The diversification of complex animal life during the Cambrian Period (541–485.4 Ma) is thought to have been contingent on an oxygenation event sometime during ~850 to 541 Ma in the Neoproterozoic Era. Whilst abundant geochemical evidence indicates repeated intervals of ocean oxygenation during this time, the timing and magnitude of any changes in atmospheric $pO_2$ remain uncertain. Recent work indicates a large increase in the tectonic CO$_2$ degassing rate between the Neoproterozoic and Paleozoic Eras. We use a biogeochemical model to show that this increase in the total carbon and sulphur throughput of the Earth system increased the rate of organic carbon and pyrite sulphur burial and hence atmospheric $pO_2$. Modelled atmospheric $pO_2$ increases by ~50% during the Ediacaran Period (635–541 Ma), reaching ~0.25 of the present atmospheric level (PAL), broadly consistent with the estimated $pO_2 > 0.1–0.25$ PAL requirement of large, mobile and predatory animals during the Cambrian explosion.
The transformation of CO₂ to organic carbon via photosynthesis imparts a significant isotopic fractionation. Buried organic carbon contains a reduced fraction of 13C atoms, leaving an excess in the ocean and atmosphere. Through this mechanism, changes in the rate of burial and weathering of organic carbon relative to the burial and weathering of carbonates alter the δ13C value of seawater, which is recorded in sedimentary carbonates. This effect is dampened at low pO2 by the rapid adjustment of oxidative weathering rates to match carbon burial rates (through changes in O₂), but not completely nullified unless oxidative weathering is the only O₂ sink. Whilst a step change in

The oxidation of the Earth system was a necessary condition for the rise of complex animal life, which occurred in several steps. The Great Oxidation Event (GOE) ~2.3 Ga saw a permanent rise in atmospheric oxygen from <10⁻⁵ PAL to 10⁻¹³ –10⁻⁴ –10⁻¹ PAL, but oxygen remained well below present levels throughout the Proterozoic. A Neoproterozoic Oxygenation Event has been proposed based on a range of indirect proxies (Fig. 1). The expansion of the oceanic inventories of Mo, V and Re, and a shift towards lower δ²⁹⁷/⁸²⁷Se values suggest a trend towards more oxidising ocean conditions across the Neoproterozoic–Phanerozoic transition, and cerium anomalies point to at least a well-oxygenated

Several hypotheses have been put forward to explain a Neoproterozoic oxygenation, in which the observed ocean oxygenation trends are the result of a broader increase in atmospheric O₂. Following the Snowball Earth glaciations, pulses of nutrients are suggested to have entered the oceans, enhancing primary production and burial of organic matter, releasing oxygen to the atmosphere, but this would only have temporarily increased pO₂ (returning to the previous state after the pulse subsided). Alternatively, a sustained increase in terrestrial chemical weathering potentially amplified through selective weathering of phosphorus by early terrestrial ecosystems.

The expansion of an early land biosphere could also have restricted the oxidative weathering of reduced crustal rock, reducing the major sink of O₂. These mechanisms can increase atmospheric O₂ concentrations, but all also imply a rise in the average δ¹³C of carbonates, either by increasing organic carbon burial relative to carbonates or by restricting organic carbon weathering, and such a rise is not observed in the geological record at the time.

Here we explore an alternative mechanism of oxygenation, where changes in plate tectonics cause a rise in pO₂ during the late Neoproterozoic. An increased fraction of young zircon grains at the Proterozoic–Phanerozoic transition points to increased continental arc volcanism, consistent with an increase in atmospheric CO₂ and warming of the planet from Cryogenian periods.

As there is no direct geochemical proxy for atmospheric oxygen levels, estimates largely rely on modelling approaches, based on our understanding of the long-term carbon cycle (Fig. 2). For oxygen to build up in the ocean-atmosphere system, photosynthetically-produced organic carbon must be shielded from being re-oxidised through the burial of organic carbon in seafloor sediments. Inorganic carbonates are also buried in sediments following precipitation from seawater, and both buried carbon species are returned to the ocean and atmosphere through uplift and weathering, as well as via metamorphism and degassing. Any change to the burial and return fluxes of organic carbon will cause a change in atmospheric oxygen concentration.
carbonate δ13C likely occurred between the mid-Proterozoic and Phanerozoic baselines, the later Neoproterozoic record does not show the sustained stepwise increase that would be expected if the long-term burial and weathering fluxes of organic carbon were increased relative to those of inorganic carbon. Least-squares regression analysis of carbonate carbon isotope data shows a gradual negative trend over the whole Neoproterozoic (decline of ~1–2‰), and no significant trend during the Ediacaran period where evidence for deep ocean oxygenation is found (see Supplementary Fig. 1).

Increasing the long-term tectonic input rate of CO2 must result in an increase in the overall carbon burial rate to maintain steady state of the ocean-atmosphere system. If some of this carbon is buried organically then O2 can rise, and if this additional burial follows the same distribution between organic carbon and carbonates as in the initial unperturbed system, then the oxygen concentration of the atmosphere can rise without any observable change in δ13C. This effect should be seen in carbon cycle models such as COPSE and GEOCARBSULF, although it has not been noted in any previous analyses using these models. In addition, a similar effect may have operated over the whole of Earth history, wherein cumulative mantle CO2 input can drive long-term burial of organic carbon and planetary oxygenation, but the model of this mechanism could not account for the timing or magnitude of any second oxygen rise after the GOE.

Here we investigate the impacts of the inferred increase in tectonic CO2 input between the late Neoproterozoic and early Phanerozoic, extending the COPSE Reloaded biogeochemical model (see Methods) to the Ediacaran. Our model predicts a ~50% increase in atmospheric O2 during the Ediacaran. The predicted magnitude and temporal dynamics of changes in δ13C in an increase in the overall carbon burial rate to maintain steady state of the ocean-atmosphere system. If some of this carbon is buried organically then O2 can rise, and if this additional burial follows the same distribution between organic carbon and carbonates as in the initial unperturbed system, then the oxygen concentration of the atmosphere can rise without any observable change in δ13C. This effect should be seen in carbon cycle models such as COPSE and GEOCARBSULF, although it has not been noted in any previous analyses using these models. In addition, a similar effect may have operated over the whole of Earth history, wherein cumulative mantle CO2 input can drive long-term burial of organic carbon and planetary oxygenation, but the model of this mechanism could not account for the timing or magnitude of any second oxygen rise after the GOE.

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Monte-Carlo setup. We now run the COPSE model forwards in time for the Ediacaran period and compare to geochemical data for $\delta^{13}$C, $\delta^{34}$S and $^{87}$Sr/$^{86}$Sr. The degassing rate follows Mills et al.\textsuperscript{37} as in Fig. 1a, and the uplift rate is set to increase linearly from 0.5 to 2 times the present day rate. The increase in uplift is chosen in order to reproduce the magnitude of the observed rise in $^{87}$Sr/$^{86}$Sr, but is also roughly consistent with the difference in reconstructed rates of sediment deposition between the Ediacaran and Cambrian\textsuperscript{44}. In order to fully capture the uncertainty in model parameterisation, we run a Monte-Carlo analysis in which the COPSE model is run 10,000 times and the most important parameters are randomly sampled from an uncertainty window shown in Table 1.

We vary the assumed present-day fluxes in the model carbon cycle because these carry large uncertainties\textsuperscript{45}, and will impact the relative effects of an increase in degassing. We vary the activation energy of seafloor weathering, as this process is a carbon sink that responds to increases in mid-ocean ridge production, thus should be increased under our assumption of increasing production and subduction rates. A highly-sensitive seafloor weathering sink would be expected to dampen the O$_2$ rise caused by an increase in degassing. Continental weathering activation energies are also varied, altering the relative strength of seafloor weathering. In the case of oxidative weathering, we test the range of possible responses to O$_2$. We also consider different values for the long-term climate sensitivity. Finally, we experiment with adding a direct mantle flux of CO$_2$ and H$_2$ into the model: COPSE does not include direct mantle input at mid-ocean ridges, and the input of reduced H$_2$ gas is an additional oxygen sink that should be amplified by increasing degassing rates. Ridge CO$_2$ input is assumed to equal H$_2$ input (in terms of mol C and mol O$_2$ equivalent) to maintain balance of the linked carbon and oxygen cycles under an additional O$_2$ sink, this value is also consistent with measurements\textsuperscript{39}. Finally, in addition to the parameter choices, the degassing forcing is resampled every 10 Myrs from the uncertainty window of Mills et al.\textsuperscript{37}. This allows for quite rapid changes in degassing rate, but not above the rates of change that have been suggested for more recent time periods\textsuperscript{50}.

The Monte-Carlo procedure follows that of Royer et al.\textsuperscript{51}, who sampled a wider range of parameters in a model of roughly equal complexity (GOCARBSULF\textsuperscript{41}), also using 10,000 runs. We choose to use a flat distribution between the parameter minimum and maximum estimates, with all values being equally likely, as we believe this is more representative of the real uncertainty than sampling from a normal distribution. The Monte-Carlo results for the carbon, oxygen and strontium cycles are shown in Fig. 5, with the dark and light shaded areas showing ± 0.5 and ± 1 standard deviation respectively over the whole experimental set.

Model predictions. Early Ediacaran pO$_2$ levels are predicted to be around ~0.2 PAL. This is consistent with recent modelling of Proterozoic oxygen regulation and with constraints on pO$_2$ from the presence of detrital pyrite\textsuperscript{12}. It is also below upper bounds of ~0.4 PAL\textsuperscript{47,52} or 0.5–0.7 PAL\textsuperscript{28} inferred from ocean models, based upon the assumption of present-day nutrient levels and the presence of widespread deep ocean anoxia. Mean atmospheric oxygen is predicted to increase by around 50% during the Ediacaran period. This is primarily due to a rise in the organic carbon burial flux from $\sim 4 \times 10^{12}$ mol yr$^{-1}$ to $\sim 8 \times 10^{12}$ mol yr$^{-1}$, which is driven by increasing phosphorus input and ocean phosphate concentration. These increases ultimately stem from the increased CO$_2$ input flux through degassing and associated increase in surface temperature and weathering, which then drive carbon burial in both organic and inorganic forms. It is possible to draw a line through the model uncertainty that represents no change or even a decrease in O$_2$ levels. However, this requires moving from one edge of the uncertainty window to the other and is therefore very unlikely. Figure 6 shows a histogram of the modelled change in pO$_2$, and shows that 97% of model runs produce an increase in atmospheric O$_2$, and more than two thirds of runs produce an O$_2$ increase of between 25 and 75% of the initial value. Consequently, we infer with a high likelihood that there was a significant increase in pO$_2$ across the Ediacaran period.

Mean estimates in Fig. 5 show a slight reduction in $t_{o_2}$ and carbonate $\delta^{13}$C, whilst the plotted Ediacaran C isotope record shows a series of positive and negative excursions, the causes of which remain the subject of much active research e.g.\textsuperscript{33,34} but the long-term average remains constant (see Methods and Supplementary Fig. 1), broadly consistent with our model. Increased weathering of carbonates, and uplift-driven weathering of older seawater $^{87}$Sr/$^{86}$Sr due to the increased weathering contributions of granites and carbonates in the model, which are relatively radiogenic.
lithologies drives an increase in $^{87}$Sr/$^{86}$Sr from ~0.7076 to ~0.7083, again generally consistent with the geological record—although this is expected as we have prescribed the uplift increase based partly on the Sr record. The supplementary information shows another Monte-Carlo experiment where an increase in continental uplift and erosion is not assumed over the model timeframe (See Supplementary Figs. 2–4 and Supplementary Note 1). This results in a much poorer fit to the $^{87}$Sr/$^{86}$Sr record, but the results for the carbon, sulphur and oxygen cycles are very similar, and as such we conclude that our proposal of degassing-driven O$_2$ rise is robust to any expected uplift rate changes.

Figure 7 shows the sulphur cycle outputs from the Monte-Carlo experiment. With increased inputs of sulphur from continental weathering and degassing, oceanic sulphate concentration, alongside pyrite and gypsum burial rates, also increase.
the ranges shown in Table 1. Light shaded windows show ± 1 std. dev, dark parameters controlling atmospheric oxygen are chosen for each run from increase linearly from 0.5 to 2 times present day. Values for the key model record, which shows little change in of ~2 × 10^12 mol yr

under enhanced degassing. This response mimics that of the carbon cycle, where increasing input of degassed sulphur species necessitates an overall greater burial rate. Indeed, the sulphur cycle generates some of the oxygen rise in our model: pyrite burial increases by around 1 × 10^{12} mol yr^-1, generating an O_2 flux of ~2 × 10^{12} mol yr^-1, or around 30% of the total additional O_2 production. Again, as in the carbon cycle, the increase in both reduced and oxidised fluxes to the sediments leads to little change in the fraction of S that is buried as pyrite (f_{py}), and thus little change to δ^{34}S. This is generally consistent with the geologic record, which shows little change in δ^{34}S over the Ediacaran, especially when considered against the variability window during the Phanerozoic (~30%). The record does indicate a shift to slightly higher values towards the Cambrian, which we do not replicate. Nevertheless, a rise in δ^{34}S would usually be interpreted as an increase in pyrite burial rates relative to gypsum (or reduction in pyrite weathering), thus it is unlikely that the process driving this change could deplete O_2. In addition to this, we note that the modelled f_{py} is lower than indicated in some reconstructions. The low f_{py} value is an inherent property of the COPSE model, which assumes relatively high rates of gypsum weathering and burial. The absolute value of f_{py} is highly uncertain, and the important prediction for this study is the change to f_{py} that might be driven by our proposed mechanism, in which our model is in agreement with available data.

Discussion

We can compare our model atmospheric pO_2 predictions to estimates of the oxygen requirements of early animal life forms. This assumes they lived in waters equilibrated with the atmosphere—e.g., in well-mixed (shallow) shelf seas or in benthic slope settings on down-welling margins or high-latitude regions of deep convection. Other locations below the surface mixed layer of the ocean—e.g., seasonally-stratified shelf seas or the open ocean thermocline—tend to be depleted in oxygen due to net respiration of organic matter. It has classically been argued that a minimum oxygen threshold exists for the evolution of animal life, but oxygen requirement clearly depends on the type of animal, including their size, mobility, nervous system (information processing) and ecological habits. Sponges (Porifera)—which are the basal animals—have low O_2 requirements. Hence their evolution was not limited by any of our predicted pO_2 levels, consistent with biomarker evidence that demosponges were present by ~660–640 Ma in the Cryogenian.

The soft-bodied Ediacaran biota ~575–540 Ma are currently interpreted as including a mix of stem- and crown-group animals. The estimated pO_2 requirement of soft-bodied, thin, sheet-like animal forms (e.g., Dickinsonia), which are assumed limited by O_2 diffusion range from ~0.01–0.03 PAL to ~0.06 PAL. Modern benthic invertebrate analogues suggest a requirement of ~0.1 PAL, closer to the levels we predict during the early Ediacaran period. Whilst it is tempting to infer that our predicted steady oxygenation during the Ediacaran period enabled the evolution of progressively more complex Ediacaran animals, pO_2 may already have been sufficient beforehand. Furthermore, once bilaterian animals with a circulatory system evolved they could have tolerated lower pO_2; small bilaterian worms with a circulatory system are estimated to only need ~0.0014–0.0036 PAL.

A better case can be made that our predicted rise in pO_2 enabled the increased size, mobility, nervous system, carnivory and eyesight of animals during the Cambrian explosion—all traits that increase physiological O_2 demand. Recent estimates of the minimum oxygen requirement for the evolution and diversification of the Cambrian fauna are ~0.1–0.2 PAL or ~0.25 PAL. Moreover the sequence of appearance of Cambrian fossil animal
subset (right, red)\textsuperscript{37}. For both, least-squares regression is performed on the whole dataset and on data that is binned into 5 Myr and 10 Myr groups. The Neoproterozoic data show an average of 2–3\texttimes{}10\textsuperscript{16} molecule\textsuperscript{-1} and an overall trend towards lower values over time. The Ediacaran data show an average of around 0\% and no clear trend. Thus we argue that there is no step-change towards more positive values over either the Neoproterozoic Era or the Ediacaran period. This absence of a step-increase is problematic for many proposed mechanisms that infer an increased burial rate of organic carbon relative to carbonates over these intervals (see main text).

**COPSE model alterations.** For this work we use the COPSE (Carbon Oxygen Phosphorus Sulphur Evolution) Reloaded model\textsuperscript{43}, which is an Earth system box model that computes changes in the C, O, P, S and N cycles over geological timescales to reconstruct long-term climate and sediment geochemistry. It was designed for the Phanerozoic Era but has been extended previously in simplified forms to test hypotheses for Proterozoic oxygen controls\textsuperscript{14,29}, reasoning that the same key processes control the major geochemical cycles. Organic carbon burial in the model is dependent on the concentrations of the limiting nutrients nitrogen and phosphorus, with \(P\) being the ultimate limiting nutrient. \(P\) input is controlled by weathering fluxes, which are dependent on global temperature and also supply alkalinity and cations, resulting in carbonate precipitation. COPSE is a fully-dynamic predictive model in which all fluxes are controlled by the internal processes, rather than being prescribed. Only external forcings (e.g., degassing rate, uplift rate) are prescribed and the resulting predicted changes in global biogeochemical cycling can be tested against isotopic records of carbon, sulphur and strontium\textsuperscript{44}.

Tectonic changes and biosphere evolution are imposed as external forcings. See Lenton et al.\textsuperscript{43} for the Phanerozoic COPSE model runs and comparisons to \(\delta^{13}\mathrm{C}\), \(\delta^{34}\mathrm{S}\) and \(87\mathrm{Sr}/86\mathrm{Sr}\) data. In this work, we run the model for the Ediacaran period to test the global response to an increase in \(\mathrm{CO}_2\) degassing rates. The degassing rate \((D)\) forcing is prescribed following a quantitative reconstruction for the late Neoproterozoic\textsuperscript{37}, and the uplift/erosion \((U)\) forcing is assumed to linearly increase based on the model fit to the strontium isotope system. Land area forcings for weathering of carbonates, granites and basalts are held at their present-day value given the lack of data, and terrestrial biosphere forcings are turned off (as in the Cambrian part of the Phanerozoic run). We run the model 10,000 times using the Monte-Carlo approach of Royer et al.\textsuperscript{31}. Full details of the Monte-Carlo parameter changes and procedure are in the main text. Aside from the standard run denoted above, we also run the model with constant uplift, the results of which are shown in the Supplementary Information (Supplementary Note 1, Supplementary Figs. 2–4).

The model equations used in this version of the model are documented below. Whilst a number of external forcings are set for this work, all model processes remain the same as the published model\textsuperscript{43}, with the exception of the addition of direct mantle input of carbon and reducing power (modelled as \(H_2\) gas). We do not include equations relating to the impact of vegetation on the long-term Carbon cycle (i.e., plant-assisted weathering) as these processes were not occurring in the Precambrian and the forcing set used here reduces them to zero. Full model equations including those omitted are documented in Lenton et al.\textsuperscript{43}, and we direct the reader to this publication for more detail on the model itself. \(\mathrm{RO}_2\) and \(\mathrm{RCO}_2\) denote concentrations of oxygen and carbon dioxide relative to present-day.

Optional oxygen dependence for mocb:

\[
\text{mocb} = k_2 \cdot U \cdot \left( \frac{\text{newp}}{\text{newp} + 2} \right)^2 \cdot f(O_2) 
\]

Methods

**Regression analysis of carbonate carbon isotopes.** Supplementary Fig. 1 shows plots of carbonate \(\delta^{13}\mathrm{C}\) for the Neoproterozoic (left, yellow) and the Ediacaran (right, red). For both, least-squares regression is performed on the whole dataset and on data that is binned into 5 Myr and 10 Myr groups. The Neoproterozoic data show an average of 2–3\texttimes{}10\textsuperscript{16} molecule\textsuperscript{-1} and an overall trend towards lower values over time. The Ediacaran data show an average of around 0\% and no clear trend. Thus we argue that there is no step-change towards more positive values over either the Neoproterozoic Era or the Ediacaran period. This absence of a step-increase is problematic for many proposed mechanisms that infer an increased burial rate of organic carbon relative to carbonates over these intervals (see main text).

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List of fluxes

**Phosphorus weathering:**

\[
\text{phosw} = k_{\text{phosw}} \left( 0.8 \frac{sibw}{sibw} + 1.14 \frac{carbw}{carbw} + 0.06 \frac{oxidw}{oxidw} \right) 
\]

**P delivery to land surface:**

\[
\text{plan} = k_{\text{plan}} \cdot V \cdot \text{phosw} \cdot \left( k_3 \cdot U + \left( 1 - k_8 \right) \cdot b_{\text{coal}} \right) 
\]

**Land organic carbon burial:**

\[
\text{lob} = C\text{Pland} \cdot \text{plan} = k_5 \cdot C\text{Pland} \cdot \text{plan} 
\]

**P delivery to oceans:**

\[
\text{psea} = \text{phosw} - \text{plan} 
\]

**Marine new production:**

\[
\text{newp} = r_{\text{CP}} \cdot \min \left( 30.9 \frac{N_{\text{bo}}}{\text{r}_{\text{P}}}, 2.2 \left( P_{\text{P}} \right) \right) 
\]

**Marine organic carbon burial:**

\[
\text{mocb} = k_2 \cdot U \cdot \left( \frac{\text{newp}}{\text{newp} + 2} \right)^2 \cdot f(O_2) 
\]

Optional oxygen dependence for mocb:

\[
f(O_2) = \frac{1}{2.1276} - 0.755 \left( \frac{O_2}{P_{\text{O}_2}} \right) 
\]
Marine organic phosphorus burial:
\[ m_{opb} = \frac{m_{op}}{C_{Psea}} \]

Calcium-bound phosphorus burial:
\[ c_{apb} = k_{c} \cdot newp^2 \cdot f_{anax} \]

Iron-sorbed phosphorus burial:
\[ f_{ipb} = k_{i} \cdot \left( 1 - \text{anox} \right) \cdot \left( \frac{P}{P_0} \right) \]

Nitrogen fixation:
\[ n_{fix} = k_{i} \left( \frac{P - N_{f}}{P_0 - N_{f}} \right)^2 \quad \text{for} \quad N_{f} < P \text{, else} 0 \]

Marine organic nitrogen burial:
\[ m_{onb} = \frac{m_{on}}{C_{Nsea}} \]

Denitrification:
\[ denit = k_{j} \left( 1 + \text{anox} \right) \cdot \frac{N_{f}}{N} \]

Granite weathering:
\[ \frac{g}{w_{fw}} = k_{gfw} \cdot U \cdot P_{G} \cdot \alpha_{fw} \cdot f_{frunoff} \cdot f_{biota} \]

Basalt weathering:
\[ \frac{b}{w_{fw}} = k_{bfw} \cdot P_{G} \cdot \alpha_{w} \cdot f_{basw} \cdot f_{frunoff} \cdot f_{biota} \]

Silicate weathering:
\[ s_{w} = g_{w} + b_{w} \]

Carbide weathering:
\[ \frac{c}{w_{fw}} = k_{cwe} \cdot C \cdot U \cdot P_{G} \cdot \alpha_{gew} \cdot f_{biota} \]

Oxidative weathering:
\[ o_{w} = k_{o} \cdot U \cdot g \cdot \theta^{0.35} \]

Marine carbonate carbon burial:
\[ m_{ccpb} = s_{w} + c_{w} + m_{ps} - pyw - pydeg \]

Seafloor weathering:
\[ s_{w} = k_{sw} \cdot D \cdot e^{\frac{\Delta T}{42}} \]

Pyrite sulphur weathering:
\[ p_{yw} = k_{pyw} \cdot U \cdot pyr \]

Gypsum sulphur weathering:
\[ g_{ypw} = k_{gypw} \cdot U \cdot P_{G} \cdot \alpha_{gypw} \cdot f_{biota} \]

Pyrite sulphur burial:
\[ m_{ps} = k_{mps} \cdot s \cdot m_{ccpb} \]

Gypsum sulphur burial:
\[ m_{gs} = k_{mps} \cdot s \cdot c_{cal} \]

Organic carbon degassing:
\[ o_{cdg} = k_{oc} \cdot D \cdot g \]

Carbonate carbon degassing:
\[ c_{cdg} = k_{cc} \cdot D \cdot B \cdot \epsilon \]

Pyrite sulphur degassing:
\[ p_{ydeg} = k_{pydeg} \cdot D \cdot pyr \]

Gypsum sulphur degassing:
\[ g_{ypdeg} = k_{gypdeg} \cdot D \cdot gyp \]

Other calculations

Atmospheric CO2:
\[ CO_2 = a^2 \]

COPSE Reloaded uses the global temperature function from Berner and Kothavala\(^{39}\) rather than that of Caldeira and Kasting\(^{37}\).

Global Temperature:
\[ \Delta T = k_{T} \cdot \ln CO_2 - k_{T} \cdot t/570 \]

where \( k_{T} = 4.328^\circ C \) and \( k_{T} = 7.4^\circ C \).

Ocean anoxic fraction:
\[ \text{anox} = \left( \frac{1}{1 + e^{-k_{anox} \left( \frac{\Delta T}{570} \right)}} \right) \]

Reduced Gas Flux:
\[ rf = k_{rf} \cdot D \]

A flux of reduced gas, modelled as H2, is added to the model to explore the possibility that increased subduction and degassing rates may act to lower O2 levels by delivering more redundant from the mantle. The rate of input is defined by an assumed present-day rate (\( k_{rf} \)) and scales with the relative degassing rate. To maintain balance of the oxygen cycle at present day, the present day oxidative weathering flux is reduced by \( k_{rf} \). This modification, in turn, requires an additional source of carbon to the surface system to maintain balance, which is represented by mid-ocean ridge degassing of CO2 with magnitude equal to \( k_{rf} \). We also assume that the large sedimentary reservoirs in the model (C, G, PYR, GYP) do not change over 100 Myrs in the model of Hayes and Waldhauser\(^{71}\).

**Strontium isotope system.** This study follows Lenten et al.\(^{40}\), whereby the strontium cycle and its isotopes are implemented following Francois and Walker\(^{72}\) and Vollstaedt et al.\(^{74}\) with some improvements to the formulation described in Mills et al.\(^{3}\).

**Strontium fluxes**

Mantle Sr Input:
\[ Sr_{mantle} = k_{Srmantle} \cdot D \]

Basalt weathering input:
\[ Sr_{basw} = k_{Srbasw} \cdot \frac{b_{w}}{b_{w}} \]

Granite weathering input:
\[ Sr_{grunoff} = k_{Srgrunoff} \cdot \frac{g_{w}}{g_{w}} \]

Inputs from carbonate sediments:
\[ Sr_{adw} = k_{Sradw} \cdot \frac{c_{cal}}{c_{cal}} \]

Burial in carbonate sediments:
\[ Sr_{adw} = k_{Sradw} \cdot \frac{m_{ccpb}}{m_{ccpb}} \]

Removal in sea floor weathering:
\[ Sr_{fw} = k_{Srfw} \cdot \frac{s_{w}}{s_{w}} \]

The relative proportions of the burial and sea floor weathering removal fluxes of strontium are assumed to follow the same proportions as the corresponding fluxes in the carbon system, with the total flux dictated by assuming present-day steady state for oceanic Sr concentration.

Output from metamorphism:
\[ Sr_{mantle} = k_{Smantle} \cdot D \cdot \frac{Sr_{mantle}}{Sr_{mantle}} \]

Although there is no fractionation of Sr isotopes associated with the input and output fluxes to the ocean, decay of \(^{87}\)Rb to \(^{87}\)Sr influences the \(^{87}\)Sr/\(^{86}\)Sr ratio over long timescales (and is responsible for the differing \(^{87}\)Sr/\(^{86}\)Sr values between different rock types). The decay process is represented explicitly in the model:
\[ \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} = \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} \cdot \left( 1 - e^{-3.8 \times 10^{-12} \times t} \right) \]

\[ \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} = \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} \cdot \left( 1 - e^{-3.8 \times 10^{-12} \times t} \right) \]

\[ \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} = \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} \cdot \left( 1 - e^{-3.8 \times 10^{-12} \times t} \right) \]

Where \( t \) is in years from Earth formation (taken to be 4.5 billion years ago). For each rock type, the rubidium-strontium ratio is then calculated such that the observed present-day \(^{87}\)Sr/\(^{86}\)Sr ratio is achieved for each rock type after 4.5 billion years:
\[ \frac{^{87}\text{Rb}}{^{86}\text{Sr}} = \frac{\frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}} - \frac{^{87}\text{Sr}}{^{86}\text{Sr}}_{\text{mantle}}}{ \left( 1 - e^{-3.8 \times 10^{-12} \times t} \right) } \]
The isotopic composition of the ocean and the sediments are calculated by first creating reservoirs consisting of Sr concentrations multiplied by their isotopic ratios, where $\delta^{87}Sr$ denotes the $^{87}Sr/^{86}Sr$ ratio of reservoir X:

\[
\frac{d(\delta^{87}Sr - \delta^{87}Sr_{\text{sediment}})}{dt} = -\frac{\delta^{87}Sr_{\text{sediment}}}{\delta^{87}Sr_{\text{ocean}} + \delta^{87}Sr_{\text{mante}} + \delta^{87}Sr_{\text{mantle}} - \delta^{87}Sr_{\text{e}} - \delta^{87}Sr_{\text{basalt}}} - \sum_{f i} \delta^{87}Sr_{\text{basalt}} (1 - e^{-\lambda t})
\]

The ocean $^{87}Sr/^{86}Sr$ ratio is calculated by dividing the new reservoir by the known concentration:

\[
\delta^{87}Sr_{\text{ocean}} = \frac{\delta^{87}Sr_{\text{sediment}}}{\delta^{87}Sr_{\text{ocean}}} - \frac{\delta^{87}Sr_{\text{sediment}}}{\delta^{87}Sr_{\text{ocean}}}
\]

The carbonate sediment $^{87}Sr/^{86}Sr$ ratio includes an additional term to account for rubidium decay within the sedimentary reservoir:

\[
\delta^{87}Sr_{\text{sediment}} = \frac{\delta^{87}Sr_{\text{ocean}}}{\delta^{87}Sr_{\text{ocean}}} + \delta^{87}Sr_{\text{carbonate}} (1 - e^{-\lambda t})
\]

Where here $\lambda t$ is time elapsed since the start of the model run. The rubidium-strontium ratio of sediments is calculated to achieve the average crustal $^{87}Sr/^{86}Sr$ of 0.73.$^3$

Data availability

The model data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability

The COPSE code is freely available at https://github.com/sjdaines/COPSE/releases

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