potential for ocean
165 state transitions in deeper time has received much less attention but is no less important (e.g.
166 ref.[21]). We also have good reason to conclude that the occurrence of oscillatory ocean
167 circulation modes is not an artifact of the particular model used here and may occur as a
168 transitional regime between different stable steady-states (Extended Data Fig. 10). For
169 instance, oscillations have previously been identified in both (ocean-only) 3D ocean
170 circulation models[34,35] and 3D ocean circulation models coupled to simplified representations
171 of atmospheric dynamics (Earth System Models of intermediate complexity)[36,37]. Non-steady
172 solutions in volume-integrated ocean temperature are also hinted at in a number of recent
173 fully coupled GCM simulations under specific continental configurations and climate
174 states[16]. Further work conducted using higher-resolution Earth system models, e.g. of the

175 Coupled Model Intercomparison Project phase 6 generation, will be important to distinguish
176 robust from model-dependent modes of ocean circulation, although identifying the boundary
177 conditions giving rise to oscillatory modes will be computationally challenging.

178 Our finding of a fundamental decoupling of subsurface and benthic [O_2] during the
179 Phanerozoic (Fig. 1e; $R^2 = 0.001$) implies that no simple relationship exists during the
180 Phanerozoic amongst the concentrations of oxygen in the atmosphere, the subsurface ocean,
181 and at the seafloor. Furthermore, the highly non-linear and chaotic nature of the system
182 means that even very minor changes in continental configuration (e.g. contrast 460 vs. 440
183 Ma, Figure 2) can induce dramatic re-organizations of large-scale circulation and hence
184 ocean oxygenation, and similarly, confusticate any predictable relationship between changes
185 in atmospheric pCO_2 (and climate) and ocean oxygenation. This has implications not only for
186 how we interpret deep-ocean redox proxy records and specifically proxies for the global areal
187 extent of seafloor anoxia[5] (e.g., $\delta^{238}U$[12], $\delta^{98}Mo$[9]), but also how we understand the underlying
188 controls on ocean anoxia and infer changes in atmospheric composition. For instance, Stolper
189 and Keller[38] analyzed the ratio of Fe^{3+} to total Fe ($Fe^{3+}/\Sigma Fe$) in hydrothermally altered basalts
190 formed in ocean basins to quantitatively reconstruct deep-ocean [O_2] over the last 3500
191 Myrs. Their results suggest that the deep ocean became oxygenated only in the Phanerozoic
192 and probably not until the late Paleozoic (<420 Myr). Our simulations support the vision of a
193 poorly oxygenated early Paleozoic ocean[4,5,38] (until ca. 440 Ma in the model, see Figs. 1d,
194 3d). However, while $Fe^{3+}/\Sigma Fe$ data is interpreted as reflecting a rise in atmospheric oxygen
195 concentrations[38], our Earth System simulations in contrast suggest that deep-ocean
196 oxygenation around 440–420 Ma could have been a consequence of continental
197 rearrangement and concomitant changes in ocean circulation and ventilation. The implication
198 is that early Phanerozoic atmospheric pO_2 need not have been appreciably lower than
199 modern, which aligns with the measurements of atmospheric oxygen trapped in fluid-gas

inclusions of halite[39]. Furthermore, the step changes in early Paleozoic seafloor oxygenation are indicative of bistability between deep-ocean circulation states; that is, for certain continental configurations multiple advection and convection patterns will co-exist (what is observed depends on the initial conditions of the simulation). Switches between such states could provide an explanation to the swings[5] in early Paleozoic global anoxia extent documented on grounds of $\delta^{238}U$[40–42] and $\delta^{98}Mo$[41,43]. Uncertainties in both the model and geological data preclude us from determining if our simulated scenario may have actually taken place in the geological past, and we recognize that continental rearrangement is also not exclusive of secular variation in other drivers of ocean anoxia, such as atmospheric oxygen, ocean nutrient inventory, and global warming[13,19,21,26]. That said, and despite our idealized boundary conditions and invariant atmospheric chemistry, there are shared temporal trends (albeit with different timings and interval durations) with recent I/Ca-based oxygen proxy compilations[13], namely: low oxygenation in the early and late Paleozoic with a high during the Devonian, and peak values occurring prior to late Cenozoic cooling.

Finally, our results have implications for the evolution of marine animal ecosystems through the Phanerozoic. If kyr-scale oscillations in ocean oxygenation were a characteristic feature of early Paleozoic oceans, as supported by the high-resolution Mo record of ref.[44] and our modelling (Extended Data Fig. 8), this would lend support to arguments linking the progressive (here: paleogeographical) stabilization of a steady-state Earth system to decreasing extinction rates through the Phanerozoic[6,45].

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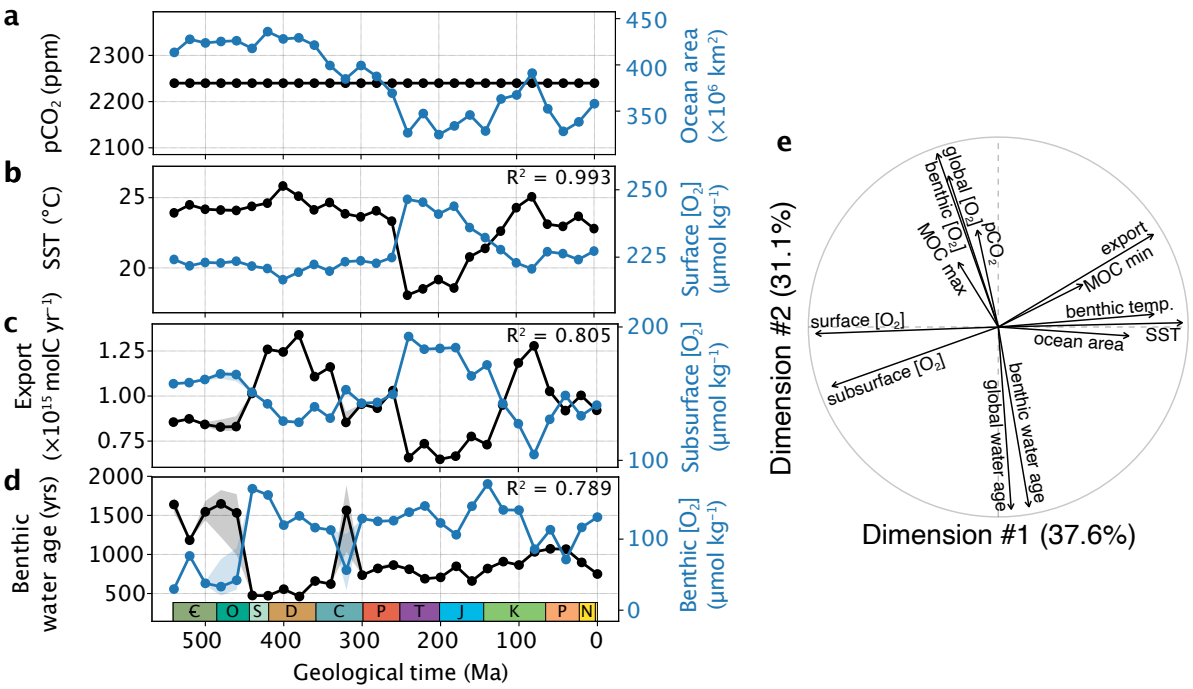
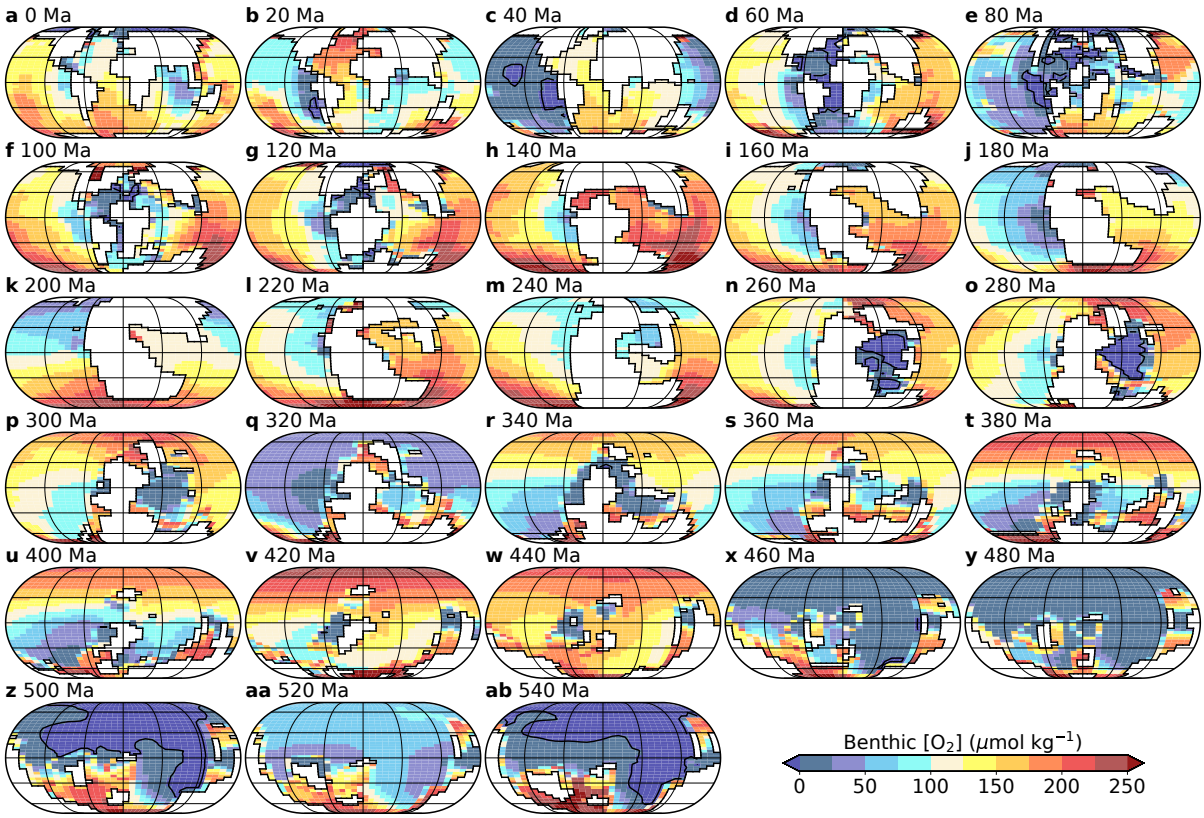


Figure 1. Earth System Model results for simulations at 2240 ppm CO_2 (series #1). (a) Atmospheric pCO_2 and global ocean area. (b) Globally averaged sea-surface temperatures and globally averaged ocean-surface oxygen concentrations. (c) Total export production and globally averaged subsurface (ca. 90–190 m depth) oxygen concentrations. (d) Globally averaged benthic water age and benthic oxygen concentrations, both extracted below 1000 m depth. (e) Principal component analysis (Methods). In panels b–d, the linear correlation coefficient (R^2) value is provided in the upper-right corner. For each variable and age, the mean value simulated over the last 5000 years of the model run is shown (point), while envelopes (shading) represent the range of values simulated over the same time interval (for simulations exhibiting oscillations). MOC: meridional overturning circulation.



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344 Figure 2. Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (series #1). Eckert
345 IV projection. Emerged continental masses are shaded white. Results are averaged over the last
346 5000 years. See Extended Data Fig. 2 for magnified versions of 7 panels with redox proxy data
347 points and Extended Data Fig. 3 for the meridional overturning circulation and regions of deep-
348 water formation.

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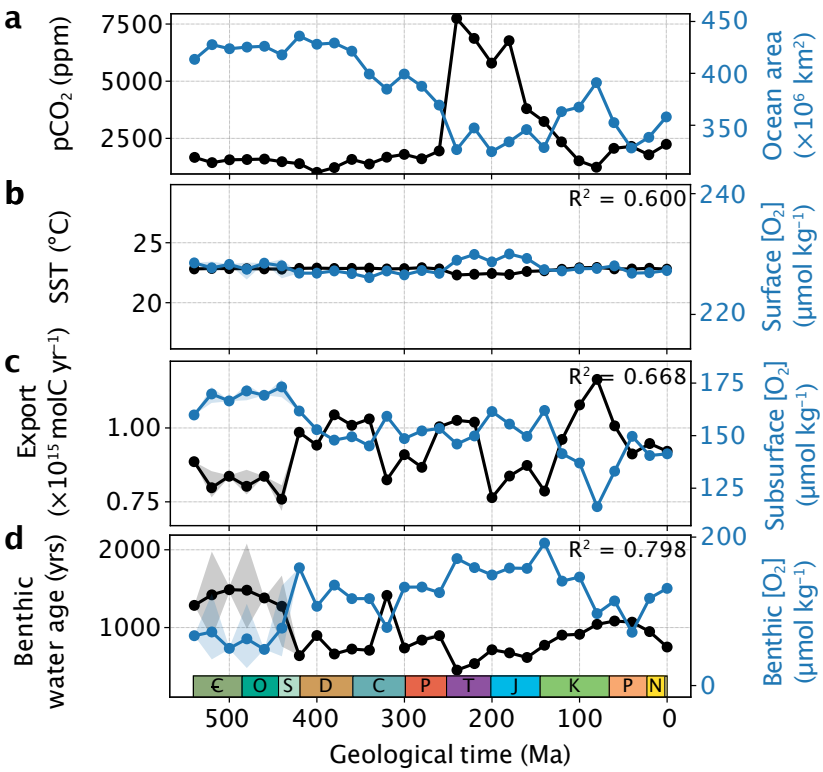

350

351 Figure 3. Earth System Model results for simulations in which we varied pCO_2 in order to
352 approximately 'correct' for the paleogeographical impacts on climate (series #2). Panels (a-d)
353 and panel description as per for Fig. 1. Note that in this series of experiments, surface
354 oxygenation and mean global SST (b) are largely invariant.

355

METHODS

Description of the model

cGENIE[20] – an 'Earth System Model of intermediate complexity' – is based around a 3-dimensional ocean circulation model which, for speed, is coupled to a 2D energy-moisture-balance atmospheric component. We configured the model on a 36×36 equal-area grid with 16 unevenly spaced vertical levels to a maximum 5500 m depth in the ocean. The cycling of carbon and associated tracers in the ocean is based on a single (phosphate) nutrient limitation of biological productivity accounting for plankton ecology based on Ward et al.[22] and Wilson et al.[46], but adopts the Arrhenius-type temperature-dependent scheme for the remineralization of organic matter exported to the ocean interior of Crichton et al.[23]. We further modify the ecological model of Ward et al.[22] to account for limitation of productivity under sea ice, re-scale the global mean annual C/P ratio of exported particulate organic matter to match that of the standard model (106)[47], and only diagnose the ocean surface mixed layer depth for calculating light attenuation rather than entrain this into the physical circulation. We include a sulphate (SO_4^{2-}) tracer as an electron acceptor in the model in addition to dissolved oxygen, such that when O_2 starts to approach zero, sulphate reduction occurs in association with the remineralization of organic matter. The hydrogen sulphide (H_2S) thereby created is transported via ocean circulation and oxidized in the presence of O_2 to re-form sulphate. Note that we do not include a nitrogen cycle (and hence nitrate reduction), nor methanogenesis in our model tracer configuration. See ref.[48] and ref.[49] for details of the overall ocean redox scheme.

Despite its low spatial resolution, cGENIE satisfactorily simulates first-order ocean [O_2] spatial patterns and values for the present-day ocean when configured with pre-industrial boundary conditions such as 278 ppm CO_2 (Extended Data Fig. 1 and ref.[20]), as well as in the geological past[19,21]. For instance, simulations for Oceanic Anoxic Event 2 conducted using

cGENIE (ref.[19], their Fig. 2f,g) compare well with simulations conducted using the more complex model IPSL-CM5A2 (ref.[28], their Fig. 10), in terms of both global extent of anoxia and response to gateway alteration.

Description of the numerical experiments

We adopted the (flat-bottomed) Phanerozoic continental reconstructions of Scotese and Wright[24], but substituted the deep-ocean bathymetry of Müller et al.[50] when available (140 Ma – 0 Ma) in order to account for mid-ocean ridges. In order to specifically quantify the impact of paleogeographical evolution, we kept solar luminosity (1368 W m^{-2}), atmospheric oxygen concentrations (20.95 %), and ocean nutrient inventory (2.1 μmol kg^{-1} PO_4), invariant. We employed a null eccentricity-minimum obliquity orbital configuration, which provides an equal mean annual insolation to both hemispheres with minimum seasonal contrasts. Atmospheric CO_2 concentration was kept fixed in series #1 (2240 ppm) but varied in series #2 in order to approximately 'correct' for the paleogeographical impacts on climate. These forcing combinations ensured that simulated ocean temperatures are in the right order of magnitude compared with the Phanerozoic proxy-derived trend[18]. The mean Phanerozoic tropical (25°S–25°N) sea-surface temperature is 29.67°C (standard deviation: 1.88°C) in series #1 (mean of 29.39°C and standard deviation of 0.45°C in series #2) compared to a mean of 28.1°C (standard deviation: 2.51°C) in the data compilation[18].

To generate the physical atmospheric boundary conditions required by cGENIE for each different continental configuration, we ran FOAM[51] general circulation model experiments for 2 to 3 kyrs, until deep-ocean temperature equilibrium. We then derived the 2D wind speed and wind stress, and 1D zonally-averaged albedo forcing fields required by the cGENIE model, using the 'muffingen' open-source software (DOI: 10.5281/zenodo.5500687), following the methods employed in ref[52].

Simulations were initialized with a sea-ice free ocean and homogeneous temperature and salinity in the ocean (5 °C and 33.9 ‰, respectively) and integrated for a total of 20,000 years. Data is presented reflecting either the average over the last 5,000 years of the simulation (e.g., Fig. 2), or the mean and range of any oscillation over the last 5,000 years (e.g., Figs 1, 3), as detailed in the figure captions.

Principal component analysis

Principal components analyses (PCA) of Fig. 1 and Extended Data Fig. 5 were performed using, for each variable, the mean value simulated over the last 5000 years of the model simulations. For each variable, a total of 28 values was thus obtained (one value for each of the 28 time slices, from 540 Ma to 0 Ma every 20 Myrs). We considered 13 variables: surface $[O_2]$, subsurface $[O_2]$, benthic $[O_2]$, global $[O_2]$, global water age, benthic water age, sea-surface temperature ('SST'), benthic temperature, pCO_2, meridional overturning circulation maximum ('MOC max') and minimum ('MOC min'), export production ('export'; i.e., the flux of organic carbon produced in the ocean photic zone by primary producers that is not recycled (remineralised) before sinking deeper in the water column) and total ocean area. The PCA was conducted using the 'PCA' function of the R package 'FactoMineR'[53] and the first two axes / principal components were represented (capturing ca. 68 % of the variance in both cases). The objective here is not to provide a thorough PCA analysis but rather to (1) confirm the robustness of the correlations illustrated in the form of time-series and R^2 in the other panels of Fig. 1 and Extended Data Fig. 5 and (2) provide information on the correlation (or not) of additional key variables in a synthetic and graphical manner.

Additional discussion on ocean circulation regimes

Most of the simulations in Extended Data Figs. 8a and 8b show that ocean dynamics obtain stable steady-state solutions. However, amongst these are cases where the system overshoots (for example, compare 0 Ma and 120 Ma in Extended Data Fig. 8a) before approaching a

steady-state solution. This may imply the presence of an unstable oscillatory mode, in agreement with the linear stability analysis of low-resolution GCM steady states under present-day conditions[34,35]. The simulations in Extended Data Fig. 8 reveal that, depending on changes to continental configuration, the steady-state solutions can lose stability, resulting in stable oscillations. It is known that, under certain climate conditions, advective feedbacks in the ocean circulation can destabilize the steady state[54]. Simulations for 540 Ma and 500 Ma in Extended Data Figs.8a and 8b, respectively, are cases of steady-state solutions with oscillatory modes that are linearly stable, but only weakly stable, resulting in clear examples of damped oscillations. Since the frequencies of the damped and self-sustained oscillations (500 and 520 Ma in Extended Data Fig. 8b, respectively) are very similar, the transition could represent a Hopf bifurcation, resulting in self-sustained oscillations (characterized by fluctuations in circulation pattern and strength) around an unstable steady state.

In order to better understand the model behavior and ultimately, the nature of the state transitions in the global ocean circulation, we conducted additional cGENIE simulations using two contrasting, idealized continental configurations featuring either a latitudinal strip of land from the North Pole to the Southern Hemisphere mid latitudes ('Drake world'[55]), or a strip of land extending from the North Pole to the South Pole ('ridge world'[55]) (Extended Data Fig. 10). Drake world, with a pole free of land (i.e., purely oceanic at all longitudes), schematically represents the continental configuration of the early Paleozoic (or a high latitude circumpolar path such as in the late Cenozoic), while ridge world represents an early Mesozoic-like continental arrangement with landmasses present from the North Pole to the South Pole (see Fig. 2).

With Drake world, at low pCO_2 levels, deep-water formation takes place at the North Pole, where a slightly higher hemispherical fraction of land cover with lower thermal inertia favors winter cooling over the surrounding ocean and convection (label #1 in Extended Data

Figs. 10a and 10b). As atmospheric CO_2 is steadily increased across a series of experiments, the onset of a first set of oscillations, between ×5.5 and ×7.5 CO_2 (label #2), marks the appearance of a new mode of ocean circulation that stabilizes in the subsequent stable steady state at around ×8.25 CO_2 (label #3). Then, a new set of oscillations, from ×9 to ×9.75 CO_2, marks another step toward the weakening of the deep-water formation over the North Pole and strengthening over the South Pole (label #4). A third stable equilibrium finally stabilizes above ×10.75 CO_2 (label #5). Each set of oscillations thus marks the shift to a new regime of steady-state circulation and the ultimate result is a shift in the locus of deep-water formation from the North Pole (with lands barriers) to the South Pole (oceanic) in response to global warming from ×4 to ×16 CO_2. A comparable (but latitudinally reversed) behavior was previously observed by Pohl et al.[21] for the latest Ordovician. In response to global warming (their Figs. 4e to 4i, see also Extended Data Fig. 10c), the locus of deep-water formation shifts in their simulations from the South Pole (with lands) to the North Pole (oceanic). This is very similar to the change in ocean circulation simulated between 460 Ma and 440 Ma in simulation series #1 (Fig. 2), although the state transition here involves continental rearrangement in addition to global warming (global sea-surface temperature increases from 24.1°C at 460 Ma to 24.38°C at 440 Ma). No similar state transition is observed using the ridge world configuration (Extended Data Fig. 10a).

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CODE AVAILABILITY

The version of the cGENIE code used in this paper is tagged as release v0.9.29 and has a DOI: 10.5281/zenodo.5885685. Necessary boundary condition files are included as part of the code release. Configuration files for the specific experiments presented in the paper can be found in the installation subdirectory: `genie-userconfigs/MS/pohletal.Nature.2022`. Details of the experiments, plus the command line needed to run each one, are given in the `readme.txt` file in that directory. A manual describing code installation, basic model configuration, and an extensive series of tutorials is provided (DOI: 10.5281/zenodo.5500696). The FOAM output is hosted on Zenodo (DOI: 10.5281/zenodo.5780096).

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AUTHOR CONTRIBUTIONS

A.P. and A.R. designed the study and wrote the manuscript with input from all co-authors. AP. and A.R. conducted the FOAM and cGENIE experiments. A.P., A.R. and A.K. led the analysis of the model results. C.R.S. produced the continental reconstructions.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

Correspondence and requests for materials should be addressed to A.P. and A.R.

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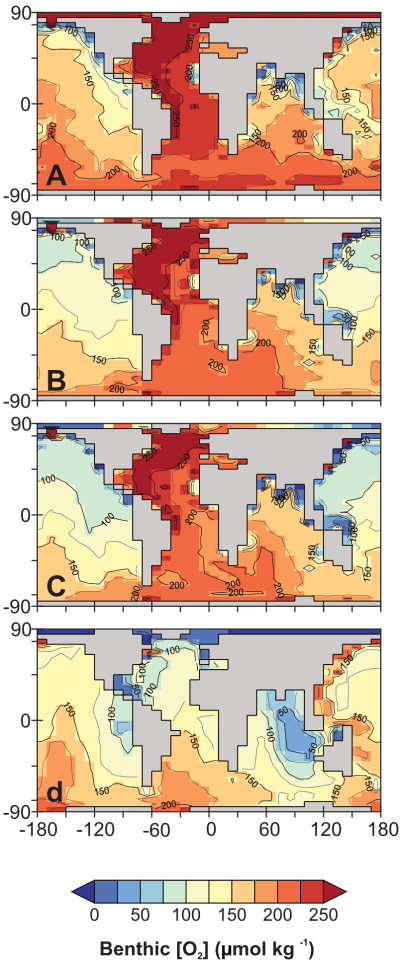
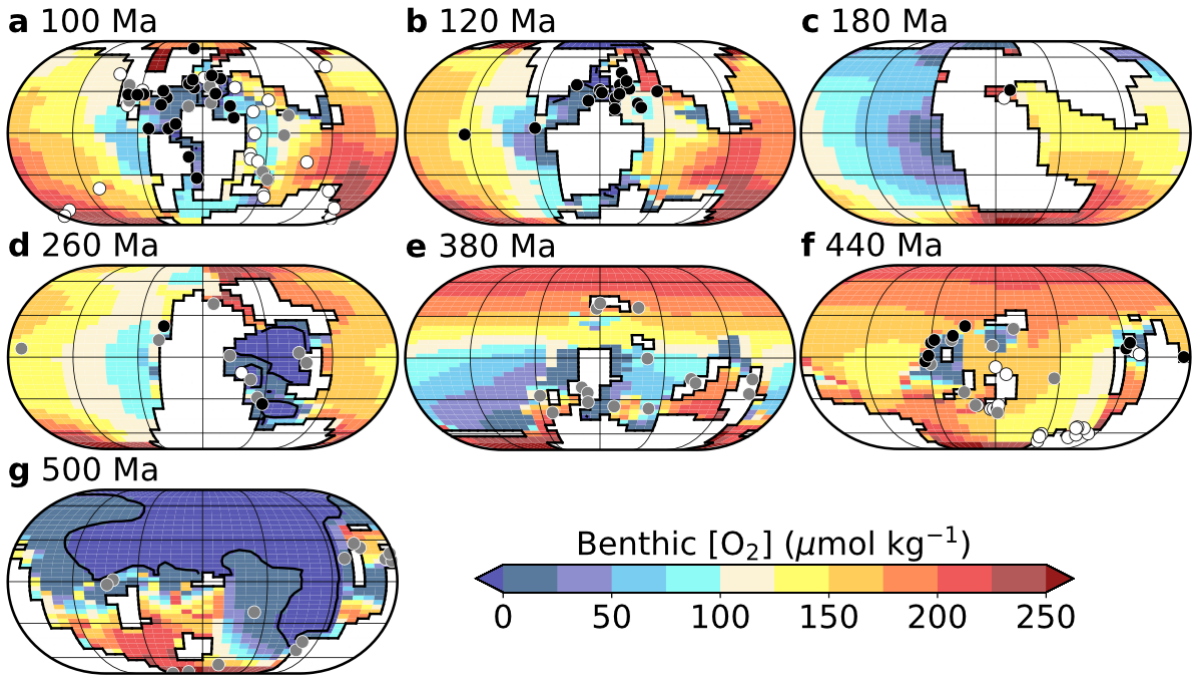


Extended Data Figure 1: Comparison of modern observations of seafloor [O_2] with the cGENIE model. Results are shown for different (modern) continental grids, boundary conditions, and biogeochemical cycling parameterization assumptions. Projection is equal-area rectangular, and the color-scale is chosen to approximately match that in Figure 2. (a) Present-day distribution of [O_2] globally at the seafloor, for which we re-grid the World Ocean Atlas 2018[56] data to the modern continental grid of ref.[47] and show the oxygen concentration in the deepest model grid point. Apparent is both the production and southwards propagation (via North Atlantic Deep Water (NADW)) of highly oxygenated waters from the North Atlantic, and oxygenated deep-water production and mixing around Antarctica. (b) Benthic [O_2] distribution for the 'standard' modern ocean circulation of ref.[47] run at 278 ppm CO_2, plus simplified biological export scheme. The large-scale patterns of benthic [O_2] are reasonably reproduced, with the exception of too weak mixing of oxygen

around the Southern Ocean, itself caused by a weak simulated Antarctic Circumpolar Current (ACC) and the difficulty in adequately representing the Drake Passage at this resolution. The slightly too-low compared to observations values in the North Pacific are an additional consequence of this. (c) Test of substituting the simplified biological export scheme of ref.[47] with the explicit ecosystem model used here in the Phanerozoic series of simulations (but still at 278 ppm CO_2). The slightly greater export simulated by the ecological model reduces benthic [O_2] by ca. 10-20 μmol kg^{-1} while leaving the large-scale patterns largely unaltered. (d) Deep-sea oxygenation in the 0 Ma Phanerozoic simulation (as per Figure 2, panel a) run at 2240 ppm CO_2. Without flux adjustment applied in the simplified cGENIE 2D EMBM atmosphere (see ref.[57]) there is virtually no NADW, explaining the relatively poor and South-to-North oxygenation of the Atlantic. The Indian Ocean is also too poorly oxygenated, although the general pattern in the Pacific is reproduced. There are several main reasons for this model-data mismatch. Firstly, directly re-gridding from a relatively coarse resolution GCM (FOAM) creates a highly restricted and shallow Drake Passage (Extended Data Figure 7a, 0 Ma), precluding a strong ACC forming. More pertinently, the Phanerozoic simulation series (Figure 2) are all run at 2240 ppm. The resulting much-warmer-than-modern ocean is associated with the absence of any sea-ice formation and lower seawater oxygen solubility, likely explaining at least some of the spatial pattern and much of the lower global mean [O_2] inventory (Extended Data Figure 8a, 0 Ma). In terms of ventilation and water mass idealized mean age (not shown), the Atlantic, lacking an AMOC is far too old, whereas the Indian and Pacific oceans are similar to the inverse modelling of ref.[58] despite the aforementioned issues with the Drake Passage and that the 0 Ma simulation is run at 2240 ppm CO_2.



583

584 Extended Data Figure 2: Selected redox proxy data vs. the corresponding model oxygenation
585 realization. Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (series #1).
586 Eckert IV projection. Emerged continental masses are shaded white. Results are averaged
587 over the last 5000 years. Black (white) dots represent anoxic (oxic) conditions and grey
588 points represent possible or intermittent anoxia, for 100 Ma after ref.[28], for 120 Ma after
589 ref.[27], for 180 Ma after ref.[30], for 260 Ma after ref.[26], for 380 and 500 Ma after ref.[59], and for
590 440 Ma after ref.[60]. These time slices have been chosen to represent regularly-spaced periods
591 during the Phanerozoic, typified by oceanic anoxic events. The last 100 Myrs are deliberately
592 left aside because (i) the ocean is overall well oxygenated during this time interval and (ii)
593 our constant boundary conditions (deliberately chosen to isolate the role of tectonics from
594 climate, see main text) do not (and indeed, do not intent to) reproduce the pronounced
595 cooling trend through the Cenozoic (especially from Early Eocene Climate Optimum (ca. 50
596 Ma) onwards), precluding direct model-data comparison.

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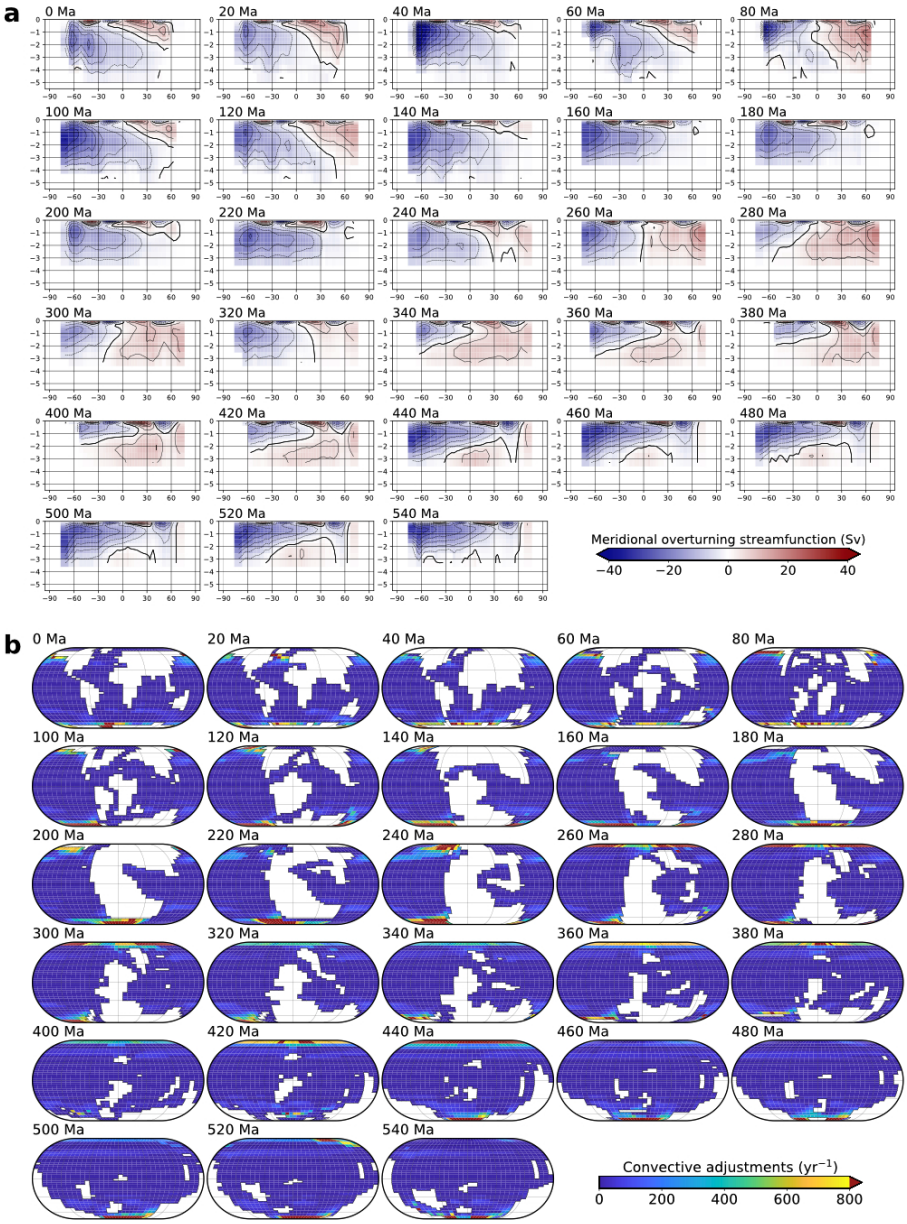
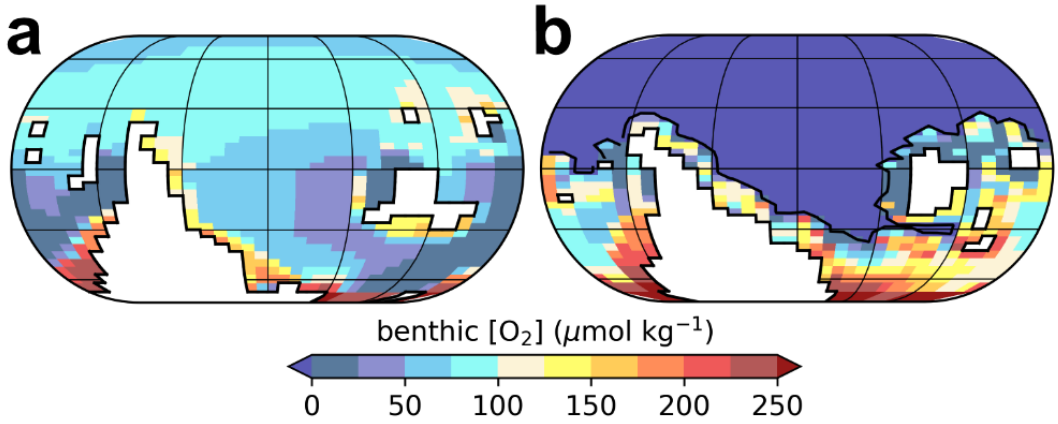


Extended Data Figure 3: Deep-ocean circulation for simulations at 2240 ppm CO_2 (series #1). (a) Meridional overturning stream function, in Sv (sverdrup, 1 Sv = 10^6 m^3 s^{-1}). A negative (blue) stream function corresponds to an anticlockwise circulation. (b) Annual distribution of convective adjustments across the water column. Emerged continental masses are shaded white. Eckert IV projection. Results are averaged over the last 5000 years.



606

607 Extended Data Figure 4: Sensitivity of benthic [O_2] to the continental reconstruction.
608 Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (like series #1) at 440 Ma
609 (a) and 460 Ma (b), using the continental reconstructions of BugPlates[31], with
610 topography/bathymetry after ref.[61]. Eckert IV projection. Emerged continental masses are
611 shaded white. Results are averaged over the last 5000 years. Panels (a) and (b) are identical to
612 panels (w) and (x) of Fig. 2 except that simulations have been conducted using another
613 continental reconstruction. Note that although we simulate sulphate reduction in cGENIE,
614 with SO_4^{2-} being used as the electron acceptor for the remineralization of organic matter in
615 the ocean interior once dissolved O_2 has become depleted (see ref.[48]), small negative O_2
616 concentrations can arise when multiple geochemical reactions compete simultaneously for
617 the same depleted oxygen pool. However, because the product of sulphate reduction –
618 hydrogen sulphide (H_2S) – has fast oxidation kinetics in the presence of free oxygen, the
619 transport of H_2S from anoxic to oxic areas closely mirrors the transport and fate of 'negative
620 oxygen' (see ref.[62]) and the overall redox landscape is largely independent of this small
621 modelled oxygen over-consumption.

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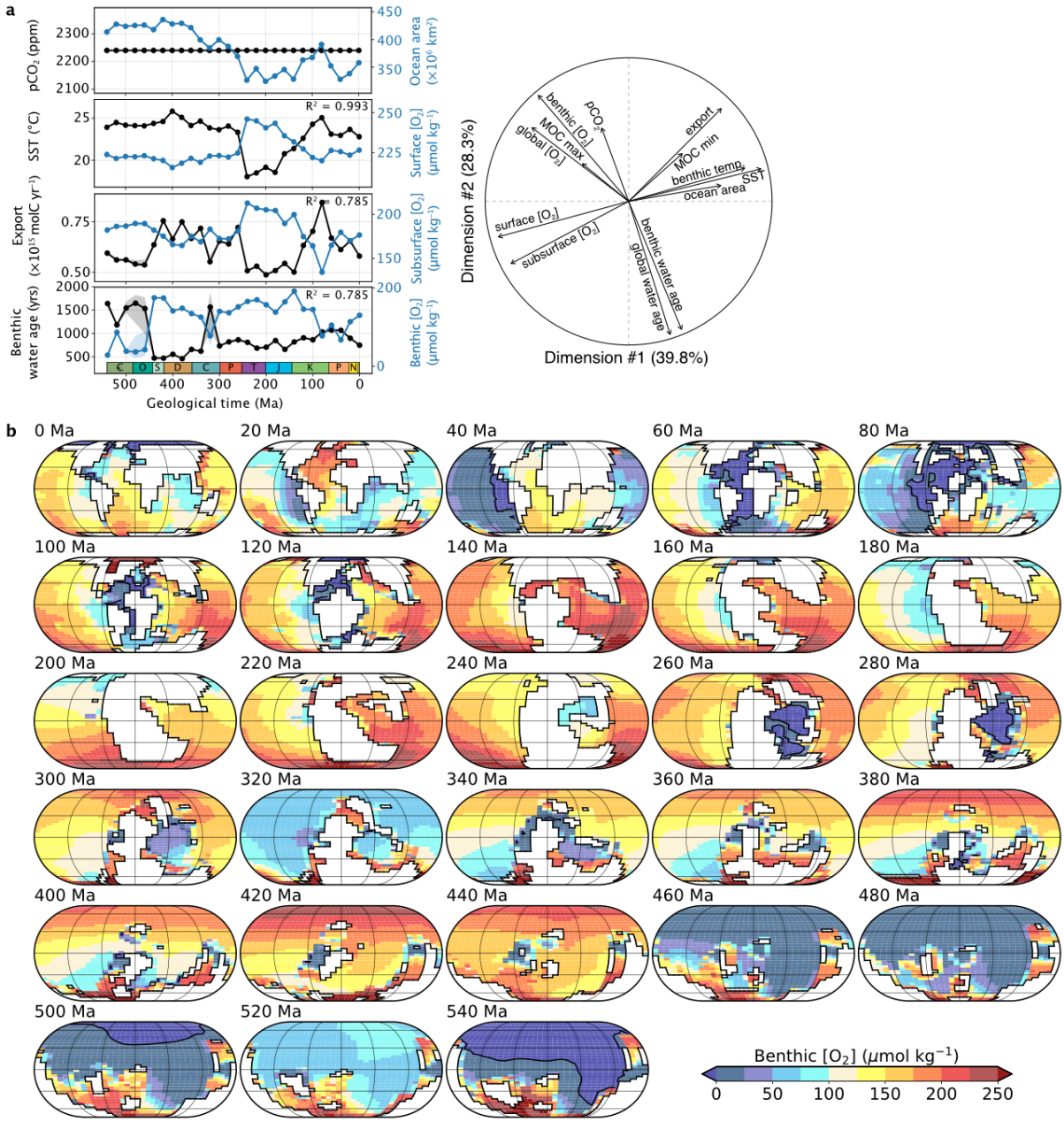

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625 Extended Data Fig. 5. Sensitivity to the remineralization scheme. Earth System Model results
626 for simulations at 2240 ppm CO_2 (like #1) but with no dependence of remineralization on
627 temperature. (a) Same as Fig. 1. (b) Same as Fig. 2.

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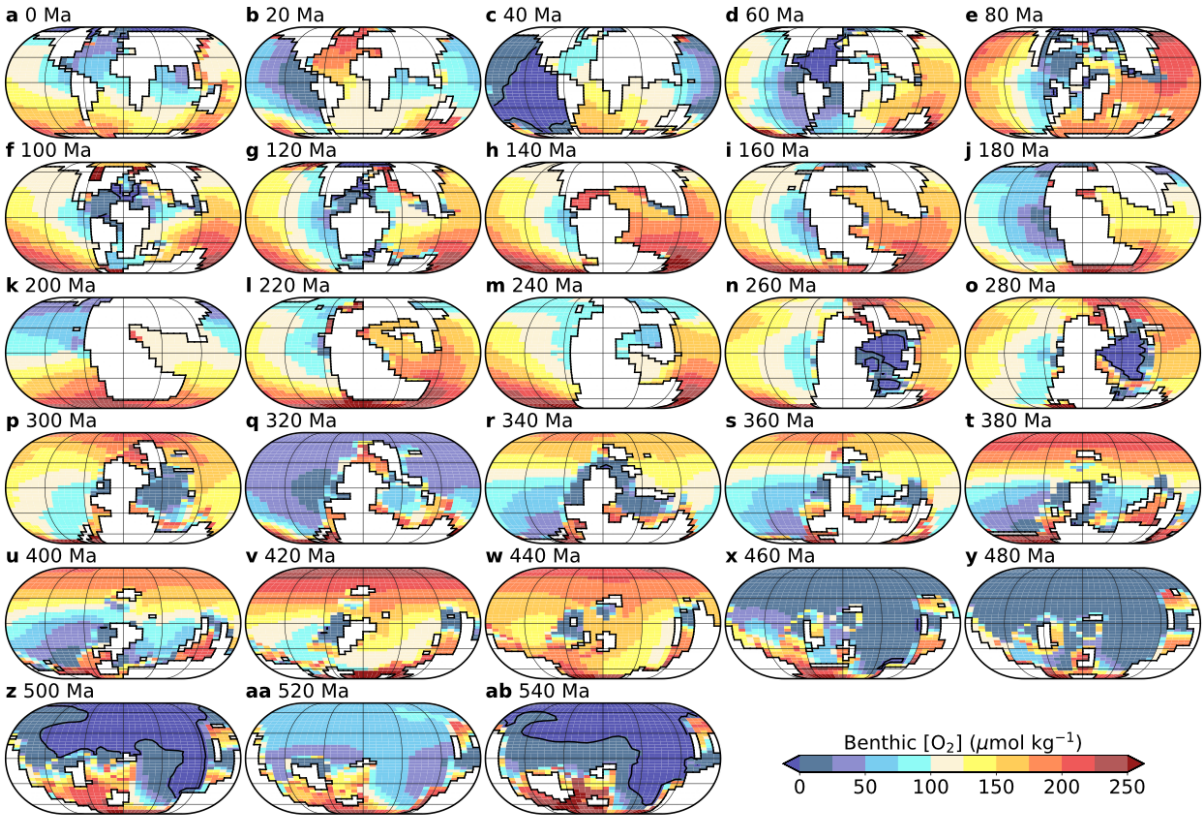


630

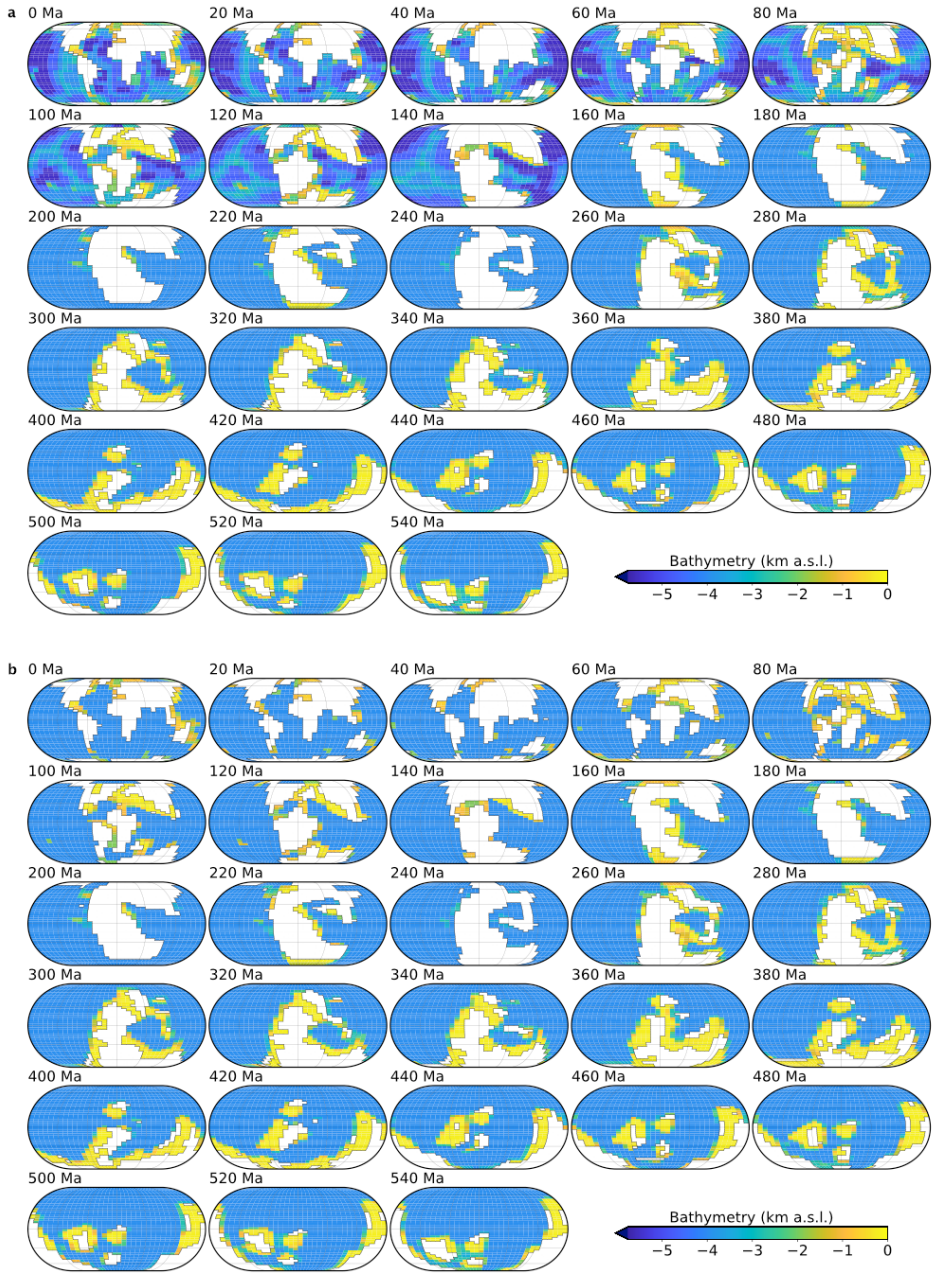
631 Extended Data Figure 6. Sensitivity of benthic [O_2] to deep-ocean bathymetry. Benthic

632 oxygen concentrations for simulations at 2240 ppm CO_2 (like #1) but with no mid-ocean

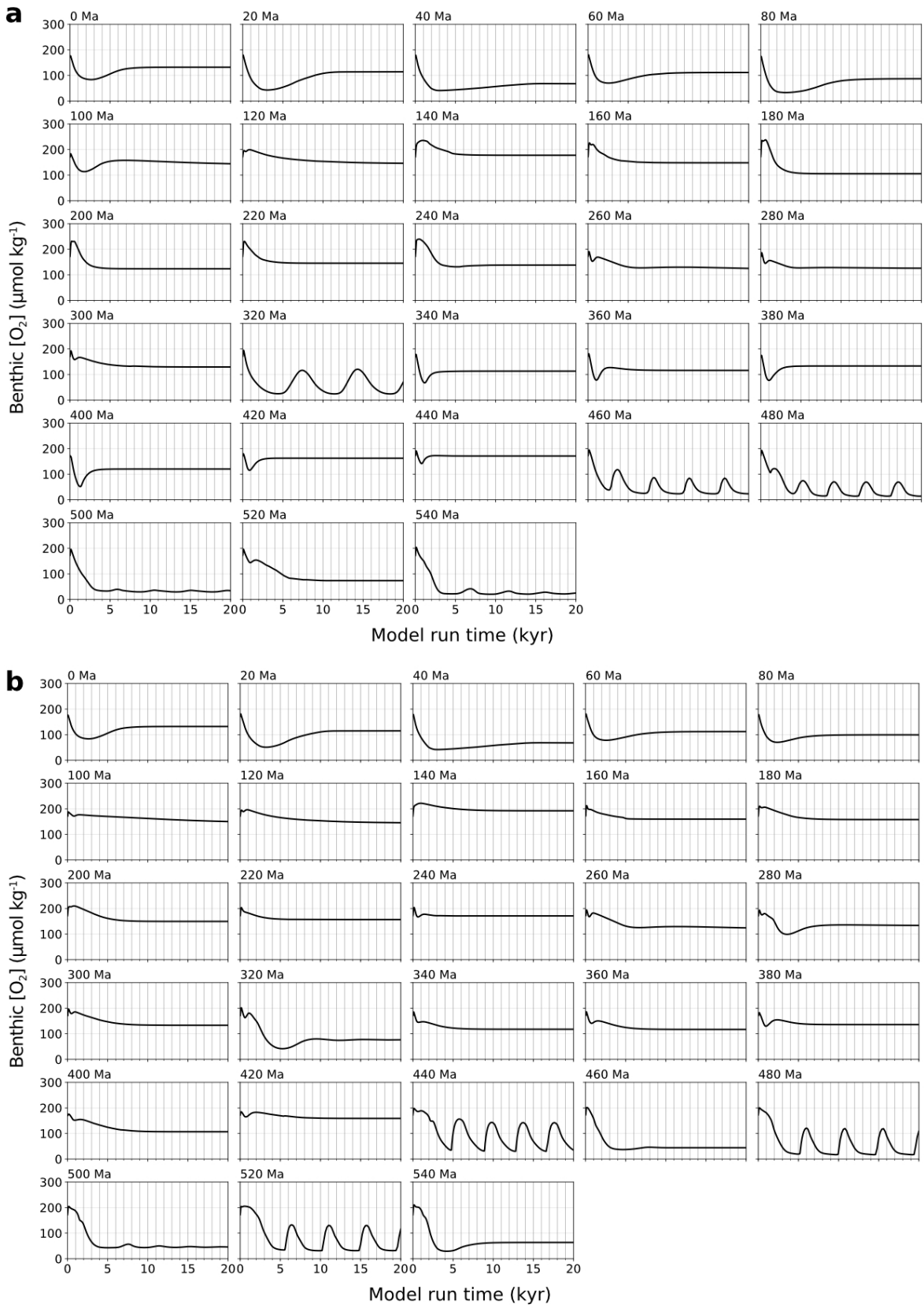
633 ridges (see Extended Data Fig. 7). Results are averaged over the last 5000 years. Emerged

634 continental masses are shaded white. Eckert IV projection.

635



Extended Data Fig. 7: Bathymetric reconstructions. Bathymetry with mid-ocean ridges used in series #1 and #2 (a), and flat-bottomed bathymetric reconstructions used in simulations with no mid-ocean ridges (b) (see Extended Data Fig. 6). Only reconstructions for 0 to 140 Ma (both included) differ (see Methods). Emerged continental masses are shaded white. Eckert IV projection.



642

643 Extended Data Figure 8. Time-evolution of benthic [O_2]. (a) Simulations at 2240 ppm CO_2

644 with temperature-dependent remineralization (series #1). (b) Simulations in which we varied

645 pCO_2 in order to approximately 'correct' for the paleogeographical impacts on climate (series
646 #2).
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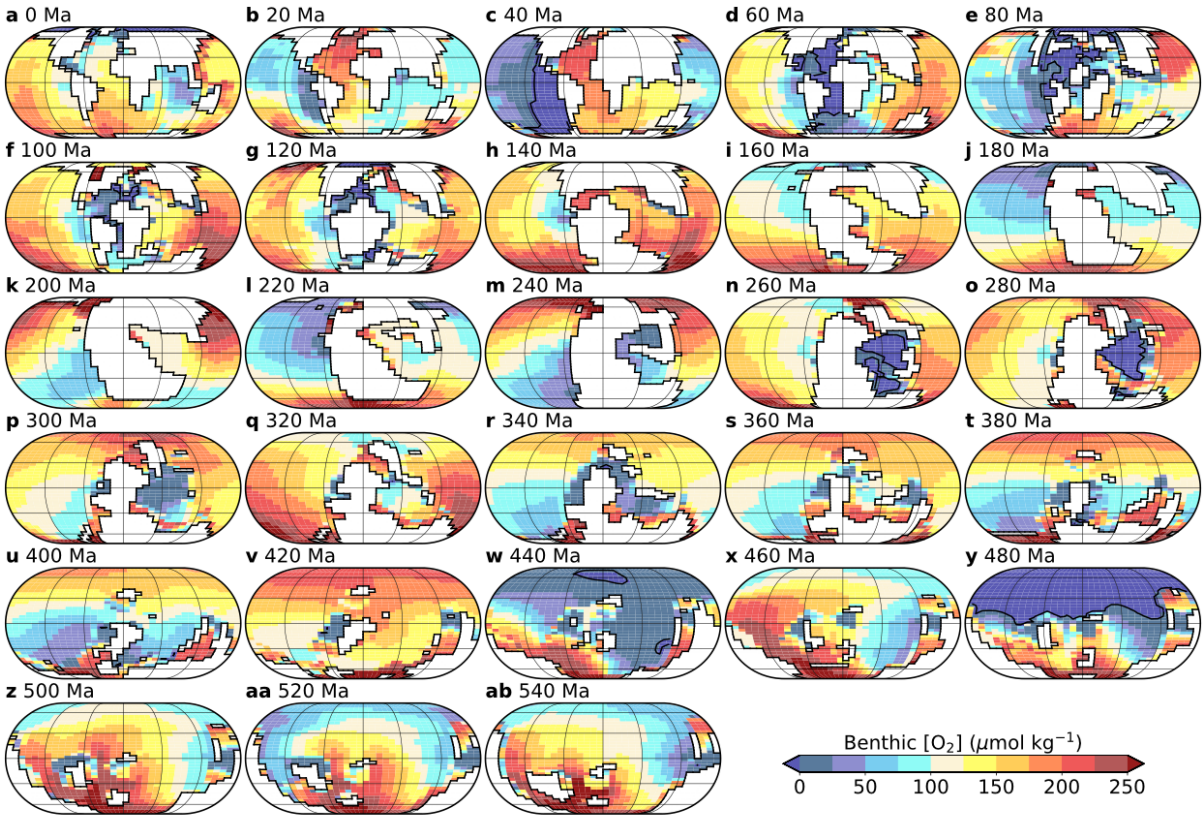
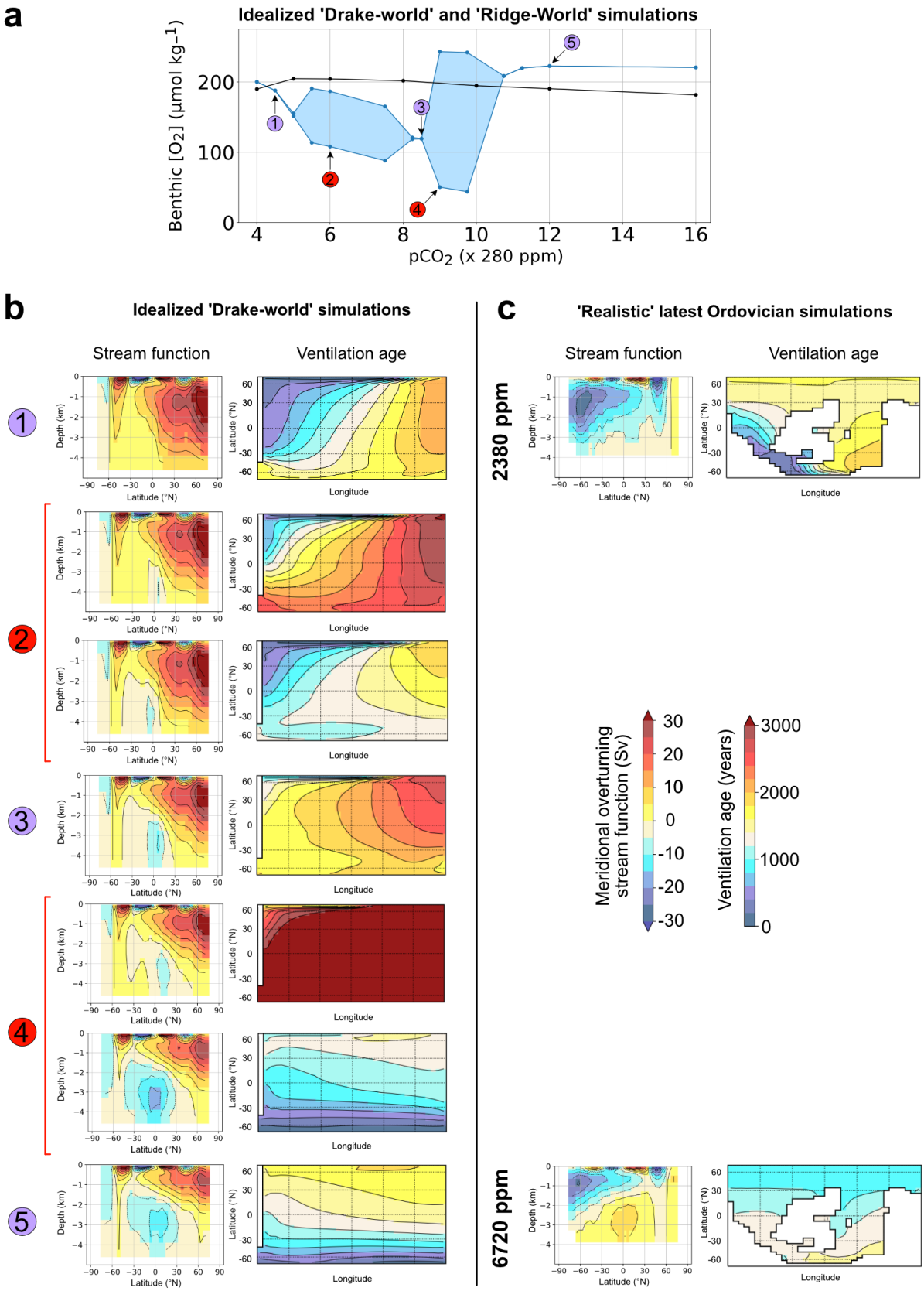


Extended Data Figure 9. Sensitivity of benthic [O_2] to atmospheric forcing (pCO_2). Benthic oxygen concentrations for simulations at 1120 ppm CO_2, with temperature-dependent remineralization and mid-ocean ridges. Emerged continental masses are shaded white. Results are averaged over the last 5000 years. Eckert IV projection.



Extended Data Figure 10: Ocean circulation regimes in the cGENIE model. (a) Envelope of benthic [O_2] values simulated at various atmospheric CO_2 levels using Drake world (in blue,

see maps in panel (b)) and ridge world (in black) (Methods). Regimes of stable equilibria and regimes of stable oscillations for Drake World simulations are numbered and labelled using a blue and red background, respectively. (b) Meridional overturning stream function in Sv (sverdrup, 1 Sv = 10^6 m^3 s^{-1}) and map of benthic ventilation age for each stable equilibrium and the 2 extreme states of each stable oscillatory regime identified in panel (a), using same numbering and color code. Lambert cylindrical equal-area projection. A negative (blue) stream function corresponds to an anticlockwise circulation. (c) Tentative comparison with the latest Ordovician simulations of Pohl et al.[21]. Results are shown at 6720 ppm and 2380 ppm CO_2, corresponding to the warm and cold states of Scenario #1 in ref.[21].