

Dear Dr Feng,

Thank you for your comments on the manuscript and for the opportunity to submit a revised version. Below we outline in blue text, our responses to the reviewers, and then a list of extra changes we have made to address your comments and several further issues we identified in the original submission.

Kind Regards,  
David Hutchinson

### **Anonymous Referee #1**

#### **General Comments**

This manuscript, entitled “The Eocene-Oligocene transition: a review of marine and terrestrial proxy data, models and model-data comparisons” by Hutchinson et al., is an outstanding review paper worthy of publication in *Climate of the Past*. This paper makes large strides and provides a comprehensive update to Eocene-Oligocene research as much has been done since the 2007 review of Coxall and Pearson. The authors take a methodical approach, first addressing terminology and a framework for the Eocene-Oligocene, then boundary conditions such as paleogeographic reconstructions, paleoceanography, and constraints on glaciation. Next, the authors move to a comprehensive review of marine and terrestrial paleoclimate and pCO<sub>2</sub> reconstructions, mechanistic modeling studies of paleogeographic, CO<sub>2</sub> and temperature changes. Finally, and most importantly, the authors end the paper with a metaanalysis of the factors affecting paleoenvironmental changes during the E-O transition and conclude that CO<sub>2</sub> decrease likely served as the primary driver of cooling and Antarctic glaciation. As this manuscript is very well written, I do not have large structural comments.

Thank you for the positive overall assessment.

Instead, I include my few specific comments along with line-by-line technical corrections below.

#### **Specific Comments and Technical Corrections**

Lines 111 and 125: This is just one example of “Fig.” vs “Figure.” Be consistent throughout.

All instances have been changed to “Figure”.

Lines 111 and 123: Again, just an example: I think it may help to structure these paragraphs in a way that really highlights these key terms such as EOGM and EOIS. This reorganization could help readers not as familiar with key E-O events as this is a review intended for a broad audience.

We have re-organised these paragraphs to set out the terms more clearly.

Figure 1. Along with the comment above, perhaps it would help to differentiate old/existing terms with your new preferred framework. Possibly a different colored font for existing terms e.g. Step 1 vs your new proposed terms e.g. EOIS.

We have now highlighted the EOIS term in blue text, since it is a new term that we define in this manuscript. All other terms in the Figure are defined previously and left in black text. We have also added a new Table 1 listing and defining terms and differentiating old/existing terms in an easily accessible form.

Line 199. Isotope

This has been fixed.

Lines 202 to 205. Possibly one more sentence to explain the mammalian phenomenon

We have added an extra sentence and minor edits to explain the mammalian evolutionary turnover.

Figure 3 caption. UK37 formatting.

This formatting has been corrected.

Line 527. Possibly one additional sentence to discuss the  $d_{18Osw}$  ice volume assumption and its robustness

This sentence has been re-ordered to come after the discussion of inter-basin similarity (previously Lines 531-533), and added a further comment on the assumption's limitations.

Line 645: Revise “multiple evidence”

This is now “multiple lines of evidence”.

Line 657: UK37 formatting

This has been fixed.

Section 5.2. Possibly a short discussion of challenges with leaf proxies (e.g. preservation bias, sampling bias) would supplement the existing discussion of challenges with chronology in terrestrial records in general.

We have added a short paragraph on the challenges of leaf proxy estimates of  $CO_2$ .

Line 920: The CCD was introduced on line 421 and should be abbreviated there.

We have used to the abbreviation here.

Lines 927-930: This sentence is very jargony and should be revised (and probably split into 3 or so sentences). At the very least, “glacio-eustatic sea level-led shelf-to-basin fractionation” and “ $C_{12}$ -enriched carbon capacitors” should be explained.

This part has been revised with improved explanations each process and simpler terms:

Carbon cycle box models suggest that the best fit to observations is achieved by a shift from shelf-to-basin carbonate fractionation (Armstrong McKay et al., 2016; Merico et al., 2008).

In this interpretation of events, the fall in sea-level due to Antarctic glaciation (i) reduces the global flux of carbonate into shallow water (reef, bank and shelf) sediments; and (ii) exposes fresh, readily dissolved shelf carbonate sediments around the world to rapid subaerial weathering (Merico et al., 2008). The first of these two mechanisms drives the sustained CCD deepening from Eocene to Oligocene. The second mechanism drives a one-off dump of carbonate into the ocean that explains the initial transient overshoot behaviour (Zachos and Kump, 2005), and the transient increase in benthic  $\delta^{13}\text{C}$  occurs because the shelf carbonate reservoir is enriched in  $^{13}\text{C}$  relative to pelagic carbonate reservoir (Swart and Eberli 2005; Swart 2008; Merico et al., 2008; Armstrong McKay et al., 2016). If the isotopic fractionation between these two carbonate sediment reservoirs is modest, however, shelf-basin fractionation can only fully explain the transient increase in oceanic  $\delta^{13}\text{C}$  if the one-off dump of weathered shelf carbonate is questionably large (Merico et al., 2008). In their follow up study, Armstrong McKay et al., (2016) considered this problem in detail and concluded that, unless shelf carbonates were substantially enriched in  $^{13}\text{C}$  relative to pelagic carbonates (by  $\sim 3\%$ ), an additional process must also have contributed, with sequestration of  $^{12}\text{C}$ -enriched carbon into carbon capacitors, and possibly increased ocean ventilation, offering the best fit to the paleorecords when combined with shelf basin fractionation.

Line 929: “C12-enriched” formatting

This term has been reformatted correctly.

Line 930: clathrates

This has been fixed.

Lines 931-935: These mechanisms require additional explanation and reduced jargon. Explain “labile and refractory components”

We now provide definitions of labile and refractory carbon and their relevance to the mechanisms discussed, as follows:

“They suggest several mechanisms are needed to explain the CCD change in addition to the shelf-basin fractionation hypothesis above: (i) perturbations to continental weathering and solute input to the deep ocean, or (ii) changes in the partition of organic carbon flux between labile (organic carbon that is readily available for oxidation and driving carbonate dissolution) and refractory (carbon that is more resistant to degradation and largely preserved and buried) components.”

Line 955: This description of GENIE is very similar to line 932

We have removed the duplicate explanation of cGENIE.

Line 968: Define SAT here and not in line 971.

This has been done.

Figure 7. This figure is perhaps the most important in the paper and possibly the hardest to interpret. At the very least, when finally published, these three panels should be much larger.

Many of the other figures can be smaller. I found 7a particularly hard to interpret, but the coastlines and proxy-model comparisons in all three panels are a bit challenging to see.

We agree – in journal form this figure would have been hard to read. For the sake of clarity, we have removed the stippling, and changed the colouring of the coastlines to make them more visible. We have also removed the numbers written adjacent to the proxy locations, since they were difficult to read, and the proxy values are already presented in table form.

Line 1082: For UVic,

The comma has been added.

Line 1085: For FOAM,

The comma has been added.

Table 2 caption: This caption requires the statement as in Table 3 about the meaning of green highlighted cells

We have added the explanation of green highlighted cells.

Line 1164: This is the first of several instances where “CO2 forcing alone” is cited as the best fit. Perhaps I’m not understanding the skill score analysis, but in Table 3 it appears that the ensemble mean skill score of 0.326 is achieved with coefficients of 0.7, 0.06 and 0.26 for alpha, beta and gamma respectively. Wouldn’t this mean that CO2 is the primary driver but that ice and paleogeography make modest contributions as well? If this is the case, the authors should clarify modify their interpretation to include these additional factors. If this is not the case, a quick mention of why this result indicates CO2 is the sole driver would be helpful.

We agree with the interpretation in this comment and have removed the references to “CO2 forcing alone”. CO2 is the primary (but not the sole) driver according to our analysis and we have clarified this.

Figure 8 caption: 910 ppm, not 900 right?

Yes, this has been corrected.

Line 1217: Here,

The comma has been added.

Line 1229: There is therefore a ... :

The sentence has been completed.

## **Anonymous Referee #2**

This paper provides a comprehensive review of the current state of understanding of climate change during the Eocene-Oligocene transition, and in the process, attempts to assess the

cause of this change, CO<sub>2</sub> versus paleogeography, the added role of ice. Published observations from marine and terrestrial archives are compiled and compared against climate simulations from a collection of modeling studies (i.e., a model inter-comparison). The observations include SAT (SST), SSS, continental ice extent, sea-ice and ocean circulation. The comparisons are for 2 broad intervals, late Eocene and early Oligocene. Presumably, the observations are binned over long (1-4 my?) windows. For the modeling studies, the boundary conditions, including ice sheets, are generally similar though not identical given the lack of coordination, and each of the models are run to equilibrium (thousands of years). The study looks at the simulated responses to changes in paleogeography (i.e., gateways), GHG levels, and Antarctica ice-sheets. For GHG levels, 900 ppm (just above the threshold for ice accumulation on Antarctica,) is used at the Eocene pCO<sub>2</sub> and 560 ppm for the Oligocene. Because the published model experiments were not coordinated and thus run with a range of CO<sub>2</sub>, for comparison the output of some models are scaled to approximate the same  $\Delta$ pCO<sub>2</sub>. The equilibrium climate states for each model and an ensemble are then assessed for a best fit with observations. Given differences in resolution and other parameters, the absolute T in the models vary widely, with a cool group and warm group, so the focus is primarily on  $\Delta$ SAT. In general, most of the models are showing ~2°C cooling in mean global SAT (figure 5). There are minor regional discrepancies which are attributed primarily to differences in ocean mixing/heat transport. In the end, the ensemble is deemed to show a good fit with observations supporting the conclusion that a reduction in atmospheric CO<sub>2</sub> was the primary driver of the EOT.

[Thank you for the overall assessment and constructive comments on improving the manuscript.](#)

I have mixed feelings about this paper. Clearly a considerable amount of time and effort went into compiling the observations, the synthesis of modeling work. This alone will be a valuable contribution to the EOT literature. However, I am not convinced that the modeling comparison is a useful exercise, at least not in the way it was intended or designed.

[We have edited the model-data comparison to better acknowledge the limitations and uncertainties that were previously missing from this section. See further discussion below.](#)

The main issue concerns the finding/conclusions about the forcing behind the transition, specifically a ~halving of pCO<sub>2</sub> (from 900 to 560 ppmv) with the EOT. To my knowledge, based on observations (see figure 5) or theory, there is no basis for a 40 to 50% reduction in atmospheric CO<sub>2</sub> across this transition. The existing B isotope data, albeit sparse, even suggests a slight increase, and the alkenones suggest a decline but not nearly of that magnitude. More importantly, just from a purely theoretical perspective, there is no reason to expect such a large decline. Recall that when the first detailed, high resolution benthic O isotope records were produced, it became clear that the EOT, or at least the appearance of continental ice-sheets on Antarctica was relatively abrupt, consistent with the threshold hypothesis; a relatively small drop in GHG would be sufficient to trigger the rapid accumulation of ice on a polar continent (i.e., climatic threshold/tipping point, e.g., Crowley and North, 1988). This concept was reinforced by the ice-sheet modeling of DeConto and Pollard 2004 which demonstrated how the local albedo feedback on summertime T could accelerate ice accumulation. Granted that by today's standards the ice-sheet model of the D/P study was relatively coarse and simplistic, but the general theory of a bifurcation point in the climate system still seems valid. We can debate the exact magnitude of the CO<sub>2</sub> drop required, but it was probably small (~ 100 ppm), especially with the proper orbital

configuration. And even with the large uncertainties, the CO<sub>2</sub> proxies are consistent with this hypothesis. This is the most compelling and important aspect of the EOT, a relatively large change in climate in response to a relatively small change in forcing. The observations of a few degrees of cooling, switches in the mode of ocean circulation are consistent with this hypothesis. The Goldner et al (2014) paper nicely illustrates the regional/global effects on ocean T of just adding the ice-sheet (w fixed pCO<sub>2</sub>). Also, why such a rapid and large reduction in pCO<sub>2</sub> at that time? Positive feedbacks involving biogeochemical cycles, ocean uptake, could potentially draw down CO<sub>2</sub> but the effect would likely be relatively small, <100 ppm, as suggested by a variety of modeling studies (& observations). More than likely, the decline in pCO<sub>2</sub> from the latest Eocene to earliest Oligocene was probably minor.

The reviewer raises some important points here regarding the conclusions drawn from the modelling work. We have considered these carefully and agree that the interpretation of the model-data comparison needs to be changed to acknowledge the limitations and uncertainties of the modelling approach. It was not our intention to suggest that the models are entirely correct and that it was a 350 ppm drop in CO<sub>2</sub> that caused the climate transition, but can see that the reader could think that from the way it was written. In order to address the reviewer's comments, we now include a discussion of the caveats; including the mismatch between observations and models, implications for model sensitivity and feedbacks, and recommendations for setting up future experiments. We have also updated the conclusion and the abstract to reflect these changes.

Regarding the CO<sub>2</sub> change, the multi-proxy compilation of Foster et al (2017) suggests 'best-fit' CO<sub>2</sub> estimates of 893 ppm and 806 ppm for our late Eocene and early Oligocene windows respectively, or a drop of 10%. We have now acknowledged in the manuscript that our scaled estimate of CO<sub>2</sub> change is larger than this best-fit estimate, however we note that there are some CO<sub>2</sub> proxies that are consistent with such a change. For example, the alkenone records of Pagani et al (2011) are consistent with a decrease of 300 ppm within a 1 Myr window of the EOT. The boron and stomatal records are more equivocal, showing that a drop of 200-300 ppm is plausible, though this can be considered an 'end-member' rather than a 'most probable' change.

The point about crossing a threshold of glaciation is an important limitation on the models used. These models must prescribe an ice sheet to be on or off, with no scope for dynamic feedbacks when crossing a glaciation threshold. We have added further comments here about the limitation in the ice sheet components of the models. However, it is still useful to compare in our ensemble: which forcing mechanisms provide the best explanation of the proxy temperature change, and how should each be relatively weighted. One clear result from our ensemble study is that the far-field temperature change (i.e. much of the global delta T at the EOT), is much better explained by CO<sub>2</sub> forcing than by imposing an ice sheet or paleogeographic changes. This highlights the fact that a global cooling mechanism is needed, whether from CO<sub>2</sub> or other feedback mechanisms, and such a change is not easily triggered by the gateway or ice sheet forcing experiments.

The results of Goldner et al (2014), included in our ensemble, also bear this out: they show a large change in Antarctic and Southern Ocean surface temperatures, but little change in the global mean. However, those results do show a cooling of the deep ocean (since the deep ocean waters are sourced from Southern Ocean sinking), which could help to explain some of the benthic temperature proxy trends. Since the models are in general not fully equilibrated, we cannot undertake a model ensemble assessment of benthic temperature changes.

With all this in mind, the fact that the model ensemble is in agreement with observations is problematic. In other words, to match climate observations, a much larger change in forcing (1.6x) is required than justified by observations or theory. This is the same recurring issue with simulating high CO<sub>2</sub> climates of the past, that a much larger forcing is required than justified by observations? The bottom line is that the models are under sensitive to GHG forcing. Arguably, this should be one of the main conclusions of this paper. As the paper is currently written, I almost get the opposite sense. Has this paper achieved the stated goal of identifying what drove the EOT, at least the abrupt appearance of ice-sheets ~34 Mya? Am sure we can all agree that over the long-term, a reduction in GHG was the primary driver of Eocene cooling and key to triggering Antarctic glaciation. What we won't agree on are the specifics of timing and magnitude, the appropriate alignment of GHG forcing with the climate response.

It is true that some of the simulations appear to be under-sensitive to CO<sub>2</sub> forcing when reconstructing Eocene climates. The climate sensitivity to doubling CO<sub>2</sub> implied by this ensemble is 3.3°C, which may be lower than necessary to fit to the Eocene proxy record, but not radically so. A recent synthesis of climate sensitivity estimates based on the DeepMIP proxy ensemble suggests that climate sensitivity during the latest Paleocene, PETM and EECO was 4.5°C, 3.6°C and 3.1°C respectively (Inglis et al, 2020), with 66% confidence intervals ranging from ~2-7°C during the three intervals combined. Thus, while there is scope for a higher climate sensitivity in the models, the current best estimates are not much higher than the ensemble mean climate sensitivity.

A large component of the Eocene warmth (compared to present day) can be attributed to non-GHG changes, including paleogeographic changes, vegetation, soil and albedo effects. These effects are illustrated more fully in the DeepMIP model ensemble of the early Eocene (Lunt et al, 2020). This shows that stronger GHG forcing is just one element that is needed to properly solve the model-data mismatch in the Eocene (or Oligocene). We have added further discussion to Section 7.2.3 to address these issues.

Recommendation: A key question for revision - what is the real purpose of this paper? If it's simply to provide a comprehensive review of the existing literature on observations and modeling of the EOT, recommendations for future research, minor/moderate revision (see comments below) would suffice. For the reasons stated above, the data model comparison (section 7) could be dropped. If retained, it would be essential to include a discussion of the caveats; the aforementioned mismatch between observations/models, implications for model sensitivity and feedbacks, and recommendations for setting up future experiments.

We have chosen to retain section 7, and as noted above, we have revised the interpretations to clarify the issues raised here. In line with the reviewer's comments, we have acknowledged the need for missing feedbacks to enable the global cooling signal seen in the proxies.

### **Additional Comments/Recommendations:**

Window of Observations (Apples vs. Oranges); Considerable effort is spent in defining the duration of the EOT, "Hence the stratigraphic interval of the EOT according to our preferred definition is now given an estimated duration of 790 kyr (fig 1)". The problem is that the collected observations (Figures 3-5) span a much wider range of time, millions of years of the

late Eocene/early Oligocene. I assume this is by necessity, especially with the inclusion of terrestrial climate proxies. However, to make the model-data comparison more meaningful, it would be best to only include climate observations that straddle the O isotope excursion at 34 Ma, let's say within windows of 500 kyr immediately above and below. This might exclude a lot of data but the comparison pre- and post EOT conditions would be more meaningful.

Using the larger window was necessary to capture an acceptable spatial extent of proxy data. This is especially the case with the terrestrial data, which generally has lower temporal resolution.

1065 -1067 A figure showing the change in sea-ice distribution would be useful.

We have added a supplementary figure showing the sea ice distribution for each model. This cannot be integrated with our scaled temperature responses, because unlike temperature, sea ice exhibits threshold behaviour that cannot be interpolated smoothly between different levels of CO<sub>2</sub>.

7.1.3 SAT response to paleogeographic change, \_TGEO I think the assessment of simulations with differing tectonic configurations, \_TGEO, is useful only for assessing how the sensitivity of a model to a given change in GHG levels varies under different configurations, e.g., an open or closed Drake passage. We already know from previous studies that the geographic changes alone produce relatively minor changes in global climate, and sometimes in the wrong direction. Also, the uncertainties about the timing of the gateways are large enough that this is not really worth focusing on. The section should be condensed or simply moved to SOM.

While we agree that the TGEO changes produce overall minor changes in global climate, this section is important to include here because the gateway cooling hypothesis is a long-standing theory of what caused the EOT cooling, and some aspects of the gateway hypothesis are still actively debated in modelling literature of the EOT (e.g. Toumoulin et al, 2020).

1121-22 yes, the CO<sub>2</sub> is somewhat arbitrary.

Agreed – but it is important to flag this here.

1124 - As we all know, the error in CO<sub>2</sub> reconstructions is quite large. Nevertheless, it is unlikely that CO<sub>2</sub> was halved pre-EOT to EOT. More likely, the change in pCO<sub>2</sub> was much smaller, at least initially with inception of glaciation (at 34 Ma) which involved a threshold CO<sub>2</sub> enhanced by regional feedbacks via ice-sheet growth. It is possible that biogeochemical feedbacks enhance the drawdown of CO<sub>2</sub>, but probably not more than 100 ppm or so.

We agree that halving CO<sub>2</sub> is not a realistic scenario, but it is a clear and useful experimental protocol for establishing the climate sensitivity to GHG changes. We scale the CO<sub>2</sub> forcing to best fit the data, and in doing so our derived estimate is much less than a halving. We have clarified that certain feedbacks are missing from these models, and thus the threshold behaviour (which requires dynamic ice sheets) cannot be simulated in them.

1165 – Based on the goodness of fit, you derive an estimate of  $\Delta$ CO<sub>2</sub>? I understand the strategy here, but it seems backwards when the primary motivation behind reconstructing



paleoclimates is to assess climate models. As stated above, I think the observations suggest that the models (as they were prior to 2017) are under sensitive to GH forcing.

As noted above, we have added further discussion on the models' climate sensitivity to CO<sub>2</sub>, including recent advances from the DeepMIP intercomparison. We note that the warmer models from that ensemble also have considerable non-CO<sub>2</sub> warming effects, i.e. climate sensitivity is not the only factor that can potentially resolve the model-data mismatch.

Figure 5 (pCO<sub>2</sub> reconstruction) – This figure made me cringe. The terrestrial proxy pCO<sub>2</sub>, given the coarse stratigraphic control, low temporal resolution, could be misleading. And let's be honest, given the concerns about the reduced sensitivity of the stomata proxy to higher CO<sub>2</sub>, who would really expect that proxy to accurately capture the  $\Delta$ pCO<sub>2</sub> across the EOT? Let's not even get into the issues with soil carbonates. As most of the climate data are marine based, it would make sense to only include the pCO<sub>2</sub> estimates from marine proxies plotted along with the benthic d18O of figure 2 over a narrower window of time. This would eliminate any uncertainties about the relative timing of changes in climate versus forcing.

We have better acknowledged the challenges of reconstructing CO<sub>2</sub> from terrestrial proxies, as noted in our response to Reviewer 1. However, these are an important branch of the EOT literature and we think it is best to include those data, with some added discussion around its limitations. We have also adjusted the age limits of Figure 5 to be shorter (38 to 30 Ma), to be more coherent with our temperature proxy compilations.

### **Extra changes to the manuscript**

- We have added a brief paragraph mentioning key regions of uncertainty in the paleogeography reconstructions to Section 2.1.
- We have added new references and discussion of terrestrial temperature change to North and South America (Section 4.1 and 4.2)
- We have added a substantial discussion (~2 paragraphs) of Tibetan Plateau uncertainties and updates to Eurasian temperature reconstructions (Section 4.4)
- We have added several new references to the terrestrial reconstruction of Australia (Section 4.5)
- We corrected a minor inconsistency in the model-data intercomparison where we had used the Coxall and Pearson (2007) 500 kyr definition of the EOT (34.2 to 33.7 Ma) to define limits on the late Eocene and early Oligocene averages. In the original submission, we excluded data from within the EOT itself. Since the definition has now changed, we have simplified the average calculation using the EO boundary (33.9 Ma) as the divider between our late Eocene and early Oligocene average windows. This caused some minor revisions to our skill score metrics and global averages (~1-2% changes), but the overall findings and interpretations are insensitive to these changes.

# The Eocene-Oligocene transition: a review of marine and terrestrial proxy data, models and model-data comparisons

David K. Hutchinson<sup>1</sup>, Helen K. Coxall<sup>1</sup>, Daniel J. Lunt<sup>2</sup>, Margret Steinhorsdottir<sup>1,3</sup>, Agatha M. De Boer<sup>1</sup>, Michiel Baatsen<sup>4</sup>, Anna von der Heydt<sup>4,5</sup>, Matthew Huber<sup>6</sup>, Alan T. Kennedy-Asser<sup>2</sup>, Lutz Kunzmann<sup>7</sup>, Jean-Baptiste Ladant<sup>8</sup>, Caroline H. Lear<sup>9</sup>, Karolin Moraweck<sup>7</sup>, Paul N. Pearson<sup>9</sup>, Emanuela Piga<sup>9</sup>, Matthew J. Pound<sup>10</sup>, Ulrich Salzmann<sup>10</sup>, Howie D. Scher<sup>11</sup>, Willem P. Sijp<sup>12</sup>, Kasia K. Śliwińska<sup>13</sup>, Paul A. Wilson<sup>14</sup>, Zhongshi Zhang<sup>15,16</sup>

1. Department of Geological Sciences and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden
2. School of Geographical Sciences, University of Bristol, UK
3. Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden
4. Institute for Marine and Atmospheric Research, Department of Physics, Utrecht University, Utrecht, the Netherlands
5. Centre for Complex Systems Studies, Utrecht University, Utrecht, the Netherlands
6. Department of Earth, Atmospheric, and Planetary Sciences, Purdue University, West Lafayette, USA
7. Senckenberg Natural History Collections Dresden, Germany
8. Department of Earth and Environmental Sciences, University of Michigan, USA
9. School of Earth and Ocean Sciences, Cardiff University, Cardiff, UK
10. Department of Geography and Environmental Sciences, Northumbria University, UK
11. School of the Earth, Ocean and Environment, University of South Carolina, USA
12. Climate Change Research Centre, University of New South Wales, Sydney, Australia
13. Department of Stratigraphy, Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark
14. University of Southampton, National Oceanography Centre Southampton, UK
15. Department of Atmospheric Science, China University of Geoscience, Wuhan, China
16. NORCE Research and Bjerknes Centre for Climate Research, Bergen, Norway

Correspondence to: David K. Hutchinson (david.hutchinson@geo.su.se)

**Abstract.** The Eocene-Oligocene transition (EOT) was a climate shift from a largely ice-free greenhouse world to an icehouse climate, involving the first major glaciation of Antarctica and global cooling occurring ~34 million years ago (Ma) and lasting ~790 kyr. The change is marked by a global shift in deep sea  $\delta^{18}\text{O}$  representing a combination of deep-ocean cooling and growth in land ice volume. At the same time, multiple independent proxies for ocean temperature indicate sea surface cooling, and major changes in global fauna and flora record a shift toward more cold-climate adapted species. The two principal suggested explanations of this transition are: a decline in atmospheric  $\text{CO}_2$ , and changes to ocean gateways, while orbital forcing likely influenced the precise timing of the glaciation. Here we review and synthesize proxy evidence of paleogeography, temperature, ice sheets, ocean circulation, and  $\text{CO}_2$  change from the marine and terrestrial realms. Furthermore, we quantitatively compare proxy records of change to an ensemble of climate model simulations of temperature change across the EOT. The simulations compare three forcing mechanisms across the EOT:  $\text{CO}_2$  decrease, paleogeographic

- Deleted: with
- Deleted: was a phase of major climate
- Deleted: environmental change
- Deleted: 500
- Deleted: global ice sheet
- Deleted: .
- Deleted: sea surface
- Deleted: a
- Deleted: ocean
- Deleted: major
- Deleted: that have been suggested
- Deleted: This work reviews
- Deleted: syntheses
- Deleted: model

changes, and ice sheet growth. ~~Our model ensemble results demonstrate the need for a global cooling mechanism beyond the imposition of an ice sheet or paleogeographic changes. We find that CO<sub>2</sub> forcing involving a large decrease in CO<sub>2</sub> of ca. 40% (~340 ppm drop) provides the best fit to the available proxy evidence, with ice sheet and paleogeographic changes playing a secondary role. While this large decrease is consistent with some CO<sub>2</sub> proxy records (the extreme end member of decrease), the positive feedback mechanisms on ice growth are so strong that a modest CO<sub>2</sub> decrease beyond a critical threshold for ice sheet initiation is well capable of triggering rapid ice-sheet growth. Thus, the amplitude of CO<sub>2</sub> decrease signalled by our data-model comparison should be considered an upper estimate and perhaps artificially large, not least because the current generation of climate models do not include dynamic ice sheets and in some cases may be under-sensitive to CO<sub>2</sub> forcing. The model ensemble also cannot exclude the possibility that paleogeographic changes could have triggered a reduction in CO<sub>2</sub>.~~

**Deleted:** We find that CO<sub>2</sub> forcing provides by far the best explanation of the combined proxy evidence, and based on our model ensemble, we estimate that a CO<sub>2</sub> decrease of about 1.6x across the EOT (e.g. from 910 to 560 ppmv) achieves the best fit to the temperature change recorded in the proxies. This model-derived CO<sub>2</sub> decrease is consistent with proxy estimates of CO<sub>2</sub> decline at the EOT

## 1 Introduction

### 1.1 Scope of Review

Since the last major review of the EOT (Coxall and Pearson, 2007) the fields of palaeoceanography and palaeoclimatology have ~~advanced~~ considerably. New proxy techniques, drilling and field archives of Cenozoic (66 Ma to present) climates, have expanded global coverage and added increasingly detailed views of past climate patterns, forcings and feedbacks. ~~From a broad perspective, statistical interrogation of an astronomically dated, continuous composite of benthic foraminifera isotope records confirms that the EOT is the most prominent climate transition of the whole Cenozoic and suggests that the polar ice sheets that ensued seem to play a critical role in determining the predictability of Earth's climatological response to astronomical forcing (Westerhold et al., 2020). New~~ proxy records capture near and far-field signals of the onset of Antarctic glaciation. Meanwhile, efforts to simulate the onset of the Cenozoic 'icehouse', using the latest and most sophisticated climate models, have also progressed. ~~Here we review both observations and the results of modelling experiments of the EOT. From the marine realm, we review records of sea surface temperature, as well as deep sea time series of the temperature and land ice proxy  $\delta^{18}\text{O}$  and carbon cycle proxy  $\delta^{13}\text{C}$ . From the terrestrial realm we cover plant records and biogeochemical proxies of temperature, CO<sub>2</sub> and vegetation change. We summarise the main evidence of temperature, glaciation and carbon cycle perturbations and constraints on the terrestrial ice extent during the EOT, and review indicators of ocean circulation change and deep water formation, including how these changes reconcile with paleogeography, in particular, ocean gateway effects.~~

**Formatted:** English (AUS)

**Deleted:** grown

**Formatted:** English (AUS)

**Deleted:** A plethora of new

**Deleted:** It is now possible to compare model outputs with one another, as well as against a growing body of climate proxy data.

**Deleted:** literature

Finally, we synthesise existing model experiments that test three major proposed mechanisms driving the EOT: (i) paleogeography changes, (ii) greenhouse forcing and (iii) ice sheet forcing upon climate. We highlight what has been achieved from these modelling studies to illuminate each of these mechanisms, and explain various aspects of the observations. We also discuss the limitations of these approaches, and highlight areas for future work. We then combine and synthesise the observational and modelling aspects of the literature in a model-data intercomparison of the available models of the EOT. This approach allows us to assess the relative effectiveness of the three modelled mechanisms in explaining the EOT observations.

The paper is structured as follows: Section 1.2 defines the chronology of events around the EOT, and clarifies the terminology of associated events, transitions, and intervals, thereby setting the framework for the rest of the review. Section 2 reviews our understanding of palaeogeographic change across the EOT, and discusses proxy evidence for changes in ocean circulation and ice sheets. Section 3 synthesises marine proxy evidence for sea surface temperatures (SST) and deep-ocean temperature change. Section 4 synthesises terrestrial proxy evidence for continental temperature change, with a focus on pollen-based reconstructions. Section 5 presents estimates of CO<sub>2</sub> forcing across the EOT, from geochemical and stomatal-based proxies. Section 6 qualitatively reviews previous modelling work, and Section 7 provides a new quantitative intercomparison of previous modelling studies, with a focus on model-data comparisons to elucidate the relative importance of different forcings across the EOT. Section 8 provides a brief conclusion.

## 105 1.2 Terminology of the Eocene-Oligocene transition

Palaeontological evidence has long established Eocene (56 to 34 Ma) warmth in comparison to a long term Cenozoic cooling trend (Lyell and Deshayes 1830, p. 99-100). As modern stratigraphic records improved, a prominent step in that cooling towards the end of the Eocene began to be resolved. This became evident in early oxygen isotope records ( $\delta^{18}\text{O}$ ) derived from deep-sea benthic foraminifera, which show an isotope shift towards higher  $\delta^{18}\text{O}$  values (Kennett and Shackleton, 1976; Shackleton and Kennett, 1975), which was subsequently attributed to a combination of continental ice growth and cooling (Lear et al., 2008). In the 1980s the search was on for a suitable Global Stratotype Section and Point (GSSP) to define the Eocene-Oligocene boundary (EOB). Much of the evidence was brought together in an important synthesis edited by Pomerol and Premoli Silva (1986). The GSSP was eventually fixed at the Massignano outcrop section in the Marche region of Italy in 1992 (Premoli Silva and Jenkins, 1993) at the 19.0 m mark which corresponds to the extinction of the planktonic foraminifer family Hantkeninidae (Coccione, 1988; Nocchi et al., 1986). By the conventions of stratigraphy, Massignano is the only place where the EOB is defined unambiguously; everywhere else the EOB must be correlated to it, whether by biostratigraphy, magnetostratigraphy, isotope stratigraphy or other methods.

Coxall and Pearson, (2007, p 352) described the EOT as "a phase of accelerated climatic and biotic change lasting 500 kyr that began before and ended after the E/O boundary". Recognizing and applying this in practice turns out to be problematic due to variability in the pattern of  $\delta^{18}\text{O}$  between records and on different timescales. Widespread records now show the positive  $\delta^{18}\text{O}$  shift with increasing detail. A high-resolution record from ODP Site 1218 in the Pacific Ocean revealed two  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  'steps' separated by a more stable 'plateau interval' (Coxall et al., 2005; Coxall and Wilson, 2011). The EOT brackets these isotopic steps with the EOB falling in the plateau between them (Coxall and Pearson, 2007; Coxall and Wilson, 2011; Dunkley Jones et al., 2008; Pearson et al., 2008). However, while two-step  $\delta^{18}\text{O}$  patterns have now been interpreted in other deep sea records, thus far largely from the Southern Hemisphere (Figure 1) (Bohaty et al., 2012; Borrelli et al., 2014; Coxall and Wilson, 2011; Langton et al., 2016; Pearson et al., 2008; Wade et al., 2012; Zachos et al., 1996), there is often ambiguity in their

**Deleted:** (Lyell and Deshayes 1830, p99-100). As modern stratigraphic records improved, a prominent step in that cooling emerged towards the end of the Eocene. This became evident in early oxygen isotope records ( $\delta^{18}\text{O}$ )

**Deleted:** ,

**Formatted:** English (UK)

**Formatted:** English (UK)

**Deleted:** the Massignano section

**Deleted:** in use

135 identification. In particular, while the second  $\delta^{18}\text{O}$  step, 'Step 2' of Coxall and Pearson (2007), is an abrupt and readily correlated feature, the first step (Step 1 of Pearson et al., 2008; EOT-1 of Katz et al. 2008) is often less prominent than at Site 1218 (Figure 1). Furthermore, some records have been interpreted to show more than two  $\delta^{18}\text{O}$  steps (e.g. Katz et al. 2008). Benthic  $\delta^{13}\text{C}$  records provide a powerful complementary stratigraphic tool. These also show a correlatable stepped pattern of increase across the EOT, although in detail  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  are not synchronous (Coxall et al., 2005; Zachos et al., 1996) and

140 further complications arise in correlation to other sites (Coxall and Wilson, 2011). In attempting to synthesize the pattern across multiple sites we suggest that attempts to define and correlate an initial 'Step-1' are premature at this point and should await better resolved records. Nonetheless, we maintain a tentative Step-1 in our terminology because it is important for differentiating phases of cooling vs ice growth during the EOT.

145 Settling on a consistent terminology for other features of the EOT is also problematic because usage of certain terms has changed through time. In order to clarify the definition of two key stratigraphic features, we recommend using the following terms: (i) for the basal Oligocene  $\delta^{18}\text{O}$  increase we suggest the term "Earliest Oligocene oxygen Isotope Step" (EOIS) to denote the large isotope step that occurs well after the EOB and within the lower part of Chron C13n (Figure 1); ii) Early Oligocene Glacial Maximum (EOGM; Liu et al. 2004; Figure 1) to denote the peak-to-peak isotope stratigraphic interval, corresponding to most of Chron C13n (starting at the top of the EOIS). Other terms for these features have been used

150 inconsistently in the literature (Table 1). For example, the term 'Oi-1' was originally defined (at DSDP Site 522) by Miller et al. (1991) as an isotope stratigraphic 'zone' between one oxygen isotope peak and another, corresponding to a duration of several millions of years. Here there was a distinction between the 'Zone Oi-1' and the 'Oi-1 Event', the latter being equivalent to our EOIS. Subsequent articles variously refer to 'Oi-1' as an extended isotope zone, the peak  $\delta^{18}\text{O}$  value at the base of that

155 zone, an extended phase of high  $\delta^{18}\text{O}$  values in the lower Oligocene approximately synonymous with the EOGM, or the 'step' that led up to the peak value (see discussion and references in Coxall and Pearson, 2007, p. 352). The terms 'Oi-1a' and 'Oi-1b', originally defined by Zachos et al. (1996) as "...two distinct, 100 to 150-kyr-long glacial maxima...separated by an 'interglacial' ", have also been inconsistently applied in the literature and are now arguably an impediment to clear communication. Due to this ambiguity, we avoid the term 'Oi-1' here. Katz et al. (2008) referred to prominent oxygen isotope

160 steps within the EOT as 'EOT-1' and 'EOT-2', which might seem a convenient nomenclature for the steps referred to here, but whereas 'EOT-1' arguably corresponds to the 'Step 1' of Coxall and Pearson (2007), 'EOT-2' was a separate feature identified in the St. Stephen's Quarry record some way below the level identified as 'Oi-1' (Katz et al. 2008, p330). Hence it is not appropriate to use 'EOT-2' to denote the second step. Note, for clarity, the EOIS is not instantaneous and several records show some 'intermediate' values; its inferred duration in the records presented here is in the tens of kyr (40 kyr at Site 1218, Coxall

165 et al., 2005).

**Deleted:** Coxall and Wilson, 2011

**Deleted:** less

**Deleted:** , particularly in benthic records (Fig. 1).

**Deleted:** in deep ocean sediments. At Site 1218

**Deleted:** prominent

**Deleted:** steps

**Deleted:** benthic

**Deleted:** , while closely coupled to those in  $\delta^{18}\text{O}$

**Deleted:** (Coxall et al., 2005)

**Deleted:**

**Deleted:** probably

**Deleted:** the

**Deleted:** The important climatic event that corresponds to the larger second  $\delta^{18}\text{O}$  step (in some records) has frequently been termed 'Oi-1' after

**Deleted:** . However, that term was originally defined

**Deleted:** In that original meaning, Oi-1 encompasses and extends well above the interval of maximum early Oligocene  $\delta^{18}\text{O}$  that corresponds to most of Chron C13n and is interpreted as the Early Oligocene Glacial Maximum (EOGM; Liu et al. 2004) (Fig. 1). Moreover, being a peak-to-peak interval, by definition it excludes the interval of  $\delta^{18}\text{O}$  increase that led up to the  $\delta^{18}\text{O}$  peak. Because Oi-1 has variously been used as a term to describe 1) an extended isotope zone, 2) the peak  $\delta^{18}\text{O}$  value at the base of that zone, 3)

**Deleted:** and 4)

**Deleted:** 352), we avoid the term here. Instead we suggest that if it is to be used, it should be employed in its original sense (Miller et al., 1991). Similarly the term 'Oi-1a' and 'Oi-1b' have been applied inconsistently in the literature and are now arguably an impediment to clear communication.

**Deleted:** ; in that paper used to denote the  $\delta^{18}\text{O}$  maximum).

**Deleted:** Insofar as it is useful to have a term for the important isotope step that occurs well after the EOB and within the lower part of Chron C13n, we here suggest "Earliest Oligocene oxygen Isotope Step" (EOIS) to distinguish it from Oi-1, EOGM, and the extended (~500 kyr) EOT isotope 'shift'.

**Deleted:** absolute

**Deleted:** that

**Deleted:** (Figure 1);

**Deleted:** krys

**Formatted:** English (US)

Event	Abbr.	Definition	Correlation	Timing	Comment	Also known as
Early Oligocene Glacial Maximum	EOGM	Period of cold climate / glaciation in the early Oligocene corresponding to most of Magnetic Chron C13n	Peak to peak $\delta^{18}\text{O}$ stratigraphic interval starting at the top of the EOIS & extending to another peak around the top of C13n	33.65 Ma to ~33.57 Ma, ~ 490 kyr duration	Defined by Liu et al. (2004). The end of the EOGM may correspond to a 2nd $\delta^{18}\text{O}$ peak sometimes referred to as Oi-1b	Oi-1 (Zachos et al., 1996) including the separate $\delta^{18}\text{O}$ maxima Oi-1a and Oi-1b
Chron C13n	C13n	Interval of normal magnetic polarity in the early Oligocene broadly correlative with the EOGM	Between specific magnetic reversals	33.705 - 33.157 Ma (GTS2012)	Very useful for correlation & dating when available	-
Eocene - Oligocene Transition	EOT	A phase of accelerated climatic & biotic change that began before and ended after the EOB	Stratigraphic interval between the extinction of <i>Discoaster saipanensis</i> & the top of the EOIS	Start = 'Top' <i>D. saipanensis</i> extinction event; End = end of EOIS $\delta^{18}\text{O}$ maximum event. Duration ~790 kyr.	Definition revised here after Coxall & Pearson (2007)	-
Earliest Oligocene oxygen isotope Step	EOIS	Short period of rapid $\delta^{18}\text{O}$ increase (0.7‰ or more) that occurred well after the EOB & within the lower part of Chron C13n	Stratigraphically above the EOB & within the lowermost part of Chron C13n	The peak is at ~33.65 Ma (GTS2012) Duration ~40 kyr.	Herein defined. Defines the end of the EOT and the start of the EOGM	The 'Oil Event' "... at the base of Zone Oil", Miller et al. (1991); Oi-1a of Zachos et al. (1996)
Eocene Oligocene boundary	EOB	The stratigraphic boundary between the Eocene and Oligocene Epochs defined at the Messignano GSSP	Denoted by the extinction of the planktonic foraminifera <i>Hantkenina</i> in the marine realm	33.9 Ma (GTS2012) 33.7 Ma (CK95)	-	Base Oligocene epoch; base Rupelian stage
Step-1	-	The first step increase in $\delta^{18}\text{O}$ occurring shortly before the EOB in some records	Harder to identify & correlate than the EOIS.	? ~34.15 Ma, Duration ~40 kyr.	-	EOT-1, Katz et al. (2008); 'Precursor glaciation', Scher et al. (2011)
Late Eocene Event	-	A transient late Eocene cool or glacial event near the start of the EOT	Transient interval of positive $\delta^{18}\text{O}$ seen in some records.	Onset is coincident (within 80 kyr analytical error; Coxall et al., 2005) with the <i>D. saipanensis</i> extinction (34.44 Ma) at Site 1218.	Defined by Katz et al. (2008) Defines the start of the EOT as defined herein	-
Priabonian oxygen isotope maximum	PrOM	A transient late Eocene cool or glacial event	Transient interval of positive $\delta^{18}\text{O}$ seen in some records well below the EOT	~37.3 Ma. Duration ~140 kyrs, tentatively placed within Chron C17n.1n	Defined by Scher et al. (2014)	-

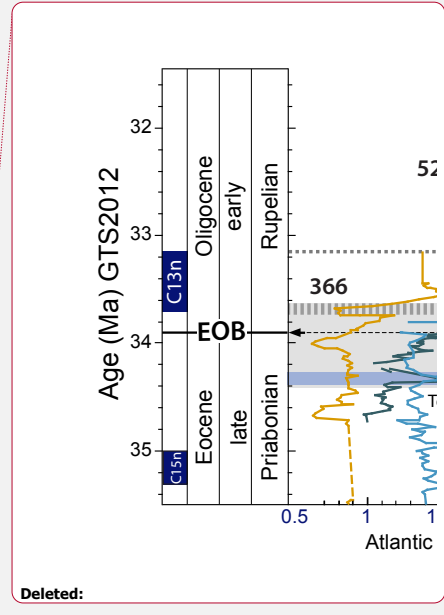
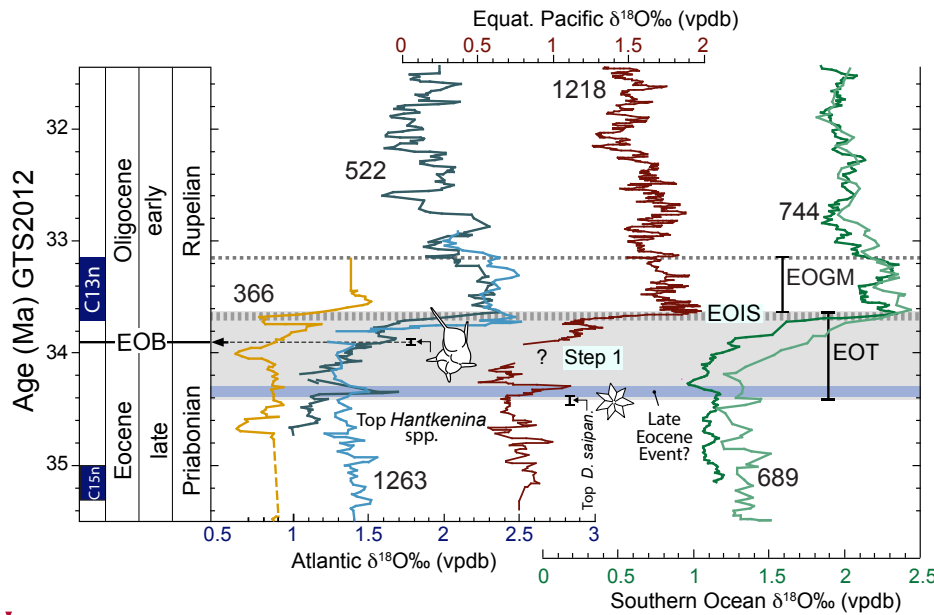
**Table 1:** Summary of Eocene Oligocene terminology and approximate timings of events, as interpreted at the time of writing. Timescales referred to are GTS2012 (Gradstein et al., 2012) and CK95 (Cande and Kent, 1995).

This brings us back to the definition of the 'EOT'. Based on the stratigraphic record from Tanzania, Dunkley Jones et al. (2008) and Pearson et al. (2008) placed the base of the EOT at the extinction of the tropical warm-water nannofossil *Discoaster saipanensis*, a reliable bioevent which they regarded as the first sign of biotic extinction associated with the late Eocene cooling. This extinction event has long been used to mark the base of nannofossil Zone NP21 (Martini, 1971) or more recently Zone CNE21 (Agnini et al., 2014). On the timescale used by Dunkley Jones et al. (2008) it was estimated to be 500 kyr before the top of the EOIS. However, a subsequent calibration from ODP Site 1218 (Blaj et al., 2009) placed this event significantly earlier than previously suggested, which is supported by recent work in Java (Jones et al., 2019). In the record from Site 1218 the *D. saipanensis* extinction is coincident (within 80 kyr analytical error; Coxall et al., 2005) with the base of a significant  $\delta^{18}\text{O}$  increase – possibly a 'failed' glaciation – that seems to be visible in many of the records (including Tanzania) and has been termed the 'Late Eocene Event' by Katz et al., (2008). It seems desirable to include these biotic and climatic events within the definition of the EOT rather than insist on an arbitrary 500 kyr duration. On the most commonly used current timescale, 'Geological Timescale 2012' (GTS2012; Gradstein et al., 2012), the critical levels are calibrated as follows: top of the EOIS at 33.65 Ma, base of Chron C13n at 33.705 Ma, EOB at 33.9 Ma, and extinction of *D. saipanensis* at 34.44 Ma. Hence the

Deleted: .

225 stratigraphic interval of the EOT according to our preferred definition is now given an estimated duration of 790 kyr (Figure 1). This terminology and the alternatives are summarized in Table 1 and illustrated below in Figure 1.

Deleted: (Figure 1).



Deleted:

230 **Figure 1:** Oxygen stable isotope and chrono-stratigraphic characteristics of the Eocene-Oligocene transition (EOT) from deep marine records and EOT terminology on the GTS 2012 time scale. Benthic foraminiferal  $\delta^{18}\text{O}$  from six deep sea drill holes are shown: [tropical Atlantic Site 366](#), [South Atlantic Sites 522 and 1263](#) (Zachos et al. 1996; Langton et al., 2016); [Southern Ocean Sites 744 and 689](#) (Zachos et al. 1996; Diester-Haass and Zahn 1996) and the [Equatorial Pacific Site 1218](#) (Coxall and Wilson 2011). Due to different sample resolutions, running means are applied using a 3-point filter for Sites 522, 689 and 1263, 5-point filter for Sites 366 and 744 and a 7-point filter for Site 1218. Time scale conversions were made by aligning common magneto-stratigraphic tie points. The EOT is defined as a [ca. 790 kyr](#) long phase of accelerated climatic and biotic change that began before and ended after the Eocene-Oligocene boundary (EOB) (after Coxall and Pearson (2007)). It is bounded at the base by the 'Top' *D. saipanensis* nannofossil extinction event, and above by the EOIS- $\delta^{18}\text{O}$  maximum. Benthic data are all *Cibicides* spp. or 'Cibs. Equivalent' and have not been adjusted to sea water equilibrium values. 'Step-1' comprises a modest  $\delta^{18}\text{O}$  increase linked to ocean cooling (Lear et al., 2008; Bohaty et al., 2012). The 'Top *Hantkenina* spp.' marker corresponds to the position of this extinction event at DSDP Site 522 (including sampling bracket) with respect to the corresponding Site 522  $\delta^{18}\text{O}$  curve. That it coincides with the published calibrated age of this event (33.9 Ma) is entirely independent. The 'Late Eocene Event'  $\delta^{18}\text{O}$  maximum (after Katz et al., 2008) may represent a failed glaciation.

Deleted: 366,

Deleted: 500

Deleted: ) 'Step-2' corresponds to the Early Oligocene oxygen Isotope Step (EOIS), defined herein.

Deleted: (T)

Deleted:

Deleted: initial

240 Combined  $\delta^{18}\text{O}$  and trace element investigations (see Section 3.2) have led to the suggestion that the  $\delta^{18}\text{O}$  increase commonly referred to as Step-1 (Figure 1) is mostly attributable to ocean cooling, with subordinate ice sheet growth, whereas the more

255 prominent  $\delta^{18}\text{O}$  increase at the end of the EOT (i.e., the EOIS in our terminology) largely represents ice growth with a little  
further cooling (Bohaty et al., 2012; Katz et al., 2008; Lear et al., 2008). Estimates of the combined total sea-level fall across  
the EOT are on the order of 70 m (Miller et al., 2008; Wilson et al., 2013) and microfacies and paleontological records from  
shelf environments (Houben et al., 2012) are consistent with this generalization. A recent shallow marine sediment record also  
indicates the onset of major glaciation at  $\sim 33.7$  Ma (Gallagher et al., 2020), in agreement with deep sea records. The EOIS is  
the sharpest feature in most records, culminating with the highest benthic  $\delta^{18}\text{O}$  values of the Eocene and Oligocene. It is widely  
260 suggested that it signifies the initiation of major sustained Antarctic glaciation, most likely an early East Antarctic Ice Sheet  
(EAIS) (Bohaty et al., 2012; Coxall et al., 2005; Galeotti et al., 2016; Miller et al., 1987; Shackleton and Kennett, 1975; Zachos  
et al., 1992). The EOGM is interpreted as an approximately 500 kyr-long glacial maximum, with lower values visible in some  
records Zachos et al., 1996; Liu et al. 2004) (Figure 1). Oxygen isotope maxima in the late Eocene imply substantial ephemeral  
precursor glaciations in the approach to the EOT (Galeotti et al., 2016; Houben et al., 2012; Katz et al., 2008; Scher et al.,  
265 2011, 2014). The oldest and most prominent of these hypothesized transient glacial events occurred at  $\sim 37.3$  Ma (within  
magnetostratigraphic C17n) and is referred to as the Priabonian Oxygen Isotope Maximum (PrOM) Event (Scher et al., 2014). The  
'Late Eocene Event' of Katz et al. (2008) at  $\sim 34.15$  Ma may be regarded as the second, the third being  $\delta^{18}\text{O}$  'Step-1' at  $\sim 34$   
Ma (the 'precursor glaciation' of Scher et al., 2011). Nevertheless, differences between  $\delta^{18}\text{O}$  curves from different water  
depths and ocean regions, combined with increasing detail in individual records afforded by high-resolution sampling  
270 emphasizes that the EOT cannot be adequately understood as a series of discrete events because it is clearly imprinted by  
orbitally paced variability throughout (Coxall et al., 2005).

A detailed discussion of the *Hantkenina* extinction and associated bioevents at the EOB was provided by Berggren et al.,  
(2018, p 30-32). The highest stratigraphic occurrence of the planktonic foraminifera family Hantkeninidae denotes the EOB  
275 in its type section (Nocchi et al., 1986). This is thought to have involved simultaneous extinction of all five morphospecies  
and two genera of late Eocene hantkeninids (Coxall and Pearson, 2007) (Figure 1). Insofar as the principles of biostratigraphy  
require a particular species to denote a biozone boundary, the commonest species *Hantkenina alabamensis* is used to define  
the base of Zone O1 (Berggren et al., 2018; Berggren and Pearson, 2005; Wade et al., 2011). The extinction of *H. alabamensis*  
can be considered the 'primary marker' for worldwide correlation of the EOB. It occurs at a slightly higher (later) level than  
280 another set of prominent planktonic foraminifer extinctions, namely *Turborotalia cerroazulensis* and related species. DSDP  
Site 522 (South Atlantic), thus far, is one of the few deep sea records to have both a detailed  $\delta^{18}\text{O}$  stratigraphy and planktonic  
foraminifera assemblages that capture these evolutionary events. Here, the *Hantkenina* extinction horizon occurs  
approximately two thirds of the way through the EOT (Figure 1). It occurs at a similar relative position in the hemipelagic  
EOT sequence in Tanzania (Pearson et al., 2008), also in unpublished data from Indian Ocean ODP Site 757 (Coxall et al.,  
285 unpublished). This finding implies that the extinction of the hantkeninids was approximately synchronous although its cause  
is currently unknown. Existing constraints on the hantkeninid extinction horizon remain rather coarse in terms of sampling

Deleted: modest

Deleted: The prominent isotope step that marks the end of the EOT (i.e., the EOIS in our terminology) is the sharpest feature in most records, culminating with the highest  $\delta^{18}\text{O}$  values of the Eocene and Oligocene.

Deleted: interval of

Deleted: early Oligocene  $\delta^{18}\text{O}$  that corresponds to most of Chron C13n is interpreted as an the Early Oligocene Glacial Maximum (EOGM)

Deleted: (Fig. 1).

Deleted: on

Deleted: occurs

Deleted: Although precise correlation of the records is uncertain due to the limited stratigraphic resolution, two younger hypothesized events are shown in Figure 1: one at about 34.15 Ma ('

Deleted: ,

Deleted: ,

Deleted: and another at  $\sim 33.9$  Ma, which corresponds to

Deleted: , and is apparently coincided with

Deleted: E/O boundary. This 33.9 Ma step has been previously referred to as the 'Precursor

Deleted: (Scher et al., 2011) and EOT-1 (Katz et al., 2008).

Formatted: English (AUS)

Deleted: recently

Deleted: (Fig. 1).

Deleted: the

Deleted: *T. coccoensis* and *T. cunialensis*

Deleted: globally

Deleted: and may have been a response to the EOT cooling phase of the late Eocene



resolution compared to many isotopic records and the matter will benefit greatly from incoming high-resolution records from Site U1411, which boasts both excellent (glassy) preservation and orbital level sampling.

320 Dating and correlation of non-marine records, which usually lack  $\delta^{18}\text{O}$  stratigraphy, is more challenging and there are far fewer well-dated records on land. Here a strict concept of the EOT is difficult to apply and relies on correlations using other stratigraphic approaches, including magnetostratigraphy and palynomorph or mammal tooth biostratigraphy that have been cross calibrated in a few marine and marginal-marine sections (Abels et al., 2011; Dupont-Nivet et al., 2007, 2008; Hooker et al., 2004). Central Asian sections are the exception, where even the step features of the EOT can be identified using magneto, bio- and cyclostratigraphy (Xiao et al., 2010). Moreover, combined  $\delta^{18}\text{O}$  and clumped isotope analyses on fresh water 325 gastropod shells from a terrestrial EOT section in the south of England has permitted the first direct correlation of marine and non-marine realms and identified coupling between cooling and hydrological changes in the terrestrial realm (Sheldon et al., 2016). This finding suggests a close timing and causal relation between the earliest Oligocene glaciation and a major Eurasian mammalian turnover event called the 'Grande Coupure' (Hooker et al., 2004; Sheldon et al., 2016). During the Grand Coupure, many endemic European mammal species became extinct and were replaced by Asian immigrant species. These changes have 330 been attributed to a combination of climate-driven extinction and species dispersal due to the closing of Turgai Strait; which provided a greater connection between Europe and Asia (Akhmetiev and Beniamovski, 2009; Costa et al., 2011; Hooker et al., 2004).

In shallow water carbonate successions, the EOB has traditionally been approximated by the prominent extinctions of a series 335 of long-ranging larger benthic foraminifers (LBFs) often called orthophragminids (corresponding to the Families Discocyclinidae and Asterocyclinidae; Adams et al. 1986). The general expectation was that these extinctions likely occurred at the time of maximum ice growth and sea level regression – in our terminology the EOIS. However, evidence from Tanzania (Cotton and Pearson, 2011) and Indonesia (Cotton et al., 2014), suggest that the extinctions occurred within the EOT. In 340 Tanzania the extinctions occur quite precisely at the level of the EOB, hinting that the EOB itself may have had a global cause affecting different environments, possibly independent of the events that caused the isotope increases (Cotton and Pearson, 2011).

The definition of the EOT used here excludes the long-term Eocene cooling trend. That trend began in the Ypresian (early Eocene) and continued through much of the Lutetian and Bartonian (middle Eocene; albeit interrupted by the Middle Eocene Climatic Optimum; MECO; Bohaty and Zachos 2003) and Priabonian (late Eocene) (Cramwinckel et al., 2018; Inglis et al., 2015; Liu et al., 2018; Šliwińska et al., 2019; Zachos et al., 2001). In particular, prominent extinctions in various marine groups occurred around the beginning of the Priabonian (late Eocene), possibly connected with global cooling (e.g. Wade and Pearson 2008; note that the base of the Priabonian has recently been defined in the Alano section in Italy; Agnini et al., 2020). These

**Deleted:** isotopes

**Deleted:** strengthens

**Deleted:** case that the large evolutionary turnover in mammals that occurred during the EOT (the 'Grande Coupure') coincides with the onset of

**Deleted:** , and therefore was linked with the associated climate change

**Deleted:** this view is not supported by

**Deleted:** , which

**Deleted:** (Cramwinckel et al., 2018; Inglis et al., 2015; Liu et al., 2018; Zachos et al., 2001)

**Deleted:** although we note that the base of the Priabonian has yet to be defined by GSSP).

data are excluded by our definition from the EOT but may be part of the same general long-term pattern. In some stratigraphic records, especially terrestrial ones, it may not be easy to distinguish these longer-term events from the EOT.

## 2 Proxy evidence for paleogeography, ocean circulation, and terrestrial ice evolution

365 Here we discuss proxy evidence for the global paleogeography of the EOT (Section 2.1) including the state and evolution of ocean gateways (Section 2.2), and proxy evidence for ocean circulation (Section 2.3) and Antarctic glaciation (Section 2.4). We then briefly discuss the timing of the Northern Hemisphere glaciation (Section 2.5).

### 2.1 Tectonic Reconstruction

The tectonic evolution of the southern continents, opening a pathway for the Antarctic Circumpolar Current, has long been linked with long-term Eocene cooling and the EOT (Kennett et al., 1975). However, there remain major challenges in reconstructing the paleogeography at or around the EOT, requiring a series of methodological steps (Baatsen et al., 2016; Kennett et al., 1975; Markwick, 2007, 2019; Markwick and Valdes, 2004; Müller et al., 2008). The first step is to use modern geography and relocate the continental and ocean plates according to a plate tectonic evolution model, used in software such as GPlates (Boyden et al., 2011). This software uses the interpretation of seafloor spreading and paleomagnetic data to reconstruct relative plate motion (e.g. Scotese et al. 1988), and an absolute reference frame to position the plates relative to the Earth's mantle (e.g. Dupont-Nivet et al. 2008). Currently, there are two such absolute reference frames: one based on a global network of volcanic hot-spots (Seton et al., 2012) and one based on a paleomagnetic reference frame (van Hinsbergen et al., 2015; Torsvik et al., 2012). Importantly, these two reference frames give virtually the same continental outlines, but the orientation of the continents is shifted. This results in differences in continental positions between the reference frames of up to 5-6° (Baatsen et al., 2016) around the EOT, creating an uncertainty in reconstructing paleogeography, especially in southern latitudes between 40 to 70 °S where important land and ocean geological archives exist. This latitudinal uncertainty also impacts the reconstruction of Antarctic glaciation, since glacial dynamics are highly sensitive to latitude.

After the plate tectonic reconstruction has been applied, adjustments are needed to capture the age-depth evolution of the seafloor (Crosby et al., 2006) and seafloor sedimentation rate (Müller et al., 2008). Adjusting land topography is more difficult, and requires knowledge of paleoaltimetry, including processes such as plate collision processes, uplift, subsidence and erosion. Several publicly available reconstructions exist for the Eocene; Markwick (2007) reconstructed paleotopography for the late Eocene (38 Ma), while Sewall et al. (2000) and more recently (Zhang et al., 2011) and Herold et al. (2014) have generated paleotopographies for the early Eocene (~55 to 50 Ma). These are based on the Hot Spot reference frame. Baatsen et al. (2016) have recently created a paleogeographic reconstruction of the late Eocene using the Paleomagnetic reference frame. Such efforts to develop realistic paleogeography for each time slice represents a major undertaking in blending geomorphic evidence with tectonic evolution, and thus includes many specific details that are beyond the scope of this review.

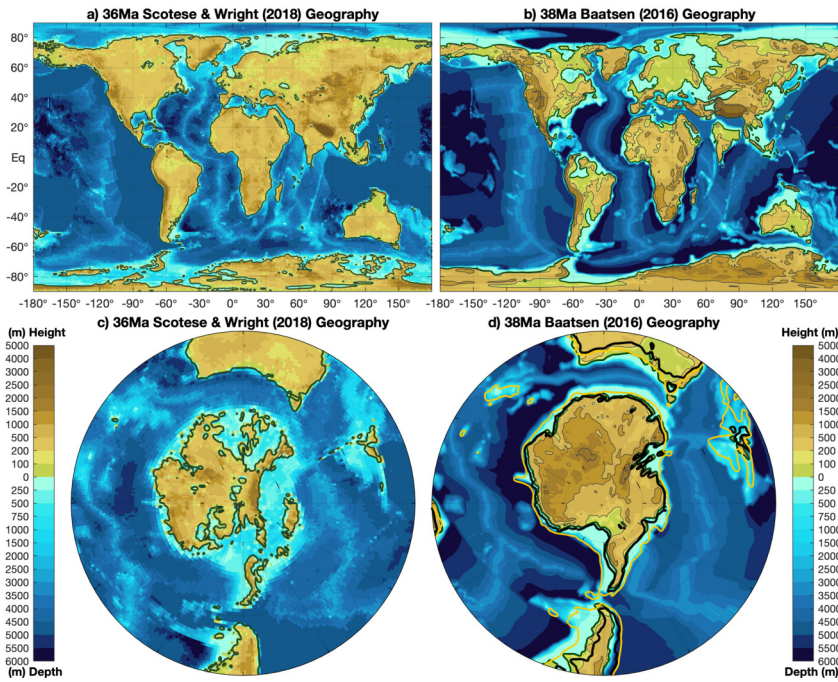
Deleted: day

395 Recently, a stage-by-stage paleogeographic reconstruction of the entire Phanerozoic has been made publicly available in digital  
format (Scotese and Wright, 2018). This includes snapshots of the Priabonian (35.9 Ma) and Rupelian (31 Ma). Another stage-  
by-stage reconstruction of Cenozoic paleogeography evolution originates from Markwick (2007); this reconstruction has been  
incorporated into a modelling study of climate dependence on paleogeography (Farnsworth et al., 2019; Lunt et al., 2016), and  
paleogeography changes across the EOT (Kennedy et al., 2015). However, the most recent versions of the (Markwick, 2007)  
400 paleogeography reconstructions are proprietary and are thus not included in this paper. Therefore, we present a summary of  
late Eocene (38 Ma) paleogeography in

Figure 2 from the publicly available datasets of Baatsen et al. (2016) and Scotese and Wright (2018). Our aim here is not to  
evaluate these reconstructions, but to present them such that their differences can be taken as broadly indicative of the  
uncertainties in paleogeography at this time. ▲

405 The reconstructions contain several notable regions of uncertainty which we briefly mention. They include (i) the Tibetan  
Plateau and the Indian subcontinent, where there are clear disagreements between the reconstructions, (ii) the Turgai strait and  
Tethys region, which has far greater shallow marine shelf regions in the Baatsen et al. (2016) reconstruction, (iii) the Fram  
Strait, which is arguably closed by the Eocene-Oligocene transition but is open in both reconstructions (Lasabuda et al., 2018),  
410 and (iv) the Rocky Mountains and North American continent exhibit key differences in elevation and coastlines, which has  
implications for Eocene-Oligocene climate evolution (Chamberlain et al., 2012). A full review of these uncertainties is beyond  
the scope of this paper, however we briefly discuss some impacts of these paleogeography uncertainties on terrestrial  
temperature reconstructions in Section 4, while we discuss the impacts on ocean circulation in Section 2.2 and 2.3.

Formatted: English (AUS)



415

420

**Figure 2:** Paleogeography at the late Eocene showing two alternative reconstructions. (a) and (c) use the Hot Spot reference frame, using the Scotese and Wright (2018) paleogeography at 36 Ma, while (b) and (d) use the Paleomagnetic reference frame showing the reconstruction of Baatsen et al. (2016) at 38 Ma. These two reconstructions use different methodologies, and are presented as broadly indicative of the uncertainties in paleogeography at this time. Also shown in (d) are post-EOT coastlines at 30 Ma (black contours) and 1000 m depth (orange contours), which illustrate the widening of the Southern Ocean gateways during the 8 Myr interval around the EOT.

## 2.2 Southern Ocean Gateways

A long-held hypothesis on the cause of the EOT glaciation is that Antarctica cooled because of tectonic opening of Southern Ocean gateways (Barker and Burrell, 1977; Kennett, 1977). This mechanism suggests that the onset of the Antarctic Circumpolar Current (ACC) reorganised ocean currents from a configuration of subpolar gyres with strong meridional heat transport to predominantly zonal flow, thereby causing thermal isolation of Antarctica (Barker and Thomas, 2004). The hypothesis is supported by foraminiferal isotopic evidence from deep sea drill cores in the Southern Ocean, which indicate a

shift from warm to cold currents (Exon et al., 2004). As such, there has been considerable effort to reconstruct the tectonic  
430 history of the Southern Ocean gateways.

The Drake Passage opening has been dated to around 50 Ma (Livermore et al., 2007) or even earlier (Markwick, 2007);  
however it was likely shallow and narrow at this time. The timing of the transition to a wide and deep gateway, potentially  
capable of sustaining a vigorous ACC, occurred on a timescale of tens of millions of years. Even with substantial widening of  
435 Drake Passage, several intervening ridges in the region are likely to have blocked the deep circumpolar flow (Eagles et al.,  
2005). These barriers may have not have cleared until the Miocene at around 22 Ma (Barker and Thomas, 2004; Dalziel et al.,  
2013). The evolution of the Tasman Gateway is better constrained. Geophysical reconstructions of continent-ocean boundaries  
(Williams et al., 2011) place the opening of a deep (greater than ~500 m) Tasmanian Gateway at  $33.5 \pm 1.5$  Ma (Scher et al.,  
2015; Stickley et al., 2004). Marine microfossil records suggest the circumpolar flow was initially westward (Bijl et al., 2013).  
440 Multiproxy based evidence from ODP Leg 189 suggests that the opening of the Tasmanian Gateway significantly preceded  
Antarctic glaciation and might therefore not been its primary cause (Huber et al., 2004; Stickley et al., 2004; Wei, 2004). The  
results also indicate that the gateway deepening at the EOT initially produced an eastward flow of warm surface waters into  
the southwestern Pacific, and not of cold surface waters as previously assumed. Subsequently, the Tasmanian Gateway steadily  
opened during the Oligocene, hypothesised to cross a threshold when the northern margin of the ACC aligned with the westerly  
445 winds (Scher et al., 2015), triggering the onset of an eastward flowing ACC at around 30 Ma. However, the westerly winds  
can also shift position due to changes in orographic barriers or an increase in the meridional temperature gradient after  
glaciation. Thus, the opening of Southern Ocean gateways approximately coincides with the EOT, but with large uncertainty  
on the timing and implications. We discuss modelling of this mechanism in Section 6.1.

### 2.3 Meridional overturning circulation

450 Throughout much of the Eocene, deep water formation is suggested to have occurred dominantly in the Southern Ocean and  
the North Pacific (Ferreira et al., 2018), based on numerical modelling and supported by stable and radiogenic isotope work  
(Cramer et al., 2009; McKinley et al., 2019; Thomas et al., 2014). A shift in the north-south gradient of  $\delta^{13}\text{C}$  and decrease in  
South Atlantic  $\epsilon_{\text{Nd}}$  around the EOT suggests that North Atlantic convection may have begun or strengthened at this time (Katz  
et al., 2011; Via and Thomas, 2006), although other studies suggest that some kind of North Atlantic overturning operated  
455 from the middle Eocene (Boyle et al., 2017; Hohbein et al., 2012; Vahlenkamp et al., 2018a, 2018b). Significant seafloor  
spreading was occurring in the Southern Hemisphere, such that these changes in ocean circulation have previously been  
explained by the opening of Southern Ocean gateways (Borrelli et al., 2014). Moreover, interactions between the Arctic and  
Atlantic oceans are gaining interest as potential triggers of a late Eocene proto Atlantic meridional overturning circulation  
(AMOC; Hutchinson et al., 2019). Data from the Labrador Sea and western North Atlantic margin indicate that North Atlantic  
460 waters became saltier and denser from 37 to 33 Ma (Coxall et al., 2018). This densification may then have strengthened or

even triggered an AMOC, suggesting a possible forcing mechanism for Antarctic cooling that predates the EOT and Southern Ocean gateway openings.

465 Proxy records suggest that the Arctic Ocean was much fresher during the Eocene than the present day, with typical surface salinities around 20-25 psu and periodic excursions to very low salinity conditions (<10 psu) (Brinkhuis et al., 2006; Kim et al., 2014; Waddell and Moore, 2008). Outflow of this fresh surface water into the North Atlantic can potentially prohibit deep water formation (Baatsen et al., 2020; Hutchinson et al., 2018). A new line of evidence suggests that deepening of the Greenland-Scotland Ridge (GSR) around the EOT may have enabled North Atlantic surface waters to become saltier (Abelson and Erez, 2017; Stürz et al., 2017), by allowing a deeper exchange between the basins. A related hypothesis derived from sea 470 level and paleo-shoreline estimates in the Nordic Seas is that the Arctic likely became isolated during the Oligocene (Hegewald and Jokat, 2013; O'Regan et al., 2011). Thus a gradual constriction of the connection between the Arctic and Atlantic presents a newly hypothesised priming mechanism for establishment of a well-developed AMOC (Coxall et al., 2018; Hutchinson et al., 2019).

#### 2.4 Antarctic glaciation

475 Although transient glacial events on Antarctica are proposed for the late Eocene, the most significant long term glaciations likely began on eastern Antarctica on the Gamburtsev Mountains and other highlands (Young et al., 2011) as a result of rapid global cooling in the early Oligocene around 33.7 Ma (EOGM, Figure 1). Evidence for glacial discharge into open ocean basins in the earliest Oligocene is long established, with ice-rafted debris (IRD) appearing in deep-sea Southern Ocean sediment cores (Zachos et al., 1992). Since these initial results, efforts have continued to document and understand early 480 Cenozoic Antarctic ice dynamics (Barker et al., 2007; Francis et al., 2008; McKay et al., 2016). Combining perspectives from marine geology, geophysics, geochemical proxies and modelling, these efforts have largely focused on the evolution and stability of the early Oligocene Antarctic ice sheets, and estimates of ice volume contributions to sea-level change. Other important developments in the study of Antarctic ice include modelled thresholds for Antarctic glaciation (DeConto et al., 2008; Gasson et al., 2014), and improved reconstructions of Eocene-Oligocene subglacial bedrock topography (from airborne 485 radar surveys). These bedrock reconstructions are important for reconstructing the nucleation centres of precursor ice sheets (Scher et al. 2011, 2014) and subsequent development of continental-sized ice sheets (Bo et al., 2009; Thomson et al., 2013; Wilson et al., 2013; Wilson and Luyendyk, 2009; Young et al., 2011).

Evidence for glaciation in the Weddell Sea and Ross Sea suggest that there was an increase in physical weathering over West 490 Antarctica around the EOT (Anderson et al., 2011; Ehrmann and Mackensen, 1992; Huang et al., 2014; Olivetti et al., 2015; Scher et al., 2011; Sorlien et al., 2007). However, in the Ross Sea, evidence suggests that an expansion over West Antarctica in Marie Byrd Land occurred after the EOT (Olivetti et al., 2013), while in the Weddell Sea sedimentation rates were still lower than recent times, suggesting the West Antarctic ice sheet was not expanded to modern proportions (Huang et al., 2014).

Deleted: Fig. 1).

495 This is consistent with approximations of ice volume based upon oxygen isotopes (Bohaty et al., 2012; Lear et al., 2008) and  
is supported by the record of relatively diverse vegetation around at least coastal regions of Antarctica through the Oligocene  
(Francis et al., 2008).

Recent evidence has emerged of transient ‘precursor’ Antarctic glaciations occurred in the late Eocene (Carter et al., 2017;  
Escutia et al., 2011; Passchier et al., 2017; Scher et al., 2014), suggesting a ‘flickering’ transition out of the greenhouse.  
500 Importantly, several Southern Ocean sites revealed evidence that Antarctic glaciation induced crustal deformation and  
gravitational perturbations resulting in local sea level rise close to the young Antarctic ice sheet (Stocchi et al., 2013). Finally,  
detailed core sedimentary records drilled close to Antarctica in the western Ross Sea invoke a transition from a modestly sized  
highly dynamic late Eocene-early Oligocene ice sheet, existing from ~34 - 32.8 Ma, to a more stable, continental-scale ice  
505 sheet thereafter, which calved at the coastline (Galeotti et al., 2016).

## 2.5 Northern hemisphere glaciation

While there is clear evidence for Antarctic glaciations at the EOT, the question of contemporaneous northern hemisphere  
glaciation ~~is contentious~~. The prevailing view is that the Oligocene represented a non-modern-like state with only Antarctica  
glaciated ~~(Westerhold et al., 2020; Zachos et al., 2001)~~. Glaciation in mountain areas around the globe is suggested to have  
510 followed through the Miocene and Pliocene, with evidence for the first significant build-up of ice on Greenland (in the southern  
highlands) traced to the late Miocene, sometime between 7.5 - 6 Ma (Bierman et al., 2016; Larsen et al., 1994; Maslin et al.,  
1998; Pérez et al., 2018) or as early as 11 Ma (Helland and Holmes, 1997). Northern Hemisphere glaciation intensified during  
the late Pliocene (~2.7 Ma) when large terrestrial glaciers began rhythmically advancing and retreating across North America,  
Greenland, and Eurasia ~~(Bailey et al., 2013; Ehlers and Gibbard, 2007; Lunt et al., 2008; Maslin et al., 1998; Raymo, 1994;  
515 De Schepper et al., 2014; Shackleton et al., 1984)~~. It is important to note that ~~a delay in northern hemisphere glaciation relative  
to Antarctica is predicted by climate models—the stabilizing effect of the hysteresis in the height-mass balance feedback  
becomes weaker with greater distance from the poles (Pollard and DeConto, 2005), because with decreasing latitude summers  
become warmer for a given radiative forcing (DeConto et al., 2008)~~.

520 ~~Nevertheless, a series of studies (Tripathi et al., 2005, 2008; Tripathi and Darby, 2018) argue that bipolar glaciation was triggered  
in the Eocene and/or Oligocene. This suggestion is based on two lines of evidence from the sedimentary record: (i) estimates  
of global seawater  $\delta^{18}\text{O}$  values (Tripathi et al., 2005) and (ii) identification of ice-transported sediment grains inferred to have  
originated from Greenland in both interior Arctic Ocean and subarctic Atlantic sediment cores associated with the EOT (Eldrett  
et al., 2007), or earlier (middle Eocene) (St. John, 2008; Tripathi and Darby, 2018; Tripathi et al., 2008). Certainly, several lines  
525 of evidence provide support for winter sea ice in the Arctic from the middle Eocene (Darby, 2014; St. John, 2008; Stickley et  
al., 2009) and perennial sea ice from 13 Ma (Krylov et al., 2008). It is possible that small mountain glaciers on East Greenland,  
perhaps comparable to the modern Franz Josef and Fox Glaciers of New Zealand (which extend from the Southern Alps~~

**Deleted:** remains equivocal.

**Deleted:** (Zachos et al., 2001)

**Deleted:** (Bailey et al., 2013; DeConto et al., 2008; Ehlers and Gibbard, 2007; Lunt et al., 2008; Maslin et al., 1998; Raymo, 1994; De Schepper et al., 2014; Shackleton et al., 1984).

**Deleted:** delayed

**Deleted:** from

**Deleted:** (Pollard and DeConto, 2005)

**Deleted:** However, a series of studies argue that bipolar glaciation happened earlier than the late Miocene. Evidence for this theory is based on global seawater  $\delta^{18}\text{O}$  budgets

**Formatted:** English (UK)

**Deleted:** (Tripathi et al., 2005) and

540 through lush rain forest), reached sea level during cooler orbital phases of the Eocene, intensifying in the late Eocene and early  
Oligocene (Eldrett et al., 2007). Yet, the results of a recent detailed analysis of expanded EOT sections from the North  
Atlantic's modern day iceberg alley on the Newfoundland margin are inconsistent with the presence of extensive ice sheets on  
southern and western Greenland and the northeastern Canadian Arctic, contradicting the suggestion of extensive early northern  
hemisphere glaciation in favour of a unipolar icehouse climate state at the EOT (Spray et al., 2019). Furthermore, it is unlikely  
545 that ice growth on land in the Northern Hemisphere was sufficiently extensive to impact global seawater  $\delta^{18}\text{O}$  budgets sea  
level at the EOT (Coxall et al., 2005; Lear et al., 2008; Mudelsee et al., 2014). Marine SSTs and floral records from the  
subarctic and Arctic imply sustained warm temperatures and extensive lowland temperate vegetation well into the middle  
Miocene (O'Regan et al. 2011), that are not readily reconciled with large continental ice sheets fringing Greenland and other  
Arctic landmasses then or before this time.

**Deleted:** found no evidence to support

550 From a theoretical perspective, climate and ice sheet modelling suggest that the  $\text{CO}_2$  threshold for Northern Hemisphere ice-  
sheet inception is fundamentally lower than for Antarctica (DeConto et al., 2008; Gasson et al., 2014), implying that the climate  
must be cooler to glaciate Greenland than Antarctica. This is also consistent with evidence that the modern Greenland ice sheet  
is highly sensitive to climatic warming and that Greenland may have been almost ice-free for extended periods even in the  
555 Pleistocene (Schaefer et al., 2016). This asymmetry between the northern and southern hemispheres in susceptibility to  
glaciation has been attributed to (i) the lower latitudes of the continents encircling the Arctic Ocean relative to the Antarctic,  
together with different ocean and atmospheric circulation patterns (DeConto et al., 2008; Gasson et al., 2012) and (ii) the ice  
sheet carrying capacity of the continents; it has been argued that Greenland topography was low during the Paleogene  
compared to Antarctica and extensive mountain building, providing high-altitude terrain needed for glaciation, did not occur  
560 until the late Miocene-Pliocene (Gasson et al., 2012; Solgaard et al., 2013).

**Deleted:** , which is hard to reconcile

**Deleted:** This asymmetry between the northern and southern hemispheres in susceptibility to glaciation has been attributed to (i) the lower latitudes of the continents encircling the Arctic Ocean relative to the Antarctic, together with different ocean and atmospheric circulation patterns (Gasson et al., 2012)

But even in the question of Greenland topography there is uncertainty. Reconstructions of plate kinematics in suspected ice  
sheet nucleation sites (e.g., northern Greenland, Ellesmere Island) are equivocal. It has been argued that Greenland topography  
was low during the Paleogene compared to Antarctica and extensive mountain building, providing high-altitude terrain needed  
565 for glaciation, did not occur until the late Miocene-Pliocene (Gasson et al., 2012; Japsen et al., 2006; Solgaard et al., 2013).  
Recent work on the plate kinematic history of the Eureka orogeny, taking into account crustal shortening (Gurnis et al., 2018),  
indicate a period of significant compression in northern Greenland and Ellesmere from 55-35 Ma (Gion et al., 2017) that was  
probably associated with uplift (Piepjohn et al., 2016). These latest tectonic insights are compatible with insights from apatite  
fission track and helium data that support the onset of a rapid phase of exhumation of the East Greenland margin around 30  
570 +/- 5 Ma (Bernard et al., 2016; Japsen et al., 2015). Together, these approaches support a view of high mountains on  
Greenland/Ellesmere that began eroding in the late Eocene to early Oligocene with a greater possibility of supporting glaciers.

**Deleted:** However, sophisticated new approaches to

**Deleted:** now

**Deleted:** The new kinematic

**Deleted:** —based on apatite fission track and helium data—



### 3 Marine observations

#### 3.1 Sea surface temperature observations

585 A key requirement for understanding the cause and consequences of the Eocene-Oligocene climatic transition is good spatial and temporal constraints on global temperatures and our most numerous and well-resolved records of this undoubtedly come from the oceans. Quantitative reconstruction of sea surface and deep ocean temperatures has been ongoing for decades. This requires use of various geochemical proxies, both to provide independent support for absolute temperature estimates and because different proxy options are available for different ocean/sedimentary settings, and deep sea versus surface ocean water masses. Each method has its own limitations and uncertainties resulting in a currently patchy but steadily improving view of global change. Quantitative assemblage-based SST proxies akin to transfer functions are not available because there are no living plankton relatives during the EOT. For a thorough review of pre-Quaternary marine SST proxies, and their strengths and weaknesses, see Hollis et al., (2019).

595 While more heterogeneous than the deep sea, reconstruction of SST in the EOT is in some ways currently more achievable than bottom water temperatures because more proxies are available, although there are still multiple confounding factors to consider. Classical marine  $\delta^{18}\text{O}$  paleothermometry extracted from the calcium carbonate shells of fossil planktonic (surface floating) foraminifera is especially complicated because of the combining influences of (i) compromised fossil preservation under the shallow late Eocene ocean calcite compensation depth, limiting the availability of planktonic records, (ii) increasing  $\delta^{18}\text{O}$  of sea water as a consequence of ice sheet expansion, which enriches ocean water and thus increases calcite  $\delta^{18}\text{O}$ ; a signal which can otherwise indicate cooling. However, a growing number of clay-rich hemipelagic marine sequences containing exceptionally well-preserved (glassy) fossil material are yielding  $\delta^{18}\text{O}$  paleotemperatures that provide useful SST perspectives.

600  $\delta^{18}\text{O}$  SSTs derived from glassy foraminifera (Haiblen et al., 2019; Norris and Wilson, 1998; Pearson et al., 2001; Wilson et al., 2002; Wilson and Norris, 2001) contrast greatly from those measured on recrystallized 'frosty' material (Sexton et al., 2006). A detailed compilation of glassy versus recrystallized foraminiferal  $\delta^{18}\text{O}$  proxies around the EOT is given in Piga (2020).

610 Planktonic foraminifera Mg/Ca paleothermometry provides another means of quantifying SSTs (Evans et al., 2016; Lear et al., 2008), however such records are even more sparse than  $\delta^{18}\text{O}$  equivalents due to the scarcity of appropriate EOT fossils. This method is especially useful since, in theory, unlike  $\delta^{18}\text{O}$  it should be independent of Antarctic glaciation and, when coupled with  $\delta^{18}\text{O}$  paleothermometry, past variations in the  $\delta^{18}\text{O}$  composition of seawater, and thus ice volume changes may also be estimated (Lear et al., 2004, 2008; Mudelsee et al., 2014). The two key existing records are from Tanzania (Lear et al., 2008) and the Gulf of Mexico (Evans et al., 2016; Wade et al., 2012). The Tanzanian planktonic Mg/Ca record provides cornerstone evidence for a permanent 2.5 °C tropical surface and bottom water, ocean cooling, and therefore likely global cooling, associated with the Step 1 of the EOT (Figure 1). The Gulf of Mexico Mg/Ca temperature record resembles the

**Deleted:**  $\delta^{18}\text{O}$  SSTs derived from glassy foraminifera

**Deleted:** (Pearson et al., 2001; Sexton et al., 2006)

620 biomarker-derived (i.e. TEX<sub>86</sub>, see below) SST record from this site (Wade et al., 2012). Both imply a distinct and slightly larger surface cooling of 3-4°C limited to Step 1. To what extent secular change in seawater Mg/Ca reconstruction might have influenced these actual numbers is an ongoing question (Evans et al., 2018). Clumped isotope paleothermometry (Ghosh et al., 2006; Zaarur et al., 2013), also independent of seawater δ<sup>18</sup>O, is still in its infancy, but this is a third method applicable to calcareous microfossils that will help address some of these problems. Thus far only one clumped isotope (Δ<sub>47</sub>) record from Maud Rise spans the EOT (Petersen and Schrag, 2015). This record shows cooling preceding the EOT, and then relatively minor changes across the EOT. Early to middle Eocene clumped isotope SST records are consistent with other proxies, specifically cooler values at high southern latitudes compared to the early and middle Eocene (Evans et al., 2018). Many new 625 SST records base on Mg/Ca and Δ<sub>47</sub> are expected in coming years.

Deleted: calcitic

630 In some regions, Eocene-Oligocene age sediments lack biogenic calcium carbonates (e.g. Bijl et al., 2009). Therefore low- and non-calcareous areas, like the Arctic and high-latitudes of the North Atlantic and North Pacific, have suffered for lack of paleotemperature data. However, the development of independent organic proxies based on biomarkers such as alkenones (U<sup>K</sup><sub>37</sub> index; Brassell et al. 1986) and glycerol dialkyl glycerol tetraethers (GDGTs) from the membrane lipids of Thaumarchaeota (TEX<sub>86</sub> index; Schouten et al. 2002), which can be preserved in high sedimentation settings close to continental margins or restricted basins where carbonate is often scarce, have helped fill this gap. Importantly, these organic biomarkers are often the only marine archive for paleothermometry at high latitudes, where SST constraints are particularly useful for model-data comparisons.

635 While the U<sup>K</sup><sub>37</sub> index is well established, the TEX<sub>86</sub> index is relatively new and its accuracy as a paleotemperature proxy is under critical review. There have been several different TEX<sub>86</sub> indices developed, with different SST calibrations (e.g. TEX<sup>\*</sup><sub>86</sub> by Sluijs et al. 2009; TEX<sub>86</sub><sup>H</sup> and TEX<sub>86</sub><sup>L</sup> by Kim et al. 2010; Bayspar by Tierney and Tingley 2015). As suggested by some of the recent studies conducted on cultures of Thaumarchaeota, GDGT composition may be sensitive not only to SST but also 640 other factors such as oxygen (O<sub>2</sub>) concentration (Qin et al., 2015) or ammonia oxidation rate (Hurley et al., 2016). Furthermore, there is uncertainty in the source of the GDGTs used for SST estimations, i.e. their production level in the water column and possible summer biases, and therefore their value as an SST proxy. Recent reviews are available for both the paleotemperatures U<sup>K</sup><sub>37</sub> (Brassell, 2014) and for TEX<sub>86</sub> (Hurley et al., 2016; Pearson and Ingalls, 2013; Qin et al., 2015; Tierney and Tingley, 2015). Despite these issues, in some studies where both U<sup>K</sup><sub>37</sub> and TEX<sub>86</sub> indices were applied, temperature estimations show 645 remarkably similar results (Liu et al., 2009) suggesting that TEX<sub>86</sub>, after an evaluation of the source and the distribution of GDGTs (Inglis et al., 2015), can successfully be applied as a paleotemperature proxy. TEX<sub>86</sub> is especially useful at lower latitudes, since the U<sup>K</sup><sub>37</sub> index saturates at about 28°C (Müller et al., 1998).

Deleted: the

650 Cross-latitude biomarker proxy records (U<sup>K</sup><sub>37</sub> and TEX<sub>86</sub>) suggest that SSTs were higher than today in both the late Eocene and early Oligocene SSTs with annual means of up to 20 °C at both 60 °N and 60 °S respectively and low meridional

temperature gradients (Hollis et al., 2009; Liu et al., 2009; Wade et al., 2012). One record from the Gulf of Mexico (Wade et al., 2012) suggests consistently higher SSTs derived from TEX<sub>86</sub> than from inorganic proxies (Hollis et al., 2009, 2012; Liu et al., 2009). Where records span the EOT (i.e. ~33-34 Ma), between 1 to 5 °C of surface cooling in both hemispheres is found. To date, temperature records from the high northern latitudes are sparse but coverage from the high southern latitudes is richer where several records suggest a cooling of subantarctic waters across the EOT of 4 to 8°C, although some records are indistinguishable from 0°C change (Figure 3). In the low latitude Pacific, Atlantic and Indian Ocean tropical SSTs were significantly warmer than today in the late Eocene, with SSTs up to 31°C (Liu et al., 2009) or even ~33°C (Lear et al., 2008; Wade et al., 2012). One TEX<sub>86</sub> record from the Gulf of Mexico implies gradual surface cooling of 3-4 °C between ~34 and 33 Ma (Wade et al., 2012). TEX<sub>86</sub> data from elsewhere in the tropical Atlantic shows a large transient cooling of up to 6°C across the EOT (Liu et al., 2009), although some equatorial records show minimal change. A summary of SST records across the EOT is shown in Figure 3.

Newly available records from the North Atlantic region are starting to challenge earlier evidence of homogeneous bipolar cooling (Liu et al., 2018; Śliwińska et al., 2019). Furthermore, comparison of a uniquely well-resolved record from the Newfoundland margin, western North Atlantic (Liu et al., 2018), with data from the subantarctic South Atlantic, confirms this in new detail, leading the authors to the conclusion that surface ocean cooling during the EOT was strongly asymmetric between hemispheres. Liu et al. (2018) interpret this finding as evidence for ‘transient thermal decoupling of the North Atlantic Ocean from the southern high latitudes’, as a result of changes in ocean circulation-driven heat transport associated with Antarctic glaciation. Recent TEX<sub>86</sub> data spanning the Oligocene suggests that the low meridional gradient similar to the late Eocene persists well after the EOT, and that warming occurs in the late Oligocene despite an apparent increase in CO<sub>2</sub> (O’Brien et al., 2020).

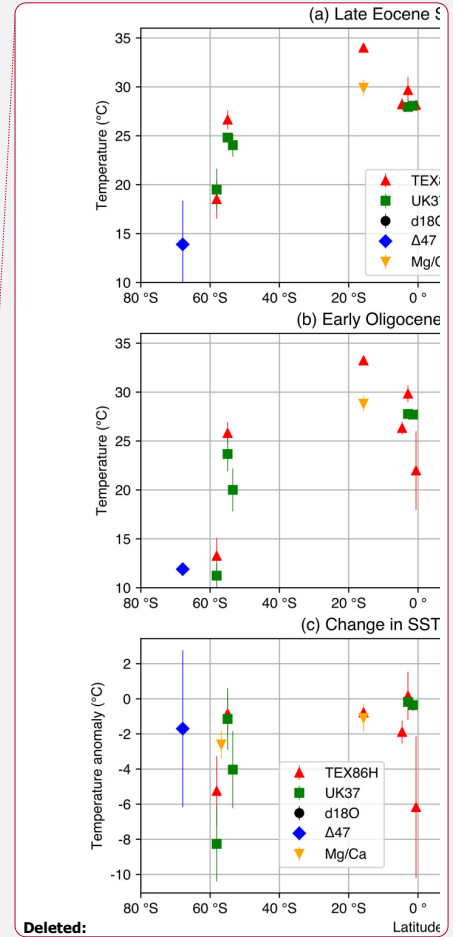
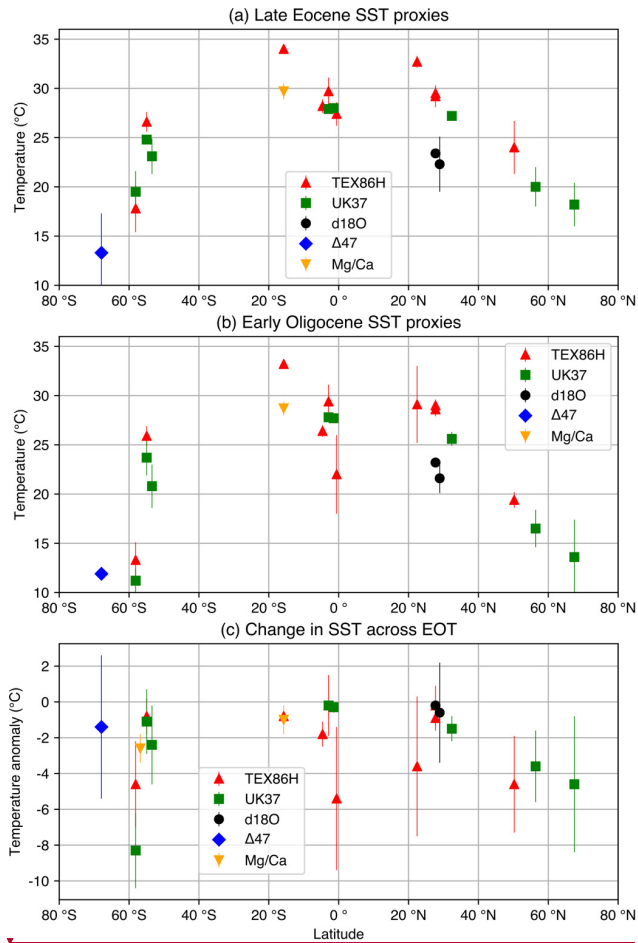
**Deleted:** suggests

**Deleted:** sea surface temperatures

**Deleted:** (

**Deleted:** ).

**Deleted:** A summary of SST records across the EOT is shown in Figure 3.



Deleted:

Deleted: UK<sup>37</sup>

Deleted: 34.2

Deleted: 7

**Figure 3:** Summary of sea surface temperature (SST) change across the EOT from proxies,  $\text{TEX}_{86}^{\text{H}}$ ,  $\text{UK}_{37}$ ,  $\delta^{18}\text{O}$ ,  $\Delta_{47}$ , and Mg/Ca. (a) Late Eocene, (b) early Oligocene and (c) change in SST across the EOT. Data shown in (a) and (b) are only from locations that record a temperature signal on both sides of the EOT. Data compiled from (Bohaty et al., 2012; Cramwinckel et al., 2018; Inglis et al., 2015; Kobashi et al., 2004; Lear et al., 2008; Liu et al., 2009, 2018; Pearson et al., 2007; Petersen and Schrag, 2015; Piga, 2020; Sliwińska et al., 2019; Wade et al., 2012; Zhang et al., 2013). The late Eocene value was calculated as an average between 38 and 33.9 Ma (pre-EOT), while the early Oligocene value was calculated as the average between 33.9 and 30 Ma (post-EOT), and the change across the EOT is the difference between these values. The data compilation is provided in digital form in Supplementary Table S1.

### 3.2 Deep sea temperature changes

695 As described in Section 1.2, the Eocene-Oligocene climate transition is defined by high-resolution benthic foraminiferal oxygen isotope ( $\delta^{18}\text{O}$ ) records from deep sea sites (Coxall et al., 2005; Zachos et al., 1996). These records describe a benthic  $\delta^{18}\text{O}$  increase of about 1.5‰, a combination of deep sea cooling and terrestrial ice growth. While surface ocean temperature changes have been constrained using organic and inorganic proxies (Section 3.1), there are fewer proxies for deep sea temperature and, thus, the picture of deep ocean cooling remains uncertain. This is because, on its own, it is impossible to deconvolve the temperature and ice volume components of  $\delta^{18}\text{O}$  records, and hence quantify the timing, magnitude and spatial distribution of deep ocean temperature change through the climate transition. Indeed, an early interpretation of the Cenozoic benthic oxygen isotope record suggested that the  $\delta^{18}\text{O}$  increase at the EOT represented a pure cooling signal (Shackleton and Kennett, 1975), whereas numerous lines of evidence have since shown that a substantial component of the  $\delta^{18}\text{O}$  shift reflects the glaciation of Antarctica (e.g. Zachos et al. 1996). Independent paleotemperature proxies provide a potential means to deconvolve the two contributors to  $\delta^{18}\text{O}$  records, and benthic foraminiferal Mg/Ca paleothermometry has been applied to several marine EOT sections (Billups and Schrag, 2003; Bohaty et al., 2012; Katz et al., 2008; Lear et al., 2000, 2004, 2008, 2010; Peck et al., 2010; Pusz et al., 2011; Wade et al., 2012). Yet, calculating absolute bottom water temperatures from benthic foraminiferal Mg/Ca ratios requires an estimate of the Mg/Ca ratio of seawater, while Mg-partitioning into foraminiferal calcite shows modest sensitivity to temperature at low temperatures and is subject to the competing influence of seawater carbonate chemistry (Evans et al., 2018; Lear et al., 2015). Relative temperature trends over short time intervals are generally considered more robust than absolute temperatures, although the residence time of calcium in seawater (~ 1 Myr; Broecker and Peng 1982) compared with the duration of the entire climate transition (~500 kyr) adds some uncertainty to calculated relative temperature changes across the EOT. High resolution reconstructions of seawater Mg/Ca are therefore required to improve both absolute and relative temperature changes using Mg/Ca paleothermometry.

715 Furthermore, although the benthic foraminiferal Mg/Ca paleothermometer appears to capture the long-term cooling trend since the early Eocene Climatic Optimum, the concomitant ~1km deepening of the calcite compensation depth (CCD) hinders its use across the EOT (Coxall et al., 2005; Lear et al., 2004). Specifically, the increase in bottom water calcite saturation state across the EOT acts to increase benthic foraminiferal Mg/Ca, and mask the deep sea cooling signal (Coxall et al., 2005; Lear et al., 2004). Attempts have been made to use Li/Ca to correct this  $\Delta\text{CO}_3^{2-}$  effect from Mg/Ca records (Lear et al., 2010; Peck et al., 2010; Pusz et al., 2011), but this approach brings with it additional uncertainties including the species-specific sensitivities to both temperature and  $\Delta\text{CO}_3^{2-}$ . An alternative, and perhaps more robust approach at present, is to combine planktonic  $\delta^{18}\text{O}$  records with salinity-independent sea surface paleotemperature records to calculate the change in the surface

Deleted: the

Deleted: the

Deleted: does add

Deleted: CCD

730 water  $\delta^{18}\text{O}$  ( $\delta^{18}\text{Osw}$ ). The overall change in surface  $\delta^{18}\text{Osw}$  across the EOT has been estimated using planktonic  $\delta^{18}\text{O}$  and Mg/Ca at many sites, including a section in Tanzania containing exceptionally well-preserved (glassy) foraminifera (Lear et al., 2008). The similarity between this  $\Delta\delta^{18}\text{Osw}$  estimate from the Indian Ocean ( $\sim 0.6\%$ ; Lear et al. 2008) and those from other sites, e.g., the Southern Ocean (Bohaty et al., 2012) and the southeast Atlantic (Peck et al., 2010) suggests that the surface  $\delta^{18}\text{Osw}$  change is dominated by a global (ice volume) signal. If we can assume that the surface  $\delta^{18}\text{Osw}$  signal is dominated by the ice volume signal (as opposed to a local change in the salinity) then these records can be used in conjunction with the benthic  $\delta^{18}\text{O}$  records to estimate changes in bottom water temperature across the climate transition (Kennedy et al., 2015). As noted above, inter-basin similarities suggest this assumption holds true in Indian Ocean, Southern Ocean and southeast Atlantic sites, whereas sites in the Pacific and North Atlantic are not as clearly constrained. The associated estimated volume of Antarctic ice depends upon the assumed isotopic composition of the ice sheet, but was likely between 70 and 110% of the size of the modern day Antarctic ice sheet (Bohaty et al., 2012; Lear et al., 2008), representing a sea level difference to modern of approximately minus 18 metres to plus 6 metres. Spatial heterogeneities in the deep ocean temperature history may therefore be inferred by calculating inter-site offsets in benthic foraminiferal  $\delta^{18}\text{O}$  records (Abelson and Erez, 2017; Bohaty et al., 2012; Cramer et al., 2009).

**Deleted:** If it can be assumed, in some regions, that the surface  $\delta^{18}\text{Osw}$  signal is dominated by

**Moved down [1]:** ice volume signal (as opposed to a local change in the salinity) then these records can be used in conjunction with the benthic  $\delta^{18}\text{O}$  records to estimate changes in bottom water temperature across the climate transition (Kennedy et al., 2015).

**Moved (insertion) [1]**

745 There is a growing consensus based on southern hemisphere and low latitude records that Step 1 of the EOT was associated with a cooling of both surface and deep waters on the order of  $2^\circ\text{C}$ , associated with a relatively minor increase in global ice volume (Bohaty et al., 2012; Lear et al., 2004, 2008, 2010; Peck et al., 2010; Pusz et al., 2011). We note that the combination of this magnitude of cooling and an overall increase in  $\delta^{18}\text{Osw}$  of  $\sim 0.6\%$  is enough to account for the average  $\sim 1.0\%$  shift in benthic foraminiferal  $\delta^{18}\text{O}$  observed in deep sea records (Mudelsee et al., 2014). However, this overall shift across the entire climate transition ignores the apparent  $\delta^{18}\text{O}$  “overshoot” (Zachos et al., 1996) observed in some high resolution records, at the base of the EOGM (Coxall and Pearson, 2007). Determining whether the “overshoot” reflects deep sea cooling, a transient further increase in global ice volume, or a combination of the two has implications for our understanding of Antarctic ice sheet dynamics and indeed the cause of the EOT itself. Unfortunately, it is Step 2 (EOIS) of the transition, into the EOGM where the CCD reaches its maximum depth and benthic foraminiferal Mg/Ca records appear most compromised by the  $\Delta\text{CO}_2$  effect (Lear et al., 2004, 2010), even at depths above the implied depth of CCD deepening (Peck et al., 2010), so we currently have no robust and direct evidence of deep ocean cooling across this step. Future work may go some way to address these problems using clumped isotopes or by generating high resolution B/Ca records across the transition, and by using deep infaunal benthic species (e.g. Elderfield et al. 2012). However, by combining benthic and planktonic records, it appears that the EOGM in the deep Pacific Ocean reflects, at least in part, a transient cooling of deep waters associated with the major expansion of the Antarctic ice sheet (Kennedy et al., 2015).

**Deleted:** the step

An additional complication is that the Mg/Ca composition of seawater may itself have shifted during the EOT, as suggested by incoming constraints from other proxies, including paired Mg/Ca and clumped isotope temperature constraints in shallow living larger benthic foraminifera (Evans et al., 2018). Further investigation into this possibility is required, which could ultimately help identify Mg/Ca adjustment factors needed to improve the ability to extract paleotemperature estimates for this geological time interval.

#### 4 The terrestrial realm at the EOT

There are several proxy indicators of past terrestrial climate change. These include geochemical indices, leaf margin analysis, Climate Leaf Analysis Multivariate Program (CLAMP) (Yang et al., 2011), and pollen assemblages (see review in Hollis et al. 2019). Here we focus on pollen assemblages as a broad indicator of terrestrial change across the EOT, because an EOT synthesis of these data already exists (Pound and Salzmann, 2017). This dataset, a global paleo-biome reconstruction of pollen and spore assemblages, indicates that the terrestrial realm of the late Eocene and early Oligocene has a vegetation distribution that in general indicates a warmer and wetter world than today. The response of the terrestrial realm to the EOT is more heterogeneous than the marine realm, and biome changes do not record a uniform global response (Pound and Salzmann, 2017). Terrestrial biomes record not only global climate change but also regional changes due to local factors. These include orographic uplift, which reduces local temperature and changes regional precipitation patterns. Further changes in precipitation are induced by the retreat of a number of inland seaways due to sea-level changes and tectonics (Chamberlain et al., 2012; Dupont-Nivet et al., 2008; Kocsis et al., 2014; Sheldon et al., 2016). These complicating factors mean that changes in vegetation must be interpreted within the context of local paleoenvironmental changes. However, there are some emerging terrestrial records that record a significant temperature drop and perturbation of the hydrological cycle, consistent with global cooling. Thus, we present the terrestrial records on a continent-by-continent basis below, with a summary of temperature change across the EOT shown in Figure 4. For a summary of strengths and limitations of deriving quantitative climate estimates from the pre-Quaternary plant record, see Hollis et al. (2019).

##### 4.1 North America

In North America, the paleobiome distribution of the EOT ranges from tropical mangroves, swamps and forests in the south of the continent to cool-temperature forests at the high latitudes (Breedlovestrout et al., 2013; Pound and Salzmann, 2017; Wolfe, 1985, 1994). Gradual cooling and drying from the middle Eocene until the late Oligocene allowed the mixed coniferous and deciduous broadleaf forests to become more dominant (Wing, 1987). Fossil leaves found in Washington State (Breedlovestrout et al., 2013) indicate no clear temperature trend from the middle Eocene to the EOT. Instead variations are attributed to differing paleoaltitude, combined with a gradual long-term cooling. Pollen records from Texas indicate a long term cooling and aridification from the middle Eocene to the early Oligocene (Yancey et al., 2003), whereas pollen records from 5° longitude further east show no turnover at the EOT boundary (Oboh-Ikuenobe and Jaramillo, 2003). Pollen from the

Deleted: with no evidence for

Deleted: global scale

Deleted: .

far north Yukon Territory show a transition from warmer adapted angiosperm forests in the Late Eocene to cooler adapted gymnosperm forests during the Early Oligocene (Ridgway and Sweet, 1995).

805 In Oregon, well dated floras and marine invertebrates show no evidence for a rapid change at the EOT (Retallack et al., 2004),  
but rather a gradual cooling during the early to middle Oligocene. By contrast, paleosols indicate a  $2.8 \pm 2.1^\circ\text{C}$  drop across the  
EOT in the same region (Gallagher and Sheldon, 2013). Isotopic data from horse teeth indicate a  $8 \pm 3.1^\circ\text{C}$  drop in [mean annual  
temperature \(MAT\)](#) across the EOT, but with a 400 kyr lag behind the marine realm (Zanazzi et al., 2007), though part of this  
shift is due to changes in the hydrological cycle (Chamberlain et al., 2012; Hren et al., 2013). [Moreover, a clumped isotope  
study of Fan et al., \(2017\) records a decrease of  \$\sim 7^\circ\text{C}\$  across the EOT in the north central USA, similar to the findings of  
810 Zanazzi et al. \(2007\).](#) Conversely a study on White River mammals interprets no significant change in MAT, but an  
aridification of the local environment (Boardman and Secord, 2013). This conclusion is in line with paleosol studies, which  
suggest a change in vegetation structure from a forest to a more open environment (Retallack, 1983).

Oxygen isotope analyses in the western North American Cordillera suggest the changing hydrological regime of North  
815 America (Chamberlain et al., 2012) was influenced by factors other than large-scale climate. Rising orography, starting in  
British Columbia at  $\sim 50$  Ma and moving south to Nevada by  $\sim 23$  Ma shifted the North American Monsoon further south during  
this time. This not only impacts terrestrial oxygen isotopes, but also the regional vegetation – creating an aridification not  
linked to global climatic events (Chamberlain et al., 2012). [There is a significant increase in dust deposition in the foothills of  
the North American cordillera \(Fan et al., 2020\), suggesting cooling and aridification.](#) No response to the EOT is evident from  
820 North American mammals (Figueirido et al., 2012; Prothero, 2012, 2004), while fossil Equidae analyses from North America  
indicate that horses had a browsing diet before, at and after the EOT (Mihlbachler et al., 2011). [One study argues that North  
American mammals had already adapted to Oligocene-like cold and arid conditions prior to the EOT \(Eronen et al., 2015\),  
suggesting that any further environmental change at the EOT would not be expressed in changes to these species.](#)

## 825 4.2 South America

Late Eocene and early Oligocene paleo-biome distributions of South America indicate tropical evergreen rainforest in the north  
and cool-temperate biomes in the south (Pound and Salzmann, 2017). In South America there was a greater change in  
vegetation from the middle Eocene into the late Eocene, rather than at the EOT (Barreda and Palazzesi, 2007). Patagonian  
pollen floras from the middle Eocene to the end of the early Oligocene are termed the “Mixed Paleoflora”. These show a long-  
830 term cooling trend rather than a step change at the EOT (Quattrocchio et al., 2013). Phytolith and oxygen isotope records from  
Patagonia show no change in vegetation across the EOT (Kohn et al., 2004, 2015; Strömberg et al., 2013). [However, this view  
has recently been challenged by a higher stratigraphic resolution study of phytoliths and magnetic properties, pointing to a  
clearer ecosystem change \(Selkin et al., 2015\). A recent stable isotope hydrology study from Patagonia indicates rapid cooling](#)



835 during the EOT (Colwyn and Hren, 2019). Faunal turnovers in South America began at approximately 42 – 39 Ma (Woodburne et al., 2014). This relates to the end of the MECO, but also correlates with the appearance of rodents from Africa. The mammal turnover associated with the EOT is no more dramatic than those during the late Eocene or late Oligocene (Woodburne et al., 2014). The Amazonian region had a diverse, primarily frugivorous fauna during the EOT, suggesting productive stable forest (Negri et al., 2009). To summarise, there are some indications of significant cooling in South America at the EOT, but overall the signal is mixed, with both faunal and plant-based proxies suggesting a heterogeneous response.

#### 840 4.3 Africa

Vegetation in Africa shows little change in structure from the Late Eocene into the Early Oligocene, but there is a documented drop in palm diversity (Jacobs et al., 2010; Pan et al., 2006; Pound and Salzmann, 2017). There are significant gaps in the paleobotanical record for Africa over this time interval, with most information coming from the region between 10° north and south of the Equator (Jacobs et al., 2010; Pound and Salzmann, 2017). One exception is the Fayum Depression in Egypt which 845 contains macrofossil and microfossil evidence for tropical vegetation in the late Eocene (Tiffney and Wing, 1991; Wing et al., 1995).

#### 4.4 Eurasia

In Eurasia there was a progressive change from para-tropical evergreen forests in the middle Eocene to warm-temperate evergreen and deciduous mixed forests by the early Oligocene (Collinson and Hooker, 2003; Teodoridis and Kvaček, 2015). 850 The paleo-biome reconstructions show a dominance of subtropical and warm-temperate mixed forests throughout Eurasia with seasonal biomes in the Iberian Peninsula and arid biomes in central Asia (Pound and Salzmann, 2017). A change from a diverse mixed broad-leaved to a cooler conifer- dominated pollen flora in North Atlantic cores through the Eocene indicates increasing seasonality in Europe (Eldrett et al., 2009). However, leaf floras from Bulgaria show no significant change in vegetation at the EOT (Bozukov et al., 2009). There is a greater change in Iberian pollen floras from the early to late Oligocene than at the EOT 855 (Postigo Mijarra et al., 2009). Between the late Eocene and early Oligocene no change in ~~MAT~~ or precipitation is reconstructed in the Ebro Basin in Spain, but there is a decrease in chemical weathering across the EOT (Sheldon et al., 2012).

In Germany and Czechia, macrofloras show a stepwise disappearance of subtropical species and immigration of evergreen and deciduous warm-temperate species during the late Eocene (Kunzmann et al., 2016). The first mixed evergreen/deciduous forest 860 in azonal biomes is recorded prior to the EOT from Roudniky ( $35.4 \pm 0.9$  Ma; ~~Kvaček et al., 2014~~) referring to a latest Eocene cooling event (Teodoridis and Kvaček, 2015). However, evergreen broadleaved forests were still present in the early Oligocene (Kovar-Eder, 2016; Teodoridis and Kvaček, 2015) indicating the low impact of global EOT changes in terrestrial central Europe. Most of the subtropical to warm-temperate genera survived in that region until the Miocene Climatic Optimum (Mai, 1995). Based on proxies from macrofloras, MAT was almost stable at the EOT (Teodoridis and Kvaček, 2015) with ongoing 865 prevailing seasonality in precipitation and a curtailment of the growing season (Moraweck et al., 2019). While cold month

~~Deleted:~~ mean annual temperature

~~Deleted:~~ (Kvaček et al., 2014)

~~Deleted:~~ but which is not monsoonal

870 mean temperatures (CMMT) in the Priabonian mostly exceed 10°C, the lower limit for the growing season, the earliest Oligocene floras from Schleenhain and Haselbach (Germany) indicate CMMT below 10°C and a growing season length of 9-11 months (Moraweck et al. 2019).

Recent investigations on late Eocene and earliest Oligocene macrofloras in SE Tibet and Yunnan revealed multiple lines of evidence for the modernization of the vegetation by establishment of present-day genera and families (Linnemann et al., 2017; Su et al., 2018). Regional vegetation change across EOT from subtropical to temperate and partly cool temperate in SW China has been argued to be influenced by the uplift of the Tibetan Plateau (Su et al., 2018). An Eocene appearance of a modern subtropical / tropical aspect of vegetation is also recorded from Chinese low latitude floras (Hainan; Guangdong) indicating an Eocene establishment of monsoonal climate linked to Tibetan uplift (Jin et al., 2017). However, the evolution of the Tibetan Plateau at the EOT is currently under debate. Earlier studies suggested that a proto-Tibetan highland of more than 4000 m elevation existed in the late Eocene based on stable isotope paleoaltimetry (Cyr et al., 2005; Quade et al., 2011; Rowley and Currie, 2006). New data-model comparisons have cast doubt on these estimates, finding that the stable isotope paleoaltimetry is influenced by different atmospheric circulation patterns than previously thought (Botsyun et al., 2019; Quade et al., 2020). These studies suggest a lower paleoaltimetry of the Tibetan Plateau (less than 3000 m) in the late Eocene (Botsyun et al., 2019; Quade et al., 2020).

885 Aside from paleoaltimetry, the timing of environmental changes suggests that climate change at the EOT had a distinct impact on Tibetan environments (Dupont-Nivet et al., 2007). Northeastern Tibet (Xining Basin) shows significant changes at the EOT in the depositional environments (Dupont-Nivet et al., 2008), pollen and clumped isotopic temperatures (Hoon et al., 2012; Page et al., 2019) and accumulation rates (Abels et al., 2011). Furthermore, temperature changes in the Xining Basin are too sudden to be driven by changes in basin altitude (Page et al., 2019). The timing of the large temperature drop suggests a coeval decrease in regional temperature linked to EOT glaciation and monsoonal rainfall (Page et al., 2019). Mongolian and northwestern Chinese faunal records indicate a large mammal turnover at the EOT: the “Mongolian Remodelling” (Kraatz and Geisler, 2010; Meng and McKenna, 1998; Sun et al., 2014), synchronous with the Grand Coupure in Europe. Significant depositional environment change in southwestern Mongolia is also shown by (Sun and Windley, 2015).

895 Freshwater gastropods from southern Britain show that growing season temperatures (Spring – Summer) may have dropped from around 34°C to about 20°C across the Eocene – Oligocene boundary (Hren et al., 2013). This has been translated into a MAT drop of 4 - 6°C (Hren et al., 2013), which is comparable to the  $\Delta U_{37}^K$  estimated SST change from the high latitude North Atlantic ODP Site 913, but not the smaller SST change at the more comparable latitude ODP Site 336 (Liu et al., 2009).  
900 Summer temperatures for the Hampshire Basin fell by around 4°C during the EOT (Grimes et al., 2005), but did not drop again during the EOIS (see section 1.2). Paleosols of the Hampshire Basin show minimal changes in temperature but an increase in precipitation (Sheldon and Tabor, 2009).

**Deleted:** However, regional

**Deleted:** is masked

**Deleted:** Paleoaltimetric studies show that the already elevated proto-Tibetan highland (Lhasa Terrain) achieved its modern elevation during EOT by uplift of (only) about 1km (Spicer, 2017; Su et al., 2018). An Eocene appearance of a modern subtropical / tropical aspect of vegetation is also recorded from Chinese low latitude floras (Hainan; Guangdong) indicating an Eocene establishment of monsoonal climate

**Deleted:** which seems to have had a much higher impact on the evolution of regional vegetation than the EOT or any later climatic event

**Deleted:** (Dupont-Nivet et al., 2008)

**Formatted:** English (UK)

**Formatted:** English (US)

**Formatted:** English (US), Superscript

**Formatted:** English (US), Subscript

#### 4.5 Australia and New Zealand

In Australia, the EOT is associated with the loss of rarer taxa in pollen records rather than significant turnovers (Macphail, 2007). There is a diversity drop from the middle to late Eocene into the latest Eocene – early Oligocene (Martin, 2006). ~~A recent review of the~~ distribution of paleo-biomes in Australia ~~showed~~ no change between the late Eocene and the early Oligocene (Pound and Salzmann, 2017), though data coverage is sparse apart from in the south of the continent. ~~However, a recent study of rainforest flora in south-eastern Australia shows a transition from warm-temperature rainforests in the late Eocene to cool-temperature rainforests in the early Oligocene (Korasidis et al., 2019). Those biome flora suggest a shift in MAT from 14-20 °C in the late Eocene to 10-14 °C in the early Oligocene (Korasidis et al., 2019). Terrestrial paleoclimate reconstructions of temperature also~~ show a cooling at around 36 Ma (Pound and Salzmann, 2017). The New Zealand records show a warm humid forest with a gradual turnover of palynomorphs through the late Eocene and the early Oligocene (Homes et al., 2015; Pocknall, 1991).

**Deleted:** The

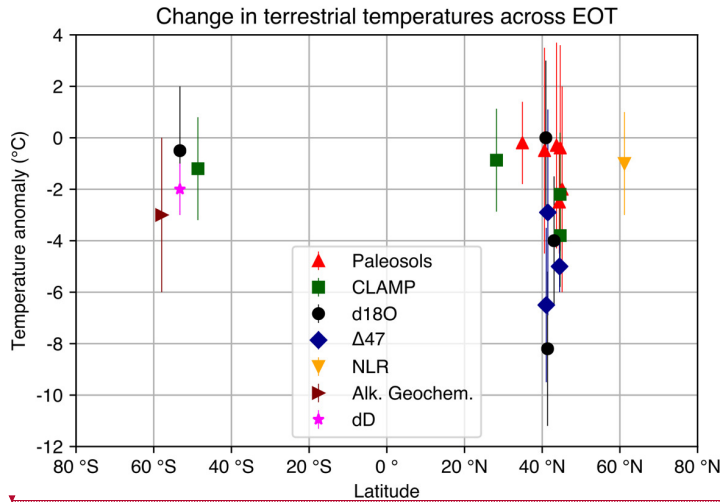
**Deleted:** shows

**Deleted:** Terrestrial paleoclimate reconstructions of temperature do

#### 4.6 Antarctica

On Antarctica it is known that from the equable climates of the middle Eocene there was a progressive drop in plant diversity and stature, from evergreen forests to low-lying vegetation (Francis et al., 2008; Pound and Salzmann, 2017). Changing  $\delta^{13}\text{C}$  measurements from late Eocene leaves and pollen have been interpreted as decreasing moisture availability on the Antarctic Peninsula (Griener et al., 2013). Vegetation at Wilkes Land, East Antarctic, changed from an early Eocene subtropical to a cool temperate forest, indicating a  $5^\circ\text{C}$  decline in ~~MAT~~ (Pross et al., 2012). A further change towards a less diverse, cool-temperate shrubland and forest indicates further cooling at Wilkes Land at the onset of the Oligocene (Strother et al., 2017). Other evidence supporting decreasing moisture availability is demonstrated by a shift from chemical weathering in a humid environment, to physical weathering associated with a colder more arid regime (Basak and Martin, 2013; Dingle et al., 1998; Ehrmann and Mackensen, 1992; Robert and Kennett, 1997; Wellner et al., 2011). This aridification of the Antarctic continent is attributable to a partly glaciated continent in the late Eocene. A new bedrock topography for Antarctica allows for an early Oligocene ice sheet of greater areal extent than today (Wilson et al., 2012), raising the possibility that the temperature component of the EOT  $\delta^{18}\text{O}$  increase was more modest than previously suggested (Wilson et al., 2013).

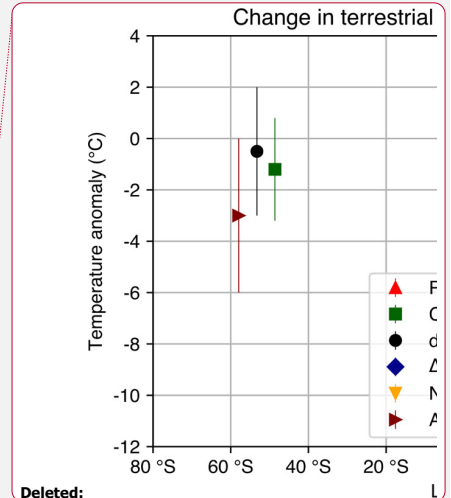
**Deleted:** mean annual temperature



**Figure 4:** Summary of terrestrial air temperature change across the EOT from proxies Paleosols, CLAMP,  $\delta^{18}\text{O}$ ,  $\Delta_{47}$ , Nearest Living Relative (NLR), alkaline geochemistry, and  $\delta\text{D}$  (hydrogen isotopes). Data is compiled from Boardman and Secord, 2013; Colwyn and Hren, 2019; Eldrett et al., 2009; Fan et al., 2017; Gallagher and Sheldon, 2013; Hérán et al., 2010; Herman et al., 2017; Hinojosa and Villagrán, 2005; Hren et al., 2013; Kohn et al., 2004; Kvaček et al., 2014; Lielke et al., 2012; Meyers, 2003; Page et al., 2019; Passchier et al., 2013; Roth-Nebelsick et al., 2017; Sheldon and Tabor, 2009; Zanazzi et al., 2007). Where possible, we apply the same method as in Figure 3, i.e. the 'late Eocene' is taken the average temperature from 38 to 33.9 Ma and the 'early Oligocene' is taken as the average from 33.9 to 30 Ma, and the temperature change shown here is the difference. However, in a number of cases, only a relative temperature change across the EOT was given in the original literature. We therefore limit our compilation to temperature anomaly only. The compilation shown above is provided in digital form in Supplementary Table S2.

## 955 5 CO<sub>2</sub> and carbon cycle dynamics

The concentration of carbon dioxide in the atmosphere ( $p\text{CO}_2$ ) is a primary driver of global climate change on geological timescales (Berner and Kothavala, 2001; Foster et al., 2017; Royer et al., 2004), and changes in  $p\text{CO}_2$  have been linked to the phase of acute climate change at the EOT (DeConto and Pollard, 2003; Heuereux and Rickaby, 2015; Pearson et al., 2009; Steinthorsdottir et al., 2016). However atmospheric  $p\text{CO}_2$  reconstructions for the EOT are sparse, variable and, in some cases, 960 contradictory and not readily reconciled with paleo-temperature proxy records or numerical model hindcasts (Beerling and Royer, 2011; Heuereux and Rickaby, 2015; Pagani et al., 2005; Pearson et al., 2009; Royer et al., 2004; Zhang et al., 2013). New well-resolved  $p\text{CO}_2$  records with strong age control are pressingly needed. Four proxies have been identified as particularly useful for Cenozoic  $p\text{CO}_2$  reconstructions by the Intergovernmental Panel on Climate Change (IPCC, 2013). These are the marine carbon and boron isotope proxies, and the terrestrial paleosol carbon and stomatal density proxies (Beerling and 965 Royer, 2011). Below, we discuss the development and state of the art of existing EOT  $p\text{CO}_2$  records constructed using marine



Deleted:

Deleted: ) and

Deleted: .

Deleted: (Boardman and Secord, 2013; Eldrett et al., 2009; Fan et al., 2017; Gallagher and Sheldon, 2013; Hérán et al., 2010; Herman et al., 2017; Hinojosa and Villagrán, 2005; Hren et al., 2013; Kohn et al., 2004; Kvaček et al., 2014; Lielke et al., 2012; Meyers, 2003; Page et al., 2019; Passchier et al., 2013; Roth-Nebelsick et al., 2017; Sheldon and Tabor, 2009; Zanazzi et al., 2007)

Deleted: 34.2

Deleted: 7

and terrestrial proxies.

### 5.1 Marine $p\text{CO}_2$ proxies

To date, the most detailed pre-Pleistocene climate records are derived from marine geochemical proxies, including boron isotopes ( $\delta^{11}\text{B}$ ) in planktonic foraminiferal calcite (Anagnostou et al., 2016; Foster et al., 2012; Greenop et al., 2017; Pearson et al., 2009; Pearson and Palmer, 1999, 2000) and carbon isotopes ( $\delta^{13}\text{C}$ ) in marine organic biomarkers (Heureux and Rickaby, 2015; Liu et al., 2009; Pagani et al., 2005, 2011; Zhang et al., 2013). Each proxy has its own limitations and uncertainties, which initially led to divergent estimates of  $p\text{CO}_2$  using these different proxies. However, recent efforts to address such uncertainties and limitations have led to a more coherent picture of the evolution of  $p\text{CO}_2$  through the Cenozoic from marine proxies.

While the theoretical basis of the boron isotope proxy is well understood, a major uncertainty in reconstructing surface ocean pH is estimating the boron isotopic composition of seawater (Greenop et al., 2017). A further major uncertainty comes into play when a second carbonate system parameter (e.g. total alkalinity) is required to calculate  $p\text{CO}_2$  from seawater pH, as well as the major ion composition of seawater, which impacts key dissociation constants. Nevertheless, significant progress has been made to reduce these uncertainties (Anagnostou et al., 2016; Greenop et al., 2017; Sosdian et al., 2018). For the Eocene  $p\text{CO}_2$  estimates, seawater  $\delta^{11}\text{B}$  has been estimated using the  $\delta^{11}\text{B}$ -pH relationship, while self-consistent estimates of the second carbonate parameter have been determined using Earth System modelling (Anagnostou et al., 2016). For the alkenone  $\delta^{13}\text{C}$  proxy, there are many factors that can impact algal growth conditions and inaccurate temperature reconstructions have also been known to bias  $p\text{CO}_2$  reconstructions (Pagani et al., 2011; Zhang et al., 2013). Algal carbon-concentrating mechanisms may also lead to biased  $p\text{CO}_2$  reconstructions when using the alkenone  $\delta^{13}\text{C}$  proxy in low- $\text{CO}_2$  intervals of the Neogene, but is unlikely to be a significant issue at the EOT (Zhang et al., 2013).

The boron isotope proxy suggests atmospheric  $p\text{CO}_2$  was  $1400\pm 470$  ppm in the early Eocene, and decreased by several hundred ppm through the Eocene over several million years (Anagnostou et al., 2016). In the late Eocene (Bartonian-Priabonian),  $p\text{CO}_2$  reconstructions are variable, but the boron isotope and alkenone proxy both indicate  $p\text{CO}_2$  concentrations around 1000 ppm (Anagnostou et al., 2016; Zhang et al., 2013). The EOT itself appears to be associated with a further, and perhaps steeper, decline in  $p\text{CO}_2$ , with both proxies supporting the passing of a modelled glaciation threshold of  $\sim 750$  ppm (DeConto and Pollard, 2003; Pagani et al., 2011; Pearson et al., 2009; Zhang et al., 2013), although this modelled threshold itself is highly uncertain (Gasson et al., 2014). A  $\delta^{11}\text{B}$ -based record from Tanzania sediments also suggests an intriguing transient  $p\text{CO}_2$  increase associated with the second  $\delta^{18}\text{O}$  step (Pearson et al., 2009).

## 5.2 Terrestrial proxies

The stomatal CO<sub>2</sub> proxy is based on the empirically and experimentally demonstrated inverse relationship between the density of stomata on the leaf surfaces of most land plants and  $p\text{CO}_2$  (Beerling, 1998; Franks et al., 2014; Hincke et al., 2016; Konrad et al., 2008; Kürschner et al., 2008; McElwain and Chaloner, 1995; Royer et al., 2001; Steinthorsdottir et al., 2016, 2019, 2020, 2011, 2013; Steinthorsdottir and Vajda, 2015; Wagner et al., 1996; Woodward, 1987). Previous studies using the stomatal proxy method of  $p\text{CO}_2$  reconstructions for the time intervals either side of the EOT (here Bartonian-Rupelian) are still relatively few, derived from mostly low-resolution datasets consisting of a variety of fossil plant taxa, and marred by limitations in chronological accuracy and correlation to marine records. Consequently, the  $p\text{CO}_2$  records have so far been highly heterogeneous.

The three current methods of stomatal  $p\text{CO}_2$  reconstruction (e.g. McElwain and Steinthorsdottir, 2017; Steinthorsdottir et al., 2020) include: 1) the semiquantitative stomatal ratio method, which compares the stomatal density (SD) or stomatal index (SI – the % of stomata relative to all leaf epidermal cells) of fossil plants with the SD/SI of its nearest living relative (NLR), to estimate paleo-  $p\text{CO}_2$  (McElwain and Chaloner, 1995), 2) the empirical transfer function method, using experimental data sets of NLR responses to variations in  $p\text{CO}_2$  (e.g. Kürschner et al., 2008; Wagner et al., 1996), and 3) mechanistic gas exchange modelling which requires numerous additional parameters such as paleotemperature and leaf  $\delta^{13}\text{C}$  (Franks et al., 2014; Konrad et al., 2008). All of these methods have been applied to reconstruct  $p\text{CO}_2$  records spanning the Eocene-Oligocene (Foster et al., 2017; Figure 5), with the highest-resolution dataset produced using the stomatal ratio method (Steinthorsdottir et al., 2016). Due to the semiquantitative approach and potential inter-method variability, these estimates are considered to be less robust in their absolute values of  $p\text{CO}_2$  than the marine estimates (Section 5.1). However, stomatal records are a valuable indicator of relative change of  $p\text{CO}_2$  in the terrestrial realm, especially in data-poor intervals including several stages of the Eocene and Oligocene (Beerling and Royer, 2011; Foster et al., 2017).

Early results based on datasets of the gymnosperms *Ginkgo biloba* and *Metasequoia glyptostroboides* from the USA suggested that  $p\text{CO}_2$  was more or less stable between 300 and 450 ppm during the Eocene and Oligocene (Royer et al., 2001) - however, the fossil leaf record was of too low resolution to draw strong conclusions. Another early study, based on data gathered mainly from published images of fossil *Ginkgo* specimens from Russia and USA, suggested a decrease in  $p\text{CO}_2$  across the EOT (Retallack, 2001), from ~1300 ppm in the Bartonian, to ~420 ppm at the EOT, and ~330 ppm in the Rupelian. A further stomatal dataset from Germany, based on fossil angiosperm leaves from the species *Eotrigonobalanus furcinervis* (Fagaceae) and *Laurophyllum acutumontanum* (Lauraceae), again of low temporal resolution, suggested that  $p\text{CO}_2$  was higher before than after the EOT (Roth-Nebelsick et al., 2004). A more recent study from a temporally restricted sedimentary succession in Canada suggested high but decreasing  $p\text{CO}_2$  at the Bartonian/Priabonian boundary (from ~1000–700 ppm to ~450 ppm), based on a dataset of *Metasequoia* fossil needles (Doria et al., 2011), but does not include the EOT or the Rupelian. In contrast, a

**Deleted:** (Beerling, 1998; Franks et al., 2014; Hincke et al., 2016; Konrad et al., 2008; Kürschner et al., 2008; McElwain and Chaloner, 1995; Royer et al., 2001; Steinthorsdottir et al., 2016, 2019, 2011, 2013; Steinthorsdottir and Vajda, 2015; Wagner et al., 1996; Woodward, 1987). Previous studies using the stomatal proxy method of  $p\text{CO}_2$  reconstructions for the time intervals either side of the EOT (here Bartonian-Rupelian) are still relatively few, derived from mostly low-resolution datasets consisting of a variety of fossil plant taxa, and marred by limitations in chronological accuracy and correlation to marine records. Consequently, the  $p\text{CO}_2$  records have so far been highly heterogeneous.

**Formatted:** English (UK)

**Deleted:** angiosperm Fagaceae

**Formatted:** English (US)

**Formatted:** Font: Not Italic, English (US)

**Formatted:** English (US)

**Deleted:** .

**Formatted:** English (US)

**Formatted:** Font: Not Italic, English (US)

study based on various angiosperm species using a leaf gas exchange model suggested more modest as well as stable  $p\text{CO}_2$  of ~470 ppm during the Bartonian and Priabonian, decreasing to ~400 ppm after the EOT in the Rupelian (Grein et al., 2013). A  
1055 subsequent study from the same region compiled all data in broad temporal bins and reconstructed early Oligocene to early  
Miocene  $p\text{CO}_2$  to ~400 ppm throughout, despite significant changes in stomatal densities (Roth-Nebelsick et al., 2012, 2014).  
Two studies with restricted temporal ranges reconstructed  $p\text{CO}_2$  in the Bartonian, indicating 400-500 ppm using *Metasequoia*  
from Canada (Maxbauer et al., 2014) and ~390 ppm using the podocarp conifer *Nageia maomigensis* from China (Liu et al.,  
2016).

1060 Recently, a new relatively high-resolution dataset consisting of *Eotrigonobalanus furcinervis* from Germany was published,  
including data points thought to be temporally located immediately before and after the EOT (Steinthorsdottir et al., 2016).  
The results show  $p\text{CO}_2$  of ~650 ppm in the Bartonian, decreasing to ~550–400 ppm in the Priabonian, and ~410 ppm at the  
EOT and the earliest Rupelian (Steinthorsdottir et al., 2016). This higher-resolution record shows a distinct ~40% Bartonian-  
1065 Priabonian decrease in  $p\text{CO}_2$ , highly comparable to the marine isotope temperature records, but reaching stable levels by the  
EOT, and not recording a significant  $p\text{CO}_2$  decrease at the EOT proper, unlike in the marine temperature records  
(Steinthorsdottir et al., 2016; Zachos et al., 2001, 2008). This discrepancy between  $p\text{CO}_2$  and temperatures suggests that there  
are factors other than greenhouse forcing that contribute to the threshold climate response of glaciation. New results based on  
Lauraceae leaf fragments from the Southern Hemisphere (Australia and New Zealand) further confirm Late Eocene  $p\text{CO}_2$   
1070 mostly in the order of 550–450 ppm, but are not sufficiently chronologically well-constrained to confirm falling  $p\text{CO}_2$  prior to  
the EOT (Steinthorsdottir et al., 2019).

Other results show a significant decrease in stomatal density values (indicating increasing  $p\text{CO}_2$ ) of extinct *Platanus neptuni*  
before the EOT (Moraweck et al., 2019). This unexpected trend, contradictory to the stomata density- $p\text{CO}_2$  relation previously  
1075 recorded, is not yet understood but is consistent with the suggestion that  $p\text{CO}_2$  change prior to the EOT caused plant responses.  
Further,  $p\text{CO}_2$  reconstructed using a mechanistic gas exchange model of Konrad et al. (2008) applied to two fossil species  
from northern central Europe, *Rhodomyrtophyllum reticulosum* and *Platanus neptuni*, records no significant decrease across  
the EOT (Moraweck et al., 2019), in agreement with Steinthorsdottir et al. (2016), but not recording decreasing  $p\text{CO}_2$  before  
the EOT. It should be noted that the gas-exchange model of Konrad et al. (2008) has recently been tested with modern material  
1080 and was shown to produce the most accurate  $p\text{CO}_2$  estimates when used with multiple species, to derive a consensus  $p\text{CO}_2$   
(Grein et al., 2013).

When focusing on datasets from central Europe, terrestrial plant based  $p\text{CO}_2$  records support the plant-derived temperature  
records by indicating no abrupt decrease or environmental change across the EOT (Kunzmann et al., 2016; Teodoridis and  
1085 Kvaček, 2015). A detectable but not fundamental change in vegetation, temperatures and  $p\text{CO}_2$  is however evident from the  
interval prior to the EOT (Kunzmann et al., 2016; Kvaček et al., 2014; Steinthorsdottir et al., 2016; Teodoridis and Kvaček,

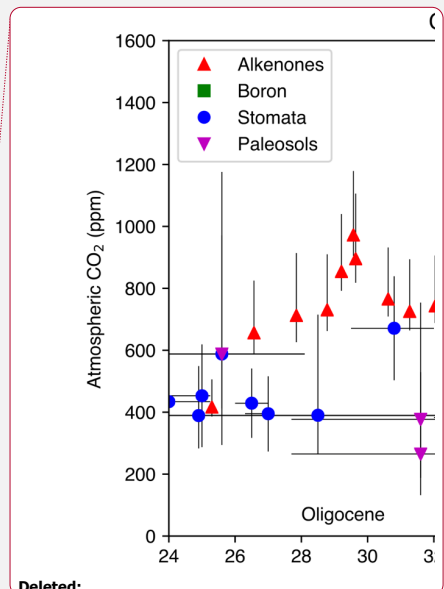
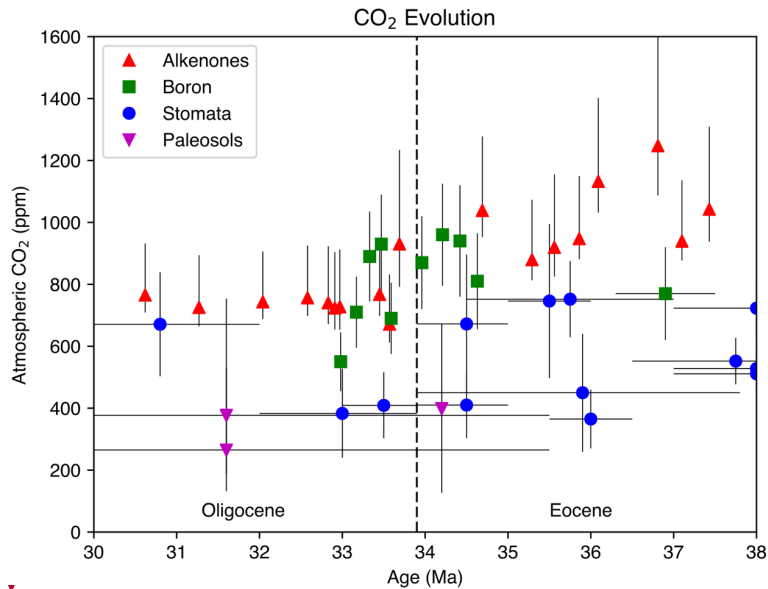
2015). Preliminary results of MAT estimations based on sedimentary GDGT values from some central German sites are in accordance with temperature estimates from plant fossils, i.e. based on CLAMP and the NLR approach. In combination these data refer to a successive decrease in MAT across the Priabonian and the EOT but not to a significant drop during the EOT.

Deleted: Nearest Living Relative (  
Deleted: )

1090 **5.3 Synthesis of EOT  $p\text{CO}_2$  change**

The most recent marine records indicate  $p\text{CO}_2$  of ~1000 ppm in the Bartonian-Priabonian, decreasing to ~700–800 ppm into the Rupelian. Stomatal proxy-based  $p\text{CO}_2$  records generally indicate elevated Bartonian-Priabonian  $p\text{CO}_2$  of ~500–1000 ppm, decreasing ~40% before the EOT to  $p\text{CO}_2$  of ~400 ppm, and continuing in the Rupelian with  $p\text{CO}_2$  of ~400 ppm or lower. The direction and approximate magnitude of  $p\text{CO}_2$  change leading up to the EOT is therefore consistent between proxies, even though the stomatal records consistently yield lower  $p\text{CO}_2$  levels than the marine proxies. We consider the higher  $p\text{CO}_2$  estimates based on marine proxies to be most robust indicator of  $p\text{CO}_2$  at this time, since they have been shown to reproduce ice-core  $\text{CO}_2$  well (Foster and Rae, 2016), and to agree better with the available modelling evidence from warm climate simulations of the Eocene, and estimated thresholds for glaciation of Antarctica (section 6.2). Some terrestrial records also indicate a decrease in  $\text{CO}_2$  but the decrease is more gradual and long term than in the marine records.

1095



Deleted:



l105 **Figure 5:** Atmospheric CO<sub>2</sub> evolution from 44 to 24 Ma from the compilation of Foster et al., (2017), incorporating data from its original  
data sources (Anagnostou et al., 2016; Doria et al., 2011; Erdei et al., 2012; Franks et al., 2014; Pearson et al., 2009; Roth-Nebelsick et al.,  
2012, 2014; Steinthorsdottir et al., 2016; Zhang et al., 2013), and Steinthorsdottir et al., (2019).

## 6 Insights into the EOT from modelling studies

In this section we qualitatively synthesise previous modelling studies that have focussed on the EOT. In particular, we discuss  
the modelled response to changing paleogeography (Section 6.1) and to changes in CO<sub>2</sub> (Section 6.2). Finally, we describe  
l110 carbon-cycle models that have explored mechanisms behind CO<sub>2</sub> changes at the EOT (Section 6.3).

### 6.1 Modelling the response to changing paleogeography at the EOT

The widening of the Southern Ocean Drake Passage and Tasman gateways has long been considered as a primary driver for  
the initiation of the AMOC and Antarctic glaciation at the EOT (Section 2.2). Many climate modelling studies have tested the  
effect of opening these Southern Ocean gateways and found cooling effects on the southern high latitudes (Cristini et al., 2012;  
l115 Elsworth et al., 2017; England et al., 2017; Mikolajewicz et al., 1993; Sijp et al., 2009, 2014; Sijp and England, 2004;  
Toggweiler and Bjornsson, 2000; Viebahn et al., 2016; Yang et al., 2014). These studies have variously found that opening  
Southern Ocean gateways can decrease southward heat transport (e.g. Sijp et al., 2009), trigger the onset of an AMOC (e.g.  
Yang et al. 2014), and enable some degree of cooling over Antarctica. However, these approaches do not reconcile the timing  
and evolution of the gateway evolution of the EOT, since they employed either modern-day or idealised geography with  
specific gateway perturbations. In contrast, climate model simulations that do employ Eocene boundary conditions indicate  
l120 that Southern Ocean gateway opening caused only a modest change in ocean poleward heat transport and could therefore not  
be directly responsible for the initiation of the AIS (Goldner et al., 2014; Huber et al., 2004; Huber and Nof, 2006; Huber and  
Sloan, 2001; Sijp et al., 2011; Zhang et al., 2011). Furthermore, opening the Southern gateways under Eocene-like CO<sub>2</sub> forcing  
may result in a weaker ACC than under pre-industrial conditions (Lefebvre et al., 2012). The long-term evolution of Southern  
l125 Ocean gateway opening has been found to cause ~3°C of bottom water cooling (Sijp et al., 2014), which may explain some of  
the observed benthic cooling (Section 3.2). However, Drake Passage opening probably affected deep ocean temperatures and  
the strength of the ACC. Hill et al. (2013) showed that despite deep water connections through both Drake Passage and the  
Tasman Gateway, a coherent ACC could not develop until the Australian continent was sufficiently equatorward such that it  
no longer inhibited strong zonal flow in the Southern Ocean.

l130 Imposing an ice sheet in a climate model has been shown to have a significant impact on the ocean circulation and deep water  
formation regions (Goldner et al., 2014; Kennedy et al., 2015). In particular, the presence of an [Antarctic](#) ice sheet may enhance  
westerly winds over the Southern Ocean, leading to enhanced Southern Ocean deep ocean formation and benthic cooling  
(Goldner et al., 2014). This [result](#) suggests that [Southern Ocean gateway changes play a secondary role to radiative forcing](#),  
l135 since the ocean circulation change are a consequence of the glaciation, rather than a cause. Other ocean gateways may also

Deleted: theory

play an important role. In the late Eocene continental configuration, the Central American Seaway and the Tethys gateway, connecting the Indian and Atlantic oceans, were wider than today. The importance of the open Tethys gateway for the EOT circulation has not received much attention but Zhang et al. (2011) found that the tropical seaways need to be sufficiently constricted before the southern high latitudes can cool substantially. This cooling is related to a transition from an ocean circulation with southern hemisphere deep water formation to the modern-like circulation with deep water formation in the North Atlantic.

Recently, focus has shifted to the role of Arctic-Atlantic gateways around the EOT. The evolution of the Arctic-Atlantic gateways has been shown to have a strong influence on the salinity of the North Atlantic and therefore on the AMOC (Hutchinson et al., 2019; Roberts et al., 2009; Stürz et al., 2017; Vahlenkamp et al., 2018b). The deepening of the Greenland-Scotland ridge at the EOT has been proposed as a trigger for the AMOC (Abelson and Erez, 2017; Stürz et al., 2017). According to this hypothesis, the deepening changes the flow across the ridge from a shallow unidirectional flow to a deeper bi-directional flow which allows salty subtropical water to penetrate further north and enable North Atlantic sinking. Hutchinson et al. (2019) recently proposed that it is the tectonic closing of the shallow Barents Sea gateway, just prior to the EOT, that initiated the AMOC, by closing off the pathway of extremely fresh Arctic water to the North Atlantic. Neither Southern Ocean gateway changes, Greenland-Scotland Ridge changes, or CO<sub>2</sub> forcing changes could similarly overcome the freshening effect of the Arctic to allow an AMOC. However, their study did not test the feedback of these circulation changes on the carbon cycle, making it unclear what the climatic impact of the Arctic closure would have been. Using an Earth System Model, (Vahlenkamp et al., 2018a, 2018b) experimented with similar changes in the North Atlantic gateways to investigate an alternative idea of significant AMOC behaviour since the early–middle Eocene. They were able to initiate an AMOC when the Greenland Scotland Ridge reached a threshold depth of deeper than 200 m but, only when the Arctic Ocean brackish water outlets were shut off from the North Atlantic. Timing of changes in Arctic-Atlantic ‘plumbing’, thus, appear to be a critical factor in allowing an AMOC to start up in the Warm Paleogene, and a key area for future research.

In all these studies, it is assumed that the final state of the simulation is the only steady solution for that climate and boundary conditions. While there is no consensus yet (Nof et al., 2007), the present day climate is thought to have two global circulation modes; the observed AMOC with sinking in the north, and a southern-sinking only mode with no AMOC (Liu et al., 2017; Srokosz and Bryden, 2015). In continental geometries other than the present day different circulation patterns and co-existing equilibria may be possible but have not been systematically searched for so far (Baatsen et al., 2018). In coupled Eocene simulations, centers of deepwater formation include the North and South Pacific (Hutchinson et al., 2018; Thomas et al., 2014) and the North and South Atlantic (Huber et al., 2003; Huber and Sloan, 2001). Conceptual climate models have suggested a potential role for meridional overturning circulation transitions in the EOT (Tigchelaar et al., 2011).

## 6.2 Modelling the response to CO<sub>2</sub> decrease at the EOT

1170 A reduction in atmospheric CO<sub>2</sub> is hypothesised to be a primary cause of the EOT, because it can plausibly explain both long  
term cooling during the Eocene, and provide a trigger for the glaciation of Antarctica (DeConto and Pollard, 2003). Although  
proxy reconstructions of atmospheric CO<sub>2</sub> during the Eocene have large uncertainties (Section 5), there is general agreement  
that climate cooled and CO<sub>2</sub> declined through the Eocene (Anagnostou et al., 2016; Foster et al., 2017), making long-term CO<sub>2</sub>  
1175 drawdown from the atmosphere a prime underlying forcing mechanism for the EOT. Furthermore, CO<sub>2</sub>-forced climate-ice  
sheet model experiments yield  $\delta^{18}\text{O}$  series (DeConto and Pollard, 2003) that closely match the overall form of our best-resolved  
EOT data sets (Coxall et al., 2005; Coxall and Wilson, 2011).

A long-standing problem in modelling the Eocene climate is to reproduce the low meridional temperature gradient recorded  
in observations. Proxies suggest that high latitude SSTs were more than 20°C warmer than present day during the early Eocene  
1180 (Bijl et al., 2009), terrestrial anomalies were 20-40°C (Huber and Caballero, 2011), while tropical temperatures were some 5-  
10°C warmer than modern (Huber, 2008; Huber and Sloan, 2000). Evidence of frost intolerant flora and fauna in high latitudes  
(Greenwood and Wing, 1995) provides a challenge to explain how the climate maintained such a low meridional temperature  
gradient.

1185 When climate models are forced using proxy data-based estimates of Eocene CO<sub>2</sub>, they generally fail to capture these flatter  
meridional temperature gradients (Huber et al., 2003; Roberts et al., 2009; Shellito et al., 2003). One method that has been  
used to address this high-latitude cold bias is to increase the CO<sub>2</sub> to extremely high values (2240 or 4480 ppm) (Cramwinckel  
et al., 2018; Eldrett et al., 2009; Huber and Caballero, 2011; Winguth et al., 2010). These extremely high CO<sub>2</sub> experiments  
yield an improved match to high-latitude temperature proxies and temperature gradients (Huber and Caballero, 2011; Lunt et  
1190 al., 2012). Because these extremely high CO<sub>2</sub> concentrations are greater than those implied by proxies, this finding also  
suggests that modelled climate sensitivity to CO<sub>2</sub> forcing may be too low, probably because of positive feedbacks that are  
either missing or too weak in the models. Several missing feedbacks suggested recently are those associated with cloud physics  
and/or greenhouse gases in addition to CO<sub>2</sub> (Beerling et al., 2011; Kiehl and Shields, 2013; Sagoo et al., 2013; Zhu et al.,  
2019). We also note that recent proxy data from the warmest regions of the tropics (Tanzania, Java) indicate tropical  
1195 temperatures of up to 35°C in the middle-late Eocene (Evans et al., 2018; Pearson et al., 2007). These temperatures imply a  
somewhat larger meridional gradient than previously suggested, helping to reduce the magnitude (but not eliminate) the model-  
data mismatch. In addition, several models have now achieved lower meridional temperature gradients through a combination  
of higher resolution, which tends to increase poleward heat transport, and improved Eocene boundary conditions (Baatsen et  
al., 2020; Hutchinson et al., 2019; Zhu et al., 2019). [A recent model-data comparison demonstrates that the Oligocene retains  
200 a low meridional temperature gradient similar to the late Eocene, which is not well explained by currently available climate  
models \(O'Brien et al., 2020\). In the Oligocene, CO<sub>2</sub> proxy estimates are lower than in the Eocene, making it arguably more](#)

difficult to model the low temperature gradient with realistic CO<sub>2</sub> forcing (O'Brien et al., 2020), although the CO<sub>2</sub> proxies carry large uncertainty.

1205 Despite the challenges faced in modelling the early Eocene, the observed cooling during the Eocene of bottom waters (Zachos et al., 2001) and high latitude SSTs (Bijl et al., 2009) and terrestrial temperatures can plausibly be explained by a reduction in CO<sub>2</sub> in climate model simulations (Eldrett et al., 2009; Liu et al., 2009). Furthermore, crossing a CO<sub>2</sub> threshold of Antarctic glaciation may also explain several degrees of bottom water cooling, through consequent shifts in Southern Ocean winds and changes to Southern Ocean circulation (Goldner et al., 2014). A key challenge to adequately testing the CO<sub>2</sub> forcing hypothesis

1210 is to derive a threshold level of CO<sub>2</sub> for glaciation from climate model reconstructions. The first study to do so found a glaciation threshold of around 780 ppm (DeConto and Pollard, 2003), in approximate agreement with CO<sub>2</sub> proxies. However, a recent inter-comparison of Eocene climate models used to force an ice sheet model found that this threshold varied significantly between models, from roughly 560 to 920 ppm (Gasson et al., 2014). Differences in the lapse-rate feedback were identified as the leading cause of this spread, although there were also differences in the paleogeographic boundary conditions.

1215 All ice-sheet modelling studies of the EOT to date have used prescribed climate states to force the glaciation. Likewise, coupled ocean-atmosphere-sea ice models currently prescribe ice sheets as either present or absent. Running a full-complexity climate model synchronously with an ice sheet model remains a major technical challenge, and has yet to be implemented for the Eocene or Oligocene. However, innovative asynchronous coupling, such as the “matrix-method” (Pollard, 2010), has shown

1220 some promise by allowing a better representation of the ice albedo feedback, leading to a similar yet slightly revised upward glaciation threshold of ~900 ppm (Ladant et al., 2014b).

### 6.3 Carbon Cycle Modelling

1225 A slow decline in atmospheric CO<sub>2</sub> remains a likely priming mechanism for the inception of large ice sheets on Antarctica and this pivotal transition in Cenozoic climate was associated during the EOT with pronounced rapid perturbation to the global carbon cycle as indicated by a transient increase in ocean δ<sup>13</sup>C and a permanent deepening of the CCD (Coxall et al., 2005). Thus, numerical carbon cycle model experiments provide useful insight to forcing mechanisms and feedback processes involved.

1230 Many hypotheses have been posited to explain the carbon cycle perturbations at the EOT (Armstrong McKay et al., 2016; Coxall et al., 2005; Coxall and Wilson, 2011; Merico et al., 2008). Some of the leading hypotheses include a shift from shelf to basin carbonate fractionation (Opdyke and Wilkinson, 1988), increases in organic carbon burial (Olivarez Lyle and Lyle, 2006), feedbacks between ice sheet coverage and silicate weathering (Zachos and Kump, 2005), and an ecological shift from calcareous to siliceous plankton (Falkowski et al., 2004). Carbon cycle box models suggest that the best fit to observations is

**Deleted:** Slow

**Deleted:** calcite compensation depth (

**Deleted:** )

**Deleted:** (Armstrong McKay et al., 2016; Coxall and Wilson, 2011; Merico et al., 2008)

**Deleted:** model experiment results

245 achieved by a shift from shelf-to-basin carbonate fractionation, (Armstrong McKay et al., 2016; Merico et al., 2008). In this interpretation of events, the fall in sea-level due to Antarctic glaciation (i) reduces the global flux of carbonate into shallow water (reef, bank and shelf) sediments and (ii) exposes fresh, readily dissolved shelf carbonate sediments around the world to rapid subaerial weathering (Merico et al., 2008). The first of these two mechanisms drives the sustained CCD deepening from Eocene to Oligocene and the second drives a one-off dump of carbonate into the ocean that explains the observed initial transient overshoot behaviour (Zachos and Kump, 2005) and, because the shelf carbonate reservoir is enriched in  $^{13}\text{C}$  relative to pelagic carbonate reservoir (Swart, 2008; Swart and Eberli, 2005), the transient increase in benthic  $\delta^{13}\text{C}$  (Armstrong McKay et al., 2016; Merico et al., 2008). If the isotopic fractionation between these two carbonate sediment reservoirs is modest, however, shelf-basin fractionation can only fully explain the transient increase in oceanic  $\delta^{13}\text{C}$  if the one-off dump of weathered shelf carbonate is questionably large (Merico et al., 2008). In their follow up study, Armstrong McKay et al. (2016) considered this problem in detail and concluded that, unless shelf carbonates were substantially enriched in  $^{13}\text{C}$  relative to pelagic carbonates (by  $\sim 3\%$ ), an additional process must also have contributed, with sequestration of  $^{12}\text{C}$ -enriched carbon into carbon capacitors, and possibly increased ocean ventilation, offering the best fit to the paleorecords when combined with shelf basin fractionation.

**Deleted:** glacio-eustatic sea level-led

**Deleted:** in global carbonate burial and a spike in riverine carbonate weathering together with carbon sequestration in  $\text{C}_{12}$ -enriched carbon capacitors such as terrestrial peatlands or marine methane clathrate

**Deleted:** .

255 Palike et al. (2012) investigated causes of carbon cycle changes over the Eocene using the intermediate complexity climate model cGENIE. They suggest several mechanisms are needed to explain the CCD change in addition to the shelf-basin fractionation hypothesis above: (i) perturbations to continental weathering and solute input to the deep ocean, or (ii) changes in the partition of organic carbon flux between labile organic carbon that is readily available for oxidation and driving carbonate dissolution and refractory (carbon that is more resistant to degradation and largely preserved and buried).

**Deleted:** ;

**Deleted:** and refractory components.

260 The longer-term decline in  $\text{CO}_2$  over the Eocene needs to be reconciled with the negative feedback between silicate weathering and surface temperature (Walker et al., 1981). Higher  $\text{CO}_2$  causes warming and enhances the hydrological cycle, which leads to an increase in silicate weathering. The increase in weathering eventually lowers  $\text{CO}_2$  and subsequent cooling, creating a dynamic equilibrium. This silicate weathering feedback is regulated by tectonic processes (Raymo and Ruddiman, 1992), since mountain ranges give rise to greater weathering than low-lying regions (Maher and Chamberlain, 2014).

**Formatted:** Tab stops: 5.36 cm, Left

270 A climate model study suggests that opening and deepening of the Drake Passage could lower atmospheric  $\text{CO}_2$  via the silicate weathering feedback (Elsworth et al., 2017). They suggested that the gateway transition enhanced the AMOC, leading to greater precipitation over land regions and a warmer northern hemisphere, both of which enhance silicate weathering and thus drawdown of  $\text{CO}_2$  (Maher and Chamberlain, 2014). However, this study used modern geography with selected gateway perturbations, whereas climate models using paleogeography from the late Eocene have yielded different patterns of overturning (Baatsen et al., 2020; Hutchinson et al., 2019). Furthermore, a hypothesised change in silicate weathering must be weighed against the CCD record, because silicate weathering changes have implications for carbonate weathering and

1285 bicarbonate ion supply to the ocean (Armstrong McKay et al., 2016; Merico et al., 2008). Fyke et al. (2015) found opening Drake Passage led to a decrease in Atlantic carbon storage and an increase in Pacific and Southern Ocean storage, due to the enhancement of a modern-like AMOC. This led to an overall increase in global carbon storage in the ocean, though their implied drop in atmospheric CO<sub>2</sub> is relatively small (10-30 ppm). Incorporating carbon cycle processes into full complexity climate models with Eocene or Oligocene paleogeography thus remains an outstanding challenge (e.g. Godd ris et al., 2014).

1290 Experiments using cGENIE report an increase in carbon re-mineralisation near the ocean surface when temperatures are very warm, such as in the early Eocene (John et al., 2013, 2014). The more temperature dependent re-mineralisation results in a shallower CCD, and a decrease in organic carbon burial, an effect which then decreased over the Eocene as temperatures decreased. This modelled mechanism is consistent with tropical records of  $\delta^{13}\text{C}$  during the Eocene (John et al., 2013, 2014), providing a positive feedback on carbon dioxide changes, in opposition to the silicate weathering feedback.

Deleted: a model of intermediate complexity,

Deleted: ,

## 7 Model-data intercomparison of temperature change across the EOT

1295 Until this point, this review paper has synthesised the existing literature but has not presented any new quantitative analysis. Furthermore, we have in general presented the proxy and model-derived insights separately. Here, we combine the information from proxies and models and present a new model-data comparison and quantitative analysis of the mechanisms behind temperature change at the EOT. This section is in two parts: (7.1) a quantitative intercomparison of temperature change across the EOT from a subset of these previous studies, in which we identify those changes that are robust across models; and (7.2) 1300 a comparison of the modelled temperature changes with proxy SST and surface air temperature (SAT) data, in which we assess which models best fit the proxy reconstructions, and which mechanisms most likely explain the observed proxy temperature changes.

Deleted: SAT

### 7.1 Intercomparison of modelled SAT change across the EOT

1305 Here we present an intercomparison of some previous model results of SAT change across the EOT. We use SAT data because it provides a consistent surface temperature over both ocean and land regions that reflects changes across the globe. It also enables comparison with proxies of both marine and terrestrial data to be readily included. We include those models and studies for which the authors have provided their model results in digital form. The models and simulations included in this intercomparison are shown in Table 2. This itself is a subset of the simulations that were available – here we show only those 1310 simulations that allow us to compare the response of the models to a consistent forcing, for as many models as possible.

Deleted: surface air temperature (

Deleted: )

Deleted: Table 7.1.

We first consider pairs of simulations that represent the response of the climate system to a perturbation in forcing that may have occurred across the EOT. These pairs can broadly be divided into three categories corresponding to three forcings: a CO<sub>2</sub> decrease, an increase in the volume and extent of the Antarctic ice sheet, and a paleogeographic change. Although these forcing

1320 factors are in reality interdependent (for example the ice sheet change may itself be caused by a CO<sub>2</sub> change), for the purposes  
of modelling they are treated as independent mechanisms.

For the CO<sub>2</sub> forcing, we consider a halving of atmospheric CO<sub>2</sub>, which for most models is from 1120 to 560 ppmv. However,  
for GFDL this is from 800 to 400 ppmv, and for ~~NorESM-L~~ there are CO<sub>2</sub> simulations at 980 and 560 ppmv. For the ~~NorESM-~~  
1325 ~~L~~ case, we scale the anomaly by a factor of  $\log(2)/\log(980/560)$  in order to approximate the radiative forcing of halving CO<sub>2</sub>.  
We emphasise here that halving CO<sub>2</sub> is not intended to be a realistic forcing perturbation for the EOT, but rather a standardised  
experimental protocol that can be used to establish the CO<sub>2</sub> climate sensitivity of the models. For the ice sheet forcing, we  
consider a change from an ice-free Antarctic, to an ice sheet similar in volume and area to that of today. However, the  
configuration of these ice sheets, and the ice-free state, does vary from model to model (see Supplementary Figure S1). The  
1330 paleogeographic forcing is less consistent across the models, and includes modelled changes to gateways only (CESM and  
UVic), to west Antarctic geography (FOAM), or to global paleogeography (HadCM3BL) (see Supplementary Figure S3).

Before examining the SAT response of the system to these three forcings, it is useful to explore the absolute temperatures in  
the model simulations. The annual global mean SAT in each simulation is shown in Figure 6, while the spatial patterns for  
1335 each individual model are shown in Supplementary Figures S1-S3. In terms of global mean surface temperature, the models  
fall approximately into two groups: (i) a cooler group, consisting of CESM\_H, FOAM, HadCM3BL, NorESM-L, have global  
mean surface temperatures of around 17-19 °C at 560 ppm, and 21 to 23 °C at 1120 ppm; and (ii) a warmer group consisting  
of CESM\_B, CESM\_H (x2) and GFDL CM2.1, where temperatures are roughly 4 °C warmer for the equivalent level of CO<sub>2</sub>  
(Figure 6). A common factor in this split is that the warmer models have higher horizontal resolution (~1° ocean for CESM\_B  
1340 and GFDL CM2.1; ~2° atmosphere for CESM\_H (x2) and CESM\_B), although this is likely to be depend strongly on the  
individual model and boundary conditions used. It is also clear from Figure 6 and Supplementary Figures S1-S3 that the CO<sub>2</sub>  
forcing has a much greater effect on global mean SST than the ice or paleogeographic forcing.

Deleted: NORESM

Deleted: NORESM

Model	Atmos resolution	Ocean resolution	Publication	Paleogeography	CO2 [ppm]	Antarc. ice	Tasman	Drake	CO2 expts	ICE expts	GEO expts	Model years
CESM_B (CESM1.0.5)	144 x 96 x 26	384 x 320 x 60	Baatsen et al (2020)	38 Ma Baatsen et al (2016)	560 1120	N N	open open	open open	L H			3600 4600
CESM_H (CESM1.1)	96 x 48 x 26	122 x 100 x 25	Goldner et al (2014)	45 Ma Sewall et al (2000)	560 560 1120 1120 560	N Y N N N	closed closed closed open closed	open open open closed open	L H	NI I		3400 3000 3300 1300 1000 1500
CESM_H (x2)	144 x 96 x 26	122 x 100 x 25	* 2° atmosphere									
FOAM	48 x 40 x 18	128 x 128 x 24	Ladant et al (2014a) Ladant et al (2014b)	34Ma 30Ma	560 560 1120 560	N Y N N	open open open open	open open open open	L H	NI I	B A	2000 2000 2000 2000
GFDL CM2.1	96 x 60 x 24	240 x 175 x 50	Hutchinson et al (2018)	38 Ma Baatsen et al (2016)	400 800 800	N N N	open open open	open open open	L H		B A	6500 6500 6500
HadCM3BL	96 x 73 x 19	96 x 73 x 20	Kennedy et al (2015)	Rupelian (28-34Ma) Chattian (23-28Ma) Priabonian (34-38Ma)	560 1120 560 560 560	N N Y N N	open open open open open	open open open open open	L H	NI I		1422 1422 1422 1422 1422
NorESM-L	96 x 48 x 26	100 x 116 x 32	Zhang et al (2012, 2014)	35 Ma (Scotese, 2001)	560 980 560	N N N	open open open	open open open	L H		B A	2200 2200 2200
UVic	150 x 100 x 1	150 x 140 x 40	Sijp et al (2016)	45 Ma Sewall et al (2000)**	1600 1600	N N	open open	open closed			A B	9000 9000

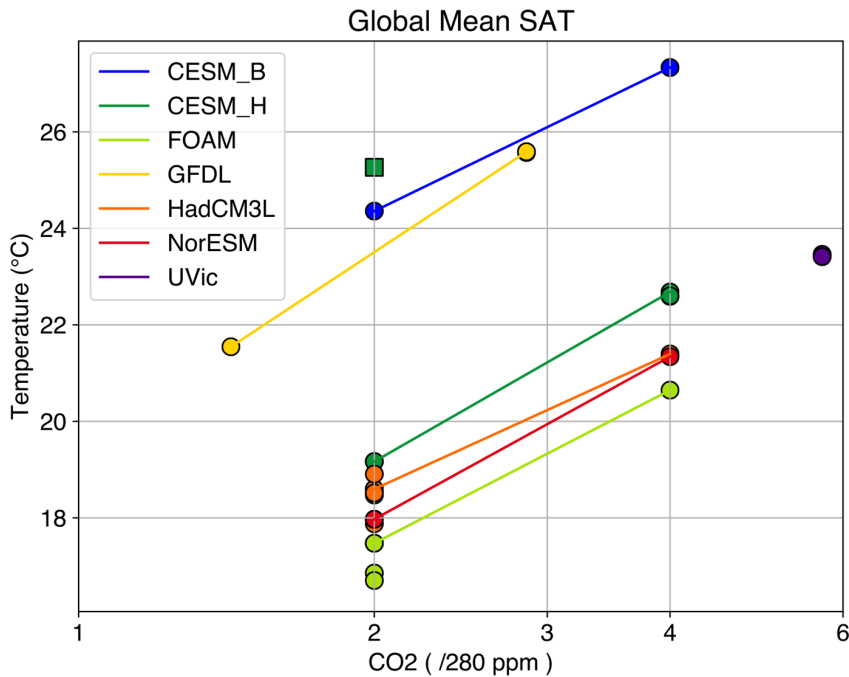
**Table 2:** Details of model simulations that are included in this intercomparison. For each model, the response to CO<sub>2</sub>, ΔT<sub>CO2</sub>, is given by H-L; ΔT<sub>ICE</sub> is given by I-NI; and ΔT<sub>GEO</sub> is given by A-B.

Model	Atmos resolution	Ocean resolution	Publication
CESM_B (CESM1.0.5)	144 x 96 x 26	384 x 320 x 60	Baatsen et al (2020)
CESM_H (CESM1.1)	96 x 48 x 26	122 x 100 x 25	Goldner et al (2014)
CESM_H (x2)	144 x 96 x 26	122 x 100 x 25	* 2° atmosphere
FOAM	48 x 40 x 18	128 x 128 x 24	Ladant et al (2014a) Ladant et al (2014b)
GFDL CM2.1	96 x 60 x 24	240 x 175 x 50	Hutchinson et al (2018)
HadCM3BL	96 x 73 x 19	96 x 73 x 20	Kennedy et al (2015)
NorESM-L	96 x 48 x 26	100 x 116 x 32	Zhang et al (2012, 2014)
UVic	150 x 100 x 1	150 x 140 x 40	Sijp et al (2016)

Deleted:

Deleted:





1350 **Figure 6:** Global mean surface air temperature (SAT) for all models included in this intercomparison as a function of CO<sub>2</sub> concentration. The lines join simulations from a single model at different CO<sub>2</sub> concentrations. References for each model are CESM\_H: (Goldner et al., 2014), UVic: (Sijp et al., 2016), FOAM: (Ladant et al., 2014a, 2014b), GFDL: (Hutchinson et al., 2018, 2019), HadCM3BL: (Kennedy et al., 2015), NorESM-L: (Zhang et al., 2014), CESM\_B: (Baatsen et al., 2020). The dark green square is an additional simulation of CESM\_H with 2° atmosphere resolution (Table 2).

1355 The SAT responses of each of the individual models to the three forcings,  $\Delta T_{CO_2}$ ,  $\Delta T_{ICE}$ ,  $\Delta T_{GEO}$ , are shown in Supplementary Figures S1, S2, and S3 respectively. We also include the annual mean sea ice distribution in each of CO<sub>2</sub>, ICE and GEO experiments in Supplementary Figures S4, S5 and S6 respectively. It is important to highlight that the changes shown have not necessarily been chosen to best represent the EOT transition. In particular, the CO<sub>2</sub> forcing shown is a halving of CO<sub>2</sub> in all models, and although proxy CO<sub>2</sub> estimates are not inconsistent with this change (Pagani et al., 2011; Pearson et al., 2009), the data come with large uncertainties, albeit more so for absolute concentrations than for relative changes. In Section 7.3 we will explore this further, but here we recognise that the model responses are highly idealised and we treat them as sensitivity studies.

Formatted: English (AUS)

Deleted: (Table 1).

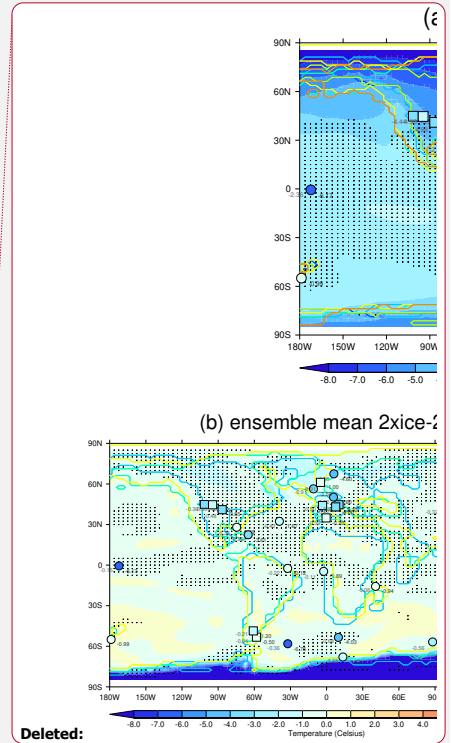
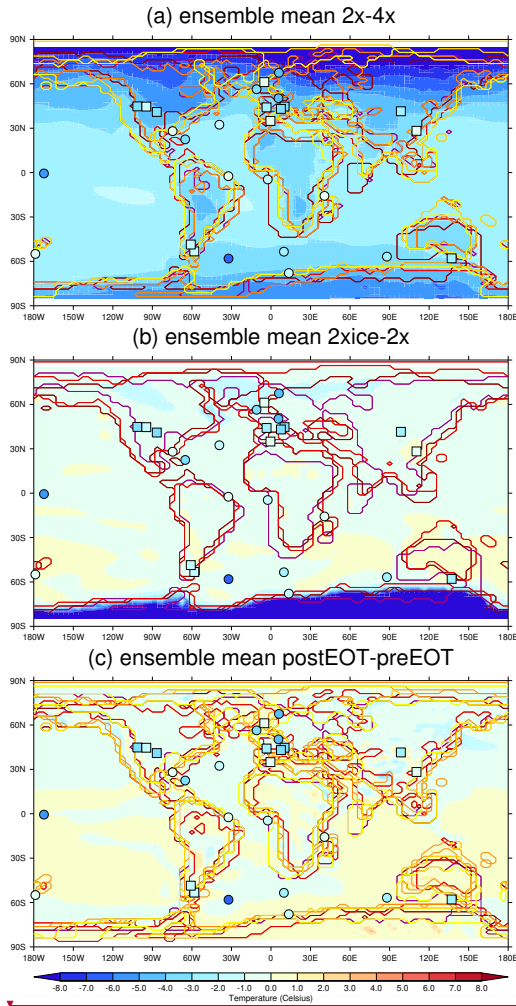
Deleted: also

Deleted: ,

### 7.1.1 SAT response to CO<sub>2</sub> decrease, $\Delta T_{CO_2}$

Here we consider the response to halving CO<sub>2</sub> in the absence of an ice sheet. There appear to be two different modes of SAT response to a halving of CO<sub>2</sub> (Supplementary Figure S1). In the first mode, CESM\_H, CESM\_B, FOAM, and GFDL respond with a cooling over all the globe, with greatest cooling in the higher latitudes. In the second mode, HadCM3BL and NorESM-L respond with cooling in most regions (with greatest cooling in the north Pacific), but with warming in the Pacific sector of the Southern Ocean. In HadCM3BL, this is associated with a switch in regions of deep water formation from dominant sinking in the southern Atlantic and north Atlantic at high CO<sub>2</sub>, to dominant sinking in the southern Pacific and north Atlantic at low CO<sub>2</sub>. The onset of sinking in the southern Pacific at low CO<sub>2</sub> leads to increased heat transport from the equatorial Pacific southwards, to such an extent that it leads to net warming in the Pacific sector of the Southern Ocean, despite the decrease in CO<sub>2</sub>. Similar but weaker changes in ocean circulations happen in the NorESM-L. However, this warming response is highly sensitive to the boundary conditions, with other qualitatively similar simulations behaving very differently in the region, with some showing only cooling (Kennedy-Asser et al., 2019). In CESM, a switch in the mode of ocean circulation does not occur, with deep water formation in the Pacific sector of the Southern Ocean at both high and low CO<sub>2</sub> (albeit increased in intensity at low CO<sub>2</sub>). Similarly, for GFDL there is no switch, with deep water formation in the South and North Pacific at high and low CO<sub>2</sub>, and for FOAM there is no switch, with deep water formation predominantly in the North Pacific at high and low CO<sub>2</sub>. The patterns of change in HadCM3BL and NorESM-L are remarkably similar except in the Arctic, where NorESM-L shows much more cooling than HadCM3BL. In this region FOAM also has very little cooling. This is because both HadCM3BL and FOAM have Arctic sea ice in both high and low CO<sub>2</sub> simulations, which maintains the SST close to 0°C.

The ensemble mean SAT change due to a halving of CO<sub>2</sub> is shown in Figure 7a. This shows that the greatest cooling is in the North Pacific and in the Atlantic and Indian sectors of the Southern Ocean. Most of the regional cooling is “robust” in that all models show a change of the same sign and are all within  $\pm 2$  °C of the ensemble mean change. Exceptions are in the south Pacific (because some models show warming rather than cooling) and in the North Pacific and Arctic (because there is large variability in the amount of cooling predicted). Overall, the zonal mean cooling is approximately symmetric about the equator, with equatorial cooling of -2.6 °C and mid-high latitude cooling of -5.0 °C. While this symmetry is at odds with an inferred northward migration of the intertropical convergence zone from dust geochemistry (Hyeong et al., 2016), we stress that this result reflects the fact that the far-field cooling induced by imposing an Antarctic ice sheet (see Figure 7b) is much smaller than the global cooling induced by CO<sub>2</sub> forcing in these models.



Deleted:

Deleted: Stippled regions are those where the change is defined as 'robust', in that all models have a response of the same sign and within  $\pm 2$  °C of the ensemble mean.

Deleted: The values of SAT change at each proxy site are shown for the data and model on the left and right of each site respectively.

**Figure 7:** Ensemble mean modelled SAT response to (a) CO<sub>2</sub> halving ( $\Delta\text{TCO}_2$ ), (b) onset of ice on Antarctica ( $\Delta\text{TICE}$ ), and (c) paleogeographic change ( $\Delta\text{TGEO}$ ) across the EOT. The continental outlines for all models in each ensemble are shown. The marine proxy data are shown as filled circles, while the terrestrial proxy data are shown as filled squares.

1405

### 7.1.2 SAT response to Antarctic ice, $\Delta T_{ICE}$

The three models that have carried out simulations with and without an Antarctic ice sheet show differing responses to the forcing (Supplementary Figure S2). CESM shows a cooling around the margins of Antarctica, and in the Pacific and Atlantic sectors of the Southern Ocean; FOAM shows cooling around the margins of Antarctica but warming throughout much of the Southern Ocean, and HadCM3BL shows cooling in the Southern Ocean except in the southern Pacific. The mechanisms behind the changes are described in the respective papers. In brief, Kennedy et al. (2015) attribute the warming in the Pacific sector of the Southern Ocean in HadCM3BL to an increased N-S pressure gradient close to the polar front leading to stronger westerlies, intensification of the Ross Sea gyre, and a resulting increase in oceanic poleward heat transport. Goldner et al. (2014) focus on changes to deep ocean temperatures, highlighting the importance of increased easterly winds around the margins of Antarctica and resulting Ekman transport for bringing cold water to depths. They do not discuss mechanisms for the warming around Australia. Ladant et al. (2014a) do not discuss the mechanism of SST change following glaciation, but Ladant et al. (2014b) do, for a similar pair of simulations. In their model, the presence of the Antarctic ice sheet enhances the strength of the Antarctic Circumpolar Current, and as a result, the Ross Gyre and Weddell Gyre initiate. They also highlight the importance of sea ice changes in amplifying the changes in SSTs. More recent work (Kennedy-Asser et al., 2019) has highlighted that the particularly strong Southern Ocean warming response in the HadCM3BL simulations could be an artefact of insufficient spin-up, with very long simulations showing a more muted temperature response. As a result, these HadCM3BL results should be treated with caution.

In terms of the ensemble mean (Figure 7b), there are only a few regions where there is a robust SST signal. Robust cooling in response to the addition of the Antarctic ice sheet are around the margins of the East Antarctic ice sheet, in the Drake Passage, south of southern Africa, and the tropical and North Atlantic. There is a seemingly robust warming east of Australia, but this is a small region and as such it is unclear if it occurs by chance.

### 7.1.3 SAT response to paleogeographic change, $\Delta T_{GEO}$

For examining the response to paleogeographic change (Supplementary Figure S3), for each model we first identify the pair of simulations for each model that represents the largest change in paleogeography across the EOT. For CESM this is an idealised gateway change from a closed Tasman and Drake Passages to open Tasman and Drake Passages. This forcing results in a cooling in the Pacific sector of the Southern Ocean, and a slight warming in the rest of the Southern Ocean, but these changes are all small compared with those caused by CO<sub>2</sub> or ice sheet changes. For UVic, the forcing is an idealised gateway change from a closed to an open Drake Passage. This has a large impact on SSTs in the Southern Ocean, with cooling south of southern Africa, and a N-S dipole of warming and cooling in the Pacific sector of the Southern Ocean, associated with the transition from a gyre circulation to an Antarctic Circumpolar Current. For FOAM, the forcing consists of a localised change

in West Antarctica in which continent becomes ocean. However, despite the relatively small forcing the response is quite substantial, leading to global cooling of about 1 °C (Figure 6), especially in the south west Pacific. For HadCM3BL, the forcing is global in nature, but consists of relatively small changes to continental position and topography and bathymetry associated with plate tectonic movements from the Priabonian (34-38 Ma) to the Chattian (23-28 Ma). As a global mean the response is very small, but regionally it is quite large, for example in the North Pacific where there is a N-S dipole response, cooling in the North Atlantic, and warming in the Southern Ocean. These changes are associated with the strengthening of deep water formation in the Atlantic sector of the Southern Ocean. NorESM-L shows a relatively muted response, but a substantial cooling of about 2 °C in the southwest Pacific.

Given that all models have carried out different simulations to differing forcings, interpreting the differences in response is challenging. However, the ensemble mean response, shown in Figure 7c, can be interpreted as the best estimate of the SAT-response to paleogeographic change across the EOT, given the uncertainty in the paleogeographic forcing itself, as well as in the different models. The only substantial region of robust change is in the tropical Atlantic, where all models indicate a cooling response of about 1 °C.

Deleted:

## 7.2 Model-data comparison across the EOT

It is important to assess the realism (or otherwise) of the model simulations by comparison with evidence from the geological record. Such model-data comparison can also improve our understanding of the likely mechanisms that drove change. Given the ‘snapshot’ nature of the model simulations, and uncertainties in dating and limitations due to sparse data coverage, it is necessary to use data that extend throughout the EOT, and that are clearly either ‘pre-EOT’ or ‘post-EOT’. Here we use an updated compilation of SST (Figure 3) and terrestrial surface temperature proxies (Figure 4), which we present in Supplementary Tables S1 and S2 respectively. In total there are 23 data points from marine sources and 20 data points from terrestrial sources. Before performing the intercomparison, we first combine and average data points that either come from different proxies from the same location, or from neighbouring data points when they are less than one grid cell apart. This process yields a final proxy dataset of 28 data points, shown in Supplementary Table S3. Each data point is then given an equal weight in determining a root mean square error skill score.

Deleted: 19

### 7.2.1 Comparison of model simulations with proxy data

The observed proxy temperature changes compared with the individual model responses to CO<sub>2</sub>, Antarctic ice and paleogeography are shown in Supplementary Figures S1-S3. As discussed in Section 7.1.1, when CO<sub>2</sub> is halved, all models predict a cooling at all sites, in agreement with the data, except NorESM-L that warms at one of the Arctic sites. There are no data to evaluate the warming signal in the southern Pacific in HadCM3BL and NorESM-L. When an Antarctic ice sheet is imposed, the agreement is not so good, with all models showing warming for at least 2 of the sites. When paleogeographic

1470 changes are imposed, the model-data agreement is worse again for most models, with all models showing warming for at least  
 3 of the sites. The exception is FOAM, for which all sites cool, in agreement with the data. The ensemble means capture the  
 broad changes reasonably well, with all sites cooling for the CO<sub>2</sub> case, and all but one site cooling for the ice and  
 paleogeographic changes.

1475 This model-data comparison is limited by the fact that the models have carried out idealised simulations, especially for CO<sub>2</sub>  
 forcing for which the halving of CO<sub>2</sub> is somewhat arbitrary. Although some proxy CO<sub>2</sub> records do indicate a drop of this order  
 of magnitude (Pagani et al., 2011; Pearson et al., 2009), the associated uncertainties are large. Similarly, the changes to the  
 Antarctic ice sheet imposed in the model may be greater or less than in reality, or the imposed changes in paleogeography may  
 be too extreme. As such, we carry out the model-data comparison such that each model SAT response to each forcing is scaled  
 1480 by a constant in such a way that it best fits the data. To assess the goodness-of-fit, we calculate a skill score, *s*, for each pair  
 of model simulations, simply as the RMS difference between the proxy temperature and modelled temperature, calculated  
 from model gridpoint that is in closest proximity to the data. For the purposes of the skill score we treat neighbouring sites  
 (e.g. tropical sites 925 and 929) as a single data point by averaging the proxy and the scaled modelled temperatures at the two  
 sites. The values of *s* for each modelled best-fit change to the proxy SATs are shown in Table 3. When comparing models and  
 1485 proxies, it is informative to consider what may be called a “good agreement”, and to provide a point of reference for assessing  
 the skill scores. As such, in Table 3 we also show the skill score that would be obtained in the case of an idealised model  
 simulating (i) no SAT change across the EOT, (ii) a global mean change that best fits the data, and (iii) a zonal-mean change  
 of the form  $\Delta SST = A + B \cos(\theta)$ , (where  $\theta$  is latitude), that best fits the data.

Model	s for best-fit $\Delta T_{CO_2}$	s for best-fit $\Delta T_{ice}$	s for best-fit $\Delta T_{geog}$
CESM_B	0.297		
CESM_H	0.313	0.539	0.562
FOAM	0.302	0.509	0.425
GFDL	0.305		0.562
HadCM3BL	0.329	0.481	0.562
NorESM-L	0.334		0.562
UVic			0.556
Ensemble mean	0.298	0.498	0.562
	s for idealised $\Delta T$		
No change	0.562		
Constant change	0.305		
cos( $\theta$ ) change	0.298		

- Deleted: SSTs
- Deleted: Table 7.2.
- Deleted: Table 7.2
- Deleted: 328
- Deleted: 343
- Deleted: 564
- Deleted: 588
- Formatted Table
- Deleted: 330
- Deleted: 533
- Deleted: 455
- Deleted: 329
- Deleted: 588
- Deleted: 361
- Deleted: 509
- Deleted: 588
- Deleted: Nor-ESM
- Deleted: 360
- Deleted: 588
- Deleted: 577
- Deleted: 326
- Deleted: 523
- Deleted: 588
- Deleted: 588
- Deleted: 329
- Deleted: 322

1515

**Table 3:** Skill scores,  $s$ , for the best-fit modelled changes in response to CO<sub>2</sub>, ice, and paleogeographic forcing, for each model and for the ensemble mean (a lower value of  $s$  represents a better fit to data). Also shown are the values of  $s$  for three idealised SAT changes. The models all achieve their best skill performance with CO<sub>2</sub> forcing (UVic does not include CO<sub>2</sub> forcing). **Three models (CESM\_B, FOAM, and GFDL) achieve a better skill than an idealised constant temperature change, while CESM\_B and the ensemble mean achieve better than the idealised cos( $\theta$ ) case. However, the spread in skill across the different models is narrow. Changes highlighted in green are better than or equal to the idealised constant change case.**

1520

- Deleted: Only one model (
- Deleted: ) achieves
- Deleted: however
- Formatted: English (AUS)

It is clear from Table 3 that the best modelled fit to the SAT proxy data arises from changes to CO<sub>2</sub>. In particular, the ensemble mean response to a decrease in atmospheric CO<sub>2</sub> has the best (lowest) skill score, and better than a constant change fit, but slightly poorer than a cos( $\theta$ ). We note however, that a cos( $\theta$ ) fit to the data produces only a 2% improved skill score over the constant change fit. The CESM\_B, FOAM and GFDL models perform marginally better than the constant change fit to the data, while CESM\_H, HadCM3BL and NorESM-L all perform slightly worse than this, but all skills scores are within a margin of 10% of the constant change fit. The CO<sub>2</sub> change provides by far the best temperature fit over the ICE and GEOG changes. The UVic model does not apply a CO<sub>2</sub> change, and consequently achieves a poorer skill score. We note however, that the ICE changes improve the skill score in the CESM\_H, FOAM and HadCM3BL models, while the GEOG changes improve the skill score in the FOAM and NorESM-L models. Since those forcing factors are independent to CO<sub>2</sub>, they also improve the overall skill score in combination, as we show below. These results broadly agree with a recent Southern Ocean-only model-data comparison, which showed that CO<sub>2</sub> forcing provided the best explanation of temperature changes across the EOT, with secondary improvements made from ice and paleogeography changes (Kennedy-Asser et al., 2020).

1525

1530

- Deleted: FOAM,
- Deleted: Nor-ESM
- Deleted: in several cases (CESM\_H, FOAM and HadCM3BL),
- Deleted: also
- Deleted: model
- Deleted: (Kennedy-Asser et al., 2020)

### 1535 7.2.2 Mechanisms of change

The above analysis implies that the change in SST at the EOT can be best explained by a decrease in CO<sub>2</sub>, as opposed to changes in ice or paleogeography. However, it is possible that changes in ice or paleogeography, combined with CO<sub>2</sub> change, may fit even better with the data. To test this possibility, we assume that the various responses add together linearly, and find the best scaled combination of each mechanism, i.e. we find  $\alpha$ ,  $\beta$ ,  $\gamma$  such that the skill score,  $s$ , of  $(\alpha\Delta T_{CO_2} + \beta\Delta T_{ice} + \gamma\Delta T_{geo})$  is minimised. The result of this exercise for each model and for the ensemble mean is shown in Table 4. This shows that CESM\_H and HadCM3BL achieve a better fit to the data when including the full response to ice sheet change and no paleogeographic change, while FOAM achieves a better fit when including a paleogeographic change and no ice sheet change. The ensemble mean agrees best with the proxies when incorporating a CO<sub>2</sub> shift of 897 to 560 ppm ( $\alpha=0.68$ ), with the GEO forcing providing further improvement to the fit ( $\gamma=0.15$ ) while the ICE forcing does not improve the ensemble mean skill score. This best-fit ensemble mean change is shown in Figure 8. Given the close agreement between the models in fitting a CO<sub>2</sub> change to the data, we can estimate from the full model spread that the CO<sub>2</sub> drop was by a factor of  $1.60 \pm 0.15$ . If for example we assume an Oligocene CO<sub>2</sub> value of 2x pre-industrial levels, the CO<sub>2</sub> drop would be from 897  $\pm$  90 ppmv to 560 ppmv. However, we would caution that this estimate reflects the model spread in matching this particular set of data, and that the true uncertainty is larger. Additionally, the models that included changes due to ice sheet forcing or paleogeographic forcing

1540

1545

- Deleted: both
- Deleted: a small fraction of
- Deleted: 910
- Deleted: 7), which is achieved from CO<sub>2</sub>
- Deleted: alone in
- Formatted: Font color: Black
- Deleted: case
- Deleted: 13
- Deleted: 910

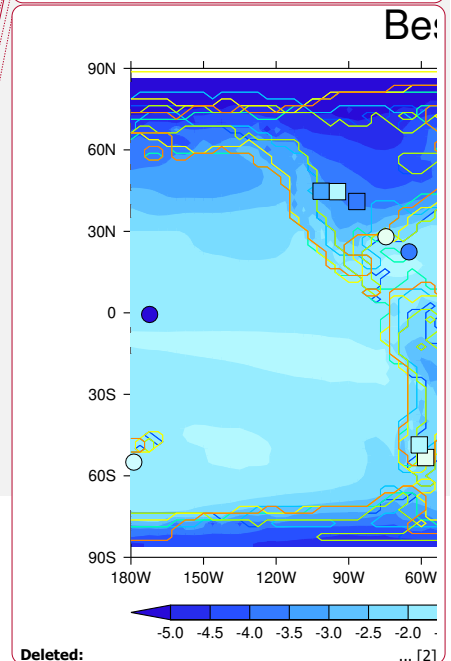
achieved some improvement in fitting the data, but this played a lesser role than CO<sub>2</sub> forcing, as measured by these skill metrics.

A 340 ppmv decrease is within the range of CO<sub>2</sub> proxy estimates, shown in Figure 5, with alkenone records in particular suggesting a drop of this magnitude across the EOT (Pagani et al., 2011; Zhang et al., 2013). Boron and stomatal records indicate that such a change is plausible but is likely of lesser magnitude. The recent multi-proxy compilation of Foster et al. (2017) uses a smoothed regression to derive ‘best fit’ CO<sub>2</sub> estimates of 893 ppmv and 806 ppm during the late Eocene (38-34 Ma) and early Oligocene (33.5-30 Ma) respectively, or a decrease of ~10%. Thus, our model-derived CO<sub>2</sub> decrease is likely to be an overestimate of the change across the EOT. There are several reasons why this mismatch may occur in our model ensemble, which we discuss in Section 7.2.3.

Model	s for best-fit $\alpha\Delta T_{CO_2} + \beta\Delta T_{ice} + \gamma\Delta T_{geo}$	$\alpha$ [CO <sub>2</sub> change ppmv]	$\beta$	$\gamma$
CESM_B	0.297	0.72 [922 to 560]		
CESM_H	0.300	0.58 [837 to 560]	0.94	0
FOAM	0.301	0.62 [861 to 560]	0	0.31
GFDL	0.305	0.54 [814 to 560]		0
HadCM3BL	0.328	0.64 [873 to 560]	0.30	0
NorESM-L	0.331	0.68 [897 to 560]	0	0.37
UVic	0.556			0.56
Ensemble mean	0.297	0.68 [897 to 560]	0.0	0.15
	s for idealised $\Delta T$			
No change	0.562			
Constant change	0.305			
cos( $\theta$ ) change	0.298			

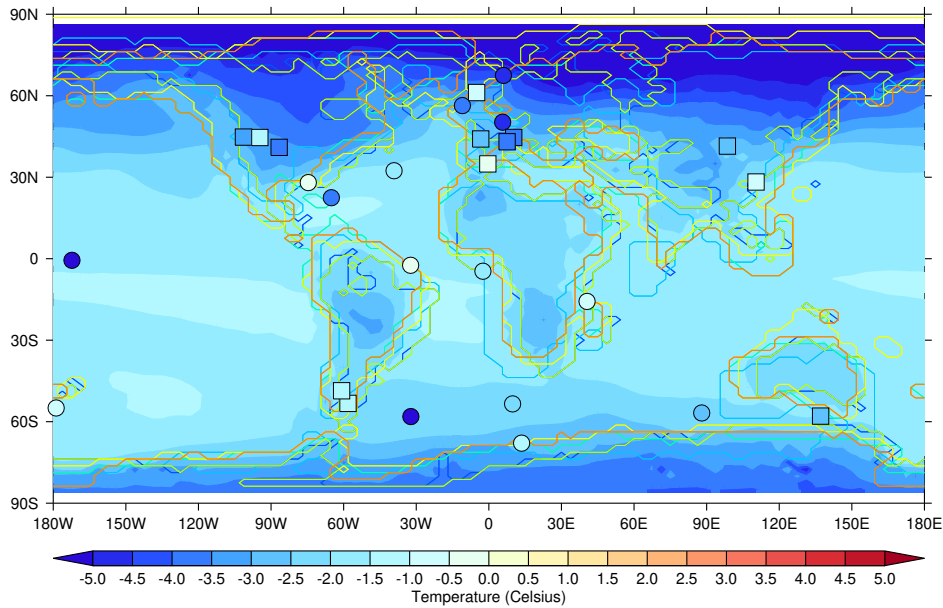
**Table 4:** Skill scores, s, for the best-fit modelled changes in response to a combination of CO<sub>2</sub>, ice, and paleogeographic forcing, for each model and for the ensemble mean (a lower value of s represents a better fit to data). Also shown are the values of  $\alpha$ ,  $\beta$ , and  $\gamma$  that give the best fit, and the CO<sub>2</sub> change corresponding to  $\alpha$ , assuming a post-EOT value of 560 ppmv. Also shown are the values of s for three idealised SAT changes. Changes highlighted in green are better than or equal to the idealised constant change case, while CESM\_B and the ensemble mean achieve better than the idealised cos( $\theta$ ) case.

- Deleted: 328
- Deleted: 74 [935]
- Deleted: 325
- Deleted: 6 [848]
- Deleted: 1.
- Deleted: 329
- Deleted: 66 [885]
- Deleted: 25
- Deleted: 329
- Deleted: 56 [826]
- Deleted: 359
- Deleted: 62 [860]
- Deleted: 49
- Deleted: Nor-ESM
- Deleted: 356
- Deleted: 72 [922]
- Deleted: 5
- Deleted: 577
- Deleted: 78
- Deleted: 326
- Deleted: 7 [910]
- Deleted: 06
- Deleted: 26
- Deleted: 588
- Deleted: 329
- Deleted: 322
- Formatted ... [1]
- Deleted: no models





## Best Fit to EOT data



645 **Figure 8:** Ensemble mean modelled SAT response to a CO<sub>2</sub> decrease from 897 to 560 ppmv, representing the best fit to the proxy data. The marine proxy data are shown as filled circles, while the terrestrial proxy data are shown as filled squares. Coastlines from each model are plotted to illustrate the uncertainties associated with the paleogeographic reconstructions.

Formatted: Subscript

Deleted: 900

### 7.2.3 Uncertainties associated with the modelling

There are several uncertainties that should be considered when interpreting the results above. Some of these are discussed  
1650 here. There is uncertainty in the models themselves. These models could be characterised as AR4-class or even TAR-class in that they were state-of-the-art at the time of the 4<sup>th</sup> or 3<sup>rd</sup> IPCC assessment report, as opposed to the most recent AR5, or the upcoming AR6. The use of less complex models can be an advantage for deep-time paleoclimate work, as these models allow greater length of simulation, which is especially important for the deep ocean where the initial condition may be far from the equilibrium state, which is unknown at the start of the simulation. However, there is a trade-off between simulation length and model complexity, and some of the model simulations presented here are relatively short (e.g. HadCM3BL; Table 2). A  
1655 potential manifestation of this lack of complexity relates to the modelled change in land-sea contrast. The EOT temperature change from marine records is larger (-2.7 °C) than that recorded from land temperature proxies (-2.3 °C). This in part reflects

Deleted: 9

Deleted: 2

the heterogeneous pattern of changes in plant species, from which the land temperature proxies are derived, but is in general a globally robust signal. On the other hand, the temperature changes recorded in the model simulations show the opposite; land temperature changes are more sensitive to greenhouse cooling than ocean temperature changes. This makes it challenging to achieve a close fit to all of the temperature records available.

**Deleted:** However, by including both marine and terrestrial temperature changes, we derive an estimate of CO<sub>2</sub> decline that of a factor of 1.6, which is broadly in line with proxy estimates (Figure 5).

There are several possible reasons why our model-derived CO<sub>2</sub> decrease is larger than the 'best fit' to the Foster et al (2017) CO<sub>2</sub> proxy compilation. First, the models may be under-sensitive to CO<sub>2</sub> forcing, as has been suggested in previous attempts to model the Eocene (Huber and Caballero, 2011; Lunt et al., 2012). The model ensemble climate sensitivity to doubling CO<sub>2</sub> is 3.3°C. A recent synthesis of Paleocene-Eocene proxy records suggests that climate sensitivity during the latest Paleocene, PETM and EECO was 4.5°C, 3.6°C and 3.1°C respectively (Inglis et al., 2020). In addition the 66% confidence interval of climate sensitivity was ~2-7°C over the three intervals combined. Thus, our model ensemble compares well with the best estimates of the early Eocene climate sensitivity, but is towards the lower end of the 'likely' confidence interval, suggesting a considerably higher climate sensitivity is possible. Second, the models do not permit dynamic feedbacks between CO<sub>2</sub> forcing and the growth of an ice sheet, which in reality would cause ice-albedo, land-albedo, and cloud radiative forcing feedbacks. These missing feedbacks may amplify the global temperature change when crossing a critical threshold of glaciation. Since these models prescribe their ice sheets as on or off, such feedbacks are not possible here. However, it is still useful to examine which forcing mechanisms provide the best explanation of the proxy record. In this sense, it is notable that CO<sub>2</sub> forcing provides the best explanation of the far-field cooling away from Antarctica, while imposing an ice sheet has a lesser effect on the global mean (Goldner et al., 2014).

The boundary conditions applied to the models is a large source of uncertainty. The spread in paleogeographic forcing between models is testament to the fact that the paleogeography both pre-EOT and post-EOT is relatively uncertain (See Section 2.1 and 2.2). Recent climate model simulations of the early Eocene suggest that the paleogeographic forcing plays a similarly important role as CO<sub>2</sub> forcing in capturing Eocene warm climates (Lunt et al., 2020). These simulations suggest that 3-5°C of the warming from pre-industrial to Eocene climates comes from non-CO<sub>2</sub> forcing, i.e. forcing from changes to geography, land surface properties and the removal of ice sheets. Therefore, while increasing the climate sensitivity may be part of solving the Eocene model-data mismatch, improving the paleogeographic boundary conditions is also a high priority for obtaining a better model-data agreement. The proxy dataset we have used is also limited in areal coverage. As such, the models remain untested in several key regions, such as the North and tropical Pacific, or the Indian Ocean. New data in the regions predicted to warm in response to a CO<sub>2</sub> drop in HadCM3BL and NorESM-L would be particularly useful for discriminating between models. The model-data comparison does not consider any uncertainty in the proxy estimates themselves. In reality, each site is associated with a different and substantial uncertainty in its estimate of SST change across the EOT.

**Deleted:** The proxy dataset we have used is somewhat limited in areal coverage.

1700 Here we have considered only the change in temperature across the EOT, rather than absolute temperatures. However, this can mask biases in the simulated base state of the pre-EOT and post-EOT simulations. Not all models do a good job of simulating the base state (see e.g. discussion of meridional temperature gradients in Section 6.2). Although the ensemble results achieve the best fit from CO<sub>2</sub> forcing (with a small contribution from ice sheet forcing), it is worth noting that the ultimate cause of the CO<sub>2</sub> drop itself remains unclear; it could itself be driven by changes to geological sources and sinks, changes in weathering rates, or feedbacks associated with ocean and land sinks due to circulation changes (see Section 6.3).

## 1705 8 Conclusions

Earth's modern 'icehouse' climate is defined by the presence of significant ice masses on land at both poles but that ice is now retreating. Understanding the drivers and scale of polar ice growth during the initial inception of this icehouse at the EOT, which involved cooling and glaciation under a yet still warm Eocene-Oligocene climate, can provide crucial insights into ice sheet stability and behaviour under a warm climate, something that is more critical than ever. Here, we have reviewed current literature regarding the EOT, in terms of stratigraphic definitions, geological records of paleogeographic and Earth system change, and modelling insights into mechanisms of change. Marine records currently provide the most extensive global record of temperature change across the EOT, with a SST cooling found across most regions. The marine records suggest a global average temperature change of approximately -2.7 °C across the EOT, although individual records range from approximately 0 to -8 °C change. Terrestrial records of temperature change are more geographically limited, with a concentration of records in the midlatitude Northern Hemisphere, and very little coverage of the Southern Hemisphere. The terrestrial records average change is -2.3 °C, but like the marine records, the change recorded at individual locations ranges from approximately 0 to -8 °C across the EOT. Records of CO<sub>2</sub> across the EOT also indicate some differences between marine and terrestrial records. Marine records suggest a higher concentration of CO<sub>2</sub> overall and a clearer transition towards lower CO<sub>2</sub> across the EOT. Terrestrial records, by contrast, indicate a lower CO<sub>2</sub> concentration overall and a more gradual CO<sub>2</sub> decline with no obvious shift coinciding with the EOT. There is an ongoing need to reconcile the different CO<sub>2</sub> signals found in the marine and terrestrial realms.

1725 A new model-data comparison presented in this paper reveals that a halving of atmospheric CO<sub>2</sub> across the EOT has a substantially greater effect on global mean and regional SAT than either the onset of Antarctic glaciation or changes in paleogeography. The response to CO<sub>2</sub> forcing is robust across models, with cooling increasing towards higher latitudes, helping to explain high latitude cooling in the marine records. While individual models achieved a better fit to the data by including paleogeographic forcing and ice sheet forcing, these changes are more variable across the models. As a result, the best fit in the ensemble mean is dominated by decreasing CO<sub>2</sub> by a factor of 1.6x, with ice sheet forcing and paleogeography forcing playing a secondary role. Assuming an Oligocene value of 560 ppmv, the corresponding pre-EOT value is 897 ppmv. However, we do not exclude the importance of contributions from other forcings. Indeed, several models in the ensemble achieve their

Deleted: terrestrial

Deleted: disappearing

Deleted: These

Deleted: 9

Deleted: Overall,

Deleted: a

Deleted: 2

Deleted: There is therefore a

Deleted: achieved

Deleted: including the

Deleted: forcing only, with

Deleted: decrease in CO<sub>2</sub>

Deleted: .

Deleted: 910

1745 best fit to the temperature records with a combination of CO<sub>2</sub> and ice-sheet induced changes, while two models show an improved fit when paleogeographic changes are combined with CO<sub>2</sub> forcing. Paleogeographic changes and ice sheet feedbacks are inherently regional and harder to aggregate across different model experiments. Nevertheless, it remains possible that gateway-induced ocean circulation change is somehow implicated in CO<sub>2</sub> decline. For a more complete understanding of these feedbacks, future climate modelling of the EOT must incorporate dynamic feedbacks between these different forcing factors.

**Deleted:** one model shows

#### 1750 **Appendix – List of Acronyms**

ACC: Antarctic Circumpolar Current

AMOC: Atlantic meridional overturning circulation

CCD: Calcite compensation depth

CMMT: cold month mean temperature

1755 CLAMP: Climate Leaf Analysis Multivariate Program

EAIS: East Antarctic ice sheet

EOGM: Early Oligocene glacial maximum

EOB: Eocene-Oligocene boundary

EOT: Eocene-Oligocene transition

1760 EOIS: Early Oligocene oxygen isotope step

GSSP: Global boundary stratotype section and point

MAT: mean annual temperature

MECO: Middle Eocene climatic optimum

NLR: Nearest Living Relative

1765 ODP: Ocean drilling program

PrOM: Priabonian oxygen isotope maximum

SAT: Surface air temperature

SST: Sea surface temperature

#### **Data Availability**

1770 The data compilation plotted in the manuscript are included in the supplementary material. The model data are available upon request from the corresponding authors listed in Table 2.

**Deleted:** lead

**Deleted:** Table 1.

## 1775 Author Contributions

The manuscript was conceived and planned by DKH, AMdB, HKC, and MS, in collaboration with all authors. Section 1 was led by HKC, PNP and PAW. Section 2 was led by DKH, MB, HDS and AvdH. Section 3 was led by KKS, HKC and CHL. Section 4 was led by MS, MJP and LK, with contributions from KM. Section 5 was led by MS, CHL and LK. Section 6 was led by DKH and AMdB. Section 7 was led by DJL and DKH. Compilations of SST records were made by KKS and MH, 1780 terrestrial records by MJP, US and MH, coordinated by DKH.  $\delta^{18}\text{O}$  records were compiled by EP. Model simulation data were contributed by DKH, ATK-A, J-BL, MB, MH, WPS, ZZ. All authors contributed to editing and review of the manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

## Acknowledgments

1785 This work originated from a workshop on the Eocene-Oligocene Transition in Stockholm in February 2017, funded by the Bolin Centre for Climate Research, Research Area 6. This work was also supported by the Swedish Research Council project 2016-03912 and FORMAS project 2018-01621. [KKS acknowledges financial support from by the Danish Council for Independent Research – Natural Sciences \(DFF/FNU; grant no. 11-107497\).](#)

## References

- 1790 Abels, H. A., Dupont-Nivet, G., Xiao, G., Bosboom, R. and Krijgsman, W.: Step-wise change of Asian interior climate preceding the Eocene–Oligocene Transition (EOT), *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 299(3), 399–412, doi:10.1016/j.palaeo.2010.11.028, 2011.
- Abelson, M. and Erez, J.: The onset of modern-like Atlantic meridional overturning circulation at the Eocene-Oligocene transition: Evidence, causes, and possible implications for global cooling, *Geochemistry, Geophys. Geosystems*, 18(6), 2177–1795 2199, doi:10.1002/2017GC006826, 2017.
- Adams, C. G., Butterlin, J. and Samanta, B. K.: Larger Foraminifera and Events at the Eocene/Oligocene Boundary in the Indo-West Pacific Region, in *termbal eocene events*, vol. 9, edited by C. Pomeroy and I. B. T.-D. in P. and S. Premoli-Silva, pp. 237–252, Elsevier., 1986.
- 1800 Agnini, C., Fornaciari, E., Raffi, I., Catanzariti, R., Pálíke, H., Backman, J. and Rio, D.: Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes, *Newsletters Stratigr.*, 47(2), 131–181, doi:10.1127/0078-0421/2014/0042, 2014.
- 1805 [Agnini, C., Backman, J., Boscolo-Galazzo, F., Condon, D. J., Fornaciari, E., Galeotti, S., Giusberti, L., Grandesso, P., Lanci, L., Luciani, V., Monechi, S., Muttoni, G., Pálíke, H., Letizia Pampaloni, M., Papazzoni, C. A., Pearson, P. N., Pignatti, J., Premoli Silva, I., Raffi, I., Rio, D., Rook, L., Sahy, D., Spofforth, D. J. A., Stefani, C. and Wade, B. S.: Proposal for the Global Boundary Stratotype Section and Point \(GSSP\) for the Priabonian Stage \(Eocene\) at the Alano section \(Italy\), Episodes, in](#)

[press, 2020.](#)

[Akhmetiev, M. A. and Beniamovski, V. N.: Paleogene floral assemblages around epicontinental seas and straits in Northern Central Eurasia: proxies for climatic and paleogeographic evolution, \*Geol. Acta\*, 7\(1–2\), 297–309, doi:10.1344/105.000000278\\_2009.](#)

- 1810 Anagnostou, E., John, E. H., Edgar, K. M., Foster, G. L., Ridgwell, A., Inglis, G. N., Pancost, R. D., Lunt, D. J. and Pearson, P. N.: Changing atmospheric CO<sub>2</sub> concentration was the primary driver of early Cenozoic climate, *Nature*, 533(7603), 380–384, doi:10.1038/nature17423, 2016.
- Anderson, J. B., Wamy, S., Askin, R. A., Wellner, J. S., Bohaty, S. M., Kirshner, A. E., Livsey, D. N., Simms, A. R., Smith, T. R., Ehrmann, W., Lawver, L. A., Barbeau, D., Wise, S. W., Kulhanek, D. K., Weaver, F. M. and Majewski, W.: Progressive Cenozoic cooling and the demise of Antarctica's last refugium, *Proc. Natl. Acad. Sci.*, 108(28), 11356 LP – 11360, doi:10.1073/pnas.1014885108, 2011.
- Armstrong McKay, D. I., Tyrrell, T. and Wilson, P. A.: Global carbon cycle perturbation across the Eocene-Oligocene climate transition, *Paleoceanography*, 31(2), 311–329, doi:10.1002/2015PA002818, 2016.
- 1820 Baatsen, M., van Hinsbergen, D. J. J., von der Heydt, A. S., Dijkstra, H. A., Sluijs, A., Abels, H. A. and Bijl, P. K.: Reconstructing geographical boundary conditions for palaeoclimate modelling during the Cenozoic, *Clim. Past*, 12(8), 1635–1644, doi:10.5194/cp-12-1635-2016, 2016.
- Baatsen, M., von der Heydt, A. S., Huber, M., Kliphuis, M. A., Bijl, P. K., Sluijs, A. and Dijkstra, H. A.: The middle-to-late Eocene greenhouse climate, modelled using the CESM 1.0.5, *Clim. Past Discuss.*, 2020, 1–44, doi:10.5194/cp-2020-29, 2020.
- 1825 Baatsen, M. L. J., von der Heydt, A. S., Kliphuis, M., Viebahn, J. and Dijkstra, H. A.: Multiple states in the late Eocene ocean circulation, *Glob. Planet. Change*, 163, 18–28, doi:https://doi.org/10.1016/j.gloplacha.2018.02.009, 2018.
- Bailey, I., Hole, G. M., Foster, G. L., Wilson, P. A., Storey, C. D., Trueman, C. N. and Raymo, M. E.: An alternative suggestion for the Pliocene onset of major northern hemisphere glaciation based on the geochemical provenance of North Atlantic Ocean ice-rafted debris, *Quat. Sci. Rev.*, 75, 181–194, doi:https://doi.org/10.1016/j.quascirev.2013.06.004, 2013.
- 1830 Barker, P. F. and Burrell, J.: The opening of Drake Passage, *Mar. Geol.*, 25(1–3), 15–34, doi:10.1016/0025-3227(77)90045-7, 1977.
- Barker, P. F. and Thomas, E.: Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current, *Earth-Science Rev.*, 66(1–2), 143–162, doi:10.1016/j.earscirev.2003.10.003, 2004.
- Barker, P. F., Filippelli, G. M., Florindo, F., Martin, E. E. and Scher, H. D.: Onset and role of the Antarctic Circumpolar Current, *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 54(21–22), 2388–2398, doi:10.1016/j.dsr2.2007.07.028, 2007.
- 1835 Barreda, V. and Palazzesi, L.: Patagonian Vegetation Turnovers during the Paleogene–Early Neogene: Origin of Arid-Adapted Floras, *Bot. Rev.*, 73(1), 31–50, doi:10.1663/0006-8101(2007)73[31:PVTDTDP]2.0.CO;2, 2007.
- Basak, C. and Martin, E. E.: Antarctic weathering and carbonate compensation at the Eocene–Oligocene transition, *Nat. Geosci.*, 6, 121, doi:10.1038/ngeo1707, 2013.
- 1840 Beerling, D. J.: Preface to Vegetation-climate-atmosphere interactions: past, present and future, the proceedings of a Discussion Meeting held at the Royal Society, *Philos. Trans. R. Soc. B Biol. Sci.*, 353(1365), 3–4, doi:10.1098/rstb.1998.0185, 1998.
- Beerling, D. J. and Royer, D. L.: Convergent Cenozoic CO<sub>2</sub> history, *Nat. Geosci.*, 4, 418, doi:10.1038/ngeo1186, 2011.

- Beerling, D. J., Fox, A., Stevenson, D. S. and Valdes, P. J.: Enhanced chemistry-climate feedbacks in past greenhouse worlds, *Proc. Natl. Acad. Sci.*, 108(24), 9770 LP – 9775, doi:10.1073/pnas.1102409108, 2011.
- 1845 Berggren, W. A. and Pearson, P. N.: A Revised Tropical to Subtropical Paleogene Planktonic Foraminiferal Zonation, *J. Foraminifer. Res.*, 35(4), 279–298, doi:10.2113/35.4.279, 2005.
- Berggren, W. A., Wade, B. S. and Pearson, P. N.: Oligocene chronostratigraphy and planktonic foraminiferal biostratigraphy: Historical review and current state-of-the-art, in *Atlas of Oligocene Planktonic Foraminifera*, edited by B. S. Wade, R. K. Olsson, P. N. Pearson, B. T. Huber, and W. A. Berggren, pp. 29–54, Cushman Foundation for Foraminiferal Research: Lawrence, USA., 2018.
- 1850 Bernard, T., Steer, P., Gallagher, K., Szulc, A., Whitham, A. and Johnson, C.: Evidence for Eocene–Oligocene glaciation in the landscape of the East Greenland margin, *Geology*, 44(11), 895–898, doi:10.1130/G38248.1, 2016.
- Berner, R. A. and Kothavala, Z.: GEOCARB III: a revised model of atmospheric CO<sub>2</sub> over Phanerozoic time, *Am. J. Sci.*, 301(2), 182–204, doi:10.2475/ajs.301.2.182, 2001.
- 1855 Bierman, P. R., Shakun, J. D., Corbett, L. B., Zimmerman, S. R. and Rood, D. H.: A persistent and dynamic East Greenland Ice Sheet over the past 7.5 million years, *Nature*, 540, 256, doi:10.1038/nature20147, 2016.
- Bijl, P. K., Schouten, S., Sluijs, A., Reichert, G.-J., Zachos, J. C. and Brinkhuis, H.: Early Palaeogene temperature evolution of the southwest Pacific Ocean, *Nature*, 461(7265), 776–779, doi:10.1038/nature08399, 2009.
- 1860 Bijl, P. K., Bendle, J. A. P., Bohaty, S. M., Pross, J., Schouten, S., Tauxe, L., Stickley, C. E., McKay, R. M., Röhl, U., Olney, M., Sluijs, A., Escutia, C., Brinkhuis, H. and Scientists, E. 318: Eocene cooling linked to early flow across the Tasmanian Gateway, *Proc. Natl. Acad. Sci.*, 110(24), 9645–9650, doi:10.1073/pnas.1220872110, 2013.
- Billups, K. and Schrag, D. P.: Application of benthic foraminiferal Mg/Ca ratios to questions of Cenozoic climate change, *Earth Planet. Sci. Lett.*, 209(1), 181–195, doi:10.1016/S0012-821X(03)00067-0, 2003.
- 1865 Blaj, T., Backman, J. and Raffi, I.: Late Eocene to Oligocene preservation history and biochronology of calcareous nannofossils from paleo-equatorial Pacific Ocean sediments, *Riv. Ital. di Paleontol. e Stratigr.*, 115, 67–85, doi:10.13130/2039-4942/5920, 2009.
- Bo, S., Siebert, M. J., Mudd, S. M., Sugden, D., Fujita, S., Xiangbin, C., Yunyun, J., Xueyuan, T. and Yuansheng, L.: The Gamburtsev mountains and the origin and early evolution of the Antarctic Ice Sheet, *Nature*, 459, 690, doi:10.1038/nature08024, 2009.
- 1870 Boardman, G. S. and Secord, R.: Stable isotope paleoecology of White River ungulates during the Eocene–Oligocene climate transition in northwestern Nebraska, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 375, 38–49, doi:https://doi.org/10.1016/j.palaeo.2013.02.010, 2013.
- Bohaty, S. M. and Zachos, J. C.: Significant Southern Ocean warming event in the late middle Eocene, *Geology*, 31(11), 1017–1020, doi:10.1130/G19800.1, 2003.
- 1875 Bohaty, S. M., Zachos, J. C. and Delaney, M. L.: Foraminiferal Mg/Ca evidence for Southern Ocean cooling across the Eocene–Oligocene transition, *Earth Planet. Sci. Lett.*, 317–318(Supplement C), 251–261, doi:10.1016/j.epsl.2011.11.037, 2012.
- Borrelli, C., Cramer, B. S. and Katz, M. E.: Bipolar Atlantic deepwater circulation in the middle-late Eocene: Effects of Southern Ocean gateway openings, *Paleoceanography*, 29(4), 308–327, doi:10.1002/2012PA002444, 2014.

- 1880 [Botsyun, S., Sepulchre, P., Donnadieu, Y., Risi, C., Licht, A. and Caves Rugenstein, J. K.: Revised paleoaltimetry data show low Tibetan Plateau elevation during the Eocene, \*Science\*, 363\(6430\), eaaq1436, doi:10.1126/science.aaq1436, 2019.](#)
- Boyden, J. A., Müller, R. D., Gurnis, M., Torsvik, T. H., Clark, J. A., Turner, M., Ivey-Law, H., Watson, R. J. and Cannon, J. S.: Next-generation plate-tectonic reconstructions using GPlates, in *Geoinformatics: Cyberinfrastructure for the Solid Earth Sciences*, edited by G. R. Keller and C. Baru, pp. 95–114, Cambridge University Press., 2011.
- 1885 Boyle, P. R., Romans, B. W., Tucholke, B. E., Norris, R. D., Swift, S. A. and Sexton, P. F.: Cenozoic North Atlantic deep circulation history recorded in contourite drifts, offshore Newfoundland, Canada, *Mar. Geol.*, 385, 185–203, doi:10.1016/j.margeo.2016.12.014, 2017.
- Bozukov, V., Utescher, T. and Ivanov, D.: Late Eocene to early Miocene climate and vegetation of Bulgaria, *Rev. Palaeobot. Palynol.*, 153(3), 360–374, doi:10.1016/j.revpalbo.2008.10.005, 2009.
- 1890 Brassell, S. C.: Climatic influences on the Paleogene evolution of alkenones, *Paleoceanography*, 29(3), 255–272, doi:10.1002/2013PA002576, 2014.
- Brassell, S. C., Eglinton, G., Marlowe, I. T., Pflaumann, U. and Sarnthein, M.: Molecular stratigraphy: a new tool for climatic assessment, *Nature*, 320, 129, doi:10.1038/320129a0, 1986.
- Breedlovestrout, R. L., Evraets, B. J. and Parrish, J. T.: New Paleogene paleoclimate analysis of western Washington using physiognomic characteristics from fossil leaves, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 392, 22–40, doi:10.1016/j.palaeo.2013.08.013, 2013.
- 1895 Brinkhuis, H., Schouten, S., Collinson, M. E., Sluijs, A., Damsté, J. S. S., Dickens, G. R., Huber, M., Cronin, T. M., Onodera, J., Takahashi, K., Bujak, J. P., Stein, R., van der Burgh, J., Eldrett, J. S., Harding, I. C., Lotter, A. F., Sangiorgi, F., Cittert, H. van K., de Leeuw, J. W., Matthiessen, J., Backman, J., Moran, K. and Scientists, the E. 302: Episodic fresh surface waters in the Eocene Arctic Ocean, *Nature*, 441(7093), 606–609, doi:10.1038/nature04692, 2006.
- 1900 Broecker, W. S. and Peng, T.-H.: *Tracers in the sea*, Eldigio Press, Columbia University, Palisades, NY., 1982.
- [Cande, S. C. and Kent, D. V.: Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic, \*J. Geophys. Res. Solid Earth\*, 100\(B4\), 6093–6095, doi:10.1029/94JB03098, 1995.](#)
- 1905 Carter, A., Riley, T. R., Hillenbrand, C.-D. and Rittner, M.: Widespread Antarctic glaciation during the Late Eocene, *Earth Planet. Sci. Lett.*, 458, 49–57, doi:10.1016/j.epsl.2016.10.045, 2017.
- Chamberlain, C. P., Mix, H. T., Mulch, A., Hren, M. T., Kent-Corson, M. L., Davis, S. J., Horton, T. W. and Graham, S. A.: The Cenozoic climatic and topographic evolution of the western North American Cordillera, *Am. J. Sci.*, 312, 213–262, doi:10.2475/02.2012.05, 2012.
- 1910 Coccione, R.: The genera *Hantkenina* and *Cribrohantkenina* (foraminifera) in the Massignano Section (Ancona, Italy), in *International Subcommission on Paleogeography and Stratigraphy, Eocene/Oligocene Meeting*, pp. 81–96., 1988.
- Collinson, M. E. and Hooker, J. J.: Paleogene vegetation of Eurasia: framework for mammalian faunas, *Deinsea*, 10(1), 41–84, 2003.
- [Colwyn, D. A. and Hren, M. T.: An abrupt decrease in Southern Hemisphere terrestrial temperature during the Eocene–Oligocene transition, \*Earth Planet. Sci. Lett.\*, 512, 227–235, doi:https://doi.org/10.1016/j.epsl.2019.01.052, 2019.](#)
- 1915 [Costa, E., Garcés, M., Sáez, A., Cabrera, L. and López-Blanco, M.: The age of the “Grande Coupure” mammal turnover: New constraints from the Eocene–Oligocene record of the Eastern Ebro Basin \(NE Spain\), \*Palaeogeogr. Palaeoclimatol.\*](#)



[Palaeoecol., 301\(1\), 97–107, doi:10.1016/j.palaeo.2011.01.005, 2011.](#)

Cotton, L. J. and Pearson, P. N.: Extinction of larger benthic foraminifera at the Eocene/Oligocene boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 311(3), 281–296, doi:10.1016/j.palaeo.2011.09.008, 2011.

1920 Cotton, L. J., Pearson, P. N. and Renema, W.: Stable isotope stratigraphy and larger benthic foraminiferal extinctions in the Melinau Limestone, Sarawak, *J. Asian Earth Sci.*, 79, 65–71, doi:https://doi.org/10.1016/j.jseas.2013.09.025, 2014.

Coxall, H. K. and Pearson, P. N.: The Eocene-Oligocene transition, Deep Time Perspect. Clim. Chang. Marrying Signal From Comput. Model. Biol. Proxies, 351–387, 2007.

1925 Coxall, H. K. and Wilson, P. A.: Early Oligocene glaciation and productivity in the eastern equatorial Pacific: Insights into global carbon cycling, *Paleoceanography*, 26(2), PA2221, doi:10.1029/2010PA002021, 2011.

Coxall, H. K., Wilson, P. A., Palike, H., Lear, C. H. and Backman, J.: Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean, *Nature*, 433(7021), 53–57, doi:10.1038/nature03135, 2005.

1930 Coxall, H. K., Huck, C. E., Huber, M., Lear, C. H., Legarda-Lisarri, A., O'Regan, M., Sliwiska, K. K., van de Fliert, T., de Boer, A. M., Zachos, J. C. and Backman, J.: Export of nutrient rich Northern Component Water preceded early Oligocene Antarctic glaciation, *Nat. Geosci.*, 11(3), 190–196, doi:10.1038/s41561-018-0069-9, 2018.

Cramer, B. S., Toggweiler, J. R., Wright, J. D., Katz, M. E. and Miller, K. G.: Ocean overturning since the Late Cretaceous: Inferences from a new benthic foraminiferal isotope compilation, *Paleoceanography*, 24(4), PA4216, doi:10.1029/2008PA001683, 2009.

1935 Cramwinckel, M. J., Huber, M., Kocken, I. J., Agnini, C., Bijl, P. K., Bohaty, S. M., Frieling, J., Goldner, A., Hilgen, F. J., Kip, E. L., Peterse, F., van der Ploeg, R., Röhl, U., Schouten, S. and Sluijs, A.: Synchronous tropical and polar temperature evolution in the Eocene, *Nature*, 559(7714), 382–386, doi:10.1038/s41586-018-0272-2, 2018.

Cristini, L., Grosfeld, K., Butzin, M. and Lohmann, G.: Influence of the opening of the Drake Passage on the Cenozoic Antarctic Ice Sheet: A modeling approach, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 339–341, 66–73, doi:10.1016/j.palaeo.2012.04.023, 2012.

1940 Crosby, A. G., McKenzie, D. and Slater, J. G.: The relationship between depth, age and gravity in the oceans, *Geophys. J. Int.*, 166(2), 553–573, doi:10.1111/j.1365-246X.2006.03015.x, 2006.

[Cyr, A. J., Currie, B. S. and Rowley, D. B.: Geochemical Evaluation of Fenghuoshan Group Lacustrine Carbonates, North-Central Tibet: Implications for the Paleosalinity of the Eocene Tibetan Plateau, \*J. Geol.\*, 113\(5\), 517–533, doi:10.1086/431907, 2005.](#)

1945 Dalziel, I. W. D., Lawver, L. A., Pearce, J. A., Barker, P. F., Hastie, A. R., Barfod, D. N., Schenke, H.-W. and Davis, M. B.: A potential barrier to deep Antarctic circumpolar flow until the late Miocene?, *Geology*, 41(9), 947–950, doi:10.1130/G34352.1, 2013.

Darby, D. A.: Ephemeral formation of perennial sea ice in the Arctic Ocean during the middle Eocene, *Nat. Geosci.*, 7, 210, doi:10.1038/ngeo2068, 2014.

1950 DeConto, R. M. and Pollard, D.: Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO<sub>2</sub>, *Nature*, 421(6920), 245–249, doi:10.1038/nature01290, 2003.

DeConto, R. M., Pollard, D., Wilson, P. A., Palike, H., Lear, C. H. and Pagani, M.: Thresholds for Cenozoic bipolar glaciation, *Nature*, 455(7213), 652–656, doi:10.1038/nature07337, 2008.

- 1955 Dingle, R. V., Marensi, S. A. and Lavelle, M.: High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula, *J. South Am. Earth Sci.*, 11(6), 571–579, doi:10.1016/S0895-9811(98)00035-2, 1998.
- Doria, G., Royer, D. L., Wolfe, A. P., Fox, A., Westgate, J. A. and Beerling, D. J.: Declining atmospheric CO<sub>2</sub> during the late Middle Eocene climate transition, *Am. J. Sci.*, 311(1), 63–75, doi:10.2475/01.2011.03, 2011.
- 1960 Dunkley Jones, T., Bown, P. R., Pearson, P. N., Wade, B. S., Coxall, H. K. and Lear, C. H.: Major shifts in calcareous phytoplankton assemblages through the Eocene-Oligocene transition of Tanzania and their implications for low-latitude primary production, *Paleoceanography*, 23(4), doi:10.1029/2008PA001640, 2008.
- Dupont-Nivet, G., Krijgsman, W., Langereis, C. G., Abels, H. A., Dai, S. and Fang, X.: Tibetan plateau aridification linked to global cooling at the Eocene–Oligocene transition, *Nature*, 445, 635, doi:10.1038/nature05516, 2007.
- Dupont-Nivet, G., Hoorn, C. and Konert, M.: Tibetan uplift prior to the Eocene-Oligocene climate transition: Evidence from pollen analysis of the Xining Basin, *Geology*, 36(12), 987–990, doi:10.1130/G25063A.1, 2008.
- 1965 Eagles, G., Livermore, R. A., Fairhead, J. D. and Morris, P.: Tectonic evolution of the west Scotia Sea, *J. Geophys. Res. Solid Earth*, 110(B2), B02401, doi:10.1029/2004JB003154, 2005.
- Ehlers, J. and Gibbard, P. L.: The extent and chronology of Cenozoic Global Glaciation, *Quat. Int.*, 164–165, 6–20, doi:10.1016/j.quaint.2006.10.008, 2007.
- 1970 Ehrmann, W. U. and Mackensen, A.: Sedimentological evidence for the formation of an East Antarctic ice sheet in Eocene/Oligocene time, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 93(1), 85–112, doi:10.1016/0031-0182(92)90185-8, 1992.
- Elderfield, H., Ferretti, P., Greaves, M., Crowhurst, S., McCave, I. N., Hodell, D. and Piotrowski, A. M.: Evolution of Ocean Temperature and Ice Volume Through the Mid-Pleistocene Climate Transition, *Science*, 337(6095), 704 LP – 709, doi:10.1126/science.1221294, 2012.
- 1975 Eldrett, J. S., Harding, I. C., Wilson, P. A., Butler, E. and Roberts, A. P.: Continental ice in Greenland during the Eocene and Oligocene, *Nature*, 446, 176, doi:10.1038/nature05591, 2007.
- Eldrett, J. S., Greenwood, D. R., Harding, I. C. and Huber, M.: Increased seasonality through the Eocene to Oligocene transition in northern high latitudes, *Nature*, 459(7249), 969–973, doi:10.1038/nature08069, 2009.
- Elsworth, G., Galbraith, E., Halverson, G. and Yang, S.: Enhanced weathering and CO<sub>2</sub> drawdown caused by latest Eocene strengthening of the Atlantic meridional overturning circulation, *Nat. Geosci.*, 10(3), 213–216, doi:10.1038/ngeo2888, 2017.
- 1980 England, M. H., Hutchinson, D. K., Santoso, A. and Sijp, W. P.: Ice–Atmosphere Feedbacks Dominate the Response of the Climate System to Drake Passage Closure, *J. Clim.*, 30(15), 5775–5790, doi:10.1175/JCLI-D-15-0554.1, 2017.
- Erdei, B., Utescher, T., Hably, L., Tamas, J., Roth-Nebelsick, A. and Grein, M.: Early Oligocene continental climate of the Palaeogene Basin (Hungary and Slovenia) and the surrounding area, *Turkish J. Earth Sci.*, 21, 153–186, doi:10.3906/yer-1005-29, 2012.
- 1985 [Eronen, J. T., Janis, C. M., Chamberlain, C. P. and Mulch, A.: Mountain uplift explains differences in Palaeogene patterns of mammalian evolution and extinction between North America and Europe, \*Proc. R. Soc. B Biol. Sci.\*, 282\(1809\), 20150136, doi:10.1098/rspb.2015.0136, 2015.](#)
- Escutia, C., Brinkhuis, H., Klaus, A. and the IODP Expedition 318 Scientists: IODP Expedition 318: From Greenhouse to Icehouse at the Wilkes Land Antarctic Margin, *Sci. Drill.*, 12, 15–23, doi:10.2204/iodp.sd.12.02.2011, 2011.

- 1990 Evans, D., Wade, B. S., Henehan, M., Erez, J. and Müller, W.: Revisiting carbonate chemistry controls on planktic foraminifera Mg / Ca: implications for sea surface temperature and hydrology shifts over the Paleocene–Eocene Thermal Maximum and Eocene–Oligocene transition, *Clim. Past*, 12(4), 819–835, doi:10.5194/cp-12-819-2016, 2016.
- Evans, D., Sahoo, N., Renema, W., Cotton, L. J., Müller, W., Todd, J. A., Saraswati, P. K., Stassen, P., Ziegler, M., Pearson, P. N., Valdes, P. J. and Affek, H. P.: Eocene greenhouse climate revealed by coupled clumped isotope-Mg/Ca thermometry, *Proc. Natl. Acad. Sci.*, 115(6), 1174 LP – 1179, doi:10.1073/pnas.1714744115, 2018.
- 1995 Exon, N. F., Kennett, J. P. and Malone, M. J.: Leg 189 Synthesis: Cretaceous – Holocene history of the Tasmanian gateway, in *Proceedings of the Ocean Drilling Program: Scientific Results*, 189. [online] Available from: [http://www.odp.tamu.edu/publications/189\\_SR/synth/synth.htm](http://www.odp.tamu.edu/publications/189_SR/synth/synth.htm), 2004.
- Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofield, O. and Taylor, F. J. R.: The Evolution of Modern Eukaryotic Phytoplankton, *Science*, 305(5682), 354 LP – 360, doi:10.1126/science.1095964, 2004.
- 2000 Fan, M., Ayyash, S. A., Tripathi, A., Passey, B. H. and Griffith, E. M.: Terrestrial cooling and changes in hydroclimate in the continental interior of the United States across the Eocene-Oligocene boundary, *GSA Bull.*, 130(7–8), 1073–1084, doi:10.1130/B31732.1, 2017.
- 1005 [Fan, M., Feng, R., Geissman, J. W. and Poulsen, C. J.: Late Paleogene emergence of a North American loess plateau, \*Geology\*, 48\(3\), 273–277, doi:10.1130/G47102.1, 2020.](#)
- Farnsworth, A., Lunt, D. J., O'Brien, C., Foster, G. L., Inglis, G. N., Markwick, P., Pancost, R. D. and Robinson, S. A.: Climate sensitivity on geological timescales controlled by non-linear feedbacks and ocean circulation, *Geophys. Res. Lett.*, doi:10.1029/2019GL083574, 2019.
- 2010 Ferreira, D., Cessi, P., Coxall, H. K., de Boer, A., Dijkstra, H. A., Drijfhout, S. S., Eldevik, T., Harnik, N., McManus, J. F., Marshall, D. P., Nilsson, J., Roquet, F., Schneider, T. and Wills, R. C.: Atlantic-Pacific Asymmetry in Deep Water Formation, *Annu. Rev. Earth Planet. Sci.*, 46(1), 327–352, doi:10.1146/annurev-earth-082517-010045, 2018.
- Figueirido, B., Janis, C. M., Pérez-Claros, J. A., De Renzi, M. and Palmqvist, P.: Cenozoic climate change influences mammalian evolutionary dynamics, *Proc. Natl. Acad. Sci.*, 109(3), 722 LP – 727, doi:10.1073/pnas.1110246108, 2012.
- 2015 Foster, G. L. and Rae, J. W. B.: Reconstructing Ocean pH with Boron Isotopes in Foraminifera, *Annu. Rev. Earth Planet. Sci.*, 44(1), 207–237, doi:10.1146/annurev-earth-060115-012226, 2016.
- Foster, G. L., Lear, C. H. and Rae, J. W. B.: The evolution of pCO<sub>2</sub>, ice volume and climate during the middle Miocene, *Earth Planet. Sci. Lett.*, 341–344, 243–254, doi:10.1016/j.epsl.2012.06.007, 2012.
- Foster, G. L., Royer, D. L. and Lunt, D. J.: Future climate forcing potentially without precedent in the last 420 million years, *Nat. Commun.*, 8, 14845, doi:10.1038/ncomms14845, 2017.
- 2020 Francis, J. E., Marenssi, S., Levy, R., Hambrey, M., Thorn, V. C., Mohr, B., Brinkhuis, H., Warnaar, J., Zachos, J., Bohaty, S. and DeConto, R.: Chapter 8 From Greenhouse to Icehouse – The Eocene/Oligocene in Antarctica, in *Antarctic Climate Evolution*, vol. 8, edited by F. Florindo and M. B. T.-D. in E. and E. S. Siegert, pp. 309–368, Elsevier., 2008.
- 2025 Franks, P. J., Royer, D. L., Beerling, D. J., Van de Water, P. K., Cantrill, D. J., Barbour, M. M. and Berry, J. A.: New constraints on atmospheric CO<sub>2</sub> concentration for the Phanerozoic, *Geophys. Res. Lett.*, 41(13), 4685–4694, doi:10.1002/2014GL060457, 2014.
- Fyke, J. G., D'Orgeville, M. and Weaver, A. J.: Drake Passage and Central American Seaway controls on the distribution of the oceanic carbon reservoir, *Glob. Planet. Change*, 128(0), 72–82, doi:10.1016/j.gloplacha.2015.02.011, 2015.

- 2030 Galeotti, S., DeConto, R., Naish, T., Stocchi, P., Florindo, F., Pagani, M., Barrett, P., Bohaty, S. M., Lanci, L., Pollard, D., Sandroni, S., Talarico, F. M. and Zachos, J. C.: Antarctic Ice Sheet variability across the Eocene-Oligocene boundary climate transition, *Science*, 352(6281), 76 LP–80, doi:10.1126/science.aab0669, 2016.
- Gallagher, S. J., Wade, B., Qianyu, L., Holdgate, G. R., Bown, P., Korasidis, V. A., Scher, H., Houben, A. J. P., McGowran, B. and Allan, T.: Eocene to Oligocene high paleolatitude neritic record of Oi-1 glaciation in the Otway Basin southeast Australia, *Glob. Planet. Change*, 191, 103218, doi:10.1016/j.gloplacha.2020.103218, 2020.
- 2035 Gallagher, T. M. and Sheldon, N. D.: A new paleothermometer for forest paleosols and its implications for Cenozoic climate, *Geology*, 41(6), 647–650, doi:10.1130/G34074.1, 2013.
- Gasson, E., Siddall, M., Lunt, D. J., Rackham, O. J. L., Lear, C. H. and Pollard, D.: Exploring uncertainties in the relationship between temperature, ice volume, and sea level over the past 50 million years, *Rev. Geophys.*, 50(1), doi:10.1029/2011RG000358, 2012.
- 2040 Gasson, E., Lunt, D. J., DeConto, R., Goldner, A., Heinemann, M., Huber, M., LeGrande, A. N., Pollard, D., Sago, N., Siddall, M., Winguth, A. and Valdes, P. J.: Uncertainties in the modelled CO<sub>2</sub> threshold for Antarctic glaciation, *Clim. Past*, 10(2), 451–466, doi:10.5194/cp-10-451-2014, 2014.
- Ghosh, P., Adkins, J., Affek, H., Balta, B., Guo, W., Schauble, E. A., Schrag, D. and Eiler, J. M.: 13C–18O bonds in carbonate minerals: A new kind of paleothermometer, *Geochim. Cosmochim. Acta*, 70(6), 1439–1456, doi:10.1016/j.gca.2005.11.014, 2006.
- 2045 Gion, A. M., Williams, S. E. and Müller, R. D.: A reconstruction of the Eureka Orogeny incorporating deformation constraints, *Tectonics*, 36(2), 304–320, doi:10.1002/2015TC004094, 2017.
- Goddéris, Y., Donnadieu, Y., Le Hir, G., Lefebvre, V. and Nardin, E.: The role of palaeogeography in the Phanerozoic history of atmospheric CO<sub>2</sub> and climate, *Earth-Science Rev.*, 128, 122–138, doi:10.1016/j.earscirev.2013.11.004, 2014.
- 2050 Goldner, A., Herold, N. and Huber, M.: Antarctic glaciation caused ocean circulation changes at the Eocene-Oligocene transition, *Nature*, 511(7511), 574–577, doi:10.1038/nature13597, 2014.
- Gradstein, F. M., Ogg, J. G., Schmitz, M. and Ogg, G.: *The geologic time scale 2012*, Elsevier., 2012.
- Greenop, R., Hain, M. P., Sosdian, S. M., Oliver, K. I. C., Goodwin, P., Chalk, T. B., Lear, C. H., Wilson, P. A. and Foster, G. L.: A record of Neogene seawater  $\delta^{11}\text{B}$  reconstructed from paired  $\delta^{11}\text{B}$  analyses on benthic and planktic foraminifera, *Clim. Past*, 13(2), 149–170, doi:10.5194/cp-13-149-2017, 2017.
- 2055 Greenwood, D. R. and Wing, S. L.: Eocene continental climates and latitudinal temperature gradients, *Geology*, 23(11), 1044–1048, doi:10.1130/0091-7613(1995)023<1044:ECCALT>2.3.CO;2, 1995.
- Grein, M., Oehm, C., Konrad, W., Utescher, T., Kunzmann, L. and Roth-Nebelsick, A.: Atmospheric CO<sub>2</sub> from the late Oligocene to early Miocene based on photosynthesis data and fossil leaf characteristics, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 374, 41–51, doi:10.1016/j.palaeo.2012.12.025, 2013.
- 2060 Griener, K. W., Nelson, D. M. and Warny, S.: Declining moisture availability on the Antarctic Peninsula during the Late Eocene, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 383–384, 72–78, doi:10.1016/j.palaeo.2013.05.004, 2013.
- Grimes, S. T., Hooker, J. J., Collinson, M. E. and Matthey, D. P.: Summer temperatures of late Eocene to early Oligocene freshwaters, *Geology*, 33(3), 189–192, doi:10.1130/G21019.1, 2005.
- Gurnis, M., Yang, T., Cannon, J., Turner, M., Williams, S., Flament, N. and Müller, R. D.: Global tectonic reconstructions

- 2065 with continuously deforming and evolving rigid plates, *Comput. Geosci.*, 116, 32–41, doi:10.1016/j.cageo.2018.04.007, 2018.
- [Haiblen, A. M., Opdyke, B. N., Roberts, A. P., Heslop, D. and Wilson, P. A.: Midlatitude Southern Hemisphere Temperature Change at the End of the Eocene Greenhouse Shortly Before Dawn of the Oligocene Icehouse, \*Paleoceanogr. Paleoclimatology\*, 34\(12\), 1995–2004, doi:10.1029/2019PA003679, 2019.](#)
- 2070 Hegewald, A. and Jokat, W.: Relative sea level variations in the Chukchi region - Arctic Ocean - since the late Eocene, *Geophys. Res. Lett.*, 40(5), 803–807, doi:10.1002/grl.50182, 2013.
- Helland, P. E. and Holmes, M. A.: Surface textural analysis of quartz sand grains from ODP Site 918 off the southeast coast of Greenland suggests glaciation of southern Greenland at 11 Ma, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 135(1), 109–121, doi:10.1016/S0031-0182(97)00025-4, 1997.
- 2075 Hérán, M., Lécuyer, C. and Legendre, S.: Cenozoic long-term terrestrial climatic evolution in Germany tracked by  $\delta^{18}\text{O}$  of rodent tooth phosphate, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 285(3–4), 331–342, doi:10.1016/j.palaeo.2009.11.030, 2010.
- Herman, A. B., Spicer, R. A., Aleksandrova, G. N., Yang, J., Kodrul, T. M., Maslova, N. P., Spicer, T. E. V., Chen, G. and Jin, J.-H.: Eocene–early Oligocene climate and vegetation change in southern China: Evidence from the Maoming Basin, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 479, 126–137, doi:10.1016/j.palaeo.2017.04.023, 2017.
- 2080 Herold, N., Buzan, J., Seton, M., Goldner, A., Green, J. A. M., Müller, R. D., Markwick, P. and Huber, M.: A suite of early Eocene (~ 55 Ma) climate model boundary conditions, *Geosci. Model Dev.*, 7(5), 2077–2090, doi:10.5194/gmd-7-2077-2014, 2014.
- Heureux, A. M. C. and Rickaby, R. E. M.: Refining our estimate of atmospheric CO<sub>2</sub> across the Eocene–Oligocene climatic transition, *Earth Planet. Sci. Lett.*, 409, 329–338, doi:10.1016/j.epsl.2014.10.036, 2015.
- 2085 Hill, D. J., Haywood, A. M., Valdes, P. J., Francis, J. E., Lunt, D. J., Wade, B. S. and Bowman, V. C.: Paleogeographic controls on the onset of the Antarctic circumpolar current, *Geophys. Res. Lett.*, 40, 5199–5204, doi:10.1002/grl.50941, 2013.
- Hincke, A. J. C., Broere, T., Kürschner, W. M., Donders, T. H. and Wagner-Cremer, F.: Multi-year leaf-level response to sub-ambient and elevated experimental CO<sub>2</sub> in *Betula nana*, *PLoS One*, 11(6), e0157400, doi:10.1371/journal.pone.0157400, 2016.
- 2090 Hinojosa, L. F. and Villagrán, C.: Did South American Mixed Paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic?, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 217(1), 1–23, doi:10.1016/j.palaeo.2004.11.013, 2005.
- van Hinsbergen, D. J. J., de Groot, L. V., van Schaik, S. J., Spakman, W., Bijl, P. K., Sluijs, A., Langereis, C. G. and Brinkhuis, H.: A Paleolatitude Calculator for Paleoclimate Studies., *PLoS One*, 10(6), e0126946, doi:10.1371/journal.pone.0126946, 2015.
- 2095 Hohbein, M. W., Sexton, P. F. and Cartwright, J. A.: Onset of North Atlantic Deep Water production coincident with inception of the Cenozoic global cooling trend, *Geology*, 40(3), 255–258, doi:10.1130/G32461.1, 2012.
- Hollis, C. J., Handley, L., Crouch, E. M., Morgans, H. E. G., Baker, J. A., Creech, J., Collins, K. S., Gibbs, S. J., Huber, M., Schouten, S., Zachos, J. C. and Pancost, R. D.: Tropical sea temperatures in the high-latitude South Pacific during the Eocene, *Geology*, 37(2), 99–102, doi:10.1130/G25200A.1, 2009.
- 2100 Hollis, C. J., Taylor, K. W. R., Handley, L., Pancost, R. D., Huber, M., Creech, J. B., Hines, B. R., Crouch, E. M., Morgans, H. E. G., Crampton, J. S., Gibbs, S., Pearson, P. N. and Zachos, J. C.: Early Paleogene temperature history of the Southwest

- Pacific Ocean: Reconciling proxies and models, *Earth Planet. Sci. Lett.*, 349–350, 53–66, doi:10.1016/j.epsl.2012.06.024, 2012.
- 2105 Hollis, C. J., Dunkley Jones, T., Anagnostou, E., Bijl, P. K., Cramwinckel, M. J., Cui, Y., Dickens, G. R., Edgar, K. M., Eley, Y., Evans, D., Foster, G. L., Frieling, J., Inglis, G. N., Kennedy, E. M., Kozdon, R., Laetano, V., Lear, C. H., Littler, K., Lourens, L., Meckler, A. N., Naafs, B. D. A., Pälike, H., Pancost, R. D., Pearson, P. N., Röhl, U., Royer, D. L., Salzmann, U., Schubert, B. A., Seebeck, H., Sluijs, A., Speijer, R. P., Stassen, P., Tierney, J., Tripathi, A., Wade, B., Westerhold, T., Witkowski, C., Zachos, J. C., Zhang, Y. G., Huber, M. and Lunt, D. J.: The DeepMIP contribution to PMIP4: methodologies for selection, compilation and analysis of latest Paleocene and early Eocene climate proxy data, incorporating version 0.1 of the DeepMIP database, *Geosci. Model Dev.*, 12(7), 3149–3206, doi:10.5194/gmd-12-3149-2019, 2019.
- 2110 Homes, A. M., Cieraad, E., Lee, D. E., Lindqvist, J. K., Raine, J. I., Kennedy, E. M. and Conran, J. G.: A diverse fern flora including macrofossils with in situ spores from the late Eocene of southern New Zealand, *Rev. Palaeobot. Palynol.*, 220, 16–28, doi:10.1016/j.revpalbo.2015.04.007, 2015.
- 2115 Hooker, J. J., Collinson, M. E. and Sille, N. P.: Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event, *J. Geol. Soc. London.*, 161(2), 161–172, doi:10.1144/0016-764903-091, 2004.
- 120 [Hooorn, C., Straathof, J., Abels, H. A., Xu, Y., Utescher, T. and Dupont-Nivet, G.: A late Eocene palynological record of climate change and Tibetan Plateau uplift \(Xining Basin, China\), \*Palaeogeogr. Palaeoclimatol. Palaeoecol.\*, 344–345, 16–38, doi:https://doi.org/10.1016/j.palaeo.2012.05.011, 2012.](https://doi.org/10.1016/j.palaeo.2012.05.011)
- Houben, A. J. P., van Mourik, C. A., Montanari, A., Coccioni, R. and Brinkhuis, H.: The Eocene–Oligocene transition: Changes in sea level, temperature or both?, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 335–336, 75–83, doi:10.1016/j.palaeo.2011.04.008, 2012.
- 2125 Hren, M. T., Sheldon, N. D., Grimes, S. T., Collinson, M. E., Hooker, J. J., Bugler, M. and Lohmann, K. C.: Terrestrial cooling in Northern Europe during the Eocene–Oligocene transition, *Proc. Natl. Acad. Sci.*, 110(19), 7562 LP – 7567, doi:10.1073/pnas.1210930110, 2013.
- Huang, X., Gohl, K. and Jokat, W.: Variability in Cenozoic sedimentation and paleo-water depths of the Weddell Sea basin related to pre-glacial and glacial conditions of Antarctica, *Glob. Planet. Change*, 118, 25–41, doi:10.1016/j.gloplacha.2014.03.010, 2014.
- 2130 Huber, M.: A Hotter Greenhouse?, *Science*, 321(5887), 353–354, doi:10.1126/science.1161170, 2008.
- Huber, M. and Caballero, R.: The early Eocene equable climate problem revisited, *Clim. Past*, 7(2), 603–633, doi:10.5194/cp-7-603-2011, 2011.
- Huber, M. and Nof, D.: The ocean circulation in the southern hemisphere and its climatic impacts in the Eocene, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 231(1–2), 9–28, doi:10.1016/j.palaeo.2005.07.037, 2006.
- 2135 Huber, M. and Sloan, L. C.: Climatic responses to tropical sea surface temperature changes on a “greenhouse” Earth, *Paleoceanography*, 15(4), 443–450, doi:10.1029/1999PA000455, 2000.
- Huber, M. and Sloan, L. C.: Heat transport, deep waters, and thermal gradients: Coupled simulation of an Eocene greenhouse climate, *Geophys. Res. Lett.*, 28(18), 3481–3484, doi:10.1029/2001GL012943, 2001.
- 2140 Huber, M., Sloan, L. and Shellito, C.: Early Paleogene oceans and climate: A fully coupled modeling approach using the NCAR CCSM, in: Causes and consequences of globally warm climates in the Early Paleogene, *Geol. Soc. Am. Spec. Pap.*, 369, 25–47, 2003.

- Huber, M., Brinkhuis, H., Stickley, C. E., Döös, K., Sluijs, A., Warnaar, J., Schellenberg, S. A. and Williams, G. L.: Eocene circulation of the Southern Ocean: Was Antarctica kept warm by subtropical waters?, *Paleoceanography*, 19(4), PA4026, doi:10.1029/2004PA001014, 2004.
- 2145 Hurley, S. J., Elling, F. J., Könneke, M., Buchwald, C., Wankel, S. D., Santoro, A. E., Lipp, J. S., Hinrichs, K.-U. and Pearson, A.: Influence of ammonia oxidation rate on thaumarchaeal lipid composition and the TEX<sub>86</sub> temperature proxy, *Proc. Natl. Acad. Sci.*, 113(28), 7762 LP – 7767, doi:10.1073/pnas.1518534113, 2016.
- Hutchinson, D. K., de Boer, A. M., Coxall, H. K., Caballero, R., Nilsson, J. and Baatsen, M.: Climate sensitivity and meridional overturning circulation in the late Eocene using GFDL CM2.1, *Clim. Past*, 14, 789–810, doi:10.5194/cp-14-789-2018, 2018.
- 2150 Hutchinson, D. K., Coxall, H. K., O'Regan, M., Nilsson, J., Caballero, R. and de Boer, A. M.: Arctic closure as a trigger for Atlantic overturning at the Eocene-Oligocene Transition, *Nat. Commun.*, 10, 3797, doi:10.1038/s41467-019-11828-z, 2019.
- Hyeong, K., Kuroda, J., Seo, I. and Wilson, P. A.: Response of the Pacific inter-tropical convergence zone to global cooling and initiation of Antarctic glaciation across the Eocene Oligocene Transition, *Sci. Rep.*, 6, 30647, doi:10.1038/srep30647, 2016.
- 2155 Inglis, G. N., Farnsworth, A., Lunt, D., Foster, G. L., Hollis, C. J., Pagani, M., Jardine, P. E., Pearson, P. N., Markwick, P., Galsworthy, A. M. J., Raynham, L., Taylor, K. W. R. and Pancost, R. D.: Descent toward the Icehouse: Eocene sea surface cooling inferred from GDGT distributions, *Paleoceanography*, 30(7), 1000–1020, doi:10.1002/2014PA002723, 2015.
- 160 [Inglis, G. N., Bragg, F., Burls, N., Evans, D., Foster, G. L., Huber, M., Lunt, D. J., Siler, N., Steinig, S., Wilkinson, R., Anagnostou, E., Cramwinckel, M., Hollis, C. J., Pancost, R. D. and Tierney, J. E.: Global mean surface temperature and climate sensitivity of the EEOC, PETM and latest Paleocene, \*Clim. Past Discuss.\*, 2020, 1–43, doi:10.5194/cp-2019-167, 2020.](#)
- Jacobs, B. F., Pan, A. D. and Scotese, C. R.: A review of the Cenozoic vegetation history of Africa, in *Cenozoic mammals of Africa*, edited by W. J. Werdelin, L., Sanders, pp. 57–72, University of California Press Berkeley., 2010.
- Japsen, P., Bonow, J. M., Green, P. F., Chalmers, J. A. and Lidmar-Bergström, K.: Elevated, passive continental margins: Long-term highs or Neogene uplifts? New evidence from West Greenland, *Earth Planet. Sci. Lett.*, 248(1), 330–339, doi:10.1016/j.epsl.2006.05.036, 2006.
- 2165 Japsen, P., Green, P. F. and Bonow, J. M.: Investigation of the Burial and Exhumation History of East Greenland Based On Apatite-fission Track Analysis, Stratigraphic Landform Analysis and the Geological Record, *OTC Arct. Technol. Conf.*, 8, doi:10.4043/25562-MS, 2015.
- Jin, J.-H., Herman, A. B., Spicer, R. A. and Kodrul, T. M.: Palaeoclimate background of the diverse Eocene floras of South China, *Sci. Bull.*, 62(22), 1501–1503, doi:10.1016/j.scib.2017.11.002, 2017.
- 2170 John, E. H., Pearson, P. N., Coxall, H. K., Birch, H., Wade, B. S. and Foster, G. L.: Warm ocean processes and carbon cycling in the Eocene, *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.*, 371(2001), doi:10.1098/rsta.2013.0099, 2013.
- John, E. H., Wilson, J. D., Pearson, P. N. and Ridgwell, A.: Temperature-dependent remineralization and carbon cycling in the warm Eocene oceans, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 413, 158–166, doi:10.1016/j.palaeo.2014.05.019, 2014.
- 2175 St. John, K.: Cenozoic ice-rafting history of the central Arctic Ocean: Terrigenous sands on the Lomonosov Ridge, *Paleoceanography*, 23(1), doi:10.1029/2007PA001483, 2008.
- [Jones, A. P., Dunkley Jones, T., Coxall, H., Pearson, P. N., Nala, D. and Hoggott, M.: Low-Latitude Calcareous Nannofossil Response in the Indo-Pacific Warm Pool Across the Eocene-Oligocene Transition of Java, Indonesia, \*Paleoceanogr. Paleoclimatology\*, 34\(11\), 1833–1847, doi:10.1029/2019PA003597, 2019.](#)

- 2180 Katz, M. E., Miller, K. G., Wright, J. D., Wade, B. S., Browning, J. V., Cramer, B. S. and Rosenthal, Y.: Stepwise transition from the Eocene greenhouse to the Oligocene icehouse, *Nat. Geosci.*, 1, 329 [online] Available from: <http://dx.doi.org/10.1038/ngeo179>, 2008.
- Katz, M. E., Cramer, B. S., Toggweiler, J. R., Esmay, G., Liu, C., Miller, K. G., Rosenthal, Y., Wade, B. S. and Wright, J. D.: Impact of Antarctic Circumpolar Current development on late Paleogene ocean structure., *Science*, 332(6033), 1076–1079, 2185 doi:10.1126/science.1202122, 2011.
- Kennedy-Asser, A. T., Lunt, D. J., Farnsworth, A. and Valdes, P. J.: Assessing Mechanisms and Uncertainty in Modeled Climatic Change at the Eocene-Oligocene Transition, *Paleoceanogr. Paleoclimatology*, 34(1), 16–34, doi:10.1029/2018PA003380, 2019.
- Kennedy-Asser, A. T., Lunt, D. J., Valdes, P. J., Ladant, J.-B., Frieling, J. and Lauretano, V.: Changes in the high-latitude Southern Hemisphere through the Eocene–Oligocene transition: a model–data comparison, *Clim. Past*, 16(2), 555–573, 2190 doi:10.5194/cp-16-555-2020, 2020.
- Kennedy, A. T., Farnsworth, A., Lunt, D. J., Lear, C. H. and Markwick, P. J.: Atmospheric and oceanic impacts of Antarctic glaciation across the Eocene–Oligocene transition, *Phil. Trans. R. Soc. A*, 373(2054), 20140419, doi:10.1098/rsta.2014.0419, 2015.
- 2195 Kennett, J. P.: Cenozoic Evolution of Antarctic Glaciation, the Circum-Antarctic Ocean, and Their Impact on Global Paleooceanography, *J. Geophys. Res.*, 82(27), 3843–3860, doi:10.1029/JC082i027p03843, 1977.
- Kennett, J. P. and Shackleton, N. J.: Oxygen isotopic evidence for the development of the psychrosphere 38 Myr ago, *Nature*, 260, 513, doi:10.1038/260513a0, 1976.
- Kennett, J. P., Houtz, R. E., Andrews, P. B., Edwards, A. R., Gostin, V. A., Hajos, M., Hampton, M., Jenkins, D. G., Margolis, 2200 S. V., Ovenshine, A. T. and Perch-Nielsen, K.: Cenozoic paleoceanography in the Southwest Pacific Ocean, Antarctic glaciation, and the development of the Circum-Antarctic Current, *Initial Rep. Deep Sea Drill. Proj.*, 29, 1155, 1975.
- Kiehl, J. T. and Shields, C. A.: Sensitivity of the Palaeocene–Eocene Thermal Maximum climate to cloud properties, *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.*, 371(2001), 20130093, doi:10.1098/rsta.2013.0093, 2013.
- 2205 Kim, J.-H., van der Meer, J., Schouten, S., Helmke, P., Willmott, V., Sangiorgi, F., Koç, N., Hopmans, E. C. and Damsté, J. S. S.: New indices and calibrations derived from the distribution of crenarchaeal isoprenoid tetraether lipids: Implications for past sea surface temperature reconstructions, *Geochim. Cosmochim. Acta*, 74(16), 4639–4654, doi:10.1016/j.gca.2010.05.027, 2010.
- Kim, S. L., Eberle, J. J., Bell, D. M., Fox, D. A. and Padilla, A.: Evidence from shark teeth for a brackish Arctic Ocean in the Eocene greenhouse, *Geology*, 42(8), 695–698, doi:10.1130/G35675.1, 2014.
- 2210 Kobashi, T., Grossman, E. L., Dockery, D. T. and Ivany, L. C.: Water mass stability reconstructions from greenhouse (Eocene) to icehouse (Oligocene) for the northern Gulf Coast continental shelf (USA), *Paleoceanography*, 19(1), PA1022, doi:10.1029/2003PA000934, 2004.
- Kocsis, L., Ozsvárt, P., Becker, D., Ziegler, R., Scherler, L. and Codrea, V.: Orogeny forced terrestrial climate variation during the late Eocene–early Oligocene in Europe, *Geology*, 42(8), 727–730, doi:10.1130/G35673.1, 2014.
- 2215 Kohn, M. J., Josef, J. A., Madden, R., Kay, R., Vucetich, G. and Carlini, A. A.: Climate stability across the Eocene-Oligocene transition, southern Argentina, *Geology*, 32(7), 621–624, doi:10.1130/G20442.1, 2004.
- Kohn, M. J., Strömberg, C. A. E., Madden, R. H., Dunn, R. E., Evans, S., Palacios, A. and Carlini, A. A.: Quasi-static Eocene–



- Oligocene climate in Patagonia promotes slow faunal evolution and mid-Cenozoic global cooling, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 435, 24–37, doi:<https://doi.org/10.1016/j.palaeo.2015.05.028>, 2015.
- 2220 Konrad, W., Roth-Nebelsick, A. and Grein, M.: Modelling of stomatal density response to atmospheric CO<sub>2</sub>, *J. Theor. Biol.*, 253(4), 638–658, doi:10.1016/j.jtbi.2008.03.032, 2008.
- [Korasidis, V. A., Wallace, M. W., Wagstaff, B. E. and Hill, R. S.: Terrestrial cooling record through the Eocene-Oligocene transition of Australia, \*Glob. Planet. Change\*, 173, 61–72, doi:https://doi.org/10.1016/j.gloplacha.2018.12.007, 2019.](https://doi.org/10.1016/j.gloplacha.2018.12.007)
- 2225 Kovar-Eder, J.: Early Oligocene plant diversity along the Upper Rhine Graben: The fossil flora of Rauenberg, Germany, *Acta Palaeobot.*, 56, 329, doi:10.1515/acpa-2016-0011, 2016.
- [Kraatz, B. P. and Geisler, J. H.: Eocene–Oligocene transition in Central Asia and its effects on mammalian evolution, \*Geology\*, 38\(2\), 111–114, doi:10.1130/G30619.1, 2010.](https://doi.org/10.1130/G30619.1)
- 2230 Krylov, A. A., Andreeva, I. A., Vogt, C., Backman, J., Krupskaya, V. V., Grikurov, G. E., Moran, K. and Shoji, H.: A shift in heavy and clay mineral provenance indicates a middle Miocene onset of a perennial sea ice cover in the Arctic Ocean, *Paleoceanography*, 23(1), doi:10.1029/2007PA001497, 2008.
- Kunzmann, L., Kvaček, Z., Teodoridis, V., Müller, C. and Moraweck, K.: Vegetation dynamics of riparian forest in central Europe during the late Eocene, *Palaeontogr. Abteilung B*, 295(1–3), 69–89, doi:10.1127/palb/295/2016/69, 2016.
- Kürschner, W. M., Kvaček, Z. and Dilcher, D. L.: The impact of Miocene atmospheric carbon dioxide fluctuations on climate and the evolution of terrestrial ecosystems, *Proc. Natl. Acad. Sci.*, 105(2), 449 LP – 453, doi:10.1073/pnas.0708588105, 2008.
- 2235 Kvaček, Z., Teodoridis, V., Mach, K., Prikryl, T. and Dvořák, Z.: Tracing the Eocene-Oligocene transition: a case study from North Bohemia, *Bull. Geosci.*, 89(1), 21–66, doi:10.3140/bull.geosci.1411, 2014.
- Ladant, J.-B., Donnadieu, Y. and Dumas, C.: Links between CO<sub>2</sub>, glaciation and water flow: reconciling the Cenozoic history of the Antarctic Circumpolar Current, *Clim. Past*, 10(6), 1957–1966, doi:10.5194/cp-10-1957-2014, 2014a.
- 2240 Ladant, J.-B., Donnadieu, Y., Lefebvre, V. and Dumas, C.: The respective role of atmospheric carbon dioxide and orbital parameters on ice sheet evolution at the Eocene-Oligocene transition, *Paleoceanography*, 29(8), 810–823, doi:10.1002/2013PA002593, 2014b.
- Langton, S. J., Rabideaux, N. M., Borrelli, C. and Katz, M. E.: Southeastern Atlantic deep-water evolution during the late-middle Eocene to earliest Oligocene (Ocean Drilling Program Site 1263 and Deep Sea Drilling Project Site 366), *Geosphere*, 12(3), 1032–1047, doi:10.1130/GES01268.1, 2016.
- 2245 Larsen, H. C., Saunders, A. D., Clift, P. D., Beget, J., Wei, W. and Spezzaferri, S.: Seven Million Years of Glaciation in Greenland, *Science*, 264(5161), 952 LP – 955, doi:10.1126/science.264.5161.952, 1994.
- [Lasabuda, A., Laberg, J. S., Knutsen, S.-M. and Høgeth, G.: Early to middle Cenozoic paleoenvironment and erosion estimates of the southwestern Barents Sea: Insights from a regional mass-balance approach, \*Mar. Pet. Geol.\*, 96, 501–521, doi:https://doi.org/10.1016/j.marpetgeo.2018.05.039, 2018.](https://doi.org/10.1016/j.marpetgeo.2018.05.039)
- 2250 Lear, C. H., Elderfield, H. and Wilson, P. A.: Cenozoic Deep-Sea Temperatures and Global Ice Volumes from Mg/Ca in Benthic Foraminiferal Calcite, *Science*, 287(5451), 269 LP – 272, doi:10.1126/science.287.5451.269, 2000.
- Lear, C. H., Rosenthal, Y., Coxall, H. K. and Wilson, P. A.: Late Eocene to early Miocene ice sheet dynamics and the global carbon cycle, *Paleoceanography*, 19(4), doi:10.1029/2004PA001039, 2004.

- 2255 Lear, C. H., Bailey, T. R., Pearson, P. N., Coxall, H. K. and Rosenthal, Y.: Cooling and ice growth across the Eocene-Oligocene transition, *Geology*, 36(3), 251, doi:10.1130/G24584A.1, 2008.
- Lear, C. H., Mawbey, E. M. and Rosenthal, Y.: Cenozoic benthic foraminiferal Mg/Ca and Li/Ca records: Toward unlocking temperatures and saturation states, *Paleoceanography*, 25(4), doi:10.1029/2009PA001880, 2010.
- Lear, C. H., Coxall, H. K., Foster, G. L., Lunt, D. J., Mawbey, E. M., Rosenthal, Y., Sosdian, S. M., Thomas, E. and Wilson, P. A.: Neogene ice volume and ocean temperatures: Insights from infaunal foraminiferal Mg/Ca paleothermometry, *Paleoceanography*, 30(11), 1437–1454, doi:10.1002/2015PA002833, 2015.
- 2260 Lefebvre, V., Donnadieu, Y., Sepulchre, P., Swingedouw, D. and Zhang, Z.-S.: Deciphering the role of southern gateways and carbon dioxide on the onset of the Antarctic Circumpolar Current, *Paleoceanography*, 27(4), PA4201, doi:10.1029/2012PA002345, 2012.
- 2265 Lielke, K., Manchester, S. and Meyer, H.: Reconstructing the environment of the northern Rocky Mountains during the Eocene/Oligocene transition: constraints from the palaeobotany and geology of south-western Montana, USA, *Acta Palaeobot.*, 52(2), 317–358 [online] Available from: <http://bomax.botany.pl/pubs-new/#article-3604>, 2012.
- Linnemann, U., Su, T., Kunzmann, L., Spicer, R. A., Ding, W.-N., Spicer, T. E. V., Zieger, J., Hofmann, M., Moraweck, K., Gärtner, A., Gerdes, A., Marko, L., Zhang, S.-T., Li, S.-F., Tang, H., Huang, J., Mulch, A., Mosbrugger, V. and Zhou, Z.-K.: New U-Pb dates show a Paleogene origin for the modern Asian biodiversity hot spots, *Geology*, 46(1), 3–6, doi:10.1130/G39693.1, 2017.
- 2270 Liu, W., Xie, S.-P., Liu, Z. and Zhu, J.: Overlooked possibility of a collapsed Atlantic Meridional Overturning Circulation in warming climate, *Sci. Adv.*, 3(1), doi:10.1126/sciadv.1601666, 2017.
- Liu, X. Y., Gao, Q., Han, M. and Jin, J. H.: Estimates of late middle Eocene CO<sub>2</sub> based on stomatal density of modern and fossil *Nageia* leaves, *Clim. Past*, 12(2), 241–253, doi:10.5194/cp-12-241-2016, 2016.
- 2275 Liu, Z., Tuo, S., Zhao, Q., Cheng, X. and Huang, W.: Deep-water Earliest Oligocene Glacial Maximum (EOGM) in South Atlantic, *Chinese Sci. Bull.*, 49(20), 2190–2197, doi:10.1007/BF03185787, 2004.
- Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S. R., Leckie, R. M. and Pearson, A.: Global Cooling During the Eocene-Oligocene Climate Transition, *Science*, 323(5918), 1187–1190, doi:10.1126/science.1166368, 2009.
- 2280 Liu, Z., He, Y., Jiang, Y., Wang, H., Liu, W., Bohaty, S. M. and Wilson, P. A.: Transient temperature asymmetry between hemispheres in the Palaeogene Atlantic Ocean, *Nat. Geosci.*, 11, 656–660, doi:10.1038/s41561-018-0182-9, 2018.
- Livermore, R., Hillenbrand, C.-D., Meredith, M. and Eagles, G.: Drake Passage and Cenozoic climate: An open and shut case?, *Geochemistry, Geophys. Geosystems*, 8(1), Q01005, doi:10.1029/2005GC001224, 2007.
- 2285 Lunt, D. J., [Ridgwell, A.](#), [Valdes, P. J.](#) and [Seale, A.](#): “Sunshade World”: A fully coupled GCM evaluation of the climatic impacts of geoengineering, *Geophys. Res. Lett.*, 35(12), n/a-n/a, doi:10.1029/2008GL033674, 2008.
- Lunt, D. J., Dunkley Jones, T., Heinemann, M., Huber, M., LeGrande, A., Winguth, A., Loptson, C., Marotzke, J., Roberts, C. D., Tindall, J., Valdes, P. and Winguth, C.: A model–data comparison for a multi-model ensemble of early Eocene atmosphere–ocean simulations: EoMIP, *Clim. Past*, 8(5), 1717–1736, doi:10.5194/cp-8-1717-2012, 2012.
- 2290 Lunt, D. J., Farnsworth, A., Loptson, C., Foster, G. L., Markwick, P., O’Brien, C. L., Pancost, R. D., Robinson, S. A. and Wrobel, N.: Palaeogeographic controls on climate and proxy interpretation, *Clim. Past*, 12(5), 1181–1198, doi:10.5194/cp-12-1181-2016, 2016.

**Deleted:** Foster, G. L., Haywood, A. M. and Stone, E. J.: Late Pliocene Greenland glaciation controlled by a decline in atmospheric CO<sub>2</sub> levels, *Nature*, 454(7208), 1102–5, doi:10.1038/nature07223

- 2295 [Lunt, D. J., Bragg, F., Chan, W.-L., Hutchinson, D. K., Ladant, J.-B., Niezgodzki, I., Steinig, S., Zhang, Z., Zhu, J., Abe-Ouchi, A., de Boer, A. M., Coxall, H. K., Donnadieu, Y., Knorr, G., Langebroek, P. M., Lohmann, G., Poulsen, C. J., Sepulchre, P., Tierney, J., Valdes, P. J., Dunkley Jones, T., Hollis, C. J., Huber, M. and Otto-Bliesner, B. L.: DeepMIP: Model intercomparison of early Eocene climatic optimum \(EECO\) large-scale climate features and comparison with proxy data, \*Clim. Past Discuss.\*, 2020, 1–27, doi:10.5194/cp-2019-149, 2020.](#)
- 2300 Lyell, C. and Deshayes, G. P.: *Principles of Geology: being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation*, John Murray., 1830.
- Macphail, M.: *Australian palaeoclimates: Cretaceous to Tertiary a review of palaeobotanical and related evidence to the year 2000*, CRC LEME Open File Report 151.,, 2007.
- 2305 Maher, K. and Chamberlain, C. P.: Hydrologic Regulation of Chemical Weathering and the Geologic Carbon Cycle, *Science*, 343(6178), 1502 LP – 1504, doi:10.1126/science.1250770, 2014.
- Mai, D. H.: Tertiäre Vegetationsgeschichte Europas, *Feddes Repert.*, 106(3–4), 331, doi:10.1002/fedr.19951060333, 1995.
- Markwick, P. J.: The palaeogeographic and palaeoclimatic significance of climate proxies for data-model comparisons, in *Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies*, pp. 251–312, *Micropalaeontol. Soc. Spec. Publ. London.*, 2007.
- 2310 Markwick, P. J.: Palaeogeography in exploration, *Geol. Mag.*, 156(2), 366–407, doi:10.1017/S0016756818000468, 2019.
- Markwick, P. J. and Valdes, P. J.: Palaeo-digital elevation models for use as boundary conditions in coupled ocean–atmosphere GCM experiments: a Maastrichtian (late Cretaceous) example, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 213(1), 37–63, doi:10.1016/j.palaeo.2004.06.015, 2004.
- 2315 Martin, H. A.: Cenozoic climatic change and the development of the arid vegetation in Australia, *J. Arid Environ.*, 66(3), 533–563, doi:10.1016/j.jaridenv.2006.01.009, 2006.
- Martini, E.: Standard Tertiary and Quaternary calcareous nannoplankton zonation, in *Proc. II Planktonic Conference, Roma 1970, Roma, Tecnoscienza*, edited by A. Farinacci, pp. 739–785., 1971.
- Maslin, M. A., Li, X. S., Loutre, M.-F. and Berger, A.: The contribution of orbital forcing to the progressive intensification of Northern Hemisphere glaciation, *Quat. Sci. Rev.*, 17(4), 411–426, doi:10.1016/S0277-3791(97)00047-4, 1998.
- 2320 Maxbauer, D. P., Royer, D. L. and LePage, B. A.: High Arctic forests during the middle Eocene supported by moderate levels of atmospheric CO<sub>2</sub>, *Geology*, 42(12), 1027–1030, doi:10.1130/G36014.1, 2014.
- McElwain, J. C. and Chaloner, W. G.: Stomatal Density and Index of Fossil Plants Track Atmospheric Carbon Dioxide in the Palaeozoic, *Ann. Bot.*, 76(4), 389–395, doi:10.1006/anbo.1995.1112, 1995.
- 2325 [McElwain, J. C. and Steinthorsdottir, M.: Paleoeecology, Ploidy, Paleoatmospheric Composition, and Developmental Biology: A Review of the Multiple Uses of Fossil Stomata, \*Plant Physiol.\*, 174\(2\), 650 LP – 664 \[online\] Available from: <http://www.plantphysiol.org/content/174/2/650.abstract>, 2017.](#)
- McKay, R. M., Barrett, P. J., Levy, R. S., Naish, T. R., Gollledge, N. R. and Pyne, A.: Antarctic Cenozoic climate history from sedimentary records: ANDRILL and beyond, *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.*, 374(2059), doi:10.1098/rsta.2014.0301, 2016.
- 2330 McKinley, C. C., Thomas, D. J., LeVay, L. J. and Rolewicz, Z.: Nd isotopic structure of the Pacific Ocean 40–10 Ma, and evidence for the reorganization of deep North Pacific Ocean circulation between 36 and 25 Ma, *Earth Planet. Sci. Lett.*, 521,

139–149, doi:10.1016/j.epsl.2019.06.009, 2019.

[Meng, J. and McKenna, M. C.: Faunal turnovers of Palaeogene mammals from the Mongolian Plateau, \*Nature\*, 394\(6691\), 364–367, doi:10.1038/28603, 1998.](#)

- 2335 Merico, A., Tyrrell, T. and Wilson, P. A.: Eocene/Oligocene ocean de-acidification linked to Antarctic glaciation by sea-level fall, *Nature*, 452(7190), 979–982, doi:10.1038/nature06853, 2008.
- Meyers, J. A.: Terrestrial Eocene-Oligocene vegetation and climate in the Pacific Northwest, in *From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition*, edited by D. R. Prothero, L. C. Ivany, and E. A. Nesbitt, pp. 171–185, Columbia University Press, New York., 2003.
- 2340 Mühlbachler, M. C., Rivals, F., Solounias, N. and Semperebon, G. M.: Dietary Change and Evolution of Horses in North America, *Science*, 331(6021), 1178 LP – 1181, doi:10.1126/science.1196166, 2011.
- Mikolajewicz, U., Maier-Reimer, E., Crowley, T. J. and Kim, K.-Y.: Effect of Drake and Panamanian Gateways on the circulation of an ocean model, *Paleoceanography*, 8(4), 409–426, doi:10.1029/93PA00893, 1993.
- Miller, K. G., Janecek, T. R., Katz, M. E. and Keil, D. J.: Abyssal circulation and benthic foraminiferal changes near the Paleocene/Eocene boundary, *Paleoceanography*, 2(6), 741–761, doi:10.1029/PA002i006p00741, 1987.
- 2345 Miller, K. G., Wright, J. D. and Fairbanks, R. G.: Unlocking the Ice House: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion, *J. Geophys. Res. Solid Earth*, 96(B4), 6829–6848, doi:10.1029/90JB02015, 1991.
- Miller, K. G., Browning, J. V., Aubry, M.-P., Wade, B. S., Katz, M. E., Kulpecz, A. A. and Wright, J. D.: Eocene–Oligocene global climate and sea-level changes: St. Stephens Quarry, Alabama, *GSA Bull.*, 120(1–2), 34–53, doi:10.1130/B26105.1, 2008.
- 2350 Moraweck, K., Grein, M., Konrad, W., Kvařáček, J., Kovač-Eder, J., Neinhuis, C., Traiser, C. and Kunzmann, L.: Leaf traits of long-ranging Paleogene species and their relationship with depositional facies, climate and atmospheric CO<sub>2</sub> level, *Palaeontogr. Abteilung B*, 298(4–6), 93–172, doi:10.1127/palb/2019/0062, 2019.
- Mudelsee, M., Bickert, T., Lear, C. H. and Lohmann, G.: Cenozoic climate changes: A review based on time series analysis of marine benthic δ<sup>18</sup>O records, *Rev. Geophys.*, 52(3), 333–374, doi:10.1002/2013RG000440, 2014.
- Müller, P. J., Kirst, G., Ruhland, G., von Storch, I. and Rosell-Melé, A.: Calibration of the alkenone paleotemperature index U<sub>37K'</sub> based on core-tops from the eastern South Atlantic and the global ocean (60°N–60°S), *Geochim. Cosmochim. Acta*, 62(10), 1757–1772, doi:10.1016/S0016-7037(98)00097-0, 1998.
- 2360 Müller, R. D., Sdrolias, M., Gaina, C. and Roest, W. R.: Age, spreading rates, and spreading asymmetry of the world's ocean crust, *Geochemistry, Geophys. Geosystems*, 9(4), Q04006, doi:10.1029/2007GC001743, 2008.
- Negri, F. R., Bocquentin-Villanueva, J., Ferigolo, J. and Antoine, P.-O.: A Review of Tertiary Mammal Faunas and Birds from Western Amazonia, in *Amazonia: Landscape and Species Evolution*, pp. 243–258, Wiley-Blackwell Publishing Ltd., 2009.
- Nocchi, M., Parisi, G., Monaco, P., Monechi, S., Madile, M., Napoleone, G., Ripepe, M., Orlando, M., Premoli Silva, I. and Bice, D. M.: The Eocene-Oligocene Boundary in the Umbrian Pelagic Sequences, Italy, in *termbal eocene events*, vol. 9, edited by C. Pomerol and I. B. T.-D. in P. and S. Premoli-Silva, pp. 25–40, Elsevier., 1986.
- 2365 Nof, D., Van Gorder, S. and de Boer, A.: Does the Atlantic meridional overturning cell really have more than one stable steady state?, *Deep Sea Res. Part I Oceanogr. Res. Pap.*, 54(11), 2005–2021, doi:10.1016/j.dsr.2007.08.006, 2007.

- Norris, R. D. and Wilson, P. A.: Low-latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera, *Geology*, 26(9), 823–826, doi:10.1130/0091-7613(1998)026<0823:LLSSTF>2.3.CO;2, 1998.
- 3370 O'Brien, C. L., Huber, M., Thomas, E., Pagani, M., Super, J. R., Elder, L. E. and Hull, P. M.: The enigma of Oligocene climate and global surface temperature evolution, *Proc. Natl. Acad. Sci.*, 202003914, doi:10.1073/pnas.2003914117, 2020.
- O'Regan, M., Williams, C. J., Frey, K. E. and Jakobsson, M.: A Synthesis of the Long-Term Paleoclimatic Evolution of the Arctic, *Oceanography*, 24, doi:10.5670/oceanog.2011.57, 2011.
- 2375 Oboh-Ikuenobe, F. E. and Jaramillo, C. A.: Palynological patterns in the uppermost Eocene to lower Oligocene sedimentary, in *From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition*, p. 269, Columbia University Press., 2003.
- Olivarez Lyle, A. and Lyle, M. W.: Missing organic carbon in Eocene marine sediments: Is metabolism the biological feedback that maintains end-member climates?, *Paleoceanography*, 21(2), PA2007, doi:10.1029/2005PA001230, 2006.
- Olivetti, V., Balestrieri, M. L., Rossetti, F. and Talarico, F. M.: Tectonic and climatic signals from apatite detrital fission track analysis of the Cape Roberts Project core records, South Victoria Land, Antarctica, *Tectonophysics*, 594, 80–90, doi:10.1016/j.tecto.2013.03.017, 2013.
- 2380 Olivetti, V., Balestrieri, M. L., Rossetti, F., Thomson, S. N., Talarico, F. M. and Zattin, M.: Evidence of a full West Antarctic Ice Sheet back to the early Oligocene: insight from double dating of detrital apatites in Ross Sea sediments., *Terra Nov.*, 27(3), 238–246, doi:10.1111/ter.12153, 2015.
- Opdyke, B. N. and Wilkinson, B. H.: Surface area control of shallow cratonic to deep marine carbonate accumulation, *Paleoceanography*, 3(6), 685–703, doi:10.1029/PA003i006p00685, 1988.
- 2385 Pagani, M., Zachos, J. C., Freeman, K. H., Tipple, B. and Bohaty, S.: Marked Decline in Atmospheric Carbon Dioxide Concentrations During the Paleogene, *Science*, 309(5734), 600 LP – 603, doi:10.1126/science.1110063, 2005.
- Pagani, M., Huber, M., Liu, Z., Bohaty, S. M., Henderiks, J., Sijp, W., Krishnan, S. and DeConto, R. M.: The Role of Carbon Dioxide During the Onset of Antarctic Glaciation, *Science*, 334(6060), 1261–1264, doi:10.1126/science.1203909, 2011.
- 2390 Page, M., Licht, A., Dupont-Nivet, G., Meijer, N., Barbolini, N., Hoorn, C., Schauer, A., Huntington, K., Bajnai, D., Fiebig, J., Mulch, A. and Guo, Z.: Synchronous cooling and decline in monsoonal rainfall in northeastern Tibet during the fall into the Oligocene icehouse, , doi:10.1130/G45480.1, 2019.
- 2395 Palike, H., Lyle, M. W., Nishi, H., Raffi, I., Ridgwell, A., Gamage, K., Klaus, A., Acton, G., Anderson, L., Backman, J., Baldauf, J., Beltran, C., Bohaty, S. M., BownPaul, Busch, W., Channell, J. E. T., Chun, C. O. J., Delaney, M., Dewangan, P., Dunkley Jones, T., Edgar, K. M., Evans, H., Fitch, P., Foster, G. L., Gussone, N., Hasegawa, H., Hathorne, E. C., Hayashi, H., Herrle, J. O., Holbourn, A., Hovan, S., Hyeong, K., Iijima, K., Ito, T., Kamikuri, S., Kimoto, K., Kuroda, J., Leon-Rodriguez, L., Malinverno, A., Moore Jr, T. C., Murphy, B. H., Murphy, D. P., Nakamura, H., Ogane, K., Ohneiser, C., Richter, C., Robinson, R., Rohling, E. J., Romero, O., Sawada, K., Scher, H., Schneider, L., Sluijs, A., Takata, H., Tian, J., Tsujimoto, A., Wade, B. S., Westerhold, T., Wilkens, R., Williams, T., Wilson, P. A., Yamamoto, Y., Yamamoto, S., Yamazaki, T. and Zeebe, R. E.: A Cenozoic record of the equatorial Pacific carbonate compensation depth, *Nature*, 488(7413), 609–614, doi:10.1038/nature11360, 2012.
- 2400 Pan, A. D., Jacobs, B. F., Dransfield, J. and Baker, W. J.: The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia, *Bot. J. Linn. Soc.*, 151(1), 69–81, doi:10.1111/j.1095-8339.2006.00523.x, 2006.
- 2405 Passchier, S., Bohaty, S. M., Jiménez-Espejo, F., Pross, J., Röhl, U., van de Flierdt, T., Escutia, C. and Brinkhuis, H.: Early Eocene to middle Miocene cooling and aridification of East Antarctica, *Geochemistry, Geophys. Geosystems*, 14(5), 1399–

- 1410, doi:10.1002/ggge.20106, 2013.
- Passchier, S., Ciarletta, D. J., Miriagos, T. E., Bijl, P. K. and Bohaty, S. M.: An Antarctic stratigraphic record of stepwise ice growth through the Eocene-Oligocene transition, *GSA Bull.*, 129(3–4), 318–330, doi:10.1130/B31482.1, 2017.
- 2410 Pearson, A. and Ingalls, A. E.: Assessing the Use of Archaeal Lipids as Marine Environmental Proxies, *Annu. Rev. Earth Planet. Sci.*, 41(1), 359–384, doi:10.1146/annurev-earth-050212-123947, 2013.
- Pearson, P. N. and Palmer, M. R.: Middle Eocene Seawater pH and Atmospheric Carbon Dioxide Concentrations, *Science*, 284(5421), 1824 LP – 1826, doi:10.1126/science.284.5421.1824, 1999.
- 2415 Pearson, P. N. and Palmer, M. R.: Atmospheric carbon dioxide concentrations over the past 60 million years, *Nature*, 406, 695, doi:10.1038/35021000, 2000.
- Pearson, P. N., Ditchfield, P. W., Singano, J., Harcourt-Brown, K. G., Nicholas, C. J., Olsson, R. K., Shackleton, N. J. and Hall, M. A.: Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs, *Nature*, 413(6855), 481–487, doi:10.1038/35097000, 2001.
- 2420 Pearson, P. N., van Dongen, B. E., Nicholas, C. J., Pancost, R. D., Schouten, S., Singano, J. M. and Wade, B. S.: Stable warm tropical climate through the Eocene Epoch, *Geology*, 35(3), 211–214, doi:10.1130/G23175A.1, 2007.
- Pearson, P. N., McMillan, I. K., Wade, B. S., Jones, T. D., Coxall, H. K., Bown, P. R. and Lear, C. H.: Extinction and environmental change across the Eocene-Oligocene boundary in Tanzania, *Geology*, 36(2), 179–182, doi:10.1130/G24308A.1, 2008.
- 2425 Pearson, P. N., Foster, G. L. and Wade, B. S.: Atmospheric carbon dioxide through the Eocene–Oligocene climate transition, *Nature*, 461(7267), 1110–1113, doi:10.1038/nature08447, 2009.
- Peck, V. L., Yu, J., Kender, S. and Riesselman, C. R.: Shifting ocean carbonate chemistry during the Eocene-Oligocene climate transition: Implications for deep-ocean Mg/Ca paleothermometry, *Paleoceanography*, 25(4), doi:10.1029/2009PA001906, 2010.
- 2430 Pérez, L. F., Nielsen, T., Knutz, P. C., Kuijpers, A. and Damm, V.: Large-scale evolution of the central-east Greenland margin: New insights to the North Atlantic glaciation history, *Glob. Planet. Change*, 163, 141–157, doi:10.1016/j.gloplacha.2017.12.010, 2018.
- Petersen, S. V and Schrag, D. P.: Antarctic ice growth before and after the Eocene-Oligocene transition: New estimates from clumped isotope paleothermometry, *Paleoceanography*, 30(10), 1305–1317, doi:10.1002/2014PA002769, 2015.
- 2435 Piepjohn, K., von Gosen, W. and Tessensohn, F.: The Eurekan deformation in the Arctic: an outline, *J. Geol. Soc. London.*, 173(6), 1007–1024, doi:10.1144/jgs2016-081, 2016.
- Piga, E.: How Hot is Hot? Tropical Ocean Temperatures and Plankton Communities in the Eocene Epoch, PhD Thesis, Cardiff University, submitted., 2020.
- Pocknall, D. T.: Palynostratigraphy of the Te Kuiti Group (late Eocene-Oligocene), Waikato Basin, New Zealand, *New Zeal. J. Geol. Geophys.*, 34(4), 407–417, doi:10.1080/00288306.1991.9514479, 1991.
- 2440 Pollard, D.: A retrospective look at coupled ice sheet–climate modeling, *Clim. Change*, 100(1), 173–194, doi:10.1007/s10584-010-9830-9, 2010.
- Pollard, D. and DeConto, R. M.: Hysteresis in Cenozoic Antarctic ice-sheet variations, *Glob. Planet. Change*, 45(1–3), 9–21,


- doi:10.1016/j.gloplacha.2004.09.011, 2005.
- 2445 Pomerol, C. and Premoli Silva, I.: The Eocene-Oligocene Transition: Events and Boundary, in Terminal Eocene Events, vol. 9, edited by C. Pomerol and I. B. T.-D. in P. and S. Premoli-Silva, pp. 1–24, Elsevier., 1986.
- Postigo Mijarra, J. M., Barrón, E., Gómez Manzaneque, F. and Morla, C.: Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic, *J. Biogeogr.*, 36(11), 2025–2043, doi:10.1111/j.1365-2699.2009.02142.x, 2009.
- 2450 Pound, M. J. and Salzmann, U.: Heterogeneity in global vegetation and terrestrial climate change during the late Eocene to early Oligocene transition, *Sci. Rep.*, 7, 43386, doi:10.1038/srep43386, 2017.
- Premoli Silva, I. and Jenkins, D. G.: Decision on the Eocene-Oligocene boundary stratotype, *Episodes*, 16(3), 379–382, 1993.
- Pross, J., Contreras, L., Bijl, P. K., Greenwood, D. R., Bohaty, S. M., Schouten, S., Bendle, J. A., Röhl, U., Tauxe, L., Raine, J. I., Huck, C. E., van de Flierdt, T., Jamieson, S. S. R., Stickley, C. E., van de Schootbrugge, B., Escutia, C. and Brinkhuis, H.: Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch, *Nature*, 488, 73, 2455 doi:10.1038/nature11300, 2012.
- Prothero, D.: Cenozoic Mammals and Climate Change: The Contrast between Coarse-Scale versus High-Resolution Studies Explained by Species Sorting, *Geosci.*, 2(2), doi:10.3390/geosciences2020025, 2012.
- Prothero, D. R.: Did impacts, volcanic eruptions, or climate change affect mammalian evolution?, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 214(3), 283–294, doi:10.1016/j.palaeo.2004.04.010, 2004.
- 2460 Pusz, A. E., Thunell, R. C. and Miller, K. G.: Deep water temperature, carbonate ion, and ice volume changes across the Eocene-Oligocene climate transition, *Paleoceanography*, 26(2), PA2205, doi:10.1029/2010PA001950, 2011.
- Qin, W., Carlson, L. T., Armbrust, E. V., Devol, A. H., Moffett, J. W., Stahl, D. A. and Ingalls, A. E.: Confounding effects of oxygen and temperature on the TEX86 signature of marine Thaumarchaeota, *Proc. Natl. Acad. Sci.*, 112(35), 10979 LP – 10984, doi:10.1073/pnas.1501568112, 2015.
- 2465 [Quade, J., Breecker, D. O., Daëron, M. and Eiler, J.: The paleoaltimetry of Tibet: An isotopic perspective, \*Am. J. Sci.\*, 311\(2\), 77–115. doi:10.2475/02.2011.01, 2011.](#)
- [Quade, J., Leary, R., Dettinger, M. P., Orme, D., Krupa, A., DeCelles, P. G., Kano, A., Kato, H., Waldrip, R., Huang, W. and Kapp, P.: Resetting Southern Tibet: The serious challenge of obtaining primary records of Palealtimetry, \*Glob. Planet. Change\*, 191, 103194, doi:https://doi.org/10.1016/j.gloplacha.2020.103194, 2020.](#)
- 2470 Quattrocchio, M. E., Martínez, M. A., Hinojosa, L. F. and Jaramillo, C.: Quantitative analysis of Cenozoic palynofloras from Patagonia, southern South America, *Palynology*, 37(2), 246–258, doi:10.1080/01916122.2013.787126, 2013.
- Raymo, M. E.: The Initiation of Northern Hemisphere Glaciation, *Annu. Rev. Earth Planet. Sci.*, 22(1), 353–383, doi:10.1146/annurev.ea.22.050194.002033, 1994.
- 2475 Raymo, M. E. and Ruddiman, W. F.: Tectonic forcing of late Cenozoic climate, *Nature*, 359(6391), 117–122, doi:10.1038/359117a0, 1992.
- Retallack, G. J.: Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota, Geological Society of America., 1983.
- Retallack, G. J.: A 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles, *Nature*, 411, 287,

- doi:10.1038/35077041, 2001.
- 2480 Retallack, G. J., Wynn, J. G. and Fremd, T. J.: Glacial-interglacial-scale paleoclimatic change without large ice sheets in the Oligocene of central Oregon, *Geology*, 32(4), 297–300, doi:10.1130/G20247.1, 2004.
- Ridgway, K. D. and Sweet, A. R.: Climatically induced floristic changes across the Eocene–Oligocene transition in the northern high latitudes, Yukon Territory, Canada, *GSA Bull.*, 107(6), 676–696, doi:10.1130/0016-7606(1995)107<0676:CIFCAT>2.3.CO;2, 1995.
- 2485 Robert, C. and Kennett, J. P.: Antarctic continental weathering changes during Eocene-Oligocene cryosphere expansion: Clay mineral and oxygen isotope evidence, *Geology*, 25(7), 587–590, doi:10.1130/0091-7613(1997)025%3C0587:ACWCDE%3E2.3.CO;2, 1997.
- Roberts, C. D., LeGrande, A. N. and Tripathi, A. K.: Climate sensitivity to Arctic seaway restriction during the early Paleogene, *Earth Planet. Sci. Lett.*, 286(3–4), 576–585, doi:10.1016/j.epsl.2009.07.026, 2009.
- 2490 Roth-Nebelsick, A., Utescher, T., Mosbrugger, V., Diester-Haass, L. and Walther, H.: Changes in atmospheric CO<sub>2</sub> concentrations and climate from the Late Eocene to Early Miocene: palaeobotanical reconstruction based on fossil floras from Saxony, Germany, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 205(1), 43–67, doi:https://doi.org/10.1016/j.palaeo.2003.11.014, 2004.
- Roth-Nebelsick, A., Grein, M., Utescher, T. and Konrad, W.: Stomatal pore length change in leaves of *Eotrigonobalanus furcinervis* (Fagaceae) from the Late Eocene to the Latest Oligocene and its impact on gas exchange and CO<sub>2</sub> reconstruction, *Rev. Palaeobot. Palynol.*, 174, 106–112, doi:10.1016/j.revpalbo.2012.01.001, 2012.
- 2495 Roth-Nebelsick, A., Oehm, C., Grein, M., Utescher, T., Kunzmann, L., Friedrich, J.-P. and Konrad, W.: Stomatal density and index data of *Platanus neptuni* leaf fossils and their evaluation as a CO<sub>2</sub> proxy for the Oligocene, *Rev. Palaeobot. Palynol.*, 206, 1–9, doi:10.1016/j.revpalbo.2014.03.001, 2014.
- 2500 Roth-Nebelsick, A., Grein, M., Traiser, C., Moraweck, K., Kunzmann, L., Kovar-Eder, J., Kvaček, J., Stiller, S. and Neinhuus, C.: Functional leaf traits and leaf economics in the Paleogene — A case study for Central Europe, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 472, 1–14, doi:10.1016/j.palaeo.2017.02.008, 2017.
- [Rowley, D. B. and Currie, B. S.: Palaeo-altimetry of the late Eocene to Miocene Lunpola basin, central Tibet, \*Nature\*, 439\(7077\), 677–681, doi:10.1038/nature04506, 2006.](https://doi.org/10.1038/nature04506)
- 2505 Royer, D. L., Wing, S. L., Beerling, D. J., Jolley, D. W., Koch, P. L., Hickey, L. J. and Berner, R. A.: Paleobotanical Evidence for Near Present-Day Levels of Atmospheric CO<sub>2</sub> During Part of the Tertiary, *Science*, 292(5525), 2310–2313, doi:10.1126/science.292.5525.2310, 2001.
- Royer, D. L., Berner, R. A., Montañez, I. P., Tabor, N. J. and Beerling, D. J.: CO<sub>2</sub> as a primary driver of phanerozoic climate, *GSA today*, 14(3), 4–10, doi:10.1130/1052-5173(2004)014<4:CAAPDO>2.0.CO;2, 2004.
- 2510 Sagoo, N., Valdes, P., Flecker, R. and Gregoire, L. J.: The Early Eocene equable climate problem: can perturbations of climate model parameters identify possible solutions?, *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.*, 371(2001), 20130123, doi:10.1098/rsta.2013.0123, 2013.
- Schaefer, J. M., Finkel, R. C., Balco, G., Alley, R. B., Caffee, M. W., Briner, J. P., Young, N. E., Gow, A. J. and Schwartz, R.: Greenland was nearly ice-free for extended periods during the Pleistocene, *Nature*, 540, 252, doi:10.1038/nature20146, 2016.
- 2515 De Schepper, S., Gibbard, P. L., Salzmann, U. and Ehlers, J.: A global synthesis of the marine and terrestrial evidence for



- glaciation during the Pliocene Epoch, *Earth-Science Rev.*, 135, 83–102, doi:10.1016/j.earscirev.2014.04.003, 2014.
- 2520 Scher, H. D., Bohaty, S. M., Zachos, J. C. and Delaney, M. L.: Two-stepping into the icehouse: East Antarctic weathering during progressive ice-sheet expansion at the Eocene–Oligocene transition, *Geology*, 39(4), 383–386, doi:10.1130/G31726.1, 2011.
- Scher, H. D., Bohaty, S. M., Smith, B. W. and Munn, G. H.: Isotopic interrogation of a suspected late Eocene glaciation, *Paleoceanography*, 29(6), 628–644, doi:10.1002/2014PA002648, 2014.
- 2525 Scher, H. D., Whittaker, J. M., Williams, S. E., Latimer, J. C., Kordesch, W. E. C. and Delaney, M. L.: Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies, *Nature*, 523(7562), 580–583, doi:10.1038/nature14598, 2015.
- Schouten, S., Hopmans, E. C., Schefuß, E. and Sinninghe Damsté, J. S.: Distributional variations in marine crenarchaeotal membrane lipids: a new tool for reconstructing ancient sea water temperatures?, *Earth Planet. Sci. Lett.*, 204(1), 265–274, doi:10.1016/S0012-821X(02)00979-2, 2002.
- 2530 Scotese, C. R. and Wright, N. M.: PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the Phanerozoic PALEOMAP Project. [online] Available from: <https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018>, 2018.
- Scotese, C. R., Gahagan, L. M. and Larson, R. L.: Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins, *Tectonophysics*, 155(1), 27–48, doi:10.1016/0040-1951(88)90259-4, 1988.
- | [Selkin, P. A., Strömberg, C. A. E., Dunn, R., Kohn, M. J., Carlini, A. A., Davies-Vollum, K. S. and Madden, R. H.: Climate, dust, and fire across the Eocene-Oligocene transition, Patagonia, \*Geology\*, 43\(7\), 567–570, doi:10.1130/G36664.1, 2015.](#)
- 2535 Seton, M., Müller, R. D., Zahirovic, S., Gaina, C., Torsvik, T., Shephard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S. and Chandler, M.: Global continental and ocean basin reconstructions since 200Ma, *Earth-Science Rev.*, 113(3), 212–270, doi:10.1016/j.earscirev.2012.03.002, 2012.
- Sewall, J. O., Sloan, L. C., Huber, M. and Wing, S.: Climate sensitivity to changes in land surface characteristics, *Glob. Planet. Change*, 26(4), 445–465, doi:10.1016/S0921-8181(00)00056-4, 2000.
- 2540 Sexton, P. F., Wilson, P. A. and Pearson, P. N.: Microstructural and geochemical perspectives on planktic foraminiferal preservation: “Glassy” versus “Frosty,” *Geochemistry, Geophys. Geosystems*, 7(12), doi:10.1029/2006GC001291, 2006.
- Shackleton, N. J. and Kennett, J. P.: Paleotemperature History of the Cenozoic and the Initiation of Antarctic Glaciation: Oxygen and Carbon Isotope Analyses in DSDP Sites 277, 279 and 281, *Initial Rep. Deep Sea Drill. Proj.*, 29, 743, 1975.
- 2545 Shackleton, N. J., Backman, J., Zimmerman, H., Kent, D. V., Hall, M. A., Roberts, D. G., Schnitker, D., Baldauf, J. G., Desprairies, A., Homrighausen, R., Huddleston, P., Keene, J. B., Kaltenback, A. J., Krumsiek, K. A. O., Morton, A. C., Murray, J. W. and Westberg-Smith, J.: Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North Atlantic region, *Nature*, 307(5952), 620–623, doi:10.1038/307620a0, 1984.
- Sheldon, N. D. and Tabor, N. J.: Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols, *Earth-Science Rev.*, 95(1), 1–52, doi:10.1016/j.earscirev.2009.03.004, 2009.
- 2550 Sheldon, N. D., Costa, E., Cabrera, L. and Garcés, M.: Continental Climatic and Weathering Response to the Eocene-Oligocene Transition, *J. Geol.*, 120(2), 227–236, doi:10.1086/663984, 2012.
- Sheldon, N. D., Grimes, S. T., Hooker, J. J., Collinson, M. E., Bugler, M. J., Hren, M. T., Price, G. D. and Sutton, P. A.: Coupling of marine and continental oxygen isotope records during the Eocene-Oligocene transition, *GSA Bull.*, 128(3–4),

- 502–510, doi:10.1130/B31315.1, 2016.
- 2555 Shellito, C. J., Sloan, L. C. and Huber, M.: Climate model sensitivity to atmospheric CO<sub>2</sub> levels in the Early–Middle Paleogene, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 193(1), 113–123, doi:10.1016/S0031-0182(02)00718-6, 2003.
- Sijp, W. P. and England, M. H.: Effect of the Drake Passage Throughflow on Global Climate, *J. Phys. Oceanogr.*, 34(5), 1254–1266, doi:10.1175/1520-0485(2004)034<1254:EOTDPT>2.0.CO;2, 2004.
- 2560 Sijp, W. P., England, M. H. and Toggweiler, J. R.: Effect of Ocean Gateway Changes under Greenhouse Warmth, *J. Clim.*, 22(24), 6639–6652, doi:10.1175/2009JCLI3003.1, 2009.
- Sijp, W. P., England, M. H. and Huber, M.: Effect of the deepening of the Tasman Gateway on the global ocean, *Paleoceanography*, 26(4), PA4207, doi:10.1029/2011PA002143, 2011.
- Sijp, W. P., von der Heydt, A. S., Dijkstra, H. A., Flögel, S., Douglas, P. M. J. and Bijl, P. K.: The role of ocean gateways on cooling climate on long time scales, *Glob. Planet. Change*, 119(0), 1–22, doi:10.1016/j.gloplacha.2014.04.004, 2014.
- 2565 Sijp, W. P., von der Heydt, A. S. and Bijl, P. K.: Model simulations of early westward flow across the Tasman Gateway during the early Eocene, *Clim. Past*, 12(4), 807–817, doi:10.5194/cp-12-807-2016, 2016.
- Śliwińska, K. K., Thomsen, E., Schouten, S., Schoon, P. L. and Heilmann-Clausen, C.: Climate- and gateway-driven cooling of Late Eocene to earliest Oligocene sea surface temperatures in the North Sea Basin, *Sci. Rep.*, 9(1), 4458, doi:10.1038/s41598-019-41013-7, 2019.
- 2570 Sluijs, A., Schouten, S., Donders, T. H., Schoon, P. L., Röhl, U., Reichert, G.-J., Sangiorgi, F., Kim, J.-H., Sinninghe Damsté, J. S. and Brinkhuis, H.: Warm and wet conditions in the Arctic region during Eocene Thermal Maximum 2, *Nat. Geosci.*, 2, 777, doi:10.1038/ngeo668, 2009.
- Solgaard, A. M., Bonow, J. M., Langen, P. L., Japsen, P. and Hvidberg, C. S.: Mountain building and the initiation of the Greenland Ice Sheet, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 392, 161–176, doi:10.1016/j.palaeo.2013.09.019, 2013.
- 2575 Sorlien, C. C., Luyendyk, B. P., Wilson, D. S., Decesari, R. C., Bartek, L. R. and Diebold, J. B.: Oligocene development of the West Antarctic Ice Sheet recorded in eastern Ross Sea strata, *Geology*, 35(5), 467–470, doi:10.1130/G23387A.1, 2007.
- Sosdian, S. M., Greenop, R., Hain, M. P., Foster, G. L., Pearson, P. N. and Lear, C. H.: Constraining the evolution of Neogene ocean carbonate chemistry using the boron isotope pH proxy, *Earth Planet. Sci. Lett.*, 498, 362–376, doi:10.1016/j.epsl.2018.06.017, 2018.
- 2580 Spray, J. F., Bohaty, S. M., Davies, A., Bailey, I., Romans, B. W., Cooper, M. J., Milton, J. A. and Wilson, P. A.: North Atlantic Evidence for a Unipolar Icehouse Climate State at the Eocene-Oligocene Transition, *Paleoceanogr. Paleoclimatology*, 34(7), 1124–1138, doi:10.1029/2019PA003563, 2019.
- Srokosz, M. A. and Bryden, H. L.: Observing the Atlantic Meridional Overturning Circulation yields a decade of inevitable surprises, *Science*, 348(6241), doi:10.1126/science.1255575, 2015.
- 2585 Stärz, M., Jokat, W., Knorr, G. and Lohmann, G.: Threshold in North Atlantic-Arctic Ocean circulation controlled by the subsidence of the Greenland-Scotland Ridge, *Nat. Commun.*, 8, 15681, doi:10.1038/ncomms15681, 2017.
- Steinhorsdottir, M. and Vajda, V.: Early Jurassic (late Pliensbachian) CO<sub>2</sub> concentrations based on stomatal analysis of fossil conifer leaves from eastern Australia, *Gondwana Res.*, 27(3), 932–939, doi:10.1016/j.gr.2013.08.021, 2015.
- Steinhorsdottir, M., Jeram, A. J. and McElwain, J. C.: Extremely elevated CO<sub>2</sub> concentrations at the Triassic/Jurassic

**Deleted:** Spicer, R. A.: Tibet, the Himalaya, Asian monsoons and biodiversity – In what ways are they related?, *Plant Divers.*, 39(5), 233–244, doi:10.1016/j.pld.2017.09.001, 2017. 

- boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 308(3), 418–432, doi:10.1016/j.palaeo.2011.05.050, 2011.
- 2595 Steinhorsdottir, M., Wohlfarth, B., Kylander, M. E., Blaauw, M. and Reimer, P. J.: Stomatal proxy record of CO<sub>2</sub> concentrations from the last termination suggests an important role for CO<sub>2</sub> at climate change transitions, *Quat. Sci. Rev.*, 68, 43–58, doi:10.1016/j.quascirev.2013.02.003, 2013.
- Steinhorsdottir, M., Porter, A. S., Holohan, A., Kunzmann, L., Collinson, M. and McElwain, J. C.: Fossil plant stomata indicate decreasing atmospheric CO<sub>2</sub> prior to the Eocene-Oligocene boundary, *Clim. Past*, 12(2), 439–454, doi:10.5194/cp-12-439-2016, 2016.
- 2600 Steinhorsdottir, M., Vajda, V., Pole, M. and Holdgate, G.: Moderate levels of Eocene pCO<sub>2</sub> indicated by Southern Hemisphere fossil plant stomata, *Geology*, doi:10.1130/G46274.1, 2019.
- [Steinhorsdottir, M., Jardine, P. E. and Rember, W. C.: Near-Future pCO<sub>2</sub> during the hot Mid Miocene Climatic Optimum, \*Paleoceanogr. Paleoclimatology\*, e2020PA003900, doi:10.1029/2020PA003900, 2020.](#)
- 2605 Stickley, C. E., Brinkhuis, H., Schellenberg, S. A., Sluijs, A., Röhl, U., Fuller, M., Grauert, M., Huber, M., Warnaar, J. and Williams, G. L.: Timing and nature of the deepening of the Tasmanian Gateway, *Paleoceanography*, 19(4), PA4027, doi:10.1029/2004PA001022, 2004.
- Stickley, C. E., St John, K., Koç, N., Jordan, R. W., Passchier, S., Pearce, R. B. and Kearns, L. E.: Evidence for middle Eocene Arctic sea ice from diatoms and ice-rafted debris, *Nature*, 460, 376–379, doi:10.1038/nature08163, 2009.
- 2610 Stocchi, P., Escutia, C., Houben, A. J. P., Vermeersen, B. L. A., Bijl, P. K., Brinkhuis, H., DeConto, R. M., Galeotti, S., Passchier, S., Pollard, D., Brinkhuis, H., Escutia, C., Klaus, A., Fehr, A., Williams, T., Bendle, J. A. P., Bijl, P. K., Bohaty, S. M., Carr, S. A., Dunbar, R. B., Flores, J. A., González, J. J., Hayden, T. G., Iwai, M., Jimenez-Espejo, F. J., Katsuki, K., Kong, G. S., McKay, R. M., Nakai, M., Olney, M. P., Passchier, S., Pekar, S. F., Pross, J., Riesselman, C., Röhl, U., Sakai, T., Shrivastava, P. K., Stickley, C. E., Sugisaki, S., Tauxe, L., Tuo, S., van de Fliedert, T., Welsh, K. and Yamane, M.: Relative sea-level rise around East Antarctica during Oligocene glaciation, *Nat. Geosci.*, 6, 380, doi:10.1038/ngeo1783, 2013.
- 2615 Strömberg, C. A. E., Dunn, R. E., Madden, R. H., Kohn, M. J. and Carlini, A. A.: Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America, *Nat. Commun.*, 4, 1478, doi:10.1038/ncomms2508, 2013.
- Strother, S. L., Salzmann, U., Sangiorgi, F., Bijl, P. K., Pross, J., Escutia, C., Salabarnada, A., Pound, M. J., Voss, J. and Woodward, J.: A new quantitative approach to identify reworking in Eocene to Miocene pollen records from offshore Antarctica using red fluorescence and digital imaging, *Biogeosciences*, 14(8), 2089–2100, doi:10.5194/bg-14-2089-2017, 2017.
- 2620 Su, T., Li, S.-F., Tang, H., Huang, Y.-J., Li, S.-H., Deng, C.-L. and Zhou, Z.-K.: *Hemitrapa Miki* (Lythraceae) from the earliest Oligocene of southeastern Qinghai-Tibetan Plateau and its phytogeographic implications, *Rev. Palaeobot. Palynol.*, 257, 57–63, doi:10.1016/j.revpalbo.2018.06.001, 2018.
- [Sun, J. and Windley, B. F.: Onset of aridification by 34 Ma across the Eocene-Oligocene transition in Central Asia, \*Geology\*, 43\(11\), 1015–1018, doi:10.1130/G37165.1, 2015.](#)
- [Sun, J., Ni, X., Bi, S., Wu, W., Ye, J., Meng, J. and Windley, B. F.: Synchronous turnover of flora, fauna, and climate at the Eocene–Oligocene Boundary in Asia, \*Sci. Rep.\*, 4, 7463 \[online\] Available from: <http://dx.doi.org/10.1038/srep07463>, 2014.](#)
- [Swart, P. K.: Global synchronous changes in the carbon isotopic composition of carbonate sediments unrelated to changes in the global carbon cycle, \*Proc. Natl. Acad. Sci.\*, 105\(37\), 13741 L.P – 13745, doi:10.1073/pnas.0802841105, 2008.](#)
- 2630 [Swart, P. K. and Eberli, G.: The nature of the  \$\delta^{13}C\$  of periplatform sediments: Implications for stratigraphy and the global](#)

[carbon cycle, \*Sediment. Geol.\*, 175\(1\), 115–129, doi:10.1016/j.sedgeo.2004.12.029, 2005.](#)

Teodoridis, V. and Kvaček, Z.: Palaeoenvironmental evaluation of Cainozoic plant assemblages from the Bohemian Massif (Czech Republic) and adjacent Germany, *Bull. Geosci.*, 90(3), 695–720, doi:10.3140/bull.geosci.1553, 2015.

2635 Thomas, D. J., Korty, R., Huber, M., Schubert, J. A. and Haines, B.: Nd isotopic structure of the Pacific Ocean 70–30 Ma and numerical evidence for vigorous ocean circulation and ocean heat transport in a greenhouse world, *Paleoceanography*, 29(5), 454–469, doi:10.1002/2013PA002535, 2014.

Thomson, S. N., Reiners, P. W., Hemming, S. R. and Gehrels, G. E.: The contribution of glacial erosion to shaping the hidden landscape of East Antarctica, *Nat. Geosci.*, 6, 203, doi:10.1038/ngeo1722, 2013.

2640 Tierney, J. E. and Tingley, M. P.: A TEX86 surface sediment database and extended Bayesian calibration, *Sci. Data*, 2, 150029, doi:10.1038/sdata.2015.29, 2015.

Tiffney, B. H. and Wing, S. L.: Paleoenvironment of the Oligocene Jebel Qatrani Formation, Fayum depression, northern Egypt, based on floral remains, in 23rd meeting of the Geological Society of America, San Diego, CA, October, pp. 21–24., 1991.

2645 Tigchelaar, M., von der Heydt, A. S. and Dijkstra, H. A.: A new mechanism for the two-step delta 18O signal at the Eocene-Oligocene boundary, *Clim. Past*, 7(1), 235–247, doi:10.5194/cp-7-235-2011, 2011.

Toggweiler, J. R. and Bjornsson, H.: Drake Passage and palaeoclimate, *J. Quat. Sci.*, 15(4), 319–328, doi:10.1002/1099-1417(200005)15:4<319::AID-JQS545>3.0.CO;2-C, 2000.

2650 Torsvik, T. H., Van der Voo, R., Preeden, U., Mac Niocaill, C., Steinberger, B., Doubrovine, P. V., van Hinsbergen, D. J. J., Domeier, M., Gaina, C., Tohver, E., Meert, J. G., McCausland, P. J. A. and Cocks, L. R. M.: Phanerozoic polar wander, palaeogeography and dynamics, *Earth-Science Rev.*, 114(3), 325–368, doi:10.1016/j.earscirev.2012.06.007, 2012.

Tripati, A. and Darby, D.: Evidence for ephemeral middle Eocene to early Oligocene Greenland glacial ice and pan-Arctic sea ice, *Nat. Commun.*, 9(1), 1038, doi:10.1038/s41467-018-03180-5, 2018.

Tripati, A., Backman, J., Elderfield, H. and Ferretti, P.: Eocene bipolar glaciation associated with global carbon cycle changes, *Nature*, 436, 341, doi:10.1038/nature03874, 2005.

2655 Tripati, A. K., Eagle, R. A., Morton, A., Dowdeswell, J. A., Atkinson, K. L., Bahé, Y., Dawber, C. F., Khadun, E., Shaw, R. M. H., Shorttle, O. and Thanabalasundaram, L.: Evidence for glaciation in the Northern Hemisphere back to 44 Ma from ice-rafted debris in the Greenland Sea, *Earth Planet. Sci. Lett.*, 265(1), 112–122, doi:https://doi.org/10.1016/j.epsl.2007.09.045, 2008.

2660 Vahlenkamp, M., Niezgodzki, I., De Vleeschouwer, D., Bickert, T., Harper, D., Kirtland Turner, S., Lohmann, G., Sexton, P., Zachos, J. and Pälike, H.: Astronomically paced changes in deep-water circulation in the western North Atlantic during the middle Eocene, *Earth Planet. Sci. Lett.*, 484, 329–340, doi:10.1016/j.epsl.2017.12.016, 2018a.

Vahlenkamp, M., Niezgodzki, I., De Vleeschouwer, D., Lohmann, G., Bickert, T. and Pälike, H.: Ocean and climate response to North Atlantic seaway changes at the onset of long-term Eocene cooling, *Earth Planet. Sci. Lett.*, 498, 185–195, doi:10.1016/j.epsl.2018.06.031, 2018b.

2665 Via, R. K. and Thomas, D. J.: Evolution of Atlantic thermohaline circulation: Early Oligocene onset of deep-water production in the North Atlantic, *Geology*, 34(6), 441–444, doi:10.1130/G22545.1, 2006.

Viebahn, J. P., von der Heydt, A. S., Le Bars, D. and Dijkstra, H. A.: Effects of Drake Passage on a strongly eddying global

- ocean, *Paleoceanography*, 31(5), 564–581, doi:10.1002/2015PA002888, 2016.
- 2670 Waddell, L. M. and Moore, T. C.: Salinity of the Eocene Arctic Ocean from oxygen isotope analysis of fish bone carbonate, *Paleoceanography*, 23(1), PA1S12, doi:10.1029/2007PA001451, 2008.
- Wade, B. S. and Pearson, P. N.: Planktonic foraminiferal turnover, diversity fluctuations and geochemical signals across the Eocene/Oligocene boundary in Tanzania, *Mar. Micropaleontol.*, 68(3), 244–255, doi:10.1016/j.marmicro.2008.04.002, 2008.
- 2675 Wade, B. S., Pearson, P. N., Berggren, W. A. and Pälike, H.: Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale, *Earth-Science Rev.*, 104(1), 111–142, doi:10.1016/j.earscirev.2010.09.003, 2011.
- Wade, B. S., Houben, A. J. P., Quaijtaal, W., Schouten, S., Rosenthal, Y., Miller, K. G., Katz, M. E., Wright, J. D. and Brinkhuis, H.: Multiproxy record of abrupt sea-surface cooling across the Eocene-Oligocene transition in the Gulf of Mexico, *Geology*, 40(2), 159–162, doi:10.1130/G32577.1, 2012.
- 2680 Wagner, F., Below, R., Klerk, P. D., Dilcher, D. L., Joosten, H., Kürschner, W. M. and Visscher, H.: A natural experiment on plant acclimation: lifetime stomatal frequency response of an individual tree to annual atmospheric CO<sub>2</sub> increase, *Proc. Natl. Acad. Sci.*, 93(21), 11705 LP – 11708, doi:10.1073/pnas.93.21.11705, 1996.
- Walker, J. C. G., Hays, P. B. and Kasting, J. F.: A negative feedback mechanism for the long-term stabilization of Earth's surface temperature, *J. Geophys. Res. Ocean.*, 86(C10), 9776–9782, doi:10.1029/JC086iC10p09776, 1981.
- 2685 Wei, W.: Opening of the Australia–Antarctica Gateway as dated by nannofossils, *Mar. Micropaleontol.*, 52(1), 133–152, doi:10.1016/j.marmicro.2004.04.008, 2004.
- Wellner, J. S., Anderson, J. B., Ehrmann, W., Weaver, F. M., Kirshner, A., Livsey, D. and Simms, A. R.: History of an Evolving Ice Sheet as Recorded in SHALDRIL Cores from the Northwestern Weddell Sea, Antarctica, in *Tectonic, Climatic, and Cryospheric Evolution of the Antarctic Peninsula*, pp. 131–151, American Geophysical Union., 2011.
- 2690 [Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretano, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A. and Zachos, J. C.: An astronomically dated record of Earth's climate and its predictability over the last 66 million years, \*Science\*, 369\(6509\), 1383 LP – 1387, doi:10.1126/science.aba6853, 2020.](#)
- 2695 Williams, S. E., Whittaker, J. M. and Müller, R. D.: Full-fit, palinspastic reconstruction of the conjugate Australian-Antarctic margins, *Tectonics*, 30(6), TC6012, doi:10.1029/2011TC002912, 2011.
- Wilson, D. S. and Luyendyk, B. P.: West antarctic paleotopography estimated at the eocene-oligocene climate transition, *Geophys. Res. Lett.*, 36(16), 10–13, doi:10.1029/2009GL039297, 2009.
- 2700 Wilson, D. S., Jamieson, S. S. R., Barrett, P. J., Leitchenkov, G., Gohl, K. and Larter, R. D.: Antarctic topography at the Eocene–Oligocene boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 335–336, 24–34, doi:10.1016/j.palaeo.2011.05.028, 2012.
- Wilson, D. S., Pollard, D., DeConto, R. M., Jamieson, S. S. R. and Luyendyk, B. P.: Initiation of the West Antarctic Ice Sheet and estimates of total Antarctic ice volume in the earliest Oligocene, *Geophys. Res. Lett.*, 40(16), 4305–4309, doi:10.1002/grl.50797, 2013.
- 2705 [Wilson, P. A. and Norris, R. D.: Warm tropical ocean surface and global anoxia during the mid-Cretaceous period, \*Nature\*, 412\(6845\), 425–429, doi:10.1038/35086553, 2001.](#)

[Wilson, P. A., Norris, R. D. and Cooper, M. J.: Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of the Turonian tropics on Demerara Rise, \*Geology\*, 30\(7\), 607–610, doi:10.1130/0091-7613\(2002\)030<0607:TTCGHU>2.0.CO;2, 2002.](#)

- 2710 Wing, S. L.: Eocene and Oligocene Floras and Vegetation of the Rocky Mountains, *Ann. Missouri Bot. Gard.*, 74(4), 748–784, doi:10.2307/2399449, 1987.
- Wing, S. L., Hasiotis, S. T. and Bown, T. M.: First ichnofossils of flank-buttressed trees (late Eocene), Fayum Depression, Egypt, *Ichnos*, 3(4), 281–286, doi:10.1080/10420949509386398, 1995.
- Winguth, A., Shellito, C., Shields, C. and Winguth, C.: Climate Response at the Paleocene–Eocene Thermal Maximum to Greenhouse Gas Forcing—A Model Study with CCSM3, *J. Clim.*, 23(10), 2562–2584, doi:10.1175/2009JCLI3113.1, 2010.
- 2715 Wolfe, J. A.: Distribution of Major Vegetational Types During the Tertiary, in *The Carbon Cycle and Atmospheric CO<sub>2</sub>: Natural Variations Archean to Present*, pp. 357–375, American Geophysical Union., 1985.
- Wolfe, J. A.: Tertiary climatic changes at middle latitudes of western North America, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 108(3), 195–205, doi:10.1016/0031-0182(94)90233-X, 1994.
- 2720 Woodburne, M. O., Goin, F. J., Bond, M., Carlini, A. A., Gelfo, J. N., López, G. M., Iglesias, A. and Zimicz, A. N.: Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity, *J. Mamm. Evol.*, 21(1), 1–73, doi:10.1007/s10914-012-9222-1, 2014.
- Woodward, F. I.: Stomatal numbers are sensitive to increases in CO<sub>2</sub> from pre-industrial levels, *Nature*, 327, 617, doi:10.1038/327617a0, 1987.
- 2725 Xiao, G. Q., Abels, H. A., Yao, Z. Q., Dupont-Nivet, G. and Hilgen, F. J.: Asian aridification linked to the first step of the Eocene-Oligocene climate Transition (EOT) in obliquity-dominated terrestrial records (Xining Basin, China), *Clim. Past*, 6(4), 501–513, doi:10.5194/cp-6-501-2010, 2010.
- Yancey, T. E., Elsik, W. C. and Sancay, R. H.: The palynological record of late Eocene climate change, northwest Gulf of Mexico, in *From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition*, pp. 252–268, Columbia University Press, New York., 2003.
- 2730 Yang, J., Spicer, R. A., Spicer, T. E. V and Li, C.-S.: ‘CLAMP Online’: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America, *Palaeobiodiversity and Palaeoenvironments*, 91(3), 163, doi:10.1007/s12549-011-0056-2, 2011.
- Yang, S., Galbraith, E. and Palter, J.: Coupled climate impacts of the Drake Passage and the Panama Seaway, *Clim. Dyn.*, 43(1–2), 37–52, doi:10.1007/s00382-013-1809-6, 2014.
- 2735 Young, D. A., Wright, A. P., Roberts, J. L., Warner, R. C., Young, N. W., Greenbaum, J. S., Schroeder, D. M., Holt, J. W., Sugden, D. E., Blankenship, D. D., van Ommen, T. D. and Siegert, M. J.: A dynamic early East Antarctic Ice Sheet suggested by ice-covered fjord landscapes, *Nature*, 474, 72, doi:10.1038/nature10114, 2011.
- Zaarur, S., Affek, H. P. and Brandon, M. T.: A revised calibration of the clumped isotope thermometer, *Earth Planet. Sci. Lett.*, 382, 47–57, doi:10.1016/j.epsl.2013.07.026, 2013.
- 2740 Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K.: Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present, *Science*, 292(5517), 686–693, doi:10.1126/science.1059412, 2001.
- Zachos, J. C. and Kump, L. R.: Carbon cycle feedbacks and the initiation of Antarctic glaciation in the earliest Oligocene,

- Glob. Planet. Change, 47(1), 51–66, doi:10.1016/j.gloplacha.2005.01.001, 2005.
- 2745 Zachos, J. C., Breza, J. R. and Wise, S. W.: Early Oligocene ice-sheet expansion on Antarctica: Stable isotope and sedimentological evidence from Kerguelen Plateau, southern Indian Ocean, *Geology*, 20(6), 569–573, doi:10.1130/0091-7613(1992)020%3C0569:EOISEO%3E2.3.CO;2, 1992.
- Zachos, J. C., Quinn, T. M. and Salamy, K. A.: High-resolution ( $10^4$  years) deep-sea foraminiferal stable isotope records of the Eocene-Oligocene climate transition, *Paleoceanography*, 11(3), 251–266, doi:10.1029/96PA00571, 1996.
- 2750 Zachos, J. C., Dickens, G. R. and Zeebe, R. E.: An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics., *Nature*, 451(7176), 279–83, doi:10.1038/nature06588, 2008.
- Zanazzi, A., Kohn, M. J., MacFadden, B. J. and Terry, D. O.: Large temperature drop across the Eocene–Oligocene transition in central North America, *Nature*, 445, 639, doi:10.1038/nature05551, 2007.
- Zhang, Y. G., Pagani, M., Liu, Z., Bohaty, S. M. and DeConto, R.: A 40-million-year history of atmospheric CO<sub>2</sub>, *Philos. Trans. R. Soc. London A Math. Phys. Eng. Sci.*, 371(2001), doi:10.1098/rsta.2013.0096, 2013.
- 2755 Zhang, Z., Nisancioglu, K. H., Flato, F., Bentsen, M., Bethke, I. and Wang, H.: Tropical seaways played a more important role than high latitude seaways in Cenozoic cooling, *Clim. Past*, 7(3), 801–813, doi:10.5194/cp-7-801-2011, 2011.
- Zhang, Z., Ramstein, G., Schuster, M., Li, C., Contoux, C. and Yan, Q.: Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene, *Nature*, 513, 401, doi:10.1038/nature13705, 2014.
- 2760 Zhu, J., Poulsen, C. J. and Tierney, J. E.: Simulation of Eocene extreme warmth and high climate sensitivity through cloud feedbacks, *Sci. Adv.*, 5(9), eaax1874, doi:10.1126/sciadv.aax1874, 2019.

**Page 47: [1] Formatted** **David Hutchinson** **10/13/20 4:38:00 PM**

Subscript

**Page 47: [1] Formatted** **David Hutchinson** **10/13/20 4:38:00 PM**

Subscript

**Page 47: [2] Deleted** **David Hutchinson** **10/13/20 4:38:00 PM**

▼

---