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Peer Review File

Manuscript Title: Continental configuration controls ocean oxygenation during the Phanerozoic

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

Pohl and colleagues conducted Earth system experiments to show that plate motion has a significant impact on oceanic redox conditions. They show that, even when solar luminosity, atmospheric pO2 and pCO2 levels, and ocean phosphate concentration were kept as constants, paleogeography alone can drive dramatic changes in dissolved oxygen concentrations in surface and deep ocean waters, through its impact on the proportion of absorptive ocean surface vs. more reflective land surface, hence planetary albedo, sea surface temperature, and ocean circulation. The most important implication is that the relationship between atmospheric pO2, surface-ocean redox conditions, and deep-ocean redox conditions are more complex than previously thought, and paleogeography plays an important role in driving this relationship. Remarkably, the model experiments recovered several features (e.g., early Paleozoic deep-water anoxia, Early Triassic anoxia in the paleo-Tethys, and early Cretaceous anoxia in central Atlantic), indicating these events may be explained by paleogeography alone. These are remarkable findings that will greatly change how we interpret proxy data and how we infer pO2 from marine sediments.
The authors also discovered self-sustained oscillations in oceanic circulation pattern (which leads to oscillations in benthic water age and redox conditions). While the drivers of these oscillations remain to be understood, they do resemble thousand-year scale variations in redox-proxy data from the rock record.
The results are novel and provocative. I am not a Earth system modeler, so I cannot comment on the modeling part of the work. The paper is well written with great clarity, very concise and to the point, and easily accessible to the broad audience. Figures are excellent and illustrate the important messages of the study. I only have a few minor comments that can be easily addressed in the revision stage.
In several places, the authors use the outdated term “continental drift” (L. 58, 72, 171, 302). I suggest that “continental drift” be replaced by paleogeography, paleogeographic configuration, or plate motion (as in the title).
L. 28: “We further identify the presence of (paleogeographical) state-dependent modes of circulation instability (oscillations), which allows for pO2 to already be close to modern by the beginning of the Phanerozoic despite the deep ocean remaining anoxic.” Here, I would modify the sentence to read “… which allows for deep ocean anoxia in the early Phanerozoic despite modern-level pO2” because pO2 was kept constant in the modeling experiments.
L. 35, remove “both”
L. 100, change “Lower Cretaceous” to “Early Cretaceous”
L. 130, to avoid ambiguity, I would replace “420 Ma” with “prior to 420 Ma”

Fig. 1e and ED Fig. 1e: explain MOC
Fig. 2 and ED Fig. 2 caption: "Results of the last simulated year are shown (year 20 000)." Can the authors confirm this statement? The Methods section says that model was integrated for 20,000 years.

Referee #2 (Remarks to the Author):

Review of "Plate motion drives variability in ocean oxygenation through the Phanerozoic" by Alexandre Pohl et al.

This paper presents a series of simulated ocean benthic oxygen concentrations through time. It is based on the analysis of a large number of simulations integrated with the EMIC cGENIE. The simulations are done for a number of time snapshots, spanning the past 520 million years, taking into account changes in continental configuration. Some of the atmospheric boundary conditions (winds and cloud albedo) are provided by output from the FOAM model, which was also run for each of these time slices, while others are computed within cGENIE. The authors find that the continental arrangement influences ocean circulation and the ventilation of bottom water masses, and therefore benthic oxygen content. Surface oxygen concentrations co-vary with solubility (mostly temperature-driven), and changes in sub-surface oxygen concentrations are mostly driven by export production. In some configurations, the system oscillates between two different circulation states. Another series of experiments was performed where CO2 concentrations were changed through time to correct for changing global temperatures, in an attempt to better isolate the impact of continental configurations.

This is an interesting paper. While the main drivers of changes in oxygen at different depths are not a surprising or novel result, it is to my knowledge the first study analysing circulation changes, and associated O2 changes, over such a long time span. I therefore believe that this paper would be of interest for the readership of Nature.

I have a few suggestions and comments below that I hope the authors and the editor will find helpful.

1. Even state-of-the-art high-resolution models underestimate current changes in observed O2 in the ocean. cGENIE is a relatively simple low-resolution model, which is unlikely to perform very well when simulating O2. I do not think that this is a show-stopper, given that cGENIE-type models are the best tools we have currently for such large and long-term sensitivity studies given our current computing capacities. But I would suggest to add a data-model comparison for present day to the supplementary material and discuss the shortcomings of this model. In addition, there are a few published model results produced with higher resolution models (that also include O2) for some of the time snapshots presented here. It would be good to add a discussion based on these to the supplementary material, for the time periods available, to show how cGENIE is performing in comparison to other models.

2. There are many uncertainties in the simulations presented here. One of the most important ones is the crude representation of ocean dynamics in such a low resolution model. There are also important parameters that would impact O2 concentrations for which the parameter space was not evaluated here (e.g., total nutrient content, CO2, O2 in atmosphere, and so on). There are feedbacks that are not included as far as I can tell (e.g., phosphate release by sediments in low oxygen environments, denitrification, etc).

I am not saying that these should be included, that would likely not advance our understanding much and just increase the degrees of freedom, and I agree with the approach taken here to analyse just one effect (changing topography). But I would recommend rephrasing some of the statements throughout the paper. The authors need to emphasize that this is a (very valuable!) sensitivity study on ocean circulation changes due to topography changes with a physically simple and coarse resolution model, which can (maybe) give us a rough idea about past O2 concentrations in the ocean. It is certainly not a trustworthy reconstruction of past O2 concentrations.

3. One of the most interesting results in my opinion is the existence of a threshold that can tip the model into an oscillatory state. It would be really interesting to see if these simulations could help our understanding on when and why these oscillations occur. For example, I wonder if the authors could analyse if/how changes in the meridional (or vertical) temperature gradient (between the surface waters in the tropics and the surface waters in deep/bottom water formation regions; or between the surface and bottom waters in the tropics) influence the existence of such a threshold and/or the frequency of the oscillation. Another set of parameters to check would be the diffusion coefficients in the ocean, how does the frequency of these oscillation change when diffusion parameters are changed? Can the authors establish an empirical predictor for oscillations to happen (or not) based on temperature gradients, diffusivity and (maybe) the volume of the ocean basin in question? I think that this would be a very valuable addition. I have to add here that, unfortunately, part of the supplementary files were not submitted, or maybe not fully uploaded. The pdf file states "This file provides additional discussion on the oscillations" and is empty otherwise. Maybe some of my queries were actually already addressed in this file?

4. The other interesting take home message here are the changes in deep and bottom water masses over time. There are time slices where NH deep/bottom water dominates the world oceans and others where SH deep/bottom water dominates. In some configurations, convection in both hemispheres is active (e.g., 260Ma or 440Ma). At some time snapshots, there are semi-enclosed seas that are cut off from the general deep water circulation (300-240Ma). I think that this is a result that will be of interest for readers. Maybe an analysis /table/figure could be added on how (and why) the location of deep water formation sites change over time.

5. Finally, it would be great if some data could be included. For example, simple markers on top of the model results in Figure 2, at times and locations where evidence for anoxia was found in climate archives?

In summary, this is an interesting paper that I would support to be published after some level of revision taking my comments above into account.

Referee #3 (Remarks to the Author):

A. Summary of the key results

The manuscript by Pohl et al. uses numerical experiments to argue that the configuration of continents and ocean basins during the Phanerozoic strongly controls ocean oxygenation. This highlights that tectonics drives many fundamental life support systems on our planet, and can help explain some extinctions and anoxic events that are captured by the geological record.

B. Originality and significance: if not novel, please include reference

Many papers have been published that make use of ocean and atmospheric circulation models, and even those linked to biogeochemical cycling. However, this is the first time I have seen it applied to systematically testing the influence of continental arrangements in the Phanerozoic on the oxygenation of the oceans.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The approach presented here is world-leading, but I do have some queries that would improve the manuscript.

First, I get a sense that paleo-topography, and particularly orogens, were not included in the FOAM simulations. If that is correct, then why was this the case? Can the authors run one or two experiments with orogens (say during Pangea time) and compare their results? Surely that would affect the wind speeds and key inputs for the cGENIE model. I can only see the paleo-bathymetries being used, and all land being assigned a value of 0 km.

Second, although the cGENIE code is available, the key code (FOAM) and associated files that seems to drive ocean and atmosphere circulation is not available to the community. For a Nature paper, I would expect a higher level of code and data availability. And importantly - it would further increase the impact of the manuscript, as others can build on these experiments.

L304: How was the Mueller et al and the Scotese and Wright paleobathymetry merged? They have different absolute reference frames, and relative plate configurations. I realise that the resolution of these climate models is not very high, but it would be useful to show what the merged bathymetry looked like.

L307: Why and how was the solar luminosity value 1368 W m-2 and CO_2 2240 ppm value chosen? Was that to ensure that the SST in Extended Data Fig 7 was realistic? Would the results/conclusions change, say if the CO_2 value was 1000, or even 500 ppm?

L316: I can see that the cGENIE code is open source, but I cannot see anywhere that would enable someone to reproduce the ocean and atmospheric circulation presented here. Given the fact that this component is critical in reproducing the results, the fact that this code is not available to the community makes it hard to interrogate and test these results.

Maybe I cannot see the different shades of blue, but I cannot distinguish any variation in the paleobathymetry in the deeper oceans, even in more "recent" geological times.

I am confused about the equal-area grid. I see that the cells in Extended Fig 3 are not equal area – how were these resampled? Does cGENIE and also FOAM have a "regular" geographic grid or does it use an equal area grid?

D. Appropriate use of statistics and treatment of uncertainties

Figure 1e is really hard to interpret. Can you provide some explanatory text (even if it is in the Extended Data)?

Extended Data Fig 1 – what is "Export"? Explain for a novice reader.

Uncertainties are provided, but I would like to see some more discussion what would happen if a different tectonic reconstruction was applied? For example, the Torsvik et al. paleomagnetic reference frames would be very different, and they also have different continental arrangements. It would be useful for the authors to show several key timestep comparisons on the role of specifying a particular plate reconstruction.

E. Conclusions: robustness, validity, reliability

See comments above.

F. Suggested improvements: experiments, data for possible revision

See comments above.

One other point is that the title talks about plate motions, but in fact these are just static arrangements of continents. Plate motions infers some kinematics, which are at best, implicit. Perhaps a title "Continental arrangements drive variability in ocean oxygenation through the Phanerozoic" would be more suited.

G. References: appropriate credit to previous work?

References are appropriate.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The text is clear, and the manuscript is direct and succinct.

Referee #4 (Remarks to the Author):

Review

A.
This manuscript sets out to explore theoretical models for how the continental configuration (plate motions) on Earth has affected ocean circulation patterns and the transport of O2 to the deep abyssal oceans in the past 550 million years. The study finds that even if climate and atmospheric O2 had been invariant, benthic O2 level in the abyssal ocean would have varied dramatically in concert with rates of ocean ventilation and plate configuration.

B. Importantly, the study finds that ocean circulation was in a state where downwelling fluxes of water and O2 to the deep abyssal ocean was limited in the early Paleozoic and during major oceanic anoxic events. This connection provides an alternative explanation for widespread anoxia in the oceans at these times, where poor ocean ventilation drives deep ocean deoxygenation. By implication, neither ocean temperature (climate) giving lower O2 solubility in the surface ocean nor low atmospheric pO2 are necessary factors to drive anoxia in the abyssal oceans (although these factors might have mattered too). It is intriguing to see that the model predicts that deep oceans were more prone to deoxygenation by slower ocean circulation at time in the Phanerozoic when major oceanic anoxic events occurred and during the early Paleozoic were anoxia prevailed in the oceans.

C. The authors utilizes a well calibrated 3D model for the atmosphere-ocean circulation dynamics (c-GENIE), coupled with a new carbon export model.
D. Sensitivity tests were performed to distinguish the driving factor for benthic O2 change.

E. My main concern goes to the significance of the oscillating circulation modes in the early Paleozoic, which appears as an explanation for the pervasive anoxic oceans at this time. Although, the Early Paleozoic oscillations are intriguing and the period of oscillations are striking given recent observations that ocean redox conditions might have fluctuated on a ~kyr time scale, the main focus should be on the unstable steady state and why it allows for pervasive anoxic deep oceans. The oscillations appears to be of second order importance. So – why are the benthic O2 levels always far lower >440 Ma compared to <420 Ma? If this transition was driven by plate motion, why is this transition only seen to occur one time in history?

Secondly, when discussion the oscillations, the manuscript lacks figures to show the distinct ocean circulation states. The bifurcation is only vaguely described by referring to “bistable states happen” (in other situations, refering to meridional overturn in the Atlantic driven by climate change). This is an analogue argument an invalid expanation. I recommend the author produce a sketch (i.e. with ocean transects) that shows the major ocean currents fluxes in the two extreme states. Where exactly is the downwelling reduced (high latitudes, I presume) and how much – what dictates the period of oscillations, etc? Are both extrema conducive to abyssal anoxia and why?

Overall, the modeling result presented here is important, and there are potential important implications for understanding the expansion of marine dead zones and animal extinctions in the past. Thus, I find the results could be interesting for the broader scientific community. For a theoretical study, however, I believe the mechanistic details of the process that has governed downwelling fluxes is not sufficiently well explained.

Other comments

1- Correlating poor ocean ventilation to OAEs:
The authors argue that the Triassic oceans was prone to anoxia by plate configuration, but anoxia prevailed in the Paleotethys ocean from 251 to 245 Ma, and should then appear in the 240 Ma simulation (not only in the 260 Ma case).

2 – Line 104ff. Plate configuration is not necessarily causing the OAEs, but just making the system more prone to OAEs. Therefore, you should state that maybe these OAEs were triggered by larger perturbation now that paleocontinental configuration apparently were not assisting OAEs at those times.

3 –
L118ff. The opening of this paragraph is confusing, because the purpose of this sensitivity test is well explained. You should state that you run a sensitivity model where you keep surface O2 constant to see that it is the downwelling flux and not the O2 load that causes benthic deoxygenation. This would be clear if you changed the sentence from “leaving mean global SST…” to “in order to keep surface ocean oxygenation largely invariant” or so. How you manipulated pCO2 to keep SST and O2 solubility largely constant is of secondary importance to the reader and should be stated after. Also, conclude this paragraph by stating that this means that O2 load in downwelling waters will then be invariant, and so it is the water flux to the benthos that varies as a result of ocean circulation (continental configuration). This will make it clearer why you have done this sensitivity analysis.

4 – Fig. 3d. When looking at predicted benthic water ages. It would be good to state howit compares to the modern ocean (I guess benthic water age, on average, is equal to ~half the ocean mixing time (~1500 yr; Gruber & Sarmiento 2006), so it looks about right?

5 –
L141. What is the physical consequence of passing this bifurcation point? What does it mean that “oscillations happens”. I guess you refer to oscillating circulation patterns, but this could be clearer. A figure with the two modes of ocean circulation should be shown. Ideally, you should provide plots with streamlines (+ fluxes of the important ocean currents) in ocean transects. Then, explain where and why the water flux to the abyssal ocean is slower?

6–

L173. Poor referencing (35). There are much better redox constraints on the global ocean than from element concentrations in single pyrite minerals. Refer to global ocean redox proxies (Wallace et al. 2017, Dahl et al. 2010) and larger statistical comparison of local redox proxies (Sperling et al. 2018).

7–
(Minor comment)
I find the choice of the Figure 2 color scheme for benthic O2 counterintuitive. I would have expected red colors to represent anoxia (alarming conditions!) and blue colors “fresher” water.

PS. The file "409907_0_additional_review_material_3745335_qzkmk5.pdf" is corrupted and was therefore not reviewed.

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Author Rebuttals to Initial Comments:

Response to the reviewers [2021-09-14989]

Plate motion drives variability in ocean oxygenation through the Phanerozoic

Line numbers refer to the revised version of the manuscript with no revision marks.

Referee #1 (Remarks to the Author):

Pohl and colleagues conducted Earth system experiments to show that plate motion has a significant impact on oceanic redox conditions. They show that, even when solar luminosity, atmospheric pO2 and pCO2 levels, and ocean phosphate concentration were kept as constants, paleogeography alone can drive dramatic changes in dissolved oxygen concentrations in surface and deep ocean waters, through its impact on the proportion of absorptive ocean surface vs. more reflective land surface, hence planetary albedo, sea surface temperature, and ocean circulation. The most important implication is that the relationship between atmospheric pO2, surface-ocean redox conditions, and deep-ocean redox conditions are more complex than previously thought, and paleogeography plays an important role in driving this relationship. Remarkably, the model experiments recovered several features (e.g., early Paleozoic deep-water anoxia, Early Triassic anoxia in the paleo-Tethys, and early Cretaceous anoxia in central Atlantic), indicating these events may be explained by paleogeography alone. **These are remarkable findings that will greatly change how we interpret proxy data and how we infer pO2 from marine sediments**. The authors also discovered self-sustained oscillations in oceanic circulation pattern (which leads to oscillations in benthic water age and redox conditions). While the drivers of these oscillations remain to be understood, they do resemble thousand-year scale variations in redox-proxy data from the rock record. **The results are novel and provocative**.

We are happy that Referee #1 acknowledges the novelty and far-reaching implications of our results.

I am not a Earth system modeler, so I cannot comment on the modeling part of the work. The paper is well written with great clarity, very concise and to the point, and easily accessible to the broad audience. Figures are excellent and illustrate the important messages of the study. I only have a few minor comments that can be easily addressed in the revision stage.

We note that the modeling part of the work has been evaluated in detail by two other reviewers.

We thank Referee #1 for their comments and provide point-by-point responses hereafter.

In several places, the authors use the outdated term “continental drift” (L. 58, 72, 171, 302). I suggest that “continental drift” be replaced by paleogeography, paleogeographic configuration, or plate motion (as in the title).

We revised to “continental configuration” [lines 58, 75], “continental rearrangement” [line 189] and “paleogeographical evolution” [line 355].

L. 28: “We further identify the presence of (paleogeographical) state-dependent modes of circulation instability (oscillations), which allows for pO2 to already be close to modern by the beginning of the Phanerozoic despite the deep ocean remaining anoxic.” Here, I would modify the sentence to read “… which allows for deep ocean anoxia in the early Phanerozoic despite modern-level pO2” because pO2 was kept constant in the modeling experiments.

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We revised (lines 28–30) to: "*We further identify the presence of state transitions in the global ocean circulation, which lead to extensive deep-ocean anoxia in the early Phanerozoic under* pO_2 *levels as high as modern*".

L. 35, remove "both"

Done.

L. 100, change "Lower Cretaceous" to "Early Cretaceous"

Done.

L. 130, to avoid ambiguity, I would replace "420 Ma" with "prior to 420 Ma"

Done.

Fig. 1e and ED Fig. 1e: explain MOC

Done (see figure caption).

Fig. 2 and ED Fig. 2 caption: "Results of the last simulated year are shown (year 20 000)." Can the authors confirm this statement? The Methods section says that model was integrated for 20,000 years.

We integrated (ran) cGENIE for 20 000 years in order to reach equilibrium, and then, in the original manuscript, used the results of the last simulated year (i.e., year 20 000) to plot the maps of Fig. 2. In the revised version of the manuscript, we instead averaged all results over the last 5000 years of the 20 000-year long experiments in order to account for stable oscillations, and revised Fig. 2 and Extended Data Figs. 2–6 and 9 accordingly. We have also edited to clarify the total simulation duration vs. the interval that the data was extracted and averaged over (lines 376–378).

Referee #2 (Remarks to the Author):

Review of "Plate motion drives variability in ocean oxygenation through the Phanerozoic" by Alexandre Pohl et al.

This paper presents a series of simulated ocean benthic oxygen concentrations through time. It is based on the analysis of a large number of simulations integrated with the EMIC cGENIE. The simulations are done for a number of time snapshots, spanning the past 520 million years, taking into account changes in continental configuration. Some of the atmospheric boundary conditions (winds and cloud albedo) are provided by output from the FOAM model, which was also run for each of these time slices, while others are computed within cGENIE. The authors find that the continental arrangement influences ocean circulation and the ventilation of bottom water masses, and therefore benthic oxygen content. Surface oxygen concentrations co-vary with solubility (mostly temperature-driven), and changes in sub-surface oxygen concentrations are mostly driven by export production. In some configurations, the system oscillates between two different circulation states. Another series of experiments was performed where CO2 concentrations were changed through time to correct for changing global temperatures, in an attempt to better isolate the impact of continental configurations. This is an interesting paper. While the main drivers of changes in oxygen at different depths are not a

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surprising or novel result, it is to my knowledge the first study analysing circulation changes, and associated O2 changes, over such a long time span. **I therefore believe that this paper would be of interest for the readership of Nature**.

We agree that our findings are novel and will be of interest to *Nature*'s wide audience.

I have a few suggestions and comments below that I hope the authors and the editor will find helpful.

We thank Referee #2 for their valuable comments, which we address in detail below.

1. Even state-of-the-art high-resolution models underestimate current changes in observed O2 in the ocean. cGENIE is a relatively simple low-resolution model, which is unlikely to perform very well when simulating O2. I do not think that this is a show-stopper, given that **cGENIE-type models are the best tools we have currently for such large and long-term sensitivity studies given our current computing capacities**. But I would suggest to add a data-model comparison for present day to the supplementary material and discuss the shortcomings of this model. In addition, there are a few published model results produced with higher resolution models (that also include O2) for some of the time snapshots presented here. It would be good to add a discussion based on these to the supplementary material, for the time periods available, to show how cGENIE is performing in comparison to other models.

Despite the low spatial resolution of the cGENIE model, it has been shown to perform well in both the Modern and geological past. Specifically: cGENIE manages to reasonably capture the large-scale circulation of the (modern) ocean and with it the distribution of dissolved oxygen. What it does not do well are the sub-regional and local patterns of [O_2], such as upwelling zones on the margins of continents (esp. Southern America and Africa), and patterns of [O_2] associated with monsoonal variability such as the Arabian Sea and inter-annual variability such as the Peru margin. Because the focus of the paper is primarily in respect of the deep ocean and large-scale patterns of [O_2] we have some confidence in the physical plausibility of our paleo projections.

We agree that this point should be made clearer, since ocean [O_2] constitutes the focus of the present contribution. In the revised version of the manuscript, we added a statement in the main text (lines 65–69): "*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)*". This new statement also refers to a new Extended Data Fig. 1, which compares modern (World Ocean Atlas) observations of [O_2] with the 'standard' cGENIE modern continental configuration plus idealized biological export scheme, as well as the 'standard' cGENIE modern continental configuration to which the ecological model as configured in this paper, has been added (see below).

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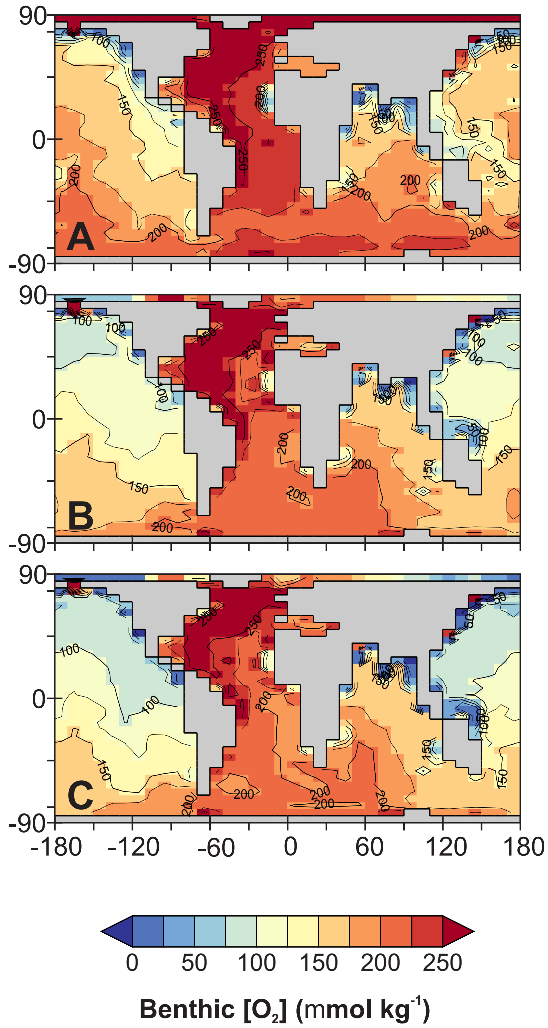

[Added] Extended Data Figure 1: Comparison of modern observations of benthic surface [O_2] with the cGENIE model. (a) Present-day distribution of [O_2] globally at the seafloor, for which we re-grid the World Ocean Atlas 2018[56] data to the modern continental grid of ref.[46] and show the oxygen concentration in the bottom most ocean layer at each model grid point. (b) Benthic [O_2] distribution for the 'standard' modern ocean circulation of ref.[46] 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 and the difficulty to adequately representing the Drake Passage at this resolution. The slightly too-low compared to data, benthic [O_2] values in the North Pacific are an additional consequence of this. (c) Test of the impact of substituting the simplified biological export scheme of ref.[46] with the explicit ecosystem model used here. 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.

We also expanded the model description in the Methods, notably following the Referee's recommendation and comparing the results of the cGENIE model to results obtained with a more complex (CMIP5-class) model (lines 347–350): "*For*

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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".

2. There are many uncertainties in the simulations presented here. One of the most important ones is the crude representation of ocean dynamics in such a low resolution model.

(We direct the reviewer to our response to their first point re. simulating distributions of dissolved oxygen in the ocean.)

There are also important parameters that would impact O2 concentrations for which the parameter space was not evaluated here (e.g., total nutrient content, CO2, O2 in atmosphere, and so on). There are feedbacks that are not included as far as I can tell (e.g., phosphate release by sediments in low oxygen environments, denitrification, etc). I am not saying that these should be included, that would likely not advance our understanding much and just increase the degrees of freedom, and I agree with the approach taken here to analyse just one effect (changing topography). But I would recommend rephrasing some of the statements throughout the paper. The authors need to emphasize that this is a (very valuable!) sensitivity study on ocean circulation changes due to topography changes with a physically simple and coarse resolution model, which can (maybe) give us a rough idea about past O2 concentrations in the ocean. It is certainly not a trustworthy reconstruction of past O2 concentrations.

Referee #2 is perfectly right: we here conduct a sensitivity test to the continental configuration. Additional parameters, such as total nutrient content, are deliberately kept unchanged. As stated by the referee, including such additional parameters would be more confusing than helpful and would distract the reader from our main message, which we believe is strong and new. We also agree that the possible limitations associated with our Earth System modeling should be more clearly stated. We revised the manuscript as follows:

- [Lines 62 and 66] We now clearly state that cGENIE is an "*Earth System Model <u>of intermediate complexity</u>*".
- [Lines 75–84] "*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). <u>We hence are not aiming to reconstruct the Phanerozoic evolution of climate here</u> (see e.g. refs[16,18]), <u>nor provide a detailed reconstruction of past [O_2] in the ocean, but rather, expose the specific impact of changes in continental configuration on gross ocean oxygenation</u>*".
- [Lines 171–174] We added the following statement: "*Further work conducted using higher-resolution Earth system models, e.g. of the Coupled Model Intercomparison Project phase 6, will be important to distinguish robust from model-dependent modes of ocean circulation, although identifying the boundary conditions giving rise to oscillatory modes will be computationally challenging*".
- [Lines 197–204] We added another statement: "*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]. However, our findings provide a very parsimonious explanation to key temporal and spatial trends observed in proxies for ocean [O_2] during the Phanerozoic, notably shedding new light on the possible environmental conditions prevailing in the early Paleozoic*".

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We believe that these changes satisfactorily draw the reader's attention on the limitations of both our model and modeling protocol to provide realistic time-series of ocean oxygen concentrations and re-emphasize that the strength of our modeling study is to specifically quantify, for the first time, the impact of continental changes on ocean [O_2].

3. One of the most interesting results in my opinion is the existence of a threshold that can tip the model into an oscillatory state. **It would be really interesting to see if these simulations could help our understanding on when and why these oscillations occur**. For example, I wonder if the authors could analyse if/how changes in the meridional (or vertical) temperature gradient (between the surface waters in the tropics and the surface waters in deep/bottom water formation regions; or between the surface and bottom waters in the tropics) influence the existence of such a threshold and/or the frequency of the oscillation. Another set of parameters to check would be the diffusion coefficients in the ocean, how does the frequency of these oscillation change when diffusion parameters are changed? Can the authors establish an empirical predictor for oscillations to happen (or not) based on temperature gradients, diffusivity and (maybe) the volume of the ocean basin in question? I think that this would be a very valuable addition. I have to add here that, unfortunately, part of the supplementary files were not submitted, or maybe not fully uploaded. The pdf file states "This file provides additional discussion on the oscillations" and is empty otherwise. Maybe some of my queries were actually already addressed in this file?

This is a very interesting point. Unfortunately, no temporal trend shows up in the equatorial vertical temperature gradient that would permit explaining the specificity of the early Paleozoic.

In order to better explain the model behavior, we took another route: we included in the revised version of the manuscript, results of experiments conducted using idealized continental configurations. These results are shown in our new Extended Data Fig. 10. They are described in the main text on lines 151–158 and more thoroughly in the Methods on lines 412–441. In short, we show that when model boundary conditions are varied (continental configuration and/or global climate state, using pCO_2 as a control parameter), early Paleozoic-like continental configurations show a succession of stable equilibria separated by regimes of stable oscillations. This behavior is described in the light of existing literature on lines 397–411. Because of the complexity of these phenomena, we decided not to include additional details in the present manuscript, but instead designed a dedicated manuscript that we attached to this response for reference and also uploaded and made available on arXiv (https://arxiv.org/abs/2201.07883). An updated version of this manuscript will be submitted to *Climate Dynamics* in the weeks to come. In this manuscript, we explain the mechanisms behind the oscillations and state transitions in ocean circulation using a box model designed specifically to reproduce key features of our cGENIE simulations. This solution permits to include a level of detail in the current manuscript that will be beneficial to *Nature*'s readers, while specific in-depth analyses will be accessible to a subset of specialists in the dedicated paper.

4. The other interesting take home message here are the **changes in deep and bottom water masses over time**. There are time slices where NH deep/bottom water dominates the world oceans and others where SH deep/bottom water dominates. In some configurations, convection in both hemispheres is active (e.g., 260Ma or 440Ma). At some time snapshots, there are semi-enclosed seas that are cut off from the general deep water circulation (300-240Ma). I think that this is a result that will be of interest for readers. Maybe an analysis /table/figure could be added on how (and why) the location of deep water formation sites change over time.

We added Extended Data Fig. 3 (copied below) representing, for each time slice, the meridional overturning stream function and the regions of convection and deep-water formation. This figure is referred to in the caption of Fig. 2, and addressed to the reader who may be interested specifically in the modes of ocean circulation.

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In terms of changes in the locus of deep-water formation through time, we think that our new analysis of the regimes of ocean circulation (Extended Data Fig. 10, lines 151–158 and 396–441), plus submitted manuscript, satisfactorily address that question – see detailed response to previous comment.

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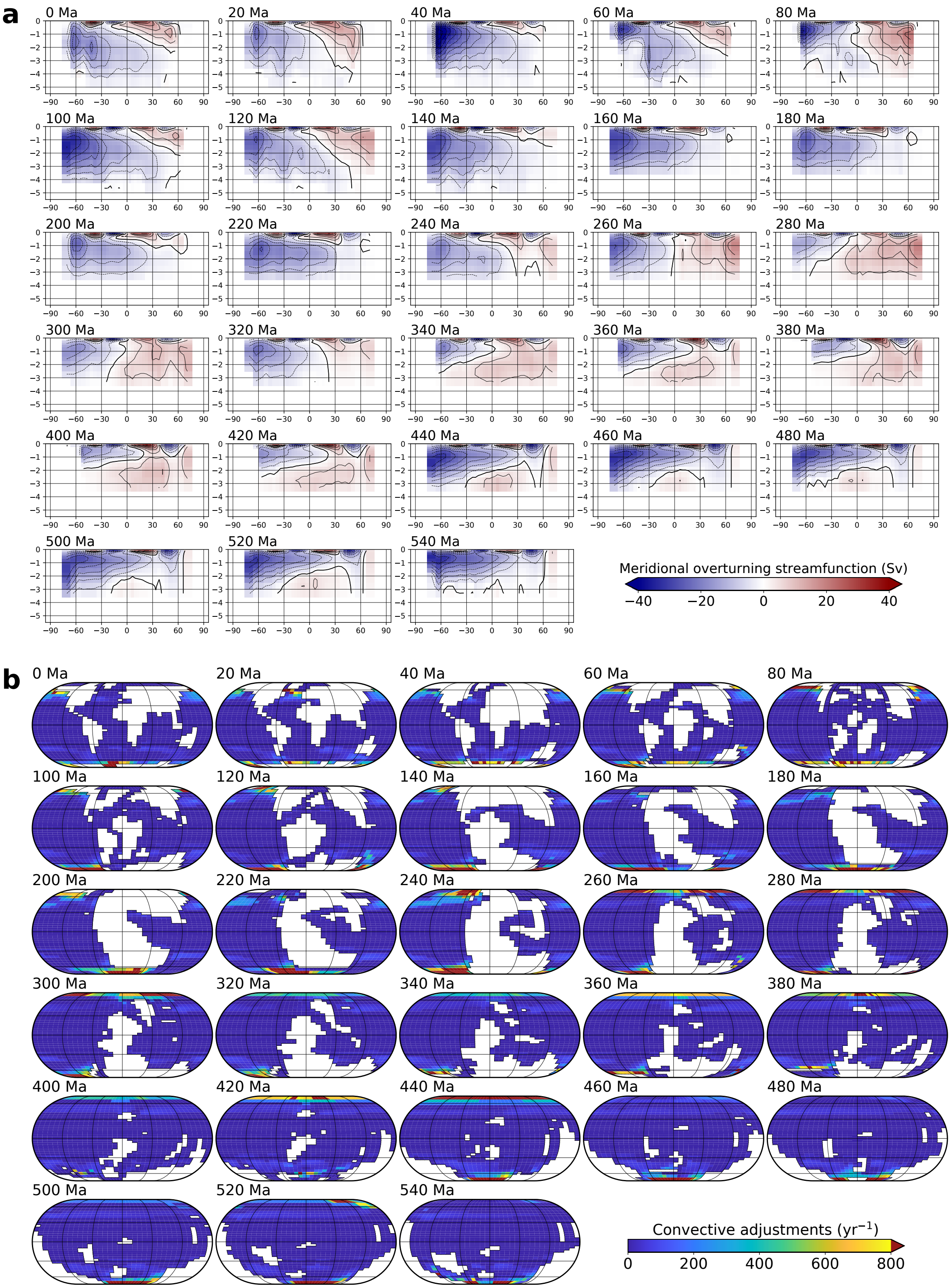
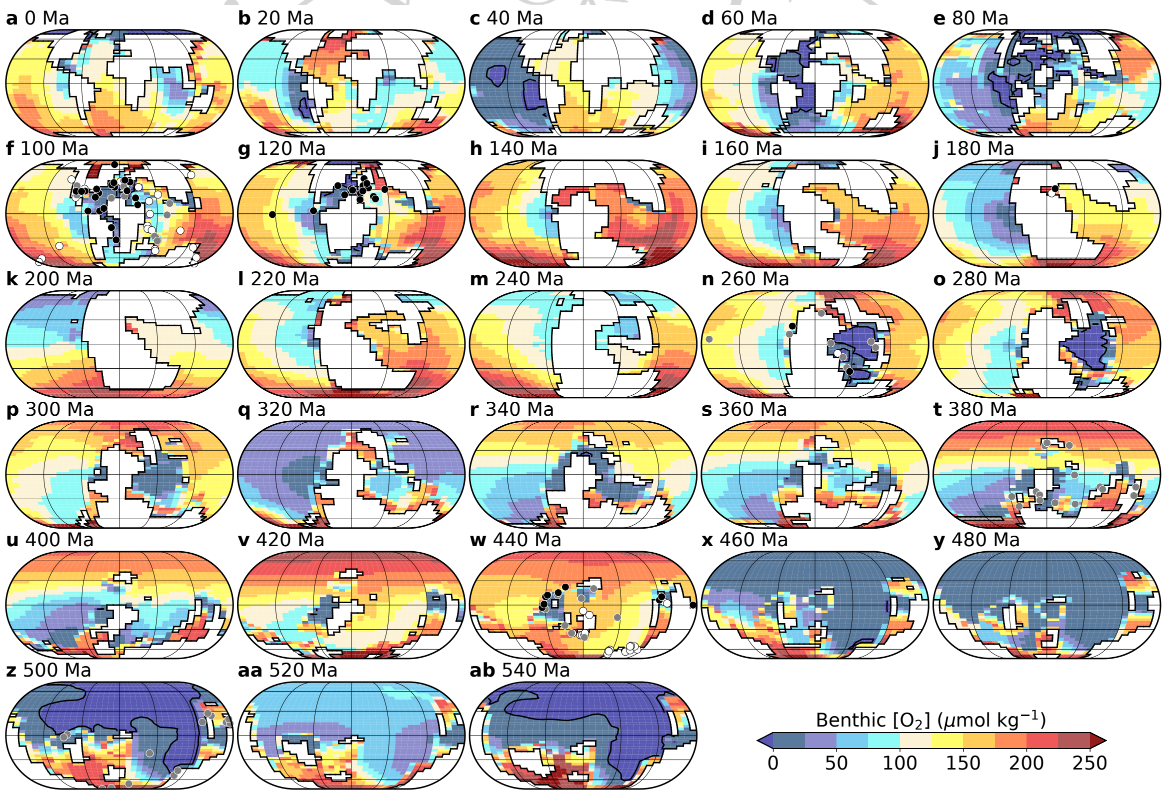


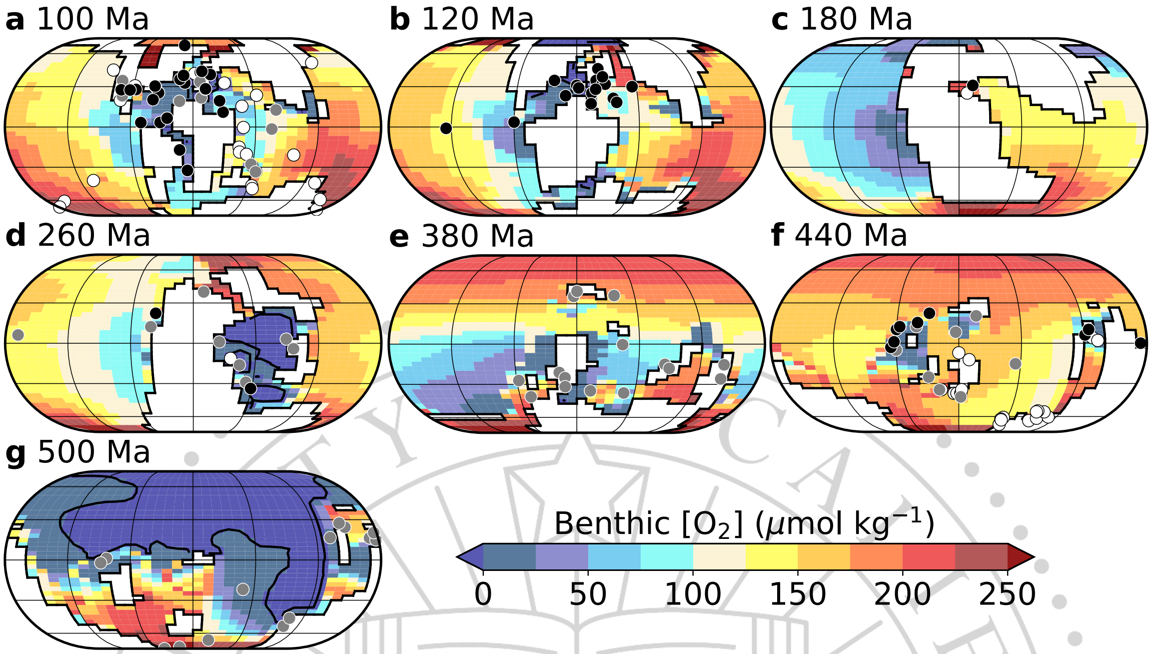
[Added] Extended Data Figure 3: Deep-ocean circulation for simulations at 2240 ppm CO_2 (series #1). (a) Meridional overturning stream function, in Sv (sverdrup, 1 Sv = 10^6 m^3 s^{-1}). A negative (blue) stream function corresponds to an anticlockwise circulation. (b) Annual distribution of convective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

5. Finally, it would be great if some data could be included. For example, simple markers on top of the model results in Figure 2, at times and locations where evidence for anoxia was found in climate archives?

We added 136 data points in Fig. 2 (see below) for key time slices discussed in the main text, based on published literature. For readability, we also replaced former Extended Data Fig. 2 (the content of which is now given in the form of text on lines 361–365) by a new figure providing magnified versions of the 7 panels of Fig. 2 with data points (included below as well).



[Revised] Figure 2. Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (series #1). Eckert IV projection. Emerged continental masses are shaded white. Thick black line delimits the extent of oceanic anoxia, defined as [O_2] ≤ 0 μmol kg^{-1}. Results are averaged over the last 5000 years. Black (white) dots represent anoxic (oxic) conditions and grey points represent possible or intermittent anoxia, for 100 Ma after ref.[28], for 120 Ma after ref.[27], for 180 Ma after ref.[30], for 260 Ma after ref.[26], for 380 and 500 Ma after ref.[47], and for 440 Ma after ref.[48]. See Extended Data Fig. 2 for magnified versions of the 7 panels with data points and Extended Data Fig. 3 for the meridional overturning circulation and regions of deep-water formation.



[Added] Extended Data Figure 2: Magnified version of the 7 panels of Fig. 2 that include data points. Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (series #1). Eckert IV projection. Emerged continental masses are shaded white. Thick black line delimits the extent of oceanic anoxia, defined as $[O_2] \leq 0$ µmol kg^{-1}. Results are averaged over the last 5000 years. Black (white) dots represent anoxic (oxic) conditions and grey points represent possible or intermittent anoxia, for 100 Ma after ref.[28], for 120 Ma after ref.[27], for 180 Ma after ref.[30], for 260 Ma after ref.[26], for 380 and 500 Ma after ref.[47], and for 440 Ma after ref.[48].

In summary, this is an interesting paper that I would support to be published after some level of revision taking my comments above into account.

We thank Referee #2 for their valuable inputs which, we believe, were successfully addressed in the revised version of the manuscript and significantly strengthened our study.

Referee #3 (Remarks to the Author):

A. Summary of the key results

The manuscript by Pohl et al. uses numerical experiments to argue that the configuration of continents and ocean basins during the Phanerozoic strongly controls ocean oxygenation. This highlights that tectonics drives many fundamental life support systems on our planet, and can help explain some extinctions and anoxic events that are captured by the geological record.

B. Originality and significance: if not novel, please include reference

Many papers have been published that make use of ocean and atmospheric circulation models, and even those linked to

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biogeochemical cycling. However, **this is the first time I have seen it applied to systematically testing the influence of continental arrangements in the Phanerozoic on the oxygenation of the oceans.**

This is indeed the first study applying spatially resolved Earth System Models to quantify the impact of continental arrangements on ocean oxygenation over the whole Phanerozoic.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The approach presented here is world-leading, but I do have some queries that would improve the manuscript.

We thank Referee #3 for both acknowledging the world-leading methodology employed and providing constructive comments permitting to improve our manuscript. We address them in detail hereafter.

First, I get a sense that paleo-topography, and particularly orogens, were not included in the FOAM simulations. If that is correct, then why was this the case? Can the authors run one or two experiments with orogens (say during Pangea time) and compare their results? Surely that would affect the wind speeds and key inputs for the cGENIE model. I can only see the paleo-bathymetries being used, and all land being assigned a value of 0 km.

Topography on land was accounted for in our FOAM simulations and derived cGENIE forcing fields. We agree that this point should me made clearer, which we did in the revised manuscript (lines 371–373): *"Importantly, the FOAM ocean-atmosphere simulations (and derived cGENIE forcing fields) account for topography on land, after ref.[24] (although topography is not shown in our maps for readability)"*.

Second, although the cGENIE code is available, the key code (FOAM) and associated files that seems to drive ocean and atmosphere circulation is not available to the community. For a Nature paper, I would expect a higher level of code and data availability. And importantly - it would further increase the impact of the manuscript, as others can build on these experiments.

Although we are engaged in open-access science – for instance the cGENIE code being open-access along with every single model experiment being reproducible – we are also mindful that not every model code is fully open-access (e.g. the UK MetOffice climate model code that is widely used and published with is the property of the UK Ministry of Defense). The code of the FOAM model is the property of Rob Jacob (Argonne National Laboratory), nor ours, and we are consequently not allowed to make it publicly available. However, Rob Jacob does plan to upload his code on GitHub. In a recent email (personal communication dated of November 18th, 2021), he explained that he delayed things because he wants to preserve the change history which will require some thought about how to use svn2git on FOAM's old CVS repository. We are thus confident that the FOAM model code will be publicly available in the near future.

In the meantime, and in an effort to make our work fully reproducible in response to the Referee's request, we have uploaded all FOAM output files on Zenodo: https://zenodo.org/record/5780097#.Ybi68RPMKCc, and added a link in the Code Availability section (lines 475–476): "*The FOAM output is hosted on Zenodo (DOI: 10.5281/zenodo.5780096)*".

L304: How was the Mueller et al and the Scotese and Wright paleobathymetry merged? They have different absolute reference frames, and relative plate configurations. I realise that the resolution of these climate models is not very high, but it would be useful to show what the merged bathymetry looked like.

We merged the Müller et al.[10] and Scotese and Wright[9] reconstructions in order to (1) substitute the flat deep-ocean bathymetry of Scotese and Wright[9] with a more realistic reconstruction, and subsequently (2) quantify the uncertainty in our simulations resulting from the poorly constrained deep-time (pre-140 Ma) bathymetry (which turns out to be of second order). The merging itself was straightforward; we replaced the deep-ocean information provided by Scotese and Wright[9] with the one provided by Müller et al.[10] for the same time slice. As illustrated in Fig. R1, both reconstructions match very well at first order. We are confident that this method is largely sufficient considering our model resolution (as stated by the Referee). Extended Data Fig. 7 compares the flat-bottomed and more realistic (i.e., merged) bathymetric reconstructions interpolated onto the cGENIE model grid.

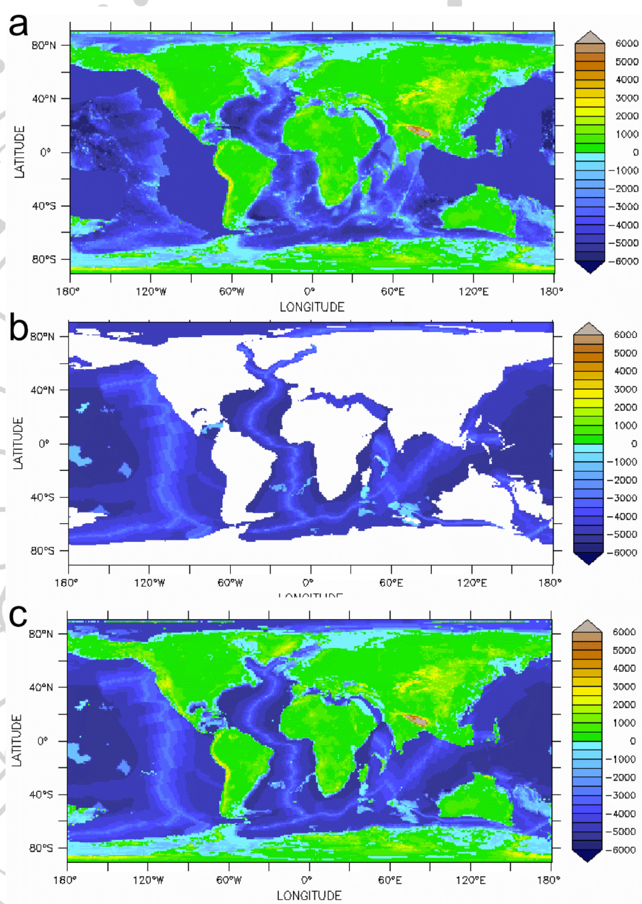

Figure R1: Illustration (for 40 Ma) of the merging of the Scotese and Wright[9] reconstruction (a) with the Müller et al.[10] ocean bathymetry (b); the merged field is shown in panel (c). All maps shown at a resolution of 1 degree. Lower-resolution maps were provided to FOAM and cGENIE to match the respective model resolutions.

L307: Why and how was the solar luminosity value 1368 W m-2 and CO2 2240 ppm value chosen? Was that to ensure that the SST in Extended Data Fig 7 was realistic? Would the results/conclusions change, say if the CO2 value was 1000, or even 500 ppm?

Yes, we chose those forcing levels to ensure that simulated climate is in the right order of magnitude compared to Phanerozoic proxy data (lines 361–365). And Referee #3 is right, our regimes of ocean circulation are climate state-dependent. Simulations run at very different pCO_2 levels would give different results for several time slices. This is a point

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that we now emphasize: we added a new Extended Data Fig. 9 showing results of simulations conducted at 1120 ppm (instead of 2240 ppm in experiment series #1) and insist on the climate state-dependence of our results on lines 149–151: "*Of course, the differences in the two simulation series illustrate that the climate state also influences the ocean circulation regimes (contrast Figs. 1 and 3; see also Extended Data Figs. 8 and 9)*".

However, we want to flag here that our simulations have no pretention to provide a "realistic" chronicle of Phanerozoic climate and ocean [O_2], which is intrinsically impossible since we kept our boundary conditions constant in order to provide a sensitivity test top the continental configuration (see lines 75–84). The strength of our work consists in (1) quantifying the impact of continental rearrangement on ocean [O_2], which is new and important, and (2) discussing the consequences for Phanerozoic proxy data interpretation. In the revised version of the manuscript, we emphasize the latter point on lines 197–204: "*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]. However, our findings provide a very parsimonious explanation to key temporal and spatial trends observed in proxies for ocean [O_2] during the Phanerozoic, notably shedding new light on the possible environmental conditions prevailing in the early Paleozoic.*".

L316: I can see that the cGENIE code is open source, but I cannot see anywhere that would enable someone to reproduce the ocean and atmospheric circulation presented here. Given the fact that this component is critical in reproducing the results, the fact that this code is not available to the community makes it hard to interrogate and test these results.

We do care a lot about open data and results reproducibility. The cGENIE model code is fully open source, and associated with this manuscript we have provided all the parameter value and boundary conditions files and run-time information needed to repeat the experiments. We included here a fairly standard 'code availability' statement which we assumed was sufficiently detailed given typical publication space constraints, but are very open to suggestions for improvement:

- "*The version of the code used in this paper is tagged as release v0.9.29 and has a DOI: 10.5281/zenodo.5885685*": the whole model code can be searched on Zenodo and downloaded (here: https://zenodo.org/record/5885685#.YepxdvXMLu4).
- "*A manual describing code installation, basic model configuration, and an extensive series of tutorials is provided (DOI: 10.5281/zenodo.5500696)*": anyone downloading the model code will then find all instructions required to install and use the model in a 400-page tutorial (https://zenodo.org/record/5500696#.YZJ5qr3MLu4).
- "*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*": once the model code downloaded and installed (see above), any user can repeat any experiment shown in the paper by simply copying the appropriate command line found in the readme.txt file provided with the model distribution. Here is a portion of the readme.txt file illustrating the instructions necessary to reproduce all the results:

```
################################################################
### readme.txt ##################################################
################################################################

For: 'Continental configuration drives variability in ocean oxygenation through the Phanerozoic'

Alexandre POHL1,2*, Andy RIDGWELL1*, Richard G. STOCKEY3, Christophe THOMAZO2, Andrew KEANE4, Emmanuelle VENNIN2, Christopher R. SCOTESE5
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2Biogéosciences, UMR 6282, UBFC/CNRS, Université Bourgogne Franche-Comté, 6 boulevard Gabriel, F-21000 Dijon, France
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5Department of Earth and Planetary Sciences, Northwestern University, Evanston, Illinois 60208, USA
*These authors contributed equally to this work

```
##################################################################
18/06/2020 -- README.txt file creation (A.P.)
18/06/2020 -- added files
15/12/2021 -- updated readme.txt and added files for series E to H
19/01/2022 -- edited to reflect new genie-userconfigs directory
20/01/2022 -- added modern oxygenation experiments
##################################################################
```

Provided are the configuration files necessary to run:
A] series #1 (i.e., all runs at 2240 ppm)
B] series #2 (i.e., like series #1 but pCO2 varied so as to approximately 'correct' for the tectonic impacts on climate)
C] like series #1 but with no dependence of remineralization on temperature
D] like series #1 but with a flat bottom, [0-140] Ma only
E] like series #1 but at 1120 ppm
F] 460 Ma and 440 Ma like series #1 but using Torsvik's BugPlates continental reconstructions
G] Drake world simulations shown in Extended Data Fig. 10
H] Ridge world simulations shown in Extended Data Fig. 10
I] present-day oxygenation experiment shown in Extended Data Figure 1:
1st experiment -- present-day ocean circulation and marine productivity of Cao et al. [2009], as shown in panel (b)
2nd experiment -- present-day ocean circulation of Cao et al. [2009] but with ecological model used in the Phanerozoic experiment, as shown in panel (c)
J] present-day ocean circulation (Cao et al. [2009]) ventillation age tracer experiment (not shown in paper)

All experiments are run from: $HOME/cgenie.muffin/genie-main
(unless a different installation directory has been used)

Remark: Phanerozoic continental configurations are not intended, and should not be used to conduct 'realistic' simulations.
Indeed, boundary conditions used in FOAM, including solar luminosity and pCO2, were designed for a simple sensitivity test to the continental configuration.
The resulting, inadapted albedo values and latitudinal temperature gradients prevent the use of these GENIE base configurations for paleo investigations beyond this very specific application.

Remark 2: Drake- and ridge- world configurations are just the ones provided in the standard model distribution, plus age tracers

```
################ A] series #1 ################

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################ B] series #2 ################
```

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… … … [readme files continues] … … …

Please note that the revised manuscript also provides a link to the raw FOAM output (see Code Availability statement, https://zenodo.org/record/5780097#.YbjBNBPMKCc).

Maybe I cannot see the different shades of blue, but I cannot distinguish any variation in the paleobathymetry in the deeper oceans, even in more "recent" geological times.

Although we were very mindful of how different people may perceive different colors, we admit that in this case the particular shades of blue chosen were indeed not optimal. We changed the colormap in Extended Data Fig. 7 to increase the contrast (see Fig. R2).

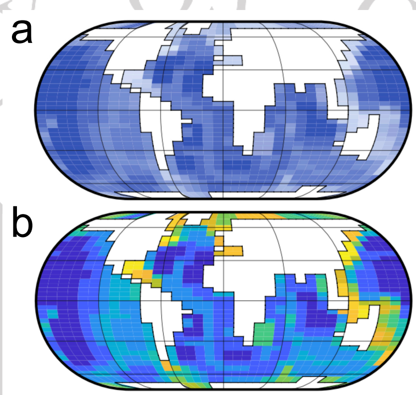

Figure R2: Original (a) and revised (b) first panel of Extended Data Fig. 7 (for 0 Ma). Note the different color scale, leading to a stronger contrast in panel (b).

I am confused about the equal-area grid. I see that the cells in Extended Fig 3 are not equal area – how were these resampled? Does cGENIE and also FOAM have a "regular" geographic grid or does it use an equal area grid?

The model description section of the Methods effectively states that cGENIE uses an equal-area grid, which it does. In previous Extended Data Fig. 3 (now Extended Data Fig. 7, see Fig. R2 above), all cells are displayed with the same size because we use an equal-area map projection. The projection name is now stated in all figure captions, where appropriate.

D. Appropriate use of statistics and treatment of uncertainties

Figure 1e is really hard to interpret. Can you provide some explanatory text (even if it is in the Extended Data)?

We added a new section the Methods:

*"**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

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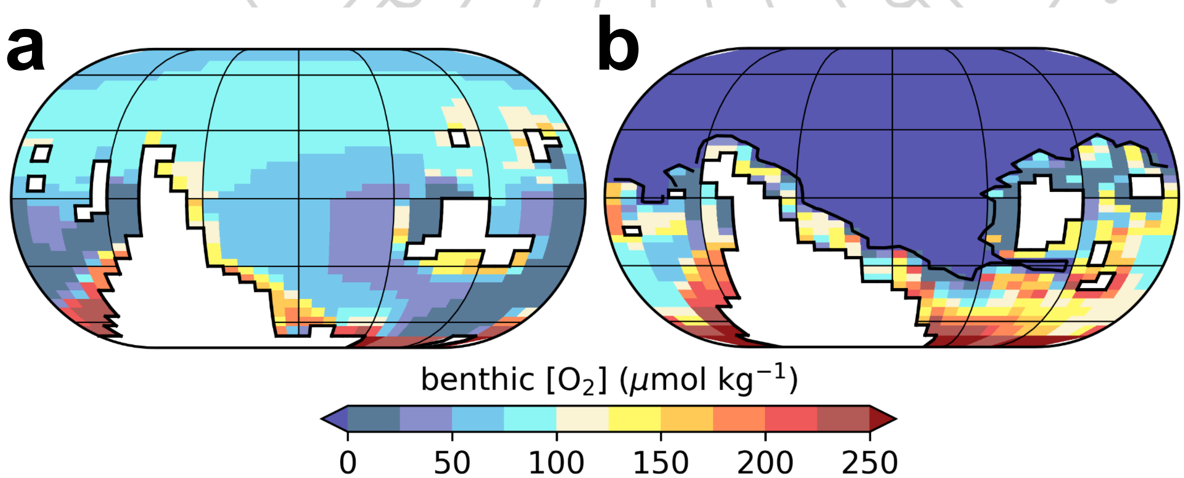
production (‘export’; i.e., the flux of organic carbon produced in the ocean photic zone by primary producers that is not recycled (remineralised) before sinking deeper in the water column) and total ocean area. The PCA was conducted using the ‘PCA’ function of the R package ‘FactoMineR’[53] and the 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”.

Extended Data Fig 1 – what is “Export”? Explain for a novice reader.

We added a definition of export production in the Methods (see underlined text in the paragraph regarding the PCA, just above).

Uncertainties are provided, but I would like to see some more discussion what would happen if a different tectonic reconstruction was applied? For example, the Torsvik et al. paleomagnetic reference frames would be very different, and they also have different continental arrangements. It would be useful for the authors to show several key timestep comparisons on the role of specifying a particular plate reconstruction.

We thank Referee #3 for this interesting suggestion. Considering another set of continental reconstructions represents a very significant amount of work, because that implies building new basemaps, running the FOAM GCM and then deriving GENIE configurations and running the model for 20 kyrs. In order to address the referee’s concerns, we therefore focused on the key, step change in ocean oxygenation simulated between 460 Ma and 440 Ma in our first series of experiments (Figs. 1 and 2). We repeated these two experiments using the alternative continental reconstructions of Torsvik (position of land masses after ref.[11], topography and bathymetry after ref.[12]). We ran FOAM and GENIE simulations using exactly the same boundary conditions as in our series #1. Results are shown in Extended Data Fig. 4 (copied below). These additional experiments show that the step change in ocean oxygenation simulated between 460 and 440 Ma is relatively robust when the continental configuration is varied in the model, which is now stated on lines 124–126: “*The step change in benthic oxygenation simulated between 460 Ma and 440 Ma is similarly observed using an alternative set of continental reconstructions*[31] *(Extended Data Fig. 4)*”. We believe that this addition significantly strengthened our manuscript.



[Added] Extended Data Figure 4: Benthic oxygen concentrations for simulations at 2240 ppm CO_2 (like series #1) at 440 Ma (a) and 460 Ma (b), using the continental reconstructions of BugPlates[31], with topography/bathymetry after ref.[57]. Eckert IV projection. Emerged continental masses are shaded white. Thick black line delimits the extent of oceanic anoxia, defined as $[O_2] \leq 0$ µmol kg^{-1}. Results are averaged over the last 5000 years. Panels (a) and (b) are identical to panels (w) and (x) of Fig. 2 except that simulations have been conducted using another continental reconstruction.

E. Conclusions: robustness, validity, reliability

See comments above.

F. Suggested improvements: experiments, data for possible revision

See comments above.

One other point is that the title talks about plate motions, but in fact these are just static arrangements of continents. Plate motions infers some kinematics, which are at best, implicit. Perhaps a title "Continental arrangements drive variability in ocean oxygenation through the Phanerozoic" would be more suited.

We agree and replaced '*plate motion*' with '*continental configuration*'.

G. References: appropriate credit to previous work?

References are appropriate.

Thank you.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The text is clear, and the manuscript is direct and succinct.

Thank you.

Referee #4 (Remarks to the Author):

Review

A.
This manuscript sets out to explore theoretical models for how the continental configuration (plate motions) on Earth has affected ocean circulation patterns and the transport of O2 to the deep abyssal oceans in the past 550 million years. The study finds that even if climate and atmospheric O2 had been invariant, benthic O2 level in the abyssal ocean would have varied dramatically in concert with rates of ocean ventilation and plate configuration.

B. Importantly, the study finds that ocean circulation was in a state where downwelling fluxes of water and O2 to the deep

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abyssal ocean was limited in the early Paleozoic and during major oceanic anoxic events. This connection provides an alternative explanation for widespread anoxia in the oceans at these times, where poor ocean ventilation drives deep ocean deoxygenation. By implication, neither ocean temperature (climate) giving lower O2 solubility in the surface ocean nor low atmospheric pO2 are necessary factors to drive anoxia in the abyssal oceans (although these factors might have mattered too). It is intriguing to see that the model predicts that deep oceans were more prone to deoxygenation by slower ocean circulation at time in the Phanerozoic when major oceanic anoxic events occurred and during the early Paleozoic were anoxia prevailed in the oceans.

C. The authors utilizes **a well calibrated 3D model for the atmosphere-ocean circulation dynamics (c-GENIE)**, coupled with a new carbon export model.

D. Sensitivity tests were performed to distinguish the driving factor for benthic O2 change.

We thank Referee #4 for this accurate summary of our work.

E. My main concern goes to the significance of the oscillating circulation modes in the early Paleozoic, which appears as an explanation for the pervasive anoxic oceans at this time. Although, the Early Paleozoic oscillations are intriguing and the period of oscillations are striking given recent observations that ocean redox conditions might have fluctuated on a ~kyr time scale, the main focus should be on the unstable steady state and why it allows for pervasive anoxic deep oceans. The oscillations appears to be of second order importance. So – why are the benthic O2 levels always far lower >440 Ma compared to <420 Ma? If this transition was driven by plate motion, why is this transition only seen to occur one time in history?

We think that part of the Referee's concern comes from the explanations that we provided in the original manuscript, which were maybe a little misleading: the oscillations themselves do not actually explain the poorly oxygenated early Paleozoic. State transitions in the global ocean circulation do. This is a point that we have now made significantly clearer in the revised version of the manuscript, on lines 140–158 and 412–441, using also our new Extended Data Fig. 10. Using theoretical continental configurations, and notably a Drake world with a strip of land extending from the North Pole to the Southern Hemisphere mid latitudes – a configuration that captures the main characteristics of the early Paleozoic land-sea mask – we demonstrate the existence of several stable equilibria and sets of stable oscillatory regimes. Extended Data Fig. 10 reveals that the opposite stable equilibria with deep waters mainly forming at one of the poles lead to high seafloor [O_2], while the intermediate equilibrium and regimes of stable oscillations are characterized by much lower seafloor [O_2]. This observation explains why early Paleozoic simulations show a poorly seafloor oxygenation. The underlying physical mechanisms are investigated and described in detail in a dedicated manuscript that we are about to submit and have already made available on arXiv (https://arxiv.org/abs/2201.07883), which uses a box model to reproduce key characteristics of our cGENIE simulations in a simplified and synthetic manner. We also revised the abstract (lines 28–30) to read: "*We further identify the presence of state transitions in the global ocean circulation, which lead to extensive deep-ocean anoxia in the early Phanerozoic under pO_2 levels as high as modern*".

Regarding the Referee's second point – the Paleozoic transition occurs in response to continental rearrangement. Extended Data Fig. 10 suggests that a pole free of land, allowing a strong circumpolar current, is required to trigger these state transitions and to permit the existence of the poorly oxygenated state (compare the blue and black lines, which represent the Drake world and ridge world configurations). Therefore, the northward drift of the low-latitude landmasses during the Ordovician and Silurian[13] must permit crossing a threshold in the land-sea mask / a tipping-point making the system mainly resilient to state transitions afterwards. Noteworthily – the position of this step change in seafloor oxygenation seems to be relatively robust when global climate is moderately varied (see experiment series #2) and when

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the continental reconstructions is varied (see Extended Data Fig. 4).

Secondly, when discussion the oscillations, the manuscript lacks figures to show the distinct ocean circulation states. The bifurcation is only vaguely described by referring to "bistable states happen" (in other situations, refering to meridional overturn in the Atlantic driven by climate change). This is an analogue argument an invalid expanation. I recommend the author produce **a sketch (i.e. with ocean transects)** that shows the major ocean currents fluxes in the two extreme states. Where exactly is the downwelling reduced (high latitudes, I presume) and how much – what dictates the period of oscillations, etc? Are both extrema conducive to abyssal anoxia and why?

We are grateful for this interesting suggestion. We designed our new Extended Data Fig. 10 in response to the Referee's comment. This new figure is no simple sketch, this is a synthesis of many simulations conducted using theoretical continental configurations. For each continental configuration (Drake and ridge world), we conducted simulations at various CO_2 levels and plotted the range of seafloor [O_2] values (Extended Data Fig. 10a) and also the meridional overturning stream function and maps of seafloor ventilation age (Extended Data Fig. 10b). Finally, we also propose a tentative comparison with the previous latest Ordovician simulations of ref.[14] (Extended Data Fig. 10c). This new figure is described on lines 152–158 and 412–441. We are confident that these important additions satisfactorily address the reviewer's request. In addition, an in-depth analysis of the mechanisms at play (going beyond this manuscript's objectives and *Nature*'s broad readership interests) is provided in a dedicated manuscript that is attached in the resubmission.

Regarding the Reviewer's specific questions:

- "what dictates the period of oscillations?": Analyses conducted using both cGENIE and the box model suggest that the period of the oscillations is a function of the strength of the circumpolar current. This conclusion was reached by varying the zonal wind stress over the Drake passage in our Drake World experiments of Extended Data Fig. 10, and similar conclusion was reached by varying the 'delay' term in the box model. We are finalizing these analyses. The latter are consequently not included in the manuscript focusing on the box modeling attached in the resubmission (and uploaded on arXiv), but we will include a dedicated section in the version of the manuscript that we are about to submit to *Climate Dynamics*.
- "Are both extrema conducive to abyssal anoxia and why?": As shown in Extended Data Fig. 10, both oscillation extrema are not conducive to abyssal anoxia. Indeed, ocean circulation regimes during stable oscillations maxima correspond to the ones of the surrounding stable steady-states. Stable steady states labeled #1 and #5 in Extended Data Fig. 10 are characterized by well-oxygenated conditions while stable steady state labeled #3 is poorly oxygenated. Therefore, each family of oscillations (labels #2 and #4) has two extrema characterized by well- and poorly-oxygenated conditions, respectively (Extended Data Fig. 10a).

Overall, **the modeling result presented here is important, and there are potential important implications for understanding the expansion of marine dead zones and animal extinctions in the past**. Thus, I find the results could be interesting for the broader scientific community. For a theoretical study, however, I believe the mechanistic details of the process that has governed downwelling fluxes is not sufficiently well explained.

We have added a significant amount of details on the processes leading to changes in modes of ocean circulation in response to the two previous comments and comments by the other referees (Referee #2 in particular) to help address this.

Other comments

1- Correlating poor ocean ventilation to OAEs:

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The authors argue that the Triassic oceans was prone to anoxia by plate configuration, but anoxia prevailed in the Paleotethys ocean from 251 to 245 Ma, and should then appear in the 240 Ma simulation (not only in the 260 Ma case).

We admit that our wording was misleading here. We here refer to the Permian-Triassic transition, not specifically to the early Triassic. This time resolution lies far beyond the 20-Myr timestep used here for the purpose of our systematic exploration covering the whole Phanerozoic. We replaced '*in the early Triassic*' with '*during the Permian-Triassic transition*' on lines 104–105, and now refer to the recent work by Hülse et al.[6]. Regarding the age itself, we here use the 260 Ma configuration because it is the continental arrangement of our dataset that is the closest to the one use for previous investigations, by Meyer et al.[15] and Hülse et al.[6]. It is also the closest temporal match with the Permian-Triassic boundary, estimated at 251.9 after the International Chronostratigraphic Chart v2021/10.

2 – Line 104ff. Plate configuration is not necessarily causing the OAEs, but just making the system more prone to OAEs. Therefore, you should state that maybe these OAEs were triggered by larger perturbation now that paleocontinental configuration apparently were not assisting OAEs at those times.

Agreed. This is what we originally wanted to convey with "*or simply a consequence of a too-cold climate state and/or an insufficient nutrient inventory*". In the revised version of the manuscript, we expanded this point to make the message clearer in response to Referee #4's comment (lines 109–112):

"It could 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.".

3 – L118ff. The opening of this paragraph is confusing, because the purpose of this sensitivity test is well explained. You should state that you run a sensitivity model where you keep surface O2 constant to see that it is the downwelling flux and not the O2 load that causes benthic deoxygenation. This would be clear if you changed the sentence from "leaving mean global SST…" to "in order to keep surface ocean oxygenation largely invariant" or so. How you manipulated pCO2 to keep SST and O2 solubility largely constant is of secondary importance to the reader and should be stated after. Also, conclude this paragraph by stating that this means that O2 load in downwelling waters will then be invariant, and so it is the water flux to the benthos that varies as a result of ocean circulation (continental configuration). This will make it clearer why you have done this sensitivity analysis.

Referee #4 makes a very good point here. The paragraph needed clarification. We rephrased as follows (lines 127–135):

"To further simplify the attribution of causes of benthic [O_2] variability through the Phanerozoic and eliminate global climate change <u>and resulting solubility-driven upper-ocean [O_2] variations as explanatory factors</u>, we carried out a second series of model experiments (#2) <u>in which we kept (mean global SST and) surface oxygenation largely invariant</u> (Fig. 3). <u>Climate detrending was achieved by varying pCO_2 in the model</u>. Variance in mean benthic [O_2] (Fig. 3d) is now if anything, even greater than in #1 (Fig. 1d) <u>and the general trend of a poorly oxygenated early Paleozoic deep ocean still stands. These results confirm that benthic anoxia in the early Paleozoic ocean results from changes in the deep-ocean circulation in the model, rather than temperature-driven variations in upper-ocean [O_2]</u>".

4 – Fig. 3d. When looking at predicted benthic water ages. It would be good to state how it **compares to the modern ocean** (I guess benthic water age, on average, is equal to ~half the ocean mixing time (~1500 yr; Gruber & Sarmiento 2006), so it looks about right?

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We have revised the caption of Fig. 1 to read: "*For comparison, the present-day value is ~1050 years in the standard Modern cGENIE simulations of ref.[46]*".

5 – L141. What is the physical consequence of passing this bifurcation point? What does it mean that "oscillations happens". I guess you refer to oscillating circulation patterns, but this could be clearer. A figure with the two modes of ocean circulation should be shown. Ideally, you should provide plots with streamlines (+ fluxes of the important ocean currents) in **ocean transects**. Then, explain where and why the water flux to the abyssal ocean is slower?

We significantly expanded the analysis of the state transitions in the large-scale ocean circulation, and included a figure corresponding to the Referee's recommendation. Please see our previous response to comment E.

6– L173. Poor referencing (35). There are much better redox constraints on the global ocean than from element concentrations in single pyrite minerals. Refer to global ocean redox proxies (Wallace et al. 2017, Dahl et al. 2010) and larger statistical comparison of local redox proxies (Sperling et al. 2018).

We deleted previous reference #35. Dahl et al. (2010) (ref.[16]) was already included in the previous version of the manuscript. Was added a reference to Sperling et al. (2021) (ref.[17]) (better adapted that Sperling et al. (2018), ref.[18]).

7– (Minor comment) I find the choice of the Figure 2 color scheme for benthic O2 counterintuitive. I would have expected red colors to represent anoxia (alarming conditions!) and blue colors "fresher" water.

We here represent [O_2] concentrations, which can be low (blue) or high (red), not anoxia per se. We think that using blue and red for respectively small and large values is standard. Considering that (1) we prefer the current color scheme, (2) only one out of the four referees questioned this choice and (3) Referee #4 considers this as a minor point, we kept the color scheme unchanged in the revised version.

PS. The file "409907_0_additional_review_material_3745335_qzkmk5.pdf" is corrupted and was therefore not reviewed

We included two Supplementary Information files: a first one containing the information itself, and another one describing the content ("*This file provides additional discussion on the oscillations*"). We are sorry that this file structure confused the Referees and will make sure to be clearer during resubmission.

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

I have read the revised manuscript and the authors' response letter. The authors have addressed my comments to my satisfaction.

Referee #2 (Remarks to the Author):

The authors have addressed all of the comments I raised in my first review. I only have minor suggestions this time (see below) and am happy to recommend publication once my last comments have been taken into account.

• It looks like GENIE forms northern hemispheric deep water in the Pacific and not in the Atlantic at 0 Ma (Extended Figure 3, 0 Ma); however the simulated O2 patterns shown in extended Figure 1 must have been extracted from a simulation forming NADW and not NPDW. I think that a short comment in the main text might be warranted.

• Don't we have any O2 proxies for time slices younger than 100 Ma? Why weren't they included?

• I really like Extended Figure 10. I think that there is a lot of necessary information in that figure. Thank you for adding it. I wonder if it can be somehow included in the main paper? Either way, can you please add titles on top of each column in the subpanels b and c (e.g., "streamfunction", "ventilation age", etc)?

• Oxygen figures: I am surprised I did not catch that earlier, but how can O2 be negative in your simulations? I guess there is no denitrification and respiration only gets cut off once O2 hits 0, therefore allowing for slightly negative values that then can get transported around? It might be good to add a sentence about this to explain to readers who are not familiar with models?

All the lines in the comments below are corresponding to the track-changed pdf.

• Please change line 33 to "a causal mechanism that *might* explain..".
• Line 98: remove "detailed"
• Line 103 and following: doesn't the position of the landmasses influence climate too?
• Line 125: "ocean deoxygenation develop" – maybe specify "benthic"?
• Lines 126/127 – twice "central Atlantic"? Please fix.
• Lines 157/158: for someone reading quickly this sentence can be misunderstood ("notions of past warm oceans necessarily…"). I would add a clear statement here that past oceans low on oxygen were likely stagnant or poorly ventilated – which is the main take-home message of the paper… i.e.

not all warm oceans were necessarily stagnant but all oxygen-deprived oceans were likely stagnant.
• Line 164: the brackets are not needed
• Line 263: change “is” to “could have been” (“could have been a consequence of continental rearrangement”)
• Line 664: “benthic surface O2”? Please fix.

Referee #3 (Remarks to the Author):

A. The manuscript by Pohl et al. uses numerical experiments to demonstrate that the configuration of continents and ocean basins
during the Phanerozoic strongly controls ocean oxygenation. This highlights that tectonics drives many fundamental life
support systems on our planet, and can help explain some extinctions and anoxic events that are captured by the geological
record. This is a very important contribution to our field, and I would like to congratulate the team for putting together such an impactful and clear study.
B. This is a very novel study, and meets the high standard of Nature papers.
C. The data and methodology has been improved and made more accessible, and now meets the high standards of Nature papers.
D. The manuscript uses a robust level of statistics and analysis, and the supplement demonstrates the author's hard work in exploring some of the key uncertainties.
E. The conclusions are well-supported by the data and models.
F. All of my concerns were addressed in the review, and I thank the authors for their meticulous work in improving the manuscript.
G. References are appropriate
H. The text remains very clear and precise, meeting the standard of Nature papers.

Referee #4 (Remarks to the Author):

The authors have greatly improved the manuscript in their revisions. The manuscript no longer reads only as a mathematical exercise exploring one Earth system model of intermediate complexity, it reads more as a contribution to improve our understanding ocean physics (and chemistry).

Specifically, it is now clear that water residence time is related to the decoupling of benthic and surface O2 levels (e.g. Fig. 3). Periods with widespread anoxia could be linked to slower downwelling at high latitudes and longer water residence times.

I must say that I'm amazed to see that a subtle difference in continental configuration between 460 and 440 Ma (Extended Figure 4) can be sufficient to dramatically amplify ocean circulation (i.e. halving the benthic water age: 1200 yr -> 600 yr) and oxygenate the deep ocean floor. The authors argue that bistability between deep-ocean circulation states occur in the cGENIE world, and while that may explain the amplification of subtle changes in ocean shape, I cannot judge whether this is reflects robust or model-dependent modes of ocean circulation.

I do find it a bit strange that the model reported in fig 3 does not give the right value for the modern ocean (1050 yr), but a value closer to 700 yr. A comment on this difference in the caption would be appropriate.

Also, I read from the extended Figure 9 that Cambrian deep anoxia depends on high $pCO_2 > 1120$ ppm (and/or higher productivity / lower pO_2). A comment on this observation would also be worth including in the ms.

In any case, I believe the paper is provocative and will stimulate debate and serve as an important contribution to the Earth science community. I recommend it for publication.

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Author Rebuttals to First Revision:

Response to the reviewers [2021-09-14989A]

Continental configuration drives variability in ocean oxygenation through the Phanerozoic

Line numbers refer to the revised version of the manuscript with no revision marks.

Referee #1 (Remarks to the Author):

I have read the revised manuscript and the authors' response letter. The **authors have addressed my comments to my satisfaction**.

We are very grateful for the Referee taking the time to read the manuscript a second time and are glad that they found our revisions satisfactory.

Referee #2 (Remarks to the Author):

The authors have addressed all of the comments I raised in my first review. I only have minor suggestions this time (see below) and **am happy to recommend publication once my last comments have been taken into account**.

• It looks like GENIE forms northern hemispheric deep water in the Pacific and not in the Atlantic at 0 Ma (Extended Figure 3, 0 Ma); however the simulated O2 patterns shown in extended Figure 1 must have been extracted from a simulation forming NADW and not NPDW. I think that a short comment in the main text might be warranted.

We may not have been sufficiently clear regarding the nature of Extended Data Figure 1 – this is a standard modern configuration of GENIE, which we added in response to the previous round of reviews in order to illustrate the capabilities of the model in reproducing large-scale patterns of observed oxygenation in the modern ocean, and is not directly related to the Phanerozoic series focused on in the paper. To make this analysis clearer, we have added to Extended Data Figure 1 a 4th panel of the 0 Ma Phanerozoic simulation and extended the model/data comparison and description included in Extended Data Figure 1 to provide a more comprehensive discussion of the reasons for the oxygenation patterns in the 0 Ma Phanerozoic simulation.
As now summarized in the extended caption to Extended Data Figure 1, there are 3 factors at play in the 0 Ma Phanerozoic simulation:

i. As discussed below – we deliberate present a predominately climate-independent set of oxygenation realizations, assuming a modern solar constant but 2240 ppm (x8 preindustrial) CO_2 in the atmosphere. At such elevated (compared to modern) warmth, collapsed NADW is a distinct possibility.
ii. Secondly, the GENIE Earth system model in its basic modern configuration lacking a dynamical atmosphere and topography on land, requires that a freshwater transport is prescribed between Atlantic and Pacific basins in order to enable the establishment of a realistic AMOC (e.g. Marsh et al.[1]). That we have not prescribed any freshwater transports in any of our time-slices including that for 0 Ma, contributes to the reversed NADW vs.

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NPDW pattern shown.
(As an aside, we note that it does not take much of a reorganization of freshwater budgets to achieve a state at 0 Ma with stronger NPDW than NADW and such a state may have transiently existed during the last deglaciation (since 18 ka) – see Rae et al.[2]).

iii. Finally, in re-gridding from a relatively coarse model grid (FOAM) to an even coarser one (GENIE) we lose a sufficient deep and wide Drake Passage, restricting the ACC and impacting global circulation patterns at 0 Ma. We made no gateway adjustment to any of the re-gridded plate configurations used including 0 Ma, in order to prevent imposing bias into any one particular realization of ocean circulation.

• Don't we have any O2 proxies for time slices younger than 100 Ma? Why weren't they included?

In short: it would be a monumental effort to compile all available [O_2] proxy data for 100 Ma onwards and set them in a consistent age scale and paleo rotation framework. Indeed, we note that even compilations and model-data evaluations for specific and restricted time intervals tend to become papers in themselves (e.g. Zhou et al.[3,4]).
More pertinently, we deliberately isolate the role of tectonics from climate in our paper, either by assuming constant (and elevated as compared to modern – 2240 ppm) CO_2, or by adjusting CO_2 to maintain an approximately constant warm mean ocean surface temperature throughout the Phanerozoic. As a result, we do not (and indeed, do not intent to) reproduce the pronounced cooling trend through the Cenozoic (esp. from Early Eocene Climate Optimum (ca. 50 Ma) onwards). Given that O_2 proxies must at least partly must reflect the dramatic cooling of the ocean interior that has occurred over the past 50 Myrs, direct comparison with a series of model realizations under much warmer-than-modern climates, would not be fully meaningful.
We also recognize that we added model-data comparisons to Figure 2 in response to a recommendation in the first round of reviews, and perhaps this addition is generating more questions (such as the referee's) than it answers. We have therefore removed the proxy data from Figure 2 (which in any case is hard to make out at the scale of the multi-panel figure), but retain the expanded view model-data comparison for the 7 time-slices in Extended Data Figure 2. We have also edited the caption to Extended Data Figure 2 so as to make it clearer as to why we have chosen these specific times and why we e.g. did not include comparisons for times younger than 100 Ma.
However, we can go some way to explicitly addressing the reviewer's suggestion by commenting on how the long-term model trends compare with an existing compilation of oxygenation (I/Ca) proxy data spanning the entire Phanerozoic (and including the last 100 Ma) – that of Lu et al.[5] (lines 205–209):
'*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*.'

• I really like Extended Figure 10. I think that there is a lot of necessary information in that figure. Thank you for adding it. I wonder if it can be somehow included in the main paper? Either way, can you please add titles on top of each column in the subpanels b and c (e.g., "streamfunction", "ventilation age", etc)?

Firstly, we have annotated the figure as requested.
Secondly, with regards to moving it to the main paper – we will happily take editorial advice on this point and whether it would be possible to have a total of 4 main figures, but we note that we already have 3 complex multi-panel figures in the main paper.
We could also move this figure to the beginning of Extended Data and make it Extended Data Figure 1, which would help increase its visibility.
Otherwise, we are glad that the Referee has found its inclusion useful and instructive.

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• Oxygen figures: I am surprised I did not catch that earlier, but how can O2 be negative in your simulations? I guess there is no denitrification and respiration only gets cut off once O2 hits 0, therefore allowing for slightly negative values that then can get transported around? It might be good to add a sentence about this to explain to readers who are not familiar with models?

We are grateful for the referee pointing out this omission in the model description summary.
Although the Referee is correct in recognizing that we did not include a nitrogen cycle (and hence denitrification) in our model configuration, we do include a sulphur cycle. Hence, once oxygen starts to run out, sulphate reduction starts to take over in providing the electron acceptor for the remineralization of organic matter in the ocean interior. However, unlike nitrate, the ocean sulphate reservoir, at least during the Phanerozoic, is effectively infinite for the purpose of providing the oxidant for organic matter remineralization and will not run out anywhere. The reason for negative values of $[O_2]$ occurring at all then is simply the nature of numerical models which only offer an approximate solution to a set of simultaneous equations. In this particular example, multiple geochemical reactions compete simultaneously for the same dissolved oxygen pool and at the same time as ocean transport of dissolved oxygen is occurring. The result is that small negative concentrations can develop, which in the example e.g. of 500 Ma (Figure 2) is never greater in magnitude at the ocean floor than ca. -5 μmol kg^{-1}.
Do the negative concentrations 'matter'? In Meyer et al.[6], we directly contrasted simulations assuming only dissolved oxygen (with negative concentrations in regions where the total organic matter remineralization oxygen demand exceeded the available $[O_2]$), with identical simulations but now also including sulphate as an electron acceptor. The projected distribution of ocean interior oxygenation was almost identical, primarily because the product of sulphate reduction – hydrogen sulphide (H_2S) – has fast oxidation kinetics in the presence of free oxygen and the transport of H_2S from anoxic to oxic areas closely mirrors the transport and fate of 'negative oxygen'.
We note that this approach is superior to higher resolution ocean biogeochemical models used to simulate earlier Phanerozoic ocean anoxia (e.g. UVic Earth system model[7] and MITgcm[8]), in which once dissolved oxygen (and nitrate) runs out, organic matter remineralization no longer takes place. Such an approach is kinetically unrealistic and will lead to a severe underestimation of the extent of ocean anoxia in the past.
A short summary of the above has been added to Methods (lines 340–347) and also highlighted in the caption of Extended Data Figure 4.

All the lines in the comments below are corresponding to the track-changed pdf.

• Please change line 33 to "a causal mechanism that *might* explain..".
Done.

• Line 98: remove "detailed"
Done.

• Line 103 and following: doesn't the position of the landmasses influence climate too?
Added this additional factor.

• Line 125: "ocean deoxygenation develop" – maybe specify "benthic"?
Added 'seafloor'.

• Lines 126/127 – twice "central Atlantic"? Please fix.
Fixed

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• Lines 157/158: for someone reading quickly this sentence can be misunderstood ("notions of past warm oceans necessarily…"). I would add a clear statement here that past oceans low on oxygen were likely stagnant or poorly ventilated – which is the main take-home message of the paper… i.e. not all warm oceans were necessarily stagnant but all oxygen-deprived oceans were likely stagnant.
Given other lengthening additions, rather than expand to better clarify this, we felt that on balance the text read better without this sentence.

• Line 164: the brackets are not needed
Done.

• Line 263: change "is" to "could have been" ("could have been a consequence of continental rearrangement")
Done.

• Line 664: "benthic surface O2"? Please fix.
(replaced with 'seafloor')

Referee #3 (Remarks to the Author):

A. The manuscript by Pohl et al. uses numerical experiments to demonstrate that the configuration of continents and ocean basins during the Phanerozoic strongly controls ocean oxygenation. This highlights that tectonics drives many fundamental life support systems on our planet, and can help explain some extinctions and anoxic events that are captured by the geological record. This is a **very important contribution to our field**, and I would like to congratulate the team for putting together such an impactful and clear study.
B. This is a very novel study, and **meets the high standard of Nature papers**.
C. The data and methodology has been improved and made more accessible, and now meets the high standards of Nature papers.
D. The manuscript uses a robust level of statistics and analysis, and the supplement demonstrates the author's hard work in **exploring some of the key uncertainties**.
E. The **conclusions are well-supported** by the data and models.
F. **All of my concerns were addressed in the review**, and I thank the authors for their meticulous work in improving the manuscript.
G. References are appropriate
H. The text remains very clear and precise, meeting the standard of Nature papers.

We are very grateful for the Referee taking the time to read the manuscript a second time and are glad that they found our revisions satisfactory.

Referee #4 (Remarks to the Author):

The authors have greatly improved the manuscript in their revisions. The manuscript no longer reads only as a mathematical exercise exploring one Earth system model of intermediate complexity, it reads more as a contribution to improve our understanding ocean physics (and chemistry). Specifically, it is now clear that water residence time is related to the decoupling of benthic and surface O2 levels (e.g. Fig. 3). Periods with widespread anoxia could be linked to slower downwelling at high latitudes and longer water residence times.

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I must say that I'm amazed to see that a subtle difference in continental configuration between 460 and 440 Ma (Extended Figure 4) can be sufficient to dramatically amplify ocean circulation (i.e. halving the benthic water age: 1200 yr -> 600 yr) and oxygenate the deep ocean floor. The authors argue that bistability between deep-ocean circulation states occur in the cGENIE world, and while that may explain the amplification of subtle changes in ocean shape, I cannot judge whether this is reflects robust or model-dependent modes of ocean circulation.

The Referee is exactly right and this is the nature of 'tipping points' in global ocean circulation – even small changes in continental position can induce a state transition and e.g. a halving of benthic ventilation age. We would argue that the existence of this phenomena is real, although the precise tectonic arrangement and pCO_2 value at which state transitions occur, will be somewhat model-dependent. Indeed, we note that the apparent presence of oscillations in some of the ocean circulation spin-ups of Valdes et al.[9] using the fully coupled HadCM3L climate model, but not in others separated by only 5 Myrs in age, supports the existence of tectonic-driven ocean tipping points. (Currently unpublished follow-on work by Paul Valdes (*pers com*) with much longer integrations of HadCM3L confirm the presence of stable oscillations in large-scale ocean circulation.)
We have gone back through all the text to make sure this point is as clear as possible, and specifically have added to the main text (lines 177–181): '*Furthermore, the highly non-linear and chaotic nature of the system means that even very minor changes in continental configuration (e.g. contrast 460 vs. 440 Ma, Figure 2) can induce dramatic re-organizations of large-scale circulation and hence ocean oxygenation, and similarly, confusticate any predictable relationship between changes in atmospheric pCO_2 (and climate) and ocean oxygenation.*'

I do find it a bit strange that the model reported in fig 3 does not give the right value for the modern ocean (1050 yr), but a value closer to 700 yr. A comment on this difference in the caption would be appropriate.

In brief – this is principally a consequence of our high pCO_2 assumption and aim to achieve a relatively warm and uniform climate across the Phanerozoic in order to expose the role of plate tectonics, which results in the climatic boundary conditions dictating ocean circulation at 0 Ma being far from modern.
For the standard modern configuration presented in Extended Data Figure 1b, c, we find that the mean benthic ventilation age is 1080 years. In other words, when the GENIE Earth system model is specifically configured for the pre-industrial ocean and with 278 ppm CO_2, we can recover the value the reviewer cites. However, we have carried out a mean zonal basin age analysis (not shown) in which we find that the Indian and Pacific zonal means of the 0 Ma Phanerozoic GENIE simulation are close to the inverse analysis of DeVries and Holzer[10], meaning that ca. 750 yrs (Figures 1, 3) could, if anything, be an over, not under-estimate. (The primary point remains that having run all the Phanerozoic series of simulations at elevated CO_2, we do not expect to recover the preindustrial ocean state for the 0 Ma time slice.)
We have revised the caption to Extended Data Figure 1 to address this as far as is possible given space constraints.

Also, I read from the extended Figure 9 that Cambrian deep anoxia depends on high pCO2 > 1120 ppm (and/or higher productivity / lower pO2). A comment on this observation would also be worth including in the ms.

We assume that the referee is hinting at the possibility that one could use the presence/absence of widespread anoxia and alternative modes of ocean circulation during the Cambrian, as a constraint on atmospheric pCO_2. If so – this is an intriguing possibility and one that had not occurred to us. However, near a state transition the system is extremely sensitive to any change in boundary condition, whether pCO_2 or continental configuration. As such, without further constraints, a small tectonic change may cause a large change in the climate (and pCO_2) threshold that divides oxic from anoxic states. (Equally, the locations of tipping points in pCO_2 space will be highly dependent on model resolution, physics, etc.)
We have added what we can to the main text given space constraint (lines 177–181):

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'Furthermore, the highly non-linear and chaotic nature of the system means that even very minor changes in continental configuration (e.g. contrast 460 vs. 440 Ma, Figure 2) can induce dramatic re-organizations of large-scale circulation and hence ocean oxygenation, and similarly, confusticate any predictable relationship between changes in atmospheric pCO_2 (and climate) and ocean oxygenation.'

In any case, I believe the paper is provocative and will stimulate debate and serve as an important contribution to the Earth science community. **I recommend it for publication**.

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7. Montenegro, A. *et al.* Climate simulations of the Permian-Triassic boundary: Ocean acidification and the extinction event. *Paleoceanography* **26**, PA3207 (2011).
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10. DeVries, T. & Holzer, M. Radiocarbon and Helium Isotope Constraints on Deep Ocean Ventilation and Mantle-3He Sources. *J. Geophys. Res. Ocean.* **124**, 3036–3057 (2019).