Evolution of continental temperature seasonality from the Eocene greenhouse to the Oligocene icehouse - A model-data comparison

Agathe Toumoulin[1], Delphine Tardif[1,2], Yannick Donnadieu[1], Alexis Licht[1], Jean-Baptiste Ladant[3], Lutz Kunzmann[4], Guillaume Dupont-Nivet[5,6]

[1] Aix Marseille Université, CNRS, IRD, INRA, Collège de France, CEREGE, 13545 Aix-en-Provence, France
[2] Université de Paris, Institut de physique du globe de Paris, CNRS, F-75005 Paris, France
[3] Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-UVSQ, Université Paris-Saclay, 91191 Gif-sur-Yvette, France
[4] Senckenberg Natural History Collections Dresden, Königsbrücker Landstraße 159, 01109 Dresden, Germany
[5] Géosciences Rennes, UMR CNRS 6118, Univ Rennes, 35042 Rennes, France
[6] Institute of Geosciences, Potsdam University, 14469 Potsdam, Germany

Correspondence to: Agathe Toumoulin (agathe.toumoulin@gmail.com)

Abstract. At the junction of greenhouse and icehouse climate stat~~phas~~es, the Eocene-Oligocene Transition (EOT) is a key moment in ~~in the history of the~~ Cenozoic climate history. W~~Yet, w~~hile it is associated with severe extinctions and biodiversity turnovers on land, the role of terrestrial climate evolution remains poorly resolved, especially the associated changes in seasonality. Some p~~P~~aleobotanical and geochemical continental records in parts of the Northern Hemisphere suggest the EOT is associated with a marked cooling in winter, leading to the development of more pronounced seasons (i.e., increase of the Mean Annual Range of Temperature, MATR) ~~in parts of the Northern Hemisphere~~. ~~However, this~~However, the MATR increase of ~~the annual temperature range~~ has been ~~poorly~~ barely studied by climate models and large~~;~~ uncertainties remain on~~about~~ its~~the~~ origin, geographical extent ~~of this phenomenon~~ and impact~~the associated climatic processes~~. ~~Although other components of the climate system vary seasonally (e.g., precipitation, wind), we therefore focus on the seasonality of temperatures only~~

In order to better understand and describe temperature ~~temperature~~ seasonality ~~patterns~~ changes between ~~from~~ the middle Eocene ~~to~~ and the early Oligocene, we use the Earth System Model IPSL-CM5A2 and a set of simulations reconstructing the EOT through three major climate forcings: pCO$_2$ decrease (1120, /840 and~~to~~ 560 ppm), the Antarctic ice-sheet (AIS) formation, and the associated sea-level decrease ~~(-70 m)~~.

Our simulations suggest that ~~seasonality~~MATR changes across the EOT reflect~~rely on~~ the combined effects of pCO$_2$ decrease, Antarctic glaciation and increased continentality,~~the different tested mechanisms~~ which result in zonal to regional climate responses. ~~Broad continental areas of increased MATR reflect a strengthening of seasonality (from 4°C to > 10°C increase of the MATR) across the EOT in agreement with MATR and Coldest Month Mean Temperatures (CMMT) changes indicated by a review of existing proxies.~~ pCO$_2$ decrease induces a zonal pattern with alternating increasing and decreasing seasonality

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bands~~, particularly strong i~~ ~~I~~n the northern high-latitudes (up to 8°C MATR increase) due to sea-ice and surface albedo feedback.~~, it results in sea-ice and surface albedo feedback, driving a strong increase in seasonality (up to 8°C MATR increase).~~ Conversely, the onset of the AIS is responsible for a more constant surface albedo yearly, which leads to a strong decrease in

35   seasonality in the southern mid- to high-latitudes (> 40°S). Finally, continental areas emerged due to the sea level lowering cause the largest increase in seasonality and explain most of the global heterogeneity in MATR changes (ΔMATR) patterns. ΔMATR patterns we reconstruct are generally consistent with the variability of the EOT biotic crisis intensity across the Northern Hemisphere and provide insights on their underlying mechanisms.

1 Introduction

40   **1.1 Context and aim of the study**

The Eocene-Oligocene Transition (EOT) is marked by an abrupt cooling event (~2.9°C from marine proxies; Hutchinson et al., 2021), considered as the hinge between the Eocene greenhouse and the later Cenozoic icehouse. This event is associated with the first major expansion of the Antarctic ice-sheet with an estimated sea level drop of ~70 m (Hutchinson et al., 2021; Miller et al., 2020). The EOT is described as a relatively brief event (~790 000 years), with two successive steps (at ca. 33.9

45   and 33.7) recognized in extensively studied marine environments, especially from deep ocean $\delta^{18}O$ values (e.g. Katz et al., 2008; Zachos et al., 2001; see the review of Hutchinson et al., 2021). ~~The Eocene-Oligocene transition is one of the major climatic events of the last 66 million years. Perceived as the hinge between a greenhouse ancient world and the present icehouse world, it has been extensively studied and described from both marine and terrestrial environments (e.g. Katz et al., 2008; Mosbrugger et al., 2005; Zachos et al., 2001; Zanazzi et al., 2007). This climate change is characterized by different phases: a~~

50   ~~progressive step between 50 and 33.9 Ma, and an abrupt cooling acceleration during the Eocene-Oligocene Transition (EOT, ca. 33.9 Ma), enabling the onset of the antarctic ice-sheet (AIS; Lear et al., 2008; Zachos et al., 2001).~~ Reported vegetation responses to the EOT appear heterogeneous across continents with important composition changes in some areas (e.g., West Coast of the United States, Greenland, Asia), notably where faunal turnover is important (e.g. Barbolini et al., 2020; Eldrett et al., 2009; Hutchinson et al., 2021; Pound and Salzmann, 2017; Wolfe, 1994). A number of~~Some~~

55   paleobotanical and geochemical studies consistently suggest that the decrease in continental temperatures was particularly marked during winter months, ~~which led~~thus leading to higher seasonal temperature contrast~~s~~, which are designated as a potential driving mechanism for biotic turnovers (e.g. Eldrett et al., 2011; Mosbrugger et al., 2005; Page et al., 2019~~20~~; Utescher et al., 2015; Zanazzi et al., 2015). Evoked forcing mechanisms explaining this enhanced winter cooling are pCO_2, AIS inception, and increased continentality, although it remains difficult to quantify and disentangle their respective

60   contribution from field data only. Understanding the drivers of the~~se~~ seasonal changes ~~between the Eocene and the Oligocene~~ is thus important, not only for assessing the climate system behaviour under major pCO_2 variations, but also to ~~since~~better describe the paleoenvironmental context ~~EOT is~~ associated with major ~~extinction~~ faunal turnover events of the EOT such as~~:~~ the "Grande Coupure" in Europe and the "Mongolian Remodelling" in central Asia (Meng and McKenna, 1998; Stehlin, 1909;

see Coxall and Pearson, 2007 for a review). ~~EOT vegetation response is heterogeneous across continents but shows important composition turnovers in some areas, notably where faunal turnover is important (e.g. Barbolini et al., 2020; Eldrett et al., 2009; Hutchinson et al., 2021; Pound and Salzmann, 2017).~~

By comparing paleoclimate simulations to a synthesis of indicators of seasonality changes (Table S1), our study attempts to reconstruct the evolution of seasonal temperature contrast from the middle Eocene to the early Oligocene. The EOT is broken down into five simulations, describing the evolution of three major forcing at that time: the pCO_2 drawdown, the AIS expansion and the resulting sea-level lowering, in order to understand the respective contribution of each component on the resulting seasonality change patterns, along with their possible synergies and retroactions.

1.2 Temperature seasonality and its evolution

Temperature seasonality can be quantified by the Mean Annual Temperature Range (MATR), which consists in the temperature difference between the warmest and coldest months of the year. Increasing MATR can occur~~be done~~ through increased summer temperatures, lowered winter temperatures, or both. MATR is practical because it can be directly calculated from temperature proxies providing an estimation of the lowest and highest temperatures within a year. This is the case for~~such as with~~ the Climate Leaf Analysis Multivariate Program (CLAMP), which reconstructs temperatures from the modern correlation between climate variables and leaf physiognomy (Wolfe, 1993; Yang et al., 2011), or~~and~~ the Coexistence Approach (CA), which uses modern relatives of fossil species to define a mutual climate range of environmental characteristics (Grimm and Potts, 2016; Mosbrugger and Utescher, 1997; Utescher et al., 2014). MATR can also be deduced from the variability of the temperature signal in geochemical proxies for temperatures, stable oxygen isotopes ($\delta^{18}O$), as the time resolution of the proxy does rarely allow for the direct reconstruction of seasonal temperatures (e.g. Ivany et al., 2000; Wade et al., 2012).

~~1.2 Evolution of temperature seasonality~~

The spatial distribution of temperature seasonality changes across the EOT appear~~is~~ heterogeneous in proxy data (e.g. Pound and Salzmann, 2017). Most changes are described in the Northern Hemisphere from paleobotanical reconstructions, and converge to show~~wards a greater~~ seasonaliti~~es~~y stronger in the early Oligocene than in the mid- to late Eocene. In North America, Western and central Europe, seasonality increase is recorded by~~in~~ the decline of species characteristic of warm paratropical to temperate environments such as ~~as conifers *Doliostrobus* sp. (conifers),~~ palms (e.g., *Nypa* sp.~~) (Palms)~~, plants from myrtle and eucalyptus family (Myrtaceae, e.g., *Rhodomyrtophyllum* sp.~~) (Myrtaceae)~~, conifers (e.g., *Doliostrobus sp.*) and some plant families with tropical elements (e.g., ~~such as~~ Annonaceae, Lauraceae, Cornaceae, ~~Flacourtiaceae,~~ Icacinaceae, Menispermaceae), and, depending on the bioclimatic zones, the expansion of temperate to boreal vegetation through the increase of deciduous and / or coniferous species (Eldrett et al., 2009; Kunzmann et al., 2016; Kvaček, 2010; Kvaček et al., 2014; Mosbrugger et al., 2005; Utescher et al., 2015; Wolfe, 1992). These vegetation changes are associated with a decrease of the Coldest Month Mean Temperatures (CMMT) across the EOT and start~~ing~~ before the EOT~~earlier~~ at some localities, during the mid- to late Eocene (Eldrett et al., 2009; Moraweck et al., 2019; Mosbrugger et al., 2005; Tanrattana et al., 2020;

Tosal et al., 2019; Utescher et al., 2015; Wolfe, 1994). Isotopic analyses have ~~also~~ documented this seasonality increase in different continental localities between the Priabonian (37.8 to 33.9 Ma) and the Rupelian (33.9 to 27.82 Ma; Grimes et al., 2005; Hren et al., 2013; Zanazzi et al., 2015). While s~~S~~ome of the~~se~~ changes are not directly quantifiable (e.g., the reduction of gastropods growing season length, United Kingdom; Hren et al., 2013; dental morphological changes for grazing perissodactyls, Europe; Joomun et al., 2010), others ~~are~~can demonstrate ~~particularly~~ strong~~, with~~ MATR increase (e.g., amplified by ~~increase up to~~15.6°C, Canada; Zanazzi et al., 2015). Temperature s~~S~~easonality increase is also documented for shallow waters of the Gulf of Mexico (increase of the MATR; Ivany et al., 2000; Wade et al., 2012). ~~Seasonality strengthening and associated vegetation changes have been proposed as driving factors for dental morphological changes for European grazing perissodactyls (Joomun et al., 2010).~~ Some studies have suggested a link between increased temperature seasonality and latitude (e.g., Eldrett et al., 2009; Zanazzi et al., 2007, 2015) but data seem insufficient to validate this relationship and this trend has not been confirmed by recent palynological compilation (Pound and Salzmann, 2017).

Data from s~~S~~outheast Europe and Anatolia show generally weaker and heterogeneous changes in temperature seasonality, with either no seasonality changes, slight seasonality lowering or slight seasonality strengthening from the mid-~~-~~Eocene to the Rupelian (Bozukov et al., 2009; Kayseri-Özer, 2013). This ~~variable signal~~variability has been ~~linked to~~explained by a strong marine influence on this ~~insular~~ part of Eocene Europe (Kayseri-Özer, 2013). Conversely, North and East Asia temperature seasonality evolution is more comparable to western Europe and North America trends (Quan et al., 2012; Utescher et al., 2015). Vegetation changes reflect an increase of the seasonal temperature range, mainly through the EOT (MATR increase of 2 to 2.5°C; CMMT decrease of ~2.2°C, ~~(~~Quan et al., 2012; Utescher et al., 2015). The appearance of tubers in lotus (*Nelumbo* sp.) during the Eocene suggests the establishment of a dormant phase in these plants and thus, of a period unfavorable to plant growth (Li et al., 2014). Fossils showing these structures have been described in Southern China (Hainan Province) and in the ~~extreme East~~easternmost ~~of~~ Russia (Kamchatka Peninsula) leading to hypothesize they could be favored by cooling ~~Eocene cooling~~ and increased seasonality on the East Asian continent during the Eocene (Budantsev, 1997; Li et al., 2014).

In the Southern Hemisphere, studies of Paleogene localities are rarer. Despite a record of late Eocene cooling in Australia, New Zealand and Patagonia, independent proxies (stable isotopes on teeth, bones and pedogenic carbonates, paleobotanical reconstructions) do not suggest a marked temperature seasonality during the Eocene (Cowlyn and Hren, 2019; Kohn et al., 2015; Laurenato et al., 2021; Nott and Owen, 1992; Pocknall, 1989). In Australia, the presence of more pronounced wood rings suggests a late Paleogene increase in seasonality starting in the mid-Oligocene at the earliest (Bishop and Bamber, 1985; Nott and Owen, 1992). Finally, the environmental and climatic impact of the EOT in continental Africa remains ~~virtually poorly un~~documented (Hutchinson et al., 2021; Saarinen et al., 2020).

1.3 Former model work

~~A first attempt to explain temperature seasonality change across the EOT was made by Eldrett et al. (2009). In their palynological and modelling study, Eldrett and coauthors explained high latitude (Greenland) seasonality strengthening by *p*CO₂ drop and the consequent increase of sea-ice formation over the Arctic Ocean. Sea-ice extension induces a strong albedo~~

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feedback in their experiment, which results in a large decrease of atmospheric temperature during the winter. In addition, Li et al. (2018) showed an important contribution of geography changes to seasonality strengthening during the Oligocene. Apart from these two studies, EOT modelling experiments mostly focused on oceans through mean annual temperature changes (Baatsen et al., 2020; Goldner et al., 2014; Hutchinson et al., 2018, *see* 2020; Kennedy et al., 2015; Kennedy Asser et al., 2019, 2020; Ladant et al., 2014b). Different modelling studies have illustrated the priming role of pCO$_2$ lowering during the EOT, but most focused on oceans through mean annual temperature changes (Baatsen et al., 2020; Goldner et al., 2014; Hutchinson et al., 2018, *see* 2020; Kennedy et al., 2015; Kennedy-Asser et al., 2019, 2020; Ladant et al., 2014b). The recent model intercomparison study of Hutchinson et al. (2021) has shown a reasonable agreement between 4X to 2X (i.e., 1120 and 560 ppm respectively) modelling experiments and proxy-data atmospheric and surface ocean temperature reconstructions from the late Eocene and the early Oligocene, respectively. They show, however, that changes in EOT SSTs were on average best represented by a pCO$_2$ shift from 910 ppm to 560 ppm (i.e., a drop of 1.6X). In addition, a recent model-data study of Lauretano et al. (2021) explored Australia climate evolution through the EOT, and estimated a pCO$_2$ drop ranging 260 – 380 ppm (drop of ~ 0.9 – 1.3X). The different simulations of the model intercomparison support once more the primary role of pCO$_2$ drop. A first attempt to explain temperature seasonality change across the EOT was made by Eldrett et al. (2009). In their palynological and modelling study, Eldrett and coauthors explained high latitude (Greenland) seasonality strengthening by pCO$_2$ drop and the consequent increase of sea-ice formation over the Arctic Ocean. In their experiment, sea-ice extension induces a strong albedo feedback, which results in a large decrease of atmospheric temperature during winter. Hutchinson et al. (2021), also quantified the general effect of AIS formation and contemporary paleogeographic changes (opening of Southern Ocean gateways, Antarctic geography or global geography). Additionally, changes in geography (topography, land-sea distribution) may have significant effects on terrestrial temperatures at a regional scale (e.g., Lunt et al., 2016; Li et al., 2018). EOT modelling experiments yield mixed answers regarding the temperature feedback resulting from both AIS and contemporary paleogeographic changes (opening of Southern Ocean gateways, Antarctic geography or global geography; (Goldner et al., 2014; Hutchinson et al., 2021; Kennedy et al., 2015; Ladant et al., 2014a, 2014b). Among these models, only one tested the The few studies testing the combined effect of both AIS and global paleogeographic changes (Kennedy et al., 2015; Lauretano et al., 2021) and suggested a moderate impact of AIS on global climate sensitivity, as previously suggested by other modelling work (Goldner et al., 2013; Kennedy et al., 2015).

1.4 Aim of the study

This study is an attempt to reconstruct temperature seasonality changes described by paleoenvironmental and paleoclimatic data between the middle Eocene and the early Oligocene. It includes both a synthesis of indicators of seasonality changes (Table S1) and paleoclimatic modelling. We reconstruct global patterns of temperature seasonality change and their main mechanisms through a set of five simulations taking into account the three major climate forcings described through this time interval: pCO$_2$ drawdown, AIS formation and concomitant sea-level lowering.

2 Material and methods

2.1 Model and simulation setting

We used the IPSL-CM5A2 general circulation model, which is built upon the CMIP5 Earth system model developed at the Institut Pierre-Simon Laplace (IPSL), IPSL-CM5A-LR (Dufresne *et al.*, 2013, Sepulchre et al., 2019). The IPSL-CM5A-LR Earth system model is composed of the LMDZ atmospheric model (Hourdin *et al.*, 2013), the ORCHIDEE land surface and vegetation model (Krinner *et al.*, 2005), and the NEMO v3.6 ocean model which includes modules for ocean dynamics (OPA8.2, Madec, 2008), biochemistry (PISCES, Aumont *et al.* 2015) and sea-ice (LIM2, Fichefet and Morales-Maqueda, 1997). The atmospheric grid has a horizontal resolution of 3.75° longitude per 1.875° latitude (96 × 95 grid points), and is divided into 39 vertical levels. For a more detailed description of the model and its different components, the reader is referred to Sepulchre *et al.* (2020).

Five simulations were carried out to reconstruct the evolution of temperature seasonality from the middle Eocene to the early Oligocene (Table 1). The applied 40 Ma paleogeography framework is the map developed by Poblete et al. (2021) and already used in Tardif et al. (2020) and Toumoulin et al. (2020). It features common late Eocene geography characteristics such as: an open Panama Seaway, an open Tethys with submerged Arabiane peninsula, a strongly maritime Europe, a Turgai land bridgeStrait connectingbetween Northern Europe withand Asia, and a narrow Southern Ocean gateways (Figure 1). The orbital parameters were set to preindustrial values and the solar constant was reduced accordingly to its Eocene value (1360.19 W/m^2; Gough, 1981). Vegetation was implemented as a boundary condition, using a zonal band of PFTs using modern vegetation distribution patterns.

Simulation	pCO$_2$	AIS	%Land (Mkm^2)	MAT (°C)	SST (°C)
4X	1120 ppm	/	132.3	26.4	28.2
3X*	**840 ppm**	**/**	**132.3**	**23.7**	**25.9**
2X	560 ppm	/	132.3	20.6	23.2
2X-ICE	560 ppm	32.5 10^{6}km^3	132.3	19.7	22.9
2X-ICE-SL*	**560 ppm**	**32.5 10^{6}km^3**	**152.7**	**18.7**	**22.2**

Table 1: Experimental design. Abbreviations: AIS: Antarctic Ice-Sheet volume (Ladant et al., 2014b); % Land: total land surface (millions of km^2: 10^{6}km^2); MAT: Mean Annual global 2-meter air Temperature (°C); SST: Sea Surface Temperatures (°C). Simulations with an asterisk constitute realistic middle Eocene (Lutetian / Bartonian) and early Oligocene (Rupelian) scenarios, others are either sensitivity experiments (2X, 2X-ICE) or use the high value of the pCO$_2$ range estimated for the time interval (4X).

Simulations were compared in pairs to highlight differences between the middle/late Eocene and the early Oligocene. The simulation set is composed of both realistic and idealized experiments (Table 1). Simulations 4X, 3X and 2X represent most of the pCO_2 range described from the mid-Eocene (Lutetian) to the early Oligocene (Rupelian; Foster et al., 2017). These pCO_2 values enable the description of the pCO_2 reduction effect on climate through this time interval and have been used in most former modelling experiments on the EOT (Hutchinson et al., 2021). Simulations 4X and 3X cover the range of potential climate values prior to the EOT (Lutetian to Priabonian). The idealized simulation 2X allows the identification of a 1 to 2 PAL (Preindustrial Atmospheric Levels, 1PAL = 280 ppm) pCO_2 lowering alone. In a complementary way, simulations 2X-ICE and 2X-ICE-SL describe the early Oligocene climate, following the Antarctic Ice-sheet formation. Both simulations are parameterized in the same way apart from theoutside sea level, which is 70 m lower in 2X-ICE-SL. The use of 2X-ICE provides a theoretical description of the effect of an ice-covered Antarctica on climate, while 2X-ICE-SL constitutes a realistic representation of the early Oligocene climate. In these experiments, the Antarctic ice cap was set to $32.5.10^6 \, \text{km}^3$ according to Ladant et al. (2014b). The 70-m sea-level drop was defined following eustatic drop estimates for the EOT (Coxall et al., 2005; Katz et al., 2008; Lear et al., 2008; Miller et al., 2020). It is responsible for important geography changes related to an increase of land proportion, such as the emergence of the Arabiane Peninsula and the retreat of the proto-Paratethys epicontinental sea. All simulations are run for 4000 years untilwhen temperatures indicate a quasi-equilibrium with only negligible temperature drifts within the global mean ocean (< 0.1°C/century; Figure S1). These trends are consistent with most model studies and do not affect the quality of atmospheric change described in this study (e.g. Hutchinson et al., 2018; Lunt et al., 2016). The results considered here are averages of the last 100 years of the model runs.
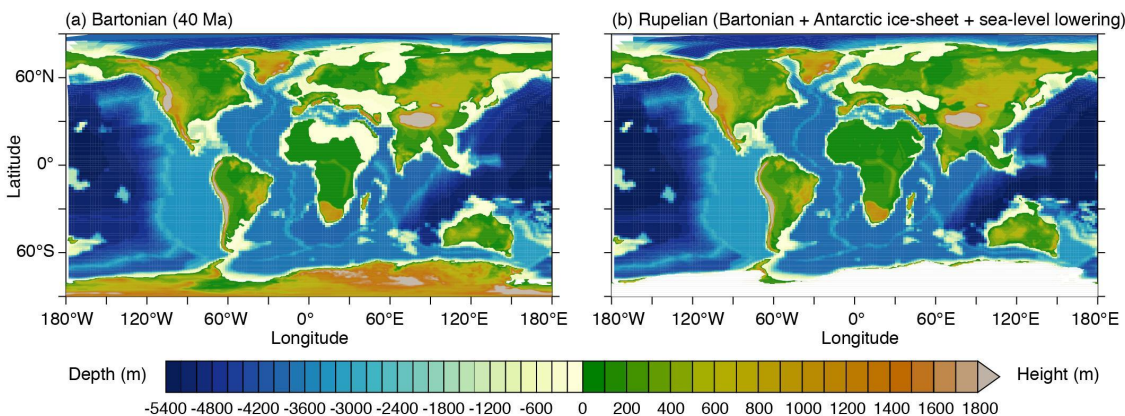
Figure 1: Paleotopographic 40 Ma map: (a) standard version as used for simulations 4X, 3X, 2X and to 2X-ICE; (b) version adjusted with a homogeneous 70 m sea-level lowering used for the simulation 2X-ICE-SL (Poblete et al., *2021*).

2.2 Data compilation

Simulation results were compared to MATR changes (ΔMATR) documented by proxy-data records (Table S1). We compiled published MATR and CMMT proxy-data from various research fields: paleobotany (macrofossils and palynology), geochemistry (isotopic measurements on various material), and paleontology. The data were selected to range from the Lutetian (47.8 Ma) to the end of the Rupelian (27.8 Ma). This large time interval allows the representation of seasonal

15 temperature changes parallel to the long-term cooling of the Eocene. The inclusion of data from the middle Eocene allows a comparison with simulations testing the effect of a pCO_2 lowering alone, before AIS formation at the EOT. It is justified by the presence of paleobotanical records suggesting a strengthening of the seasons already from the Lutetian to the Priabonian (e.g. Li et al., 2014; Mosbrugger et al., 2005). Compiled Eocene—Oligocene ΔMATR ~~Eocene—Oligocene changes~~ correspond either to the values given in original publications, when they were available and precise, or to values re-calculated from the

20 original data. For publications for which ΔMATR were recalculated, we proceeded by ~~minimizing the paleogeographic distance between sites~~ grouping the closest sites (especially in terms of latitudes) and checked that the values obtained were consistent with the authors original interpretation of the paleoenvironmental context. Half of the data come from the pollen compilation of Pound and Salzmann (2017). A selection was made through this study data to keep (1) the best dated samples, according to their dating quality indicator (data Q1 to Q3; Pound and Salzmann, 2017), and (2) sites with temperature estimates

25 for the Priabonian and Rupelian, or at least one nearby locality that could be compared. No Eocene-Oligocene site was selected for more clarity. In an effort to limit the addition of overly uncertain ΔMATR data, sites with a range of CMMT estimates (CMMTmax - CMMTmin) ≥ 10°C (either for Priabonian or Rupelian sites) were excluded.

Some previously published seasonality increases were not here associated with ~~changes~~ estimate of ~~in~~ ΔMATR, because they were either (1) ~~estimated~~ suggested from other parameters, such as the length of the growing season, which do~~es~~ not allow the

30 calculation of the MATR (Hren et al., 2013), or (2) derived from qualitative data that cannot be specifically associated with temperature values (e.g., organism morphological changes such as teeth shape or plant tuber appearance; Joomun et al., 2010; Li et al., 2014). These sites are displayed on the maps, but are not ~~analyzed quantitatively~~ included in quantitative analyses (section 2.3). In order to better estimate the impact of changes in temperature seasonality, the length of the plant growing season (i.e., the number of months with an average temperature above 10°C) was recalculated using the formula of Grein et

35 al., (2013) for coexistence approach data ~~from the approximate coexistence analyses~~ (Table s1). Paleocoordinates for every locality were reconstructed using an online service of *Gplates*, according to the 40 Ma paleogeography used for the paleoclimate models (Poblete et al., 2021) that essentially follows ~~using an online service of *Gplate*,~~ the plate tectonic reconstruction models of Matthews et al. (2016) ~~and a 40 Ma geography~~ with some modifications.

2.3 Comparison of model and data ΔMATR

40 Different analyses were made to evaluate the data-model agreement for temperature seasonality changes from the Priabonian to Rupelian (Table 2). Modelled ΔMATR values were extracted from a 3° longitude by 3° latitude area surrounding each data

locality. First, a general agreement percentage was calculated from the direction of seasonality changes alone to assert the agreement between our simulation and qualitative data. For this metric, model predictions are considered "good" for an individual site if modelled ΔMATR changes in the same direction ~~they have the same sign~~ as the data (i.e., ~~positive~~ if modeled ΔMATR increase/decrease at the location of a data point showing seasonality increase/decrease). For data indicating null ΔMATR, a good agreement was considered with model values ranging from - 0.5 to 0.5°C. ~~This first metric enables us to assert the agreement between our simulation and qualitative data.~~

In addition, Priabonian to Rupelian seasonality changes were ~~then~~ compared to ~~the~~ model predictions, by (1) assessing their correlation and (2) calculating the root of the mean squared distance between their values. These two analyses were performed using ~~Rstudio software~~R (version 4.0.3; R CoreTeam, 2020, Boston, USA). Given the limited number of quantitative Priabonian–Rupelian data (n = 29~~15~~), the statistical correlation of data-model ΔMATR was assessed from average ΔMATR with the non-parametric Spearman rank test. ~~Modelled MATR values were extracted from a 3° longitude by 3° latitude area surrounding each data locality. This test returns a coefficient, ρ (rho), which is a measure of the correlation (ranging from -1 to 1 indicating total negative and positive linear correlations respectively and 0 the absence of correlation). The statistical significance of the correlation is described through the p-value.~~ In this analysis, we used the common significance level, α, of 0.05 (i.e., *p-values* < 0.05 indicate significant correlations). Data-model agreement ~~for ΔMATR from Priabonian to Rupelian data~~ was also assessed through ~~the use of~~ the Root Mean Squared Estimate ~~(see Kennedy-Asser et al., 2020, and their figure S1 for a detailed presentation of the method).~~, which ~~This method~~ consists in calculating the root of the mean squared distance between model and data values for comparable points (RMSE, see Kennedy-Asser et al., 2020, and their figure S1 for a detailed presentation of the method). Conversely to the Spearman Rank Test for which mean ΔMATR estimations were used, the distance is here measured using the full range of estimates at each data locality (i.e., minimum and maximum ΔMATR). Note that, because it considers the full range of ΔMATR, this method tends to ~~underestimate~~ minimize the difference between model and data. The lower bound of modelled ΔMATR at each locality was calculated as the difference between the lowest~~r~~ MATR value over the 3° x 3° area ~~centered~~centred around the locality for an Oligocene-like cold simulation (2X, 2X-ICE or 2X-ICE-SL) and the highest MATR value over the 3° x 3° area for an Eocene simulation (4X or 3X). For the upper bound, we used the difference between the higher MATR value over the same area for an Oligocene-like cold simulation and the lower MATR value for an Eocene simulation.

The RMSE adjusted to ΔMATR is written as follows:

$$\text{RMSE}_{(\text{MATR-changes})} = \text{SQRT } ((\cdot(\text{MATR}_{(\text{diff-data})} - \text{MATR}_{(\text{diff-model})})^2/\text{n}) \tag{1}$$

Where *MATR_{diff-data}* and *MATR_{diff-model}* are MATR Priabonian to Rupelian changes estimated by data and model respectively, and *n* the total number of localities.
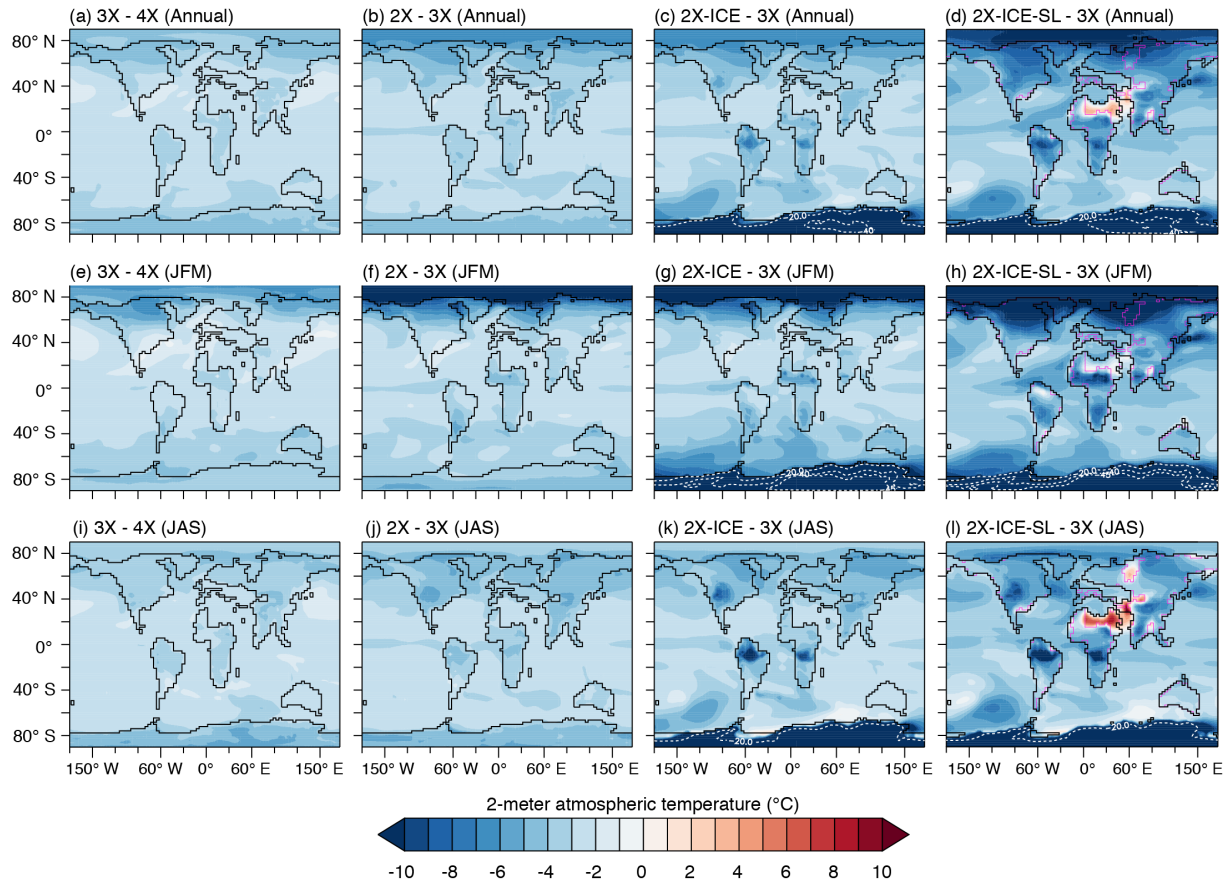
Figure 2: 2-meter air temperature changes (°C). JFM: averaged over January to March, JAS: averaged over July to September.

Magenta lines of subfigures d,h,l indicate shorelines before sea-level lowering. White dotted lines in c,d,g,h,k,l are the level lines encircling the 20, 40 and 45°C cooling zones.
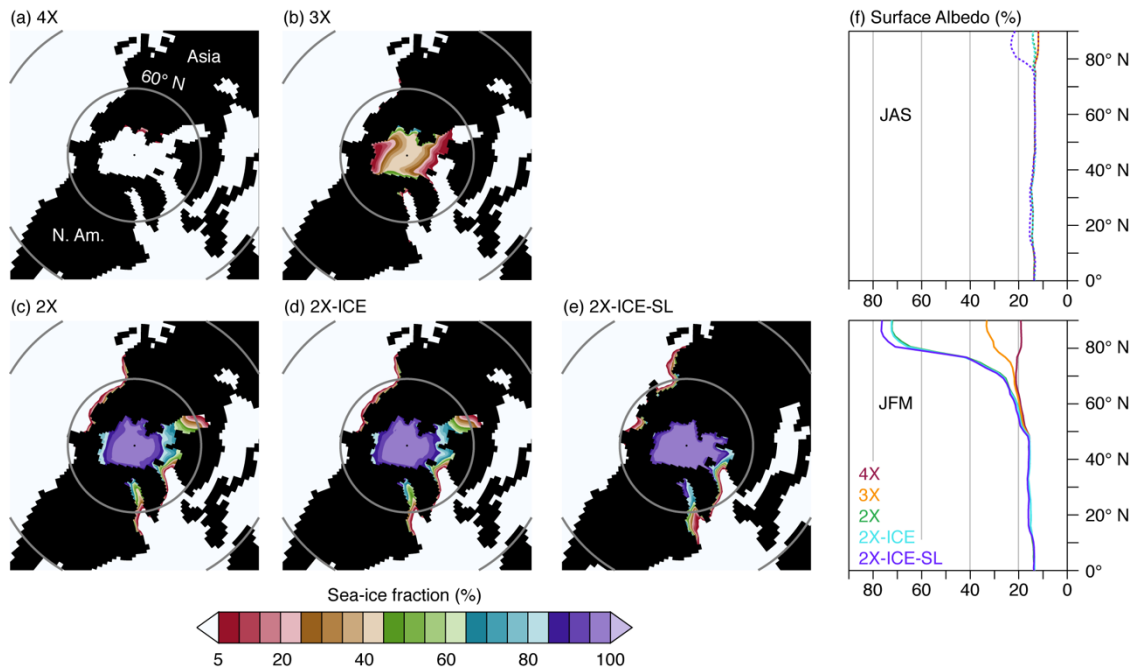
Figure 3: Northern Hemisphere winter sea-ice fraction and surface albedo (%)

3 Results

3.1 ~~Modelled~~ Simulated response to pCO$_2$ lowering

In this section, we compare the simulations 4X, 3X, 2X together to describe the effects of pCO$_2$ drawdown on climate and provide a range of possible MAT and MATR change intensities. The simulation pair 2X-4X represents the strongest possible changes, 3X-4X the weakest changes, and 2X-3X an intermediate scenario (see section 2.1).

~~3.1.1 Temperature changes~~

~~Atmospheric~~ Mean annual temperatures decrease strongly in our different experiments (Table 1, Figure 2). The halving of pCO$_2$ from 4X to 2X alone (i.e., without AIS formation and sea level drop) induces a global cooling of 5.8°C and 5.0°C for the air temperature and the surface ocean respectively (Table 1). A pCO$_2$ drop of 1 PAL induces a 2.7 to 3.1°C lowering of MAT and a 2.3 to 2.7°C cooling of the SST, for 4X to 3X and 3X to 2X changes, respectively. Along with its effect on annual temperatures and regardless of its intensity, pCO$_2$ decrease induces zonal ΔMATR including (1) an increase of MATR at high-latitudes (especially in the North), (2) a decrease of MATR across most mid-latitudes, and (3) moderate changes at low-latitudes, which we detail in the following sections 3.1.2 and 3.1.3 (for Eocene MATR values see Figure S2).

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3.1.2 ~~Areas with increased seasonality~~ MATR increase zones

~~Along with its effect on temperatures, pCO$_2$ decrease induces zonal ΔMATR including (1) an increase of MATR at high-latitudes, (2) a decrease of MATR across most mid-latitudes, and (3) moderate changes at low-latitudes (Figure 4. a,b; see also Figure S2 for absolute MATR values).~~ Temperature changes are characterized by polar amplification, with a stronger winter cooling at high-latitudes (Figure 2. a,b,e,f,i,j), likely due to ~~. This phenomenon is well explained by~~ the combined effect of albedo and sea-ice feedback. ~~The~~ Below a given threshold (situated between 2 and 3 PAL), the pCO$_2$ drop enables sea-ice growth over the Arctic and, to a lesser extent, the subsistence of snow on the ground during the cold season, which increases winter surface albedo (Figure 3). In addition, seasonal sea-ice expansion limits ocean-to-air heat transfer at highest Northern latitudes and contributes to further winter cooling of the atmosphere.

This preferential lowering of winter temperatures results in a large MATR increase of 5-20% (3X-4X and 2X-3X) and up to 40% (2X-4X; Figure 4 e and S3 b) over high northern latitudes. ~~The large MATR increase at high northern latitudes is triggered by the preferential lowering of winter temperatures aforementioned. it represents an increase in MATR of 5-20% between 3X and 2X and up to 40% between 4X and 2X (Figure 4 e and S6 b).~~ Furthermore, the areas of colder winters and ~~broader~~ high MATR ~~become larger~~widen as pCO$_2$ decreases: MATR increases from 60°N poleward between 4X and 3X, to 50°N poleward between 4X and 2X (Figures 4 and S4~~3~~). In contrast, Antarctica shows moderate ΔMATR ~~changes~~ (regionally up to 3°C from 4X to 3X, and 6°C from 3X to 2X) compared to high ~~n~~Northern latitude~~s~~ lands (6°C MATR increase from 4X to 3X~~ to 2X~~, and 10°C from 3X to 2X). This is because Antarctica is characterized by wide MATR values in all ice-sheet free experiments (4X, 3X and 2X experiments), resulting in low ΔMATR changes from one experiment to another (Figure 4 a,b). This important seasonality is induced by the continent's high albedo variability, as it oscillates from snow-free to snow-covered soil within a year. ~~This is because ice-free Antarctica is characterized by high variability of albedo as the continent oscillates from snow-free to snow-covered soil within a year, resulting in highly variable intra-annual temperatures (Figure 4).~~
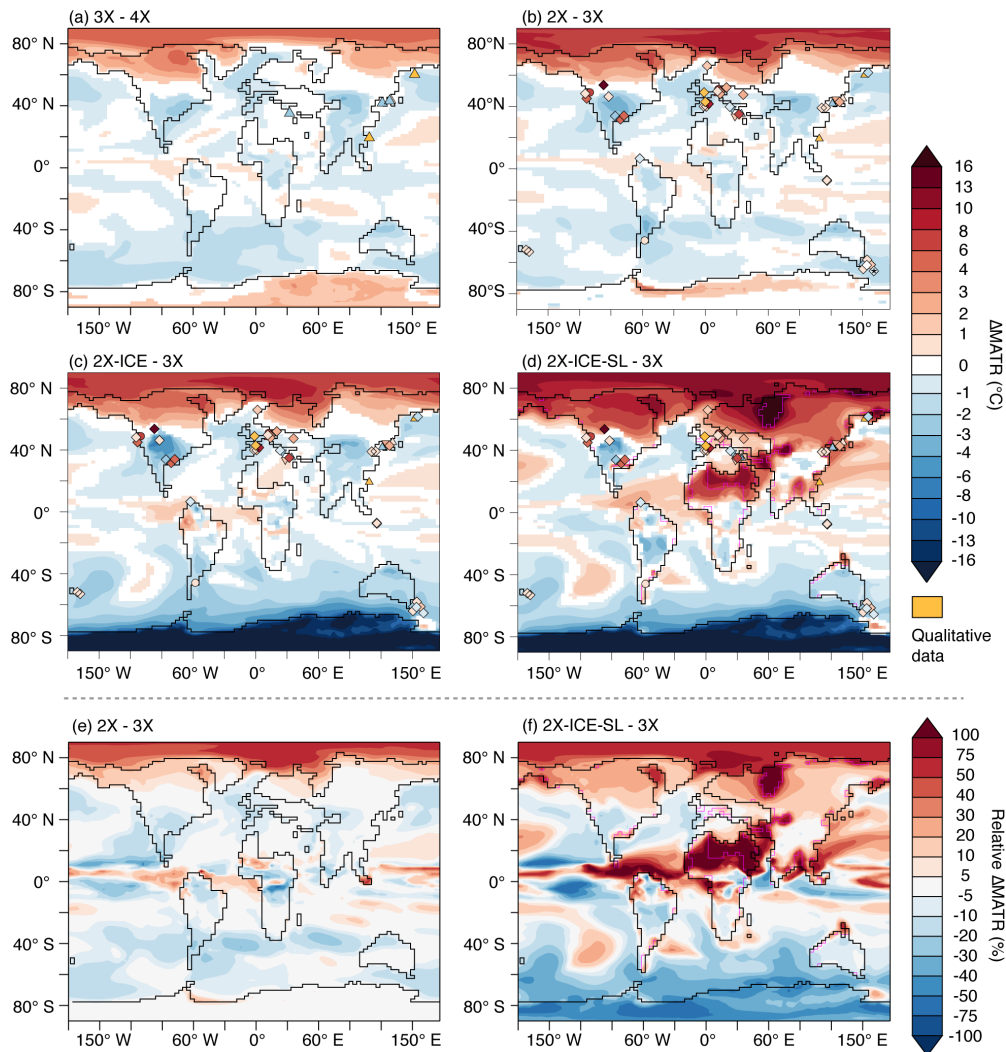
Figure 4: Changes in Mean Annual Temperature Range changes, ΔMATR (°C). Shadings are model differences calculated with a Student t-test over the last 100 years of comparative simulations (95% confidence); white areas indicate no significant change inΔ-MATR. Subfigures e,f indicate relative ΔMATR (in %), for 2X-3X and 2X-ICE-SL - 3X respectively. Symbols correspond to ΔMATR from proxy-data for different time steps: Priabonian–Lutetian (triangles); Rupelian–Lutetian (deltas); Rupelian–Bartonian (circles); Rupelian–Priabonian (diamonds). Orange symbols indicate qualitative values describing a temperature seasonality increase. In case of proxies reconstructing a range of equally probable values (e.g., Coexistence approach), values shown are mean values. References for every data site are displayed on Figure 87 and available in the data compilation provided in Table S1.

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3.1.3 ~~Areas with decreased seasonality~~MATR decrease zones

Areas with decreased seasonality are characterized by summer cooling that exceeds winter cooling, which reduces the MATR (Figure 2 and 4). The widest zones ~~with~~ of decreasing MATR are ~~located~~ continental regions located within the 30-50°N latitudinal band~~, across North America, Western Europe, Central Asia, and 30-50°S for South America and Australia~~. The magnitude of simulated MATR reduction depends on the pCO_2 drop considered~~,~~ with reduction from 3X to 2X and from 4X to 2X resulting in up to 20 and 30% of regional MATR decrease, respectively (Figure 4 and S8). At lower latitudes, in Amazonia, equatorial Africa and India~~To a lesser extent~~, seasonality decreases but to a lesser extent ~~in Amazonia, equatorial Africa and India~~ (Figure 4). A variety of atmospheric and oceanic processes are likely involved in these contrasting MATR changes, depending on the region considered.~~This phenomenon is well explained by two distinct chains of reaction. First~~ The good correlation between MATR increase (respectively decrease) and P-E ratio (i.e., precipitation *minus* evaporation, also referred to as *net precipitation*) decrease (respectively increase; i.e., North America, Central Asia, and North Australia) suggests a strong implication of the hydrological cycle on this phenomenon (Fig 5 c,d; Fig 6 a,c,h). ~~the~~ The pCO_2 drop tends to slow down the hydrological cycle, which results in flatte~~rns the~~ P-E latitudinal gradients. At high latitudes, a reduction of precipitation leads to an overall P-E decrease, while at mid to low latitudes, increased precipitation results in ~~(precipitation *minus* evaporation, also referred to as~~or net precipitation)~~, caused by~~ a general increase of P-E ~~values between 50°S and 50°N, notably in North America and East Asia (especially in part of India, Mongolia and SE Asia), and an overall P-E decrease at high latitudes in both hemispheres~~ (Figure 5 a-d). In these low to mid latitude zones, precipitation strengthening is more important in summer and associated with ~~S~~summer~~increased~~ increased evaporation, which results ~~is increased in zones with increased moisture (i.e. where P-E increases, Figure 6, not shown). This results~~ in larger latent heat fluxes ~~during summer (Figure 5 e,f)~~ and thus in a greater cooling~~decrease during~~ in summer ~~temperatures~~, consistently with decreased seasonality (Figure ~~2 j~~6 a,c). ~~In addition, s~~Summer cooling is strengthened through vegetation feedb~~b~~ack: P-E increase favors net primary productivity which in turn contributes to evaporation and summer warmth loss (Figure 6 a,c~~5 g,h~~). ~~Secondly~~In constrast, ~~changes in ocean temperature have a strong impact on continental~~decreased MATR in Europe and Southern South America appears poorly correlated to the above-mentioned parameters (Figure 6 b,g). For Europe, the presence of sea-ice over the Arctic Ocean (Figure 3 b-e;e) limits heat loss via the atmosphere during winter and results in a greater summer cooling of the SST (Figure S5), which contributes to lowering European MATR. In addition, a regional increase in low-level cloud cover during summer could also contribute to lowering ΔMATR for both Europe and southern South America through albedo feedback (5 to 15% higher low-level cloud fraction between 40-60°; Figure 7 d,h, S6). For southern South America, several parameters seem consistent with the reduction of the MATR but it is difficult to disentangle their contribution. By amplifying the latitudinal temperature gradients, the pCO_2 drop induces a northward migration of the westerly wind maximum (by about 2° of latitude, annually but less markedly during austral winter, JAS) and of the ~~polar front (boundary between the atmospheric polar and Ferrel cells), especially during austral summer, and of the westerly wind maximum (by about 2° of latitude, annually but less markedly during austral winter, JAS; Figure S4). The~~ Antarctic Circumpolar current, which delimits the southern hemisphere's subpolar

and subtropical gyres., follows tThis northward shift thereby limits the arrival of warm subtropical waters towards the poles (Figure S7). several areas at mid latitudes, such as in Patagonia and Europe. In these areas, cold air masses originating from the nearest oceans (North Atlantic and South Pacific) are brought by westerly winds during summer. They favor a lowering of temperatures during this season and thus, a lowering of the MATR This greater cooling in summer SST reinforces the ocean's buffering effect on atmospheric temperatures in southern South America and favors milder summers, and to a lesser extent, cooler winters, which is consistent with a decrease in seasonality (Figure 76). Finally, cChanges in atmospheric dynamics (decrease in the width and increase in the intensity of the Hadley cell) are also visible and could have an impact on air-ocean exchanges, but much more analysis would be needed to understand their implication, which is not the focus of this paper (Fig. S5). These cold air masses result from the regional increase in low-level cloud cover during summer (5 to 15% higher cloud fraction between 40-60°; Figure 6 d,h, S4) which increases planetary albedo. In addition, For Europe, the presence of sea-ice at the North Pole (Figure 3 b,c) limits heat loss via the atmosphere during winter and results in a greater SST cooling during summer which significantly impacts European MATR (Figure S65). to

3.2 Modelled response to Antarctic Ice Sheet and sea-level drop

3.2.1 Antarctic Ice Sheet aloneonly

AIS formation is responsible for a supplementary 0.9°C and 0.3°C cooling of the air temperature and the surface ocean respectively (Table 1). It induces striking mean annual temperature differences, reaching -35°C above the continent (Figures 2 and S6). Its direct effect on atmospheric 2 meter mean annual temperatures varies regionally and is more significant striking over Antarctica with up to -35°C cooling, and over the Southern Ocean and Australia (Figures 2 c,g,k and S8 c,d). In contrast with Arctic sea-ice which increases seasonality at highest northern latitudes, the AIS decreases southern latitude temperature seasonality (Figures 4 c and S8 c,d6). Indeed, simulations with the AIS have a year-long white Antarctica soil withand high and stable surface albedo, which reduces seasonal temperature variability (Figure 3.g-l).
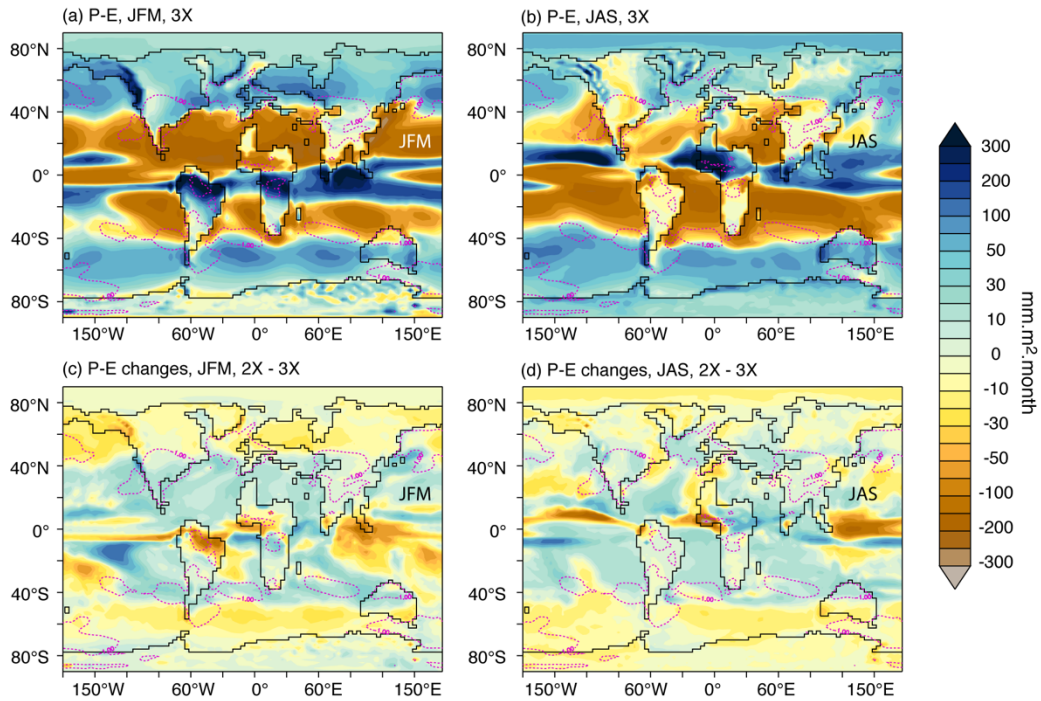
15

Figure 5: (a,b) Net precipitation (precipitation – evaporation, P-E) in JAS and JFM for the late Eocene simulation 3X. (c,d) Changes associated with pCO2 drop from 3X to 2X (differences shown are 2X *minus* 3X) for net precipitation. ~~(c,d), latent heat fluxes (e,f) and net primary production (g,h). Dashed Magenta lines contour MATR decreasing zones in 2X *minus* 3X simulations (blue zones in Figure 4.b).~~ <u>Magenta dashed lines contour areas with decreased seasonality (ΔMATR $\leq$ -1°C) in 2X minus 3X simulations (blue zones in Figure 4.b).</u>
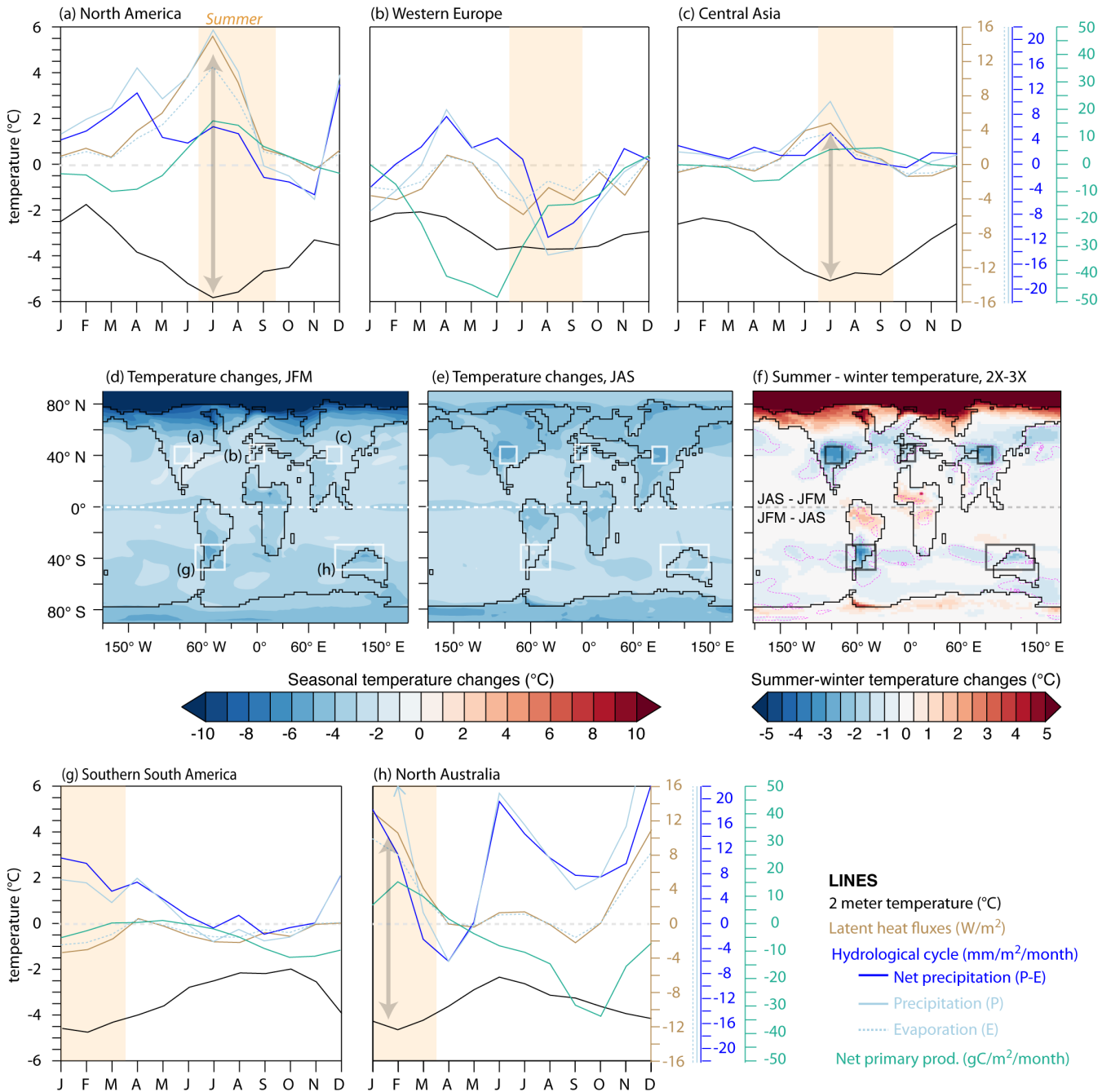
Figure 6: Annual variability of multiple climate parameters within the different areas of decreasing seasonality between 3X and 2X (a-c,g,h): atmospheric temperature (black), latent heat fluxes (soil to atmosphere; brown), hydrological cycle (incl. precipitation, evaporation and net precipitation, different shades of blue), and net primary productivity (green). (d-f) Temperature changes and summer *minus* winter temperature changes. Rectangles outline the land areas analysed in subfigures a-c,g,h (ocean zones are not taken into account in the calculation of the plots).
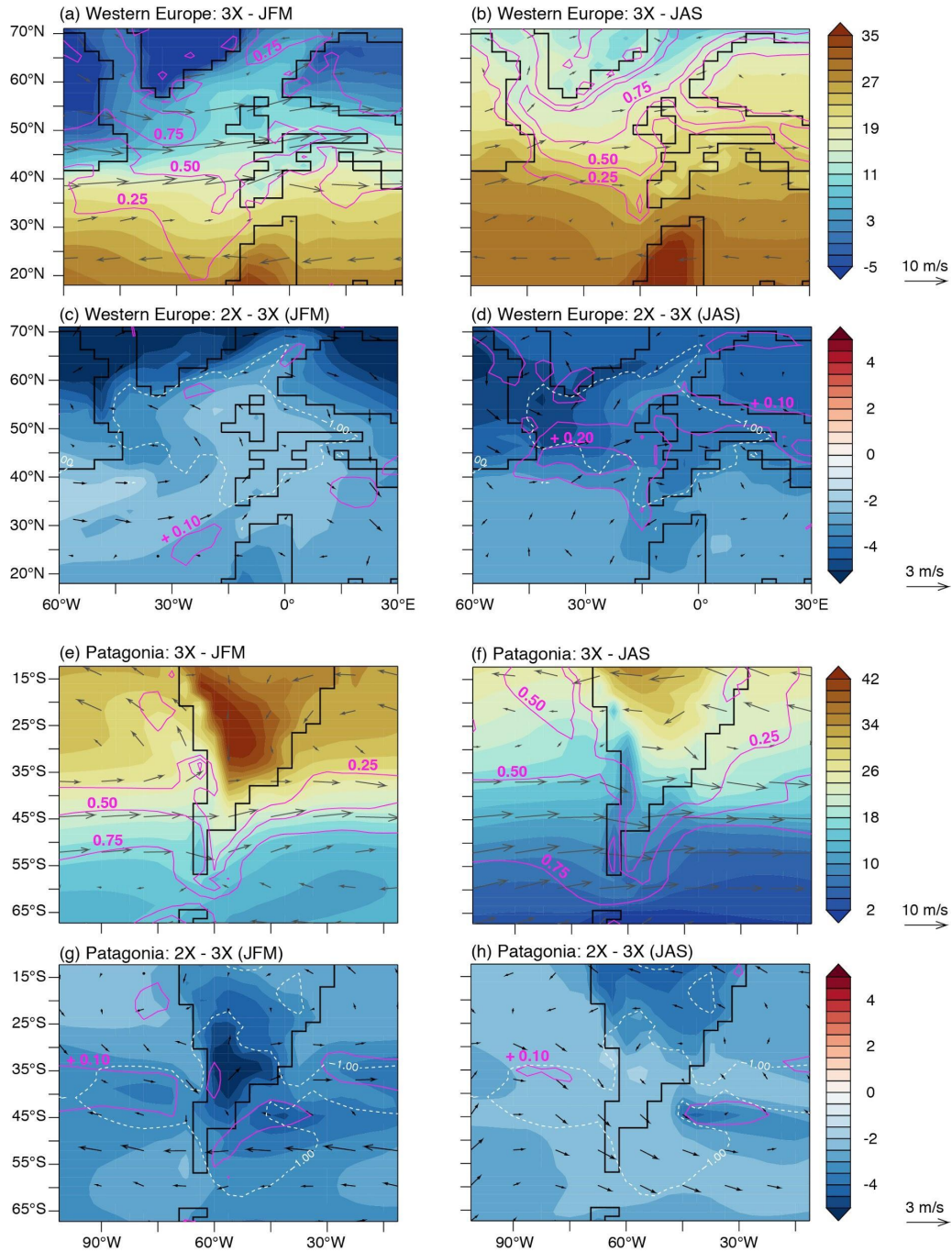
Figure 76:

Figure 7: 2-meter atmospheric temperature across western Europe and Patagonia. Shadings correspond to temperatures (a,b,e,f) and temperature differences (c,d,g,h). Similarly, magenta lines contour low-level fraction (a,b,e,f) and low-level cloud fraction changes (c,d,g,h; always expressed in %) and arrows, 850 hPa winds (a,b,e,f) and 850 hPa wind changes (c,d,g,h; always in m.s-1). White dashed lines contour areas with decreased seasonality (ΔMATR $\leq$ -1°C) in 2X minus 3X simulations (blue zones

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3.2.2 Sea-level drop

SIn addition, sea-level decrease alone is responsible for a 1.0°C mean annual global 2m air cooling of global MAT (0.7°C for surface oceans) and results in considerable regional temperature changes in areas sufferingwith important land-sea distribution changes (Table 1, and Figures 4 d,f and S3 e,f6). The increased proportion of land over ocean enhances latent and sensible heat fluxes during boreal winter, which reduces CMMT and conversely reduces energy fluxes during boreal summer, which increases summer warmth (Figures 2, S3 and S6). The marine regions that become exposed after sea level drop show the strongest increase in MATR,numerous areas of as they experience both winter cooling and summer warming, due to the lower thermal inertia of land compared to ocean warming resulting from land fraction increase provoke a wide spatial extension of the MATR reinforcement zone (Figure 4 d,f). This seasonality strengthening in newly exposed areas occurs independently of their latitude, therefore disrupting The the otherwise zonal distribution of seasonal temperature changes generated by pCO_2 drop and AIS formation (Figures 4 f and S3 f) is dismantled. The effect on seasonality of these disappearing seas expands beyond these areas adjoining the emerging landmasses due to the resulting regional perturbation in temperature. NorthernEast Africa, Western Asia and Russia are the most impacted areas, due tofollowing the proto-Pparatethys sea retreat and the emergence of the Arabic Arabian Peninsula (Figure 1). More moderate seasonality changes are also visible as a result of sea retreats of smaller extent, such as the emergence of the Florida platform and the modification of the East Asian coastlines (Figure 4 d and S3 e,f).

3.3 Model-data comparison

	2X - 4X	2X-ICE - 4X	2X-ICE-SL - 4X	2X - 3X	2X-ICE - 3X	2X-ICE-SL - 3X
Average ΔMATR model-data mismatch Mean MATR *(model - data)*	5.3 °C -3.5°C	5.8°C -3.9°C	3.9°C -1.9°C	4.6°C -2.8°C	5.1°C -3.2°C	3.2°C -1.2°C
RMSE	5.0°C 3.1°C	5.3°C 3.4°C	4.1°C 2.5°C	4.8°C 2.9°C	5.0°C 3.2°C	3.8°C 2.4°C
%	5,8 % 19.4%	5,8 % 19.4%	35,3 % 41.9%	0,0 % 22.6%	0,0 % 16.1%	58,8 % 45.2%

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rho	0.21 (*p* = ~~0.45~~ 0.28)	~~0.35~~ 0.27 (*p* = ~~0.20~~ 0.16)	~~0.57**~~ 0.29 (*p* = ~~0.02~~ 0.12)	~~0.20~~ 0.19 (*p* = ~~0.47~~ 0.32)	~~0.37~~ 0.25 (*p* = ~~0.17~~ 0.20)	~~0.56**~~ 0.29 (*p* = ~~0.03~~ 0.12)

Table 2: Priabonian-Rupelian data-model comparison. ~~RMSE for ΔMATR between the Priabonian and the Rupelian.~~ Negative mean ΔMATR values reflect a tendency of the model to underestimate ΔMATRs. The line "%" give the percentage of sites where the direction of ΔMATR is adequately modelled (e.g., the model described a MATR reinforcement in the zone where data indicate MATR increase). Modelled ΔMATR estimates were considered as positive when > 0.5, negative when < 0.5, or null when ranging [-0.5; 0.5]. "*rho*" indicates the strength of the correlation estimated with the Spearman Rank test, with associated p-values ("p"). ~~Significant correlations are indicated in bold and with **~~Note that all p-values being > 0.05, none of the correlations are significant.

3.3.1 *p*CO$_2$ lowering

The ΔMATR described by the *p*CO$_2$ drop experiments (from 3X or 4X to 2X) show neither a good agreement with middle to late Eocene, nor with late Eocene to early Oligocene data estimates (Figures 4 a,b and 6 b). The simulations predict no change, or a MATR decrease, in areas where the Lutetian–Priabonian data points (n=6, triangles, Figure 4 a) describe increased seasonality (Figure 4 a,b). Priabonian–Rupelian ΔMATR modelled through 4X to 2X and 3X to 2X *p*CO$_2$ drops ~~(1.8°C and 1.0°C)~~ are, on average, lower than data estimates at similar localities, with a mean offset of -3.5 and -2.8°C, respectively (~~3.6°C,~~ Figure ~~8~~7 b; Table 2). The use of the simulation 4X instead of 3X for the late Eocene stage has a marginal effect on ~~slightly increases~~ the percentage of agreement for the sign of the ΔMATR, although slightly higher value is observed for 3X-2X ~~but this result only depends on one high-latitude data-point for which a positive ΔMATR is predicted with a larger *p*CO$_2$ drop~~ (Table 2, line '%', ~~data-point 12 in~~ Figure~~s~~ ~~8~~7.~~b~~a and S9). In addition, *p*CO$_2$ drop alone leads to zonal ΔMATRs which do not transcribe the spatial heterogeneity visible in data. This misfit is visible through high RMSE scores and the absence of significant correlation between modelled ΔMATR resulting from *p*CO$_2$ drop (simulations 2X – 4X and 2X – 3X) and ΔMATR described by proxy-data (Table 2). Two data-model agreement patterns are nevertheless to be noted: (1) Regardless of their values (which are higher in data than in our simulations), the northernmost data points are inside or surround the high-latitude seasonality strengthening zone we modelled (Figure 4, data-points ~~9,5,12~~1,2,3 on Figure 8 a~~7~~); (2) none of the Southern Hemisphere data localities showing no seasonality change are located within ~~zones~~ MATR increase zones (Figure 4 ~~a,~~b).
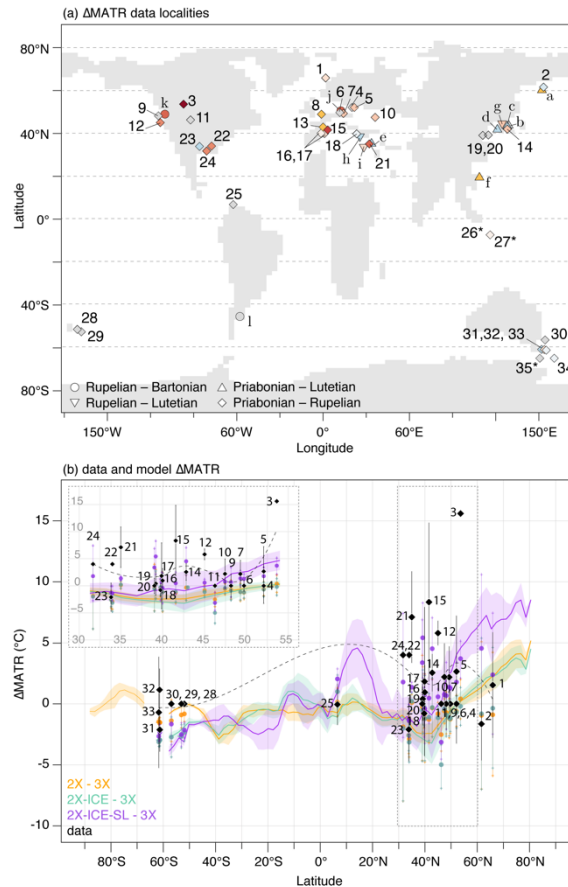
Figure 87 – Ddata-model comparison of ΔMATR from the Priabonian to the Rupelian. (a). Map of all data ΔMATR estimates compiled in this study (symbols refer to the time period compared for the calculation of the MATR shift, see ~~also~~ Table S1 for associated references). (b-db). Comparison of data estimates of Priabonian-Rupelian ΔMATR (black diamonds) to modelled ΔMATR at same localities (colored ~~squares~~circles, calculated ~~on~~ over a 3x3° area) from different pairs of simulations with 3X. Error bars are minimum and maximum data estimates of ΔMATR. Dashed black line is the LOESS curve associated to data ΔMATR estimates. Bold colored lines indicate the continental latitudinal gradient of ΔMATR on land (i.e., all longitudes averaged per degree of latitude); ~~thinner lines~~ color-shaded intervals are the standard deviation around the average. ~~-~~A subfigure similar to (b) but using the simulation 4X as a Priabonian stage is available in supporting material, Fig. S9.

3.3.2 Antarctic ice-sheet and sea-level

The formation of the AIS alone does not result in a better agreement between ~~the~~ modelled and Priabonian–Rupelian ΔMATR estimates. It is even slightly reduced (Table 2). The reinforcement of the MATR lowering zone at high-southern latitudes increases the data-model misfit ~~with the few data-points in New-Zealand, Patagonia and Australia~~because of data points

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indicating ~~which indicate~~ null ΔMATR in this zone (~~points 16, 8 and 20 on Figure 7.a;~~ Figure 4.c and Figure 8.b~~7.e~~). There is still no significant correlation between ΔMATR from the model and differences ~~observed~~ documented by proxy-data

65 (~~Spearman rank test: rho = 0.35 and p-value = 0.20 (2X-ICE – 4X) and rho: 0.37, p-value = 0.17 (2X-ICE – 3X),~~ Table 2). Geographic changes associated with sea-level drop result in a better agreement with data ΔMATR (Figure 4 -d and ~~Figure~~ 8 b~~7.d~~). The largest continental fraction changes affect the MATR on a broad geographic scale and allow for a better agreement, even with several ~~distant~~ data points standing away from the regions directly impacted by the sea-level drop, as for example ~~. For example, the retreat of the proto-paratethys reinforces the area of MATR increase at the high northern latitudes which

70 spreads toward North America and creates a better fit with~~ data estimates located on the Pacific Coast (Figure 4 d). Similarly, coastline changes along the eastern part of Africa and Western Asia cause an increase in seasonality in Anatolia and Central/Western Europe, improving the fit between model and data. These changes in temperature seasonality result in a reduction of 2 to 2.5 months in the duration of the plant growing season (as reconstructed with the formula of Grein et al., 2013; Table S1). Smaller changes in coastlines such as in Florida, Kamchatka Peninsula or along the East Asian coast increase

75 seasonality at a regional scale and improve the data-model fit (data-points ~~1, 3-5, 14, 17~~14, 22, 24). This better fit is transcribed through the RMSE analysis results, the lowest values being obtained when the simulation 2X-ICE-SL is used to simulate the Rupelian stage (Table 2). ~~The simulation still underestimates ΔMATR across the EOT (Figure 7.d; Table 2). Modelled MATR using simulation 2X-ICE-SL for the Rupelian stage are the only ones showing significant correlation with proxy-data ΔMATR (Table 2). Changes are equally correlated to~~However, there is no significant correlation between model and proxy-data

80 Priabonian–Rupelian ΔMATR, independently of the late Eocene simulation (4X or 3X) used as initial stage (for both, Spearman rank test: rho = ~~0.56 and 0.57~~0.29, *p-value* = 0.12~~< 0.05~~, Table 2). This persistent mismatch may be triggered by biases from the model or the data and from the methodology used to calculate these ΔMATR, which are further detailed in the Discussion. ΔMATR is still slightly underestimated by the model (Figure 7.d; Table 2). ~~This better agreement is also visible in RMSE analysis, with the lowest data-model distance observed for the couple 2X-ICE-SL – 3X (Table 2).~~

85 The pair of simulation that best describe the Priabonian-Rupelian transition, according to currently available data is 2X-ICE-SL – 3X as it presents(1) the lowest average model – data ΔMATR mismatch (-1.20°C) and (2) the best agreement in ΔMATR direction (45% of the data acerted, Table 2). ~~A smaller data-model difference is also described for 2X-ICE-SL – 3X (as compared to 2X-ICE-SL – 4X) by other indicators, notably (1) a 3.2°C mean difference, as compared to a 3.9°C offset for 2X-ICE-SL – 4X (2X-ICE-SL – 3X) and (2) the percentage of values for which a ΔMATR in the good direction is predicted (23.5%

90 higher with 3X; Table 2).~~

4 Discussion

4.1 Implication for mechanisms of late Eocene to early Oligocene seasonality changes

4.1.1 Model climate sensitivity and climate response to EOT forcing

ΔMATR across the EOT are better predicted when considering the changes occurring between ~~with~~ the lower pCO_2 simulation
3X for the late Eocene stage and the most realistic simulation 2X-ICE-SL for the early Oligocene stage. In addition, with a
mean ~~global~~ SST cooling of 2.7°C between 3X and 2X simulations (Table 1), surface temperature changes are also in
agreement with the mean changes described in marine proxies across the EOT (i.e., difference of 2.9°C between 38-34.2 and
33.7-30 Ma, Hutchinson et al., 2021). The best fit with a limited drop of pCO_2 reflects the high climate sensitivity of our model
(i.e., the average temperature change per doubling of the pCO_2 at model equilibrium; PALEOSENS, 2012). This high
sensitivity is also highlighted in our experiments of pCO_2 halving from 1120 to 560 ppm (2X-4X), which result in a dramatic
mean annual global cooling (5.8°C for global MAT, 5°C for SST; Table 1). Such temperature difference is high compared to
previous modelling studies which describe a 3 to 4°C surface atmospheric temperature difference under similar ~~forcing~~pCO_2
decrease, and the 2.9°C cooling found in marine proxies across the EOT (Hutchinson et al., 2021). The pCO_2 of 4X and 2X,
are more generally used in simulations to represent the transition to an icehouse world (e.g., Baatsen et al., 2020; Goldner et
al., 2014; Kennedy-Asser et al., 2019). Although 4X is likely to represent the upper end of~~too high~~ pCO_2 possible values for
the late Eocene (values rather approximate ~ 800 ppm from the Lutetian to the Priabonian; Foster et al., 2017), the use of this
value is justified to better reconstruct high-latitudes temperatures (Huber and Caballero, 2011). A good agreement between
warm conditions and Bartonian SST data has also been recently shown by other experiments using the model IPSL-CM5A2
with middle / late Eocene boundary conditions (Tardif et al., 2020; Toumoulin et al., 2020). We thus argue that the use of the
4X simulation is appropriate to study possible variations of pCO_2 during the Eocene, but the use of the 3X simulation is better
to study the changes between the Priabonian and the Rupelian.

4.1.2 Temperature seasonality changes through the late Eocene

The evolution of the different climate ~~parameters~~ features likely involved in ~~responsible for~~ ΔMATR is consistent with several
~~aspects of~~findings from ~~previou~~former studies. First, earlier modelling experiments have described albedo and sea-ice increase
resulting in polar amplification of the cooling (e.g., Baatsen et al., 2020; Kennedy-Asser et al., 2019) and a reinforcement of
temperature seasonality (Eldrett et al., 2009). The resulting strengthening and expansion of the northern high-~~Northern~~
latitudes MATR increase zone with pCO_2 lowering is a good explanation for the dramatic seasonality increase at high latitudes
suggested by some studies (Eldrett et al., 2009; Wolfe, 1992; Zanazzi et al., 2015). In addition, changes in the ~~importance~~
magnitude and distribution of net precipitation (i.e., precipitation – evaporation) resulting from the decrease in pCO_2 ~~lowering~~
agree with former theoretical and modelling work suggesting an intensified hydrological cycle under higher pCO_2
(e.g., Carmichael et al., 2016; Hutchinson et al., 2018). This phenomenon results from a greater capacity of the air to retain
moisture and more intense atmospheric convection phenomena (Allen and Ingram, 2003; Carmichael et al., 2016; Held and

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Soden, 2006). In parallel, although the implication of changes in the atmospheric circulation in the southern South American seasonality lowering zone appears non-obvious, the intensification and weakening of the Hadley cell extent in relation to

25 changing pCO$_2$ levels have been described numerous times (e.g., Lu et al., 2007; Frierson et al., 2007)~~, but the implication of these mechanisms in the South American seasonality lowering zone appears non-obvious~~. Deeper analyses would be needed to understand the atmospheric dynamics in the simulations, which is out of the scope of the study. Finally, the increase ~~of~~ in low cloud cover is consistent with former model studies describing higher fraction of low-level clouds under lower pCO$_2$ (Baatsen et al., 2020; Caballero and Huber, 2013; Zhu et al., 2019). ~~Such a trend could be explained by a higher efficiency of~~

30 ~~cloud water conversion into precipitation in warmer climates (Zhu et al., 2019).~~ Nevertheless, although a low-level cloud cover increase due to pCO$_2$ drop is consistent with increased air moisture in Western Europe at the EOT (Kocsis et al., 2014), this parameter remains poorly constrained in paleoclimate archives and modelling analysis (Lunt et al., 2020; Sagoo et al., 2013). Despite these agreements, the MATR evolution resulting from pCO$_2$ drop does not clearly match data estimates whether they correspond to both Lutetian-Priabonian or to Priabonian-Rupelian changes. This suggests that the temperature seasonality

35 ~~compiled~~ inferred from proxy data can only be partly explained by a pCO$_2$ drop. Since zonal ΔMATR patterns are simulated~~visible~~ with a pCO$_2$ drop of 1PAL (either from 4X to 3X or from 3X to 2X) we hypothesize that they likely occurred before the AIS onset, and that the strengthening of seasonality occurred in northern high-~~northern~~latitudes ~~were among the first to observe seasonality strengthening~~in the first place. However, ~~the major part~~most of Lutetian-Priabonian data ~~is~~ are ~~outside this area~~not located in the high-latitudes, which prevents ~~from~~ unambiguous testing ~~of~~ this hypothesis (Figure 4 a,b;

40 Supporting Table 1). Similarly, the presence of areas ~~of~~with decreased seasonality due to changes in the hydrological cycle (i.e., USA, Central Asia, north Australia) cannot be confirmed because of a lack of data in these areas: although some of the data associated with a decrease in the MATR share the same latitudinal bands, none of them are directly located within a zone of MATR decrease. ~~It might be of interest checking for~~ New additional seasonal temperature records in these areas would be interesting to better trace such eventual early trends. ~~This~~The general low fit of data and model values for middle to late Eocene

45 changes ~~was~~is, to some extent, predictable since the ice-free 2X simulation ~~was set ice-free and thus,~~ does not ~~either~~represent the late Eocene ~~nor the early Oligocene~~ (see Material and Method section) and was designed as a sensitivity test. Indeed, small scale glaciations (25-35% modern AIS) ~~have been described already~~may have existed during the late Eocene, before the EOT, associated with a moderate sea-level decrease (Carter et al., 2017; Miller et al., 2020; Scher et al., 2014). Interestingly, the combination of the three forcing mechanisms ~~also~~leads to a better agreement of the modelled ΔMATR ~~and~~with middle to late

50 Eocene data, especially in coastal areas of Kamchatka, and South China (triangles, Figure 4). Although the 70-m sea level decrease ~~from~~ prescribed in the 2X-ICE-SL simulation is ~~too important~~unrealistic for the late Eocene, the better data-model agreement when both AIS and sea-level decrease are considered suggests that small ice-sheet development before the EOT may have played a significant role in driving the middle to late Eocene ΔMATR. Additional sensitivity experiments, with ~~lower~~a smaller AIS and intermediate sea-level drop, may ~~enable~~allow further quantif~~ying~~ication of the sensitivity of coastal

55 localities to ~~before EOT smaller~~sea-level variations occurring before the EOT.

4.1.3 Temperature seasonality changes through the EOT

The use of two simulations to set up the effect of the AIS onset (with or without a drop -in sea level) is interesting to unravel the direct and indirect mechanisms affecting temperatures. Temperature changes resulting from the presence of the AIS alone (i.e., not taking into account sea level) are consistent with former model studies that simulate a highly regional effect on atmospheric temperature (see supporting information of Hutchinson et al., 2021), although the changes ~~we observe~~ in our simulations spread more widely over the Southern Ocean and Australia ~~(see supporting information of Hutchinson et al., 2021 for model maps)~~. ~~However, t~~The decreasing seasonality zones modelled at high and mid-latitudes of the Southern Hemisphere are mostly associated with an absence of seasonality change in the data, which often display stable vegetation and biomes from the late Eocene to the Rupelian (Hutchinson et al., 2021; Kohn et al., 2015; Nott and Owen, 1992; Pocknall, 1989; Pound and Salzmann, 2017). This apparent mismatch calls into question the capability of paleobotanical proxies to record temperature seasonality decrease in environments already characterized by low seasonality. Indeed, the decrease in the temperature seasonality is associated with a more pronounced drop in summer temperatures, which is a less limiting factor for flora distribution and thus less constrained in the fossil record than winter temperatures (Huber and Caballero, 2011).

~~The best representation of the~~The evolution of temperature seasonality ~~evolution~~ from the Priabonian to the Rupelian ~~arises~~ is better represented when the sea level drop associated with the AIS is taken into account (Table 2, Figure 4, 8). This consequence of the Antarctic glaciation has global repercussions and explains part of the heterogeneity documented in the data, as previously suggested (Pound and Salzmann, 2017). ~~Note that o~~Our results are very dependent on the paleogeography used in the simulations and of the proxy location ~~of the data we compared to~~used in our data-model comparison~~ling results~~. Because our Rupelian simulations use a late Eocene ~~are constructed from Priabonian~~ paleogeography with a global sea -level lowering, we overlook some ~~of the~~ paleogeographic changes that occurred between both periods ~~are not represented~~, which may affect our seasonality reconstruction. The gradual northward migration of Australia is not considered; the Neotethys is gradually closed during the early Oligocene but a deep-sea passage to the north of the Arabian Plate remains present in our ~~map~~paleogeography~~, to the north of the Arabian Plate~~ (Barrier et al., 2018). ~~Failure to take this difference into account could lead to a misrepresentation of ΔMATR in this area.~~ Another source of error may come from fragmented continental areas such as those seen in Europe at that time. In these zones, temperature changes recorded through the EOT are heterogeneous ~~with~~ as paleovegetation studies suggest~~ing~~ medium (1.8 - 2.1°C; Moraweck et al., 2019; Teodoridis et Kvaček, 2015; Tosal et al., 2019) to strong (up to 8.3°C; Tanrattana et al., 2020) MATR increase. The heterogeneity shown in data might thus result from smaller scale paleogeographic changes through the EOT that are not well represented by the resolution used in our simulations. This variability of data ΔMATR estimate could also be due to (1) a variable quality of MATR data related to the fragmentary nature of the fossil record and to differential recording of vegetation types, as well as (2) differences in the temperature of marine/oceanic zones before regression. Depending on their extension and depth, these seas may have buffered more or less importantly seasonal temperature variations of the nearby regions, and therefore their disappearance may have affected the MATR in different magnitude. A~~n~~ early Oligocene ~~late~~ intensification of seasonality in Central and Eastern Europe, associated

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to major phase of Antarctic ice-sheet expansion (and its effect on sea level), ~~related to changes in geography induced by sea~~

90 ~~level decline and not by the *p*CO₂ lowering,~~ is consistent with fairly stable vegetation between the middle and late Eocene (Bozukov et al., 2009; Kvaček et al., 2014; Moraweck et al., 2015). This may result from the proximity with the warm Tethys, ~~which may have~~ buffer~~ing~~ed the EOT cooling, as suggested by stable $\delta^{18}O$ describing moderate temperature changes in this area (Kocsis et al., 2014). ~~The heterogeneity shown in data might thus result from smaller-scale paleogeographic changes through the EOT that are not represented in our simulations.~~

95 Finally, ~~In addition,~~ differences between our modelling results and data may also be related to the amplitude of the sea-level drop used in our simulation compared to its variability during the Rupelian. The EOT is generally described in two steps: a first event at ~ 33.9 Ma with both a decrease in temperature and sea level (~ 25 m) and a second event, the Early Oligocene Glacial Maximum (EOGM), between approximately 33.65 and 33.15 Ma, starting after a large oxygen isotope incursion (often referred to as "Oi-1"), which is characterized by an additional 50 m sea-level decrease (see Hutchinson et al., 2021 for synthesis

00 and terminology, and Miller et al., 2020). The sum of these two steps corresponds to the boundary conditions of our simulation. However, important variations of the East Antarctic Ice-Sheet have been described until the early Miocene (50-60 m sea-level equivalent; Miller et al., 2020). Directly after the EOGM phase, a decrease in ice-volume is visible between 33.15 and 32.8 Ma, before increasing again and remaining stable between 32.8 and 29 Ma (after the "Oi-1a" event; Galeotti et al., 2016). Due to the combined effects of the drop in CO_2 and the development of the AIS (and the amplitude of the associated drop in sea

05 level, 70 m), the important changes in seasonality reconstructed here (2X-ICE-SL *minus* 3X) were probably not in place throughout the Rupelian, but rather for shorter periods during the EOGM, or later between 32.8-29 Ma. Most continental paleoclimate studies do not provide the resolution to distinguish these steps. Among the data points ~~we~~ compiled for this study, only four sites have enough temporal resolution to be linked to the EOGM phase represented by our 2X-ICE-SL simulation (Bozukov et al., 2009; Eldrett et al., 2009; Hren et al., 2013; Kohn et al., 2015; Tosal et al., 2019).

10 **4.2 Perspectives on environmental and biotic crisis**

The EOT is associated with major extinction events, of which the best known are the "Grande Coupure" in Europe and the "Mongolian Remodelling" in central Asia (Stehlin, 1909; Meng and McKenna, 1998; see Coxall and Pearson, 2007 for review). ~~Although~~ Both events were~~first~~ recognized as ~~a~~ major biotic turnover~~s~~ for ungulates (Blondel, 2001; Stehlin, 1909). ~~this biological crisis also affected~~ In addition, other vertebrates were affected by the Grande Coupure ~~, including~~ (e.g., rodents,

15 primates, amphibians and squamates), and ~~is also expressed by~~ major changes in vegetation are described, in association to the Mongolian Remodelling, and regionally, in Europe ~~that vary regionally~~ (e.g., Barbolini et al., 2020; Dolezych et al. in press; Eldrett et al., 2009; Marigó et al., 2014; Pound and Salzmann, 2017; Rage, 1986, 2013; Rage and Roček, 2003). These changes have been linked to (1) competitive interactions resulting from the dispersal of Asian taxa to Europe, and (2) EOT climate deterioration and selection processes through resource and/or habitat changes (e.g. Hooker et al., 2004; Kratz and Geisler,

20 2010; Marigó et al., 2014; Sun et al., 2015; Zhang et al., 2012). The latter mechanism is commonly related to irreversible cooling and/or aridification at the EOT (e.g., Blondel, 2001; Sun et al., 2015; Zhang et al., 2012). Climate cooling may have

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significantly reduced the habitat of well spread early Eocene tropical (and paratropical) species, ~~which are~~ characterized by narrow thermal ecological niches (Hren et al., 2009; Huang et al., 2020; Jaramillo et al., 2006; Wing, 1987). Although the distribution of fauna and flora is based on a complex set of parameters, we discuss here how ΔMATR provides an additional interpretative key for understanding biotic turnover at the EOT.

While ~~Asia and~~ North America and Asia show comparable temperature changes, our simulations highlight significant differences in the evolution of their MATR, which ~~increase and~~ decrease and either increase/decrease at a regional scale, respectively. Vegetation changes and the Mongolian Remodelling are contemporaneous to AIS growth between 32.8-29 Ma and can be compared with our 2X-ICE-SL simulation (Galeotti et al., 2016; Kraatz and Geisler, 2010; Sun et al., 2015). The MATR strengthening modelled in central Asia shows that cooling was particularly strong during winter. In addition to the aridification, this more pronounced winter-cooling may have contributed to the intensity of extinctions in this area (Barbolini et al., 2020; Dupont-Nivet et al., 2007). This seasonality strengthening is strongly driven by the proto-Parathethys retreat, which contrasts with a previous geochemistry study suggesting a weak contribution of this sea to local climate conditions (Bougeois et al., 2018). Conversely, the ~~the decrease in MATR~~zone of decreased MATR reconstructed in North America may ~~provides~~ provide an explanation for the low impact of the EOT on fauna and vegetation in this area (Coxall and Pearson, 2007; Prothero and Heaton, 1996; Stucky, 1992). Despite a similar decrease of the mean annual temperature, most of the temperature drop is in summer and ~~isn't~~is not associated with the onset of cold winters (Figure S4~~3~~). We hypothesize that these patterns enabled a greater persistence of existing warm-temperate to ~~paratropical~~paratropicale vegetation and associated biota (Pound and Salzmann, 2017). The study of Tardif et al. (~~in preparation~~2021) using the same model and similar simulations (4X and 2X-ICE) with a dynamic vegetation module shows moderate biome changes across the EOT in this ~~area~~North America decreased seasonality zone. Reduced stress on biodiversity in areas with limited or reduced MATR changes~~This hypothesis,~~ is also consistent with moderate vegetation changes across the EOT in areas with decreasing seasonality in the Southern Hemisphere (see discussion 4.1.3).

Europe stands in an intermediate position between North America and Asia with generally weaker changes in MATR (Figure 4.d); Eastern Europe ~~displays~~exhibits a slight increase in MATR, while MATR decreases in the west. Although comparable ΔMATR values could have different impacts depending on initial MATR, the types of ecosystems and their resilience, the strong consequences of moderate seasonality increase on growing season length supports the hypothesis that seasonality changes may also have contributed to shaping the biodiversity evolution in Central Europe. The late development of increased seasonality zones in this area, linked to the major phase of sea level drop, could explain the persistence of fairly stable vegetation during the Eocene (Kvaček et al., 2014; Hutchinson et al., 2021). Yet, given the fragmented nature of Europe at this time, increases in seasonality prior to EOT would also be possible as a result of smaller, but locally significant, sea level variations. These d~~D~~ifferences in the evolution of the MATR between North America, Europe and Asia support several studies suggesting different causes for EOT extinctions (Blondel, 2001; Hooker et al., 2004; Meng and McKenna 1998; Sun et al., 2015). Finally, little is known about the EOT in Africa (notably because of a few Oligocene sites), but the ~~rare~~ data available suggest moderate changes in~~stable~~ northern African flora and fauna ~~in northern Africa~~ (Hutchinson et al., 2021; Jacobs et al.,

2010; Pound and Salzmann, 2017; Rasmussen et al., 1992). The significant increase in seasonality in North Africa seen in our simulations (which results from the emergence of part of the continent), differs from the one observed in other areas, since it is linked to an increase in summer temperatures (barely no change in winter). ~~The lack of data in this area could be partly explained by the fact that much of the increase in seasonality is localized in a region that changes from marine to continental.~~

60 ~~In addition,We propose that~~ ~~U~~unchanged winter temperatures and shift of marine to terrestrial environments might ~~also~~ complicate the recording of this temperature seasonality strengthening ~~might explain the apparent lack of biotic response through the EOT in North Africa~~. Recording low latitude changes in seasonality strengthening may however be possible as shown ~~, though more data are needed on this continent to better document the EOT response.~~ by a recent study combining multiple lines of evidences (including plant and primate macrofossils), which suggest a potential shift from tropical to more

65 open deciduous vegetation through the EOT, reflecting increased seasonality in precipitation and/or temperature seasonality during the early Oligocene at low latitudes of South America (Peru, ~7°S, Antoine et al., 2021). More studies would probably enable a better understanding of the evolution of the seasonality in this low latitude area.

5 Conclusion

This study investigates the changes in temperature seasonality during the middle to late Eocene and across the EOT. MATR

70 change modelled with ~~T~~the combined effects of pCO_2 drop, AIS formation and sea-level ~~decrease~~ lowering ~~impact the seasonality in the right direction when compared to~~are qualitatively consistent with the proxy data reconstruction of the late Eocene to early Oligocene ~~changes in MATR~~. The decrease in pCO_2 leads to a marked strengthening of seasonality ~~at high northern latitudes~~ in the northern high-latitudes, which may have started earlier than the EOT, during the late Eocene. The formation of the AIS and the resulting sea-level drop lead to both an intensification and an extension of increasing seasonality

75 areas. The best agreement between data and modelled MATR evolution throughout the EOT is reached when all three parameters are combined. ~~When all three parameters are combined, a statistically significant correlation between data and modeled MATR evolution throughout the EOT is reached.~~ Accounting for sea level changes associated with the Antarctic glaciation~~freeze-up~~ appears to be the most important parameter to explain the heterogeneity of ΔMATR across the EOT. A seasonality increase is also visible in middle to late Eocene localities, which may reflect earlier sea level changes associated

80 with the incipient precursors of the Antarctic ice sheet. A discrepancy between data and model is present for quantitative MATR change estimates across the EOT, with less marked seasonality changes in the model. This is mainly due to areas where a decrease in seasonality is predicted by the model while the vegetation proxies show stable vegetation. We hypothesize that this discrepancy can be explained by a low capacity of vegetation to ~~register~~ record decreases in summer temperatures compared to winter temperatures.

85 Reconstructing changes in MATR brings additional constraints on the abiotic environmental factors~~pressure applied~~ at play on land between the middle Eocene and the early Oligocene. The different mechanisms described here likely explain the heterogeneity in seasonality changes found in data across the greenhouse-icehouse transition, and provide insights into the

diversity of continental paleoenvironments. The map of ΔMATR reconstructed here may provide new elements to better understand major extinction events at the EOT. T~~As a first step, t~~This study ~~onl~~primarily focused on the evolution of

90 temperature seasonality that has the clearest evolution~~;~~. T~~t~~he variability of other seasonality parameters, including rainfall seasonality, w~~ill~~~~ould also~~ be worth investigating in future studies to obtain a finer~~better~~ picture of the evolution of terrestrial climates and biodiversity through the EOT. In addition, further work using higher resolution Rupelian paleogeography and regional models would be of great interest to better reconstruct temperature seasonality changes, especially in highly fragmented land areas such as Europe during the Eocene.

Code availability

95 LMDZ, XIOS, NEMO and ORCHIDEE are released under the terms of the CeCILL license. OASISMCT is released under the terms of the Lesser GNU General Public License (LGPL). IPSL-CM5A2 code is publicly available through svn, with the following command lines: svn co http://forge.ipsl.jussieu.fr/igcmg/svn/modipsl/branches/publications/IPSLCM5A2.1_11192019 (last access: 16 February

00 2021, IPSL Climate Modelling Centre, 2021a) modipsl cd modipsl/util;./model IPSLCM5A2.1

The mod.def file provides information regarding the different revisions used, namely

- NEMOGCMbranchnemo_v3_6_STABLErevision666-XIOS2branchs/xios-2.5revision1763
- IOIPSL/srcsvntags/v2_2_2
- LMDZ5branches/IPSLCM5A2.1rev3591

05 - branches/publications/ORCHIDEE_IPSLCM5A2.1.r5307rev6336–OASIS3-MCT2.0_branch(rev4775IPSLserver)

The login/password combination requested for the first use to download the ORCHIDEE component is anonymous/anonymous. We recommend referring to the project website http://forge.ipsl.jussieu.fr/igcmg_doc/wiki/Doc/Config/IPSLCM5A2 (last access: 16 February 2021, IPSL Climate Modelling Centre, 2021b) for a proper installation and compilation of the environment.

Data availability

10 The key climatological outputs of the simulations are stored in the PANGAEA database (data are currently under review and may be sent to reviewers upon request).

Author contribution

YD, AT and JBL conducted the modelling experiments. AT compiled proxy-data, ~~analyzed~~analysed the model results,

15 generated figures and tables, and drafted the manuscript. AT, YD, DT and JBL discussed the paleoclimate results. LK

contributed to the paleobotanical context, and AL and GDN to the paleogeographic and geological context. All authors have provided critical feedback and contributed to the final manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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