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The relative roles of CO₂ and palaeogeography in determining Late Miocene climate: results from a terrestrial model-data comparison

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The Late Miocene (\sim 11.6–5.3 Ma) palaeorecord provides evidence for a warmer and wetter climate than that of today and there is uncertainty in the palaeo-CO₂ record of at least 150 ppmv. We present results from fully coupled atmosphere-ocean-vegetation simulations for the Late Miocene that examine the relative roles of palaeogeography (topography and ice sheet geometry) and $\rm CO_2$ concentration in the determination of Late Miocene climate through comprehensive terrestrial model-data comparisons. Assuming that the data accurately reflects the Late Miocene climate, and that the Late Miocene palaeogeographic reconstruction used in the model is robust, then results indicate that the proxy-derived precipitation differences between the Late Miocene and modern can be largely accounted for by the palaeogeographic changes alone. However, the proxy-derived temperatures differences between the Late Miocene and modern can only begin to be accounted for if we assume a palaeo- $\rm CO_2$ concentration towards the higher end of the range of estimates.

1 Introduction

The terrestrial palaeorecord contains evidence that the Late Miocene (~11.6–5.3 Ma) climate was, in many regions, much warmer and/or wetter than today (e.g. Pound et al., 2011). For example, warm temperate forests thrived in what is now the Circumboreal Region (Worobiec and Lesiak, 1998; Denk et al., 2005) and grasslands existed in modern desert regions (e.g. the Arabian peninsula, Kingston and Hill, 1999; the Sahara Desert, Vignaud et al., 2002). Moreover, although it is widely suggested that a large-scale Antarctic ice sheet has existed throughout the Late Miocene (e.g. Shackleton and Kennett, 1975; Lewis et al., 2008), Northern Hemisphere glaciation is thought to have been limited (Moran et al., 2006; Kamikuri et al., 2007; Jakobsson et al., 2007).

The Late Miocene is also a period in which significant tectonic reorganisation occurred including major tectonic uplift of the Himalayas (Harrison et al., 1992; Molnar et al., 1993; Rowley and Currie, 2006a; Fang et al., 2005), the Andes (Gregory-Wodzicki,

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2002; Garzione et al., 2008), the North American Rockies (Morgan and Swanberg, 1985), the East African Plateaus (Saggerson and Baker, 1965; Yemane et al., 1985), and the Alps (Spiegel et al., 2001; Kuhlemann, 2007); and ocean gateways, e.g. there is evidence for an open Panama Gateway between the Atlantic and Pacific Oceans (Keigwin, 1982; Duque-Caro, 1990) and an unrestricted Indonesian Seaway between the Pacific and Indian Oceans (van Andel et al., 1975; Edwards, 1975; Kennett et al., 1985; Cane and Molnar, 2001) during the Late Miocene.

Modelling studies have shown that Late Miocene-like differences in palaeogeography and ice sheet extents are likely to have resulted in large changes to both atmospheric and oceanic circulation compared to the present day (e.g. Andes uplift: Takahashi and Battisti, 2007; Rockies uplift: Seager et al., 2002; Foster et al., 2010; uplift of the Tibetan Plateau: Ramstein et al., 1997; Lunt et al., 2010; Zhongshi et al., 2007a, b; Ruddiman et al., 1997; Kutzbach and Behling, 2004; Northern Hemispheric glaciation: Crowley and Baum, 1995; Lunt et al., 2004; Tonazzio et al., 2004; Panama Gateway closure: Lohmann et al., 2006; Nisancioglu et al., 2003; Schneider and Schmittner, 2006; Lunt et al., 2008b; and closure of the Paratethys: Ramstein et al., 1997; Zhang et al., 2011).

Although there is considerable scatter in the Late Miocene atmospheric CO reconstructions deduced from a variety of proxies, the estimates are generally quite low as compared to older time periods such as the Eocene (Beerling and Royer, 2011) (Fig. 1: Freeman and Hayes, 1992; Pagani et al., 1999a, b; Pearson and Palmer, 2000; Demicco et al., 2003; Kurschner et al., 1996, 2008; Retallack, 2001; Tripati et al., 2009).

It is therefore reasonable to expect that the combination of all of these changes (Fig. 2) would result in a climate that was significantly different to that which we experience today, and this is supported by GCM modelling simulations for the Late Miocene (e.g. Steppuhn et al., 2006; Lunt et al., 2008a; Micheels et al., 2011; Knorr et al., 2011). However, in order to evaluate the simulated Late Miocene climate from a GCM it is necessary to make quantitative comparisons with the palaeorecord.

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Previous climate modelling has generally struggled to simulate the warm conditions inferred from the palaeorecord, when imposing relatively low CO2 concentrations in the models (e.g. Steppuhn et al., 2006; Micheels et al., 2007), although a recent study which also included prescribed vegetation has met with some success, highlighting the importance of vegetation (Knorr et al., 2011). For computational reasons, most of the Late Miocene modelling to date has been carried out with atmosphere-only climate models (Barron, 1985; Kutzbach et al., 1989; Ruddiman and Kutzbach, 1989; Fluteau et al., 1999; Zhongshi et al., 2007a, b; Lunt et al., 2008a), atmosphere-slab ocean climate models which are incapable of simulating dynamic changes to ocean currents or overturning circulation patterns (Prell and Kutzbach, 1992; Dutton and Barron, 1997; Ramstein et al., 1997; Ruddiman et al., 1997; Kutzbach and Behling, 2004; Steppuhn et al., 2006, 2007; Micheels et al., 2007, 2009a) or uncoupled atmosphere and ocean models (Lohmann et al., 2006). Recent work using a fully coupled atmosphere-ocean climate model has highlighted the disparity between the results obtained from atmosphere-only or atmosphere-slab ocean models and a model capable of incorporating important ocean circulation feedbacks (Micheels et al., 2011; Knorr et al., 2011). This is particularly important for simulating the Late Miocene, since major reorganisation of Atlantic, Pacific and Indian Ocean circulation patterns occurred at this time (Collins et al., 1996; Kennett et al., 1985; Duque-Caro, 1990; Kameo and Sato, 2000; Cane and Molnar, 2001). Many of the most advanced GCM's now incorporate a dynamic land surface component which both responds, and feedbacks to, the atmospheric state, therefore allowing a more stringent test of the GCM than using a fixed late Miocene vegetation reconstruction.

These lines of evidence - warm/wet Late Miocene climate, uncertain CO₂, and significant tectonic uplift and ice sheet change – demand the question, "Can modelling inform what the likely relative roles of palaeogeographic changes and CO2 concentrations are in determining Late Miocene climate". Here we present the model results from a fully coupled atmosphere-ocean-vegetation GCM for the Late Miocene, and compare our simulations with a synthesis of available climate proxies from the terrestrial

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realm. Notable differences are found to occur in the oceanographic realm for our Late Miocene simulations as compared to our control simulation, such as warming in the Indian and Pacific Oceans, reductions in overturning circulation in the North Atlantic and widespread cooling of the waters across the Panama Gateway. Most marine proxy data available for the Late Miocene comes from the $\delta^{18}O_c$ of foraminifera, much of which has not been converted to palaeotemperature estimates. Furthermore, the treatment of the uncertainties associated with that data such as $\delta^{18}O_{sw}$ reconstruction, depth habitat and seasonality considerations, and preservation requires in-depth discussion which is outside the scope of this manuscript. Consequently, although we do show and discuss near-surface oceanographic differences between out Late Miocene and CTRL simulations, these differences will be described in more depth and compared with data in a forthcoming paper (Bradshaw et al., 2012).

As the timing and magnitude of the tectonic changes during the Late Miocene are uncertain, GCM simulations for this period are representative of a large timeslab. But this also allows us to examine the impact of large changes in the palaeogeography and to assemble as large a number of palaeodata as possible. We therefore examine the compiled palaeodata for any marked differences in the climate between the Tortonian (11.6-7.25 Ma) and the Messinian (7.25-5.3 Ma) of the Late Miocene and compare the model simulations to those sub-datasets separately.

Data and model descriptions

In this section we describe the terrestrial palaeodata and the GCM that has been used, and discuss some of the uncertainties that are inherent in both.

Description of the quantitative Late Miocene palaeodata

The palaeorecord of the Late Miocene is sparse in comparison with more recent periods such as the LGM, (Farrera et al., 1999; Waelbroeck et al., 2009). We have

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compiled a total of 1109 terrestrial climate reconstructions from the literature for the climatic variables of mean annual temperature (MAT) and mean annual precipitation (MAP). As comparison is made to the dataset separately for the Messinian and the Tortonian stages, any data that had age uncertainty placing it between the two stages was duplicated, one datapoint residing in each stage. The total number of datapoints considered therefore increased to 1671.

The data synthesis largely consists of the data from the NECLIME database (Bruch et al., 2007; Utescher et al., 2011) and the NOW Neogene Mammal Database (Eronen et al., 2010; Fortelius, 2012) but also includes data from a variety of other sources including the synthesis of Steppuhn et al. (2007), as detailed in the Supplement. These reconstructions are derived from microfauna, macrofauna, microflora and macroflora proxies using a variety of different reconstruction methods including the co-existence approach (Mosbrugger and Utescher, 1997), the climatic amplitude method (Fauquette et al., 2006), nearest living relative methods (Wolfe, 1993; Spicer, 2007; Spicer et al., 2009), species characteristic approaches (Eronen et al., 2010; Jacobs and Deino, 1996), and species composition approaches (Montuire et al., 2006; Bohme et al., 2008; van Dam, 2006). All of these terrestrial data are provided in the Supplement. Comparison is also made to the Tortonian biome reconstruction dataset of Pound et al. (2011).

As a multi-proxy dataset is used, there is considerable variability in the age constraint due to uncertainty in the dating. Although the data from small mammals and microfloras are generally very well dated, large mammals and macrofloras have much looser age-determination and many macroflora datapoints are only consigned to the Messinian or the Tortonian. Therefore the data is considered in 2 timeslabs: the Messinian (5.3–7.25 Ma) and the Tortonian (7.25–11.6 Ma). We note that the proxy data used to is likely to have been generated under a range of different orbital configurations and other climatic cycles, and individual datapoints could therefore represent extremes in these cycles, but this is unlikely to have biased the entire dataset.

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For a comparison study between fossil data and GCM simulations where a palaeon-tological assemblage has been used to reconstruct climatic conditions, such as the mean annual temperature or precipitation, two main uncertainties exist: taphonomical (the death, decay, deposition and preservation of fossils) and the uncertainties associated with the data reconstruction techniques. Discussion of these are outside the scope of this paper, and the reader is referred to the source references for those details: (Taphonomy: Western and Behrensmeyer, 2009; Martin, 1999; Behrensmeyer et al., 2000. Data reconstruction techniques: Mosbrugger and Utescher, 1997; Fauquette et al., 2006; Wolfe, 1993; Spicer, 2007; Spicer et al., 2009; Eronen et al., 2010; Jacobs and Deino, 1996; Montuire et al., 2006; Bohme et al., 2008; van Dam, 2006).

2.2 Description of the modern reference climate (modern potential natural climate)

For the purpose of this study, we are interested in the Late Miocene climate because we wish to understand how and why it was different to today. In terms of understanding these differences, we are only interested in the changes that occur under natural forcing (a modern potential natural climate), however the modern instrument record contains both natural and anthropogenic forcing. In order to make an estimate of the extent of anthropogenic influence on the modern instrumental record (IR $_{20\text{thC}}$), we derive grid-based correction factors using the anomaly between the "Preindustrial" simulations (Model $_{\text{preind}}$) and the "20th Century" simulations (Model $_{20\text{thC}}$) of the CMIP-4 GCM ensemble (IPCC, 2007) as detailed in Eq. (1). Through application of the correction factors, it is assumed that the modern instrumental record is a suitable proxy for the potential natural climate state.

Modern potential natural climate =
$$IR_{20thC} - \left(\frac{1}{n}\sum_{i=1}^{n} Model_{20thC} - Model_{preind}\right)$$
 (1)

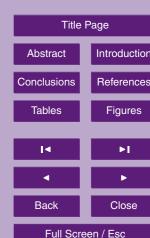
The modern instrumental record used is the CRU-TS 3.0 Climate Database (Mitchell and Jones, 2005), an interpolation of mean monthly surface weather station data to a

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 0.5×0.5 degree grid, spanning the period 1900–2006. The modern climate estimates for temperature and precipitation at any grid point will be least certain in areas of largest interpolation where no weather stations exist, but in other areas there is uncertainty in the records too due to limited temporal operation of some stations, station movement, urbanisation and other land use changes. The observational datasets are at a higher spatial resolution than the HadCM3L model, therefore when aggregating the observations to the HadCM3L model resolution the minimum and maximum values within each grid box are retained in order to account for within-grid box uncertainty.

2.3 Description of the models

2.3.1 HadCM3L

The Hadley Centre Coupled Model, version 3 (HadCM3) is a fully coupled atmosphereocean general circulation model comprising the atmospheric model HadAM3 (resolution 2.5° latitude by 3.75° longitude), and the ocean model HadOM3 (resolution 1.25° latitude by 1.25° longitude) (Gordon et al., 2000). It is computationally demanding to run HadCM3 simulations to equilibrium so we use a reduced ocean resolution version, HadCM3L (resolution 2.5° latitude by 3.75° longitude) (Cox et al., 2000). The model contains many parameterizations of atmospheric and oceanic processes, including atmospheric convection (Gregory and Rowntree, 1990), boundary layer mixing (Smith, 1993), ocean layer mixing (Gent and McWilliams, 1990), and radiation (Edwards and Slingo, 1996). HadCM3L has been used in studies of the future (e.g. Cox et al., 2000) and the past (e.g. Lunt et al., 2007, 2010). As HadCM3L has a reduced ocean resolution, model performance is degraded compared to HadCM3. For example, the ocean resolution of HadCM3L is such that the Denmark Straits are unresolved and therefore the two terrestrial grid points representing Iceland are removed to prevent an unacceptable build up of sea ice in the Nordic Sea (Jones, 2003) The version of HadCM3L used here does not therefore require the inclusion of flux corrections to maintain a stable overturning circulation for the modern ocean (Jones, 2003).

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The model land surface processes are simulated using the MOSES-2.1 (Met Office Surface Exchange Scheme) land surface scheme (Essery and Clark, 2003). There are nine surface types, five of which correspond to plant functional types (PFTs): broadleaf tree, needleleaf tree, C_3 grass, C_4 grass and shrub; the remainder representing bare soil, water bodies, ice and urban surfaces.

2.3.2 TRIFFID

The dynamic global vegetation model coupled to HadCM3L is TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics), a full description of which is given in (Cox, 2001) and (Hughes et al., 2004). TRIFFID calculates areal coverage, leaf area index and canopy height for the five PFTs, which each respond differently to climate and CO₂ forcing, and all can co-exist within the same gridbox.

Two modes of coupling between the TRIFFID and the GCM are used: a spinup equilibrium mode in which the fluxes between the land and the atmosphere are calculated by the GCM and averaged over ~5 yr, and a dynamic mode, used for the last 100 yr of the simulations, in which the fluxes are averaged over 10 days. The averaged fluxes are then passed to TRIFFID which calculates the growth and expansion of the existing vegetation, and updates the land surface parameters based on the new vegetation distribution and structure.

2.3.3 BIOME4

In order to make model-data comparisons with a recently published biome reconstruction dataset for the Late Miocene (Pound et al., 2011), the HadCM3L model climatologies are used to drive the BIOME4 vegetation model offline (Kaplan, 2001). The 28 different vegetation classes used by Pound et al. (2011) match the vegetation classifications of the BIOME4 model, which has successfully been used for previous pre-Quaternary vegetation model-data comparisons (e.g. Salzmann et al., 2009).

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No GCM is able to reproduce exactly the modern climate, and a discussion of the biases in the HadCM3 version of our GCM is given in Gordon et al. (2000). The HadCM3L version of the model suffers from temperature biases, particularly for toocool ocean temperatures at high latitudes. Temperatures over the land surface are generally within the range of uncertainty of the CRU-TS 3.0 modern instrumental data (Mitchell and Jones, 2005), but there is still a marked cold bias at high northern latitudes of up to 10 °C above 70° N. Similar biases exist for precipitation, with the mean annual precipitation being underestimated by up to a third in parts of northern South America and southern India, and overestimated by the same amount in some tropical regions of South America, Africa and Australia.

Both TRIFFID and BIOME4 are based on physiological constraints that influence vegetation distributions, and are therefore attempting to model the potential natural vegetation for a given climatology. Estimates of anthropogenic land surfaces (urban and agricultural) amount to some 16% of the total land surface area (CIESIN, 2004; Matthews, 1983; Ramankutty and Foley, 1999; Schneider et al., 2009) and therefore discrepancies will exist in those areas between reference maps of reconstructed natural vegetation (the vegetation that might exist if human influence were to cease, based on extrapolation of remnants of natural vegetation) and model-produced maps of potential natural vegetation (the vegetation that might exist if human influence had never existed), and these may be significant in areas of deforestation (Prentice et al., 1992).

The TRIFFID model has been compared to IGBP-DIS land cover dataset, which represents the modern distribution of vegetation as derived from satellite image interpretation (Loveland and Belward, 1997; Betts et al., 2004). This suggests that the shrub PFT is overestimated at high latitudes, that the broadleaf tree PFT is overestimated in equatorial regions, and that grasses tend to be globally slightly underestimated. The discrepancies between the satellite imagery and the TRIFFID model are suggested to be a combination of orographic representation leading to underestimation of precipitation, differences between the anthropogenic masks used in their version of the

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model and that found on the satellite imagery, and the inadequate treatment of natural disturbance mechanisms such as fire (Betts et al., 2004). The version of the model used here aims to reproduce the vegetation of a modern potential natural climate, and therefore evaluation of the predicted PFTs is difficult. It is also hard to identify, when the modern predicted PFTs are likely wrong (e.g. needleleaf forests in south-east Asia and extensive broadleaf forests in Australia), whether those inadequacies are due to the climate model or the vegetation model.

The BIOME4 model has been shown to produce a fair comparison to the vegetation data of Olson et al. (1983), with most of the areas of discrepancy being attributed to differences between potential natural vegetation and actual modern vegetation as a result of human influence. Other suggested sources of error include incorrect climatological forcing due to the difficulty in representing orographic extremes, and missing parameterisations in the model, particularly related to seasonality (Prentice et al., 1992).

The GCM simulations were integrated over 2100 model years. Particular attention is given to the question of equilibrium in the climate system, particularly for the deep ocean as it has been shown the global mean air temperature may not be a good indicator of model equilibrium (Brandefelt and Otto-Bliesner, 2009). The trend in the global mean ocean temperatures is very small for the Late Miocene simulations (<0.0008 °C century⁻¹) and our control simulation (0.0005 °C century⁻¹), although it is not possible to rule out some remaining disequilibrium. The analysis in this paper is carried out using the climatological means of the last 50 yr of the simulations, after the TRIFFID dynamic mode had used for 100 yr to ensure full consideration of interannual variability in the vegetation component.

3 Experiment design

For the Late Miocene, the palaeogeography (including ice sheet geometry) derived by Markwick (2007) is used, which is representative of the timeslab 11.6 to 5.3 Ma. The length of this palaeogeographic timeslab is necessarily long due to difficulties (

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associated with the poorly constrained chronology and age estimates uncertainty for the various tectonic and ice sheet changes (Markwick and Valdes, 2004).

The orography, ice sheet configuration and continental positions assumed for the model simulations are shown in Fig. 2, and are now discussed in more detail. As we perform both changes in palaeogeography and CO_2 concentration, there is the possibility that non-linearity in the climate system could produce a different result to that which we present here (i.e. if we were to consider the impact of CO_2 changes independently of palaeogeography changes). However, recent work for the Pliocene, using the HadCM3 version of the model used here, suggests that any non-linearity would be small (refer to Fig. 6c of Lunt et al., 2012).

3.1 Modern configuration

For the modern control (CTRL) simulation we use the standard UK Meteorological Office configurations for modern continental positions and both terrestrial and ice sheet elevations as defined in the ETOPO5 dataset (NOAA, 1988). Land ice grid boxes and soil type distributions used in CTRL are based on the identification of Wilson and Henderson-Sellers (1985). The two land grid boxes that represent Iceland are converted to ocean grid boxes as discussed in Sect. 2.3.4.

We also use modern ETOPO5 bathymetry (NOAA, 1988). The two new ocean grid boxes replacing Iceland are assigned the average depth of the surrounding ocean grid boxes. We note that the land-sea mask generation algorithms that map the high resolution data onto the HadCM3L grid also results in the non-representation of many other small islands.

For the purpose of this study we wish to model a modern potential natural climate, and therefore assume a preindustrial atmospheric CO_2 concentration in the range 275–284 ppm (Etheridge et al., 1996) and use a value of 280 ppm in CTRL, consistent with the Climate Model Intercomparison Project standard (Meehl et al., 2007).

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3.2.1 Orography

The orography for the Late Miocene has been reconstructed by (Markwick, 2007) using a methodology of establishing relationships between modern elevations and their tectonophysiographic settings and applying those same relationships to the geological record (a full description of the technique is described in Markwick, 2007; Markwick and Valdes, 2004). The methodology results in significant reductions in the Miocene elevations of most of the world's highest regions compared to modern. We now describe those reductions in relation to the palaeoelevation estimates of other authors; however, given the uncertainties associated with reconstructing past mountain elevation (e.g. Ehlers and Poulsen, 2009), any inconsistencies with that of Markwick (2007) would require further sensitivity experiments.

The Tibetan Plateau in the Late Miocene simulations is an average 30 % lower than in CTRL. The timing of Tibetan uplift is debated, with many studies indicating an elevation during the Late Miocene similar to today (e.g. Currie et al., 2005; DeCelles et al., 2007; Spicer et al., 2003; Garzione et al., 2000; Rowley et al., 2001; Rowley and Currie, 2006b). There is evidence that the uplift did not occur in a spatially uniform pattern (England and Searle, 1986; Clark et al., 2005; Rowley and Garzione, 2007), but a recent study has shown that modelled SSTs in the Indian and Pacific Oceans were very similar for three simulations assuming different uplift histories (Lunt et al., 2010).

The Andes are 45% lower in the Late Miocene simulations than the CTRL. This is consistent with palaeobotanical and geomorphological data which suggests that the elevation of the Andes was no more than half of the modern elevation at \sim 11–10 Ma (Gregory-Wodzicki, 2000).

The Alps are on average 30 % lower in the Late Miocene simulations than the CTRL. Palaeoaltitude estimates for the Eastern Alps are between 500 and 2000 m (Jimenez-Moreno et al., 2008; Kuhlemann, 2007). These estimates are consistent with the Markwick (2007) reconstruction.

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The Western Cordillera of North America, is on average 25% higher in the Late Miocene simulations than in the CTRL. The evolution of topographic changes in the Western Cordillera are debated. There is evidence for high elevation in the Western Cordillera of North America since the Eocene (Sjostrom et al., 2006) or even the Cretaceous (Chase et al., 1998), with the elevation in Nevada during the Middle Miocene being some 1-1.5 km higher than it is today. The dating of the collapse to present day elevation in Nevada is put at ~13 Ma by Wolfe et al. (1997) but the palaeoelevation reconstruction from Markwick (2007) differs in that Nevada is ~9 % lower in LM than CTRL. Orographic lowering in Wyoming is believed to have occurred during the Eocene (Chase et al., 1998), and the methodology used by Markwick (2007) puts Wyoming 27 % lower in the Late Miocene simulations than in the CTRL. A recent study of the Western Cordillera of North America also considers that elevations were generally lower during the Late Miocene than today, but argues for considerable evidence of surface uplift during the Late Miocene in the westernmost regions north of 45° N (Foster et al., 2010).

Ice sheet configuration 3.2.2

The extent of Late Miocene glaciation is much debated (Shackleton and Kennett, 1975; Webb and Harwood, 1991; Wilson, 1995; Pekar and DeConto, 2006; Huybrechts, 1993; Marchant et al., 1996) and perhaps highly variable (Lear et al., 2000). For the Late Miocene, the Markwick (2007) reconstruction assumes the East and West Antarctic ice sheets cover the whole Antarctic continent, although ice thickness is generally less than CTRL. The sensitivity experiments of DeConto et al. (2008) and Micheels et al. (2009a) support the evidence for the onset of some glaciation in the Northern Hemisphere during the Miocene (Moran et al., 2006; Kamikuri et al., 2007; Jakobsson et al., 2007; Denton and Armstrong, 1969; Thiede and Myhre, 1995 and references therein; Talwani and Udintsev, 1976; Warnke and Hansen, 1977). Markwick (2007) assumes much reduced Northern Hemisphere ice for the Late Miocene compared with the extent

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of the present day Greenland ice sheet. Future work will investigate the impact of ice sheet extent assumptions on the simulated Late Miocene climate.

The high latitude topography is lowered in the Late Miocene simulations compared to the CTRL, due to the removal of continental ice rather than post-Miocene uplift: Greenland is 60 % lower and Antarctica is very spatially variable, but is on average 4 % lower.

All non-ice covered land grid boxes were initialised with the TRIFFID shrub PFT before the TRIFFID model was switched on as the simulations were continuations of pre-existing simulations with global homogenous shrub coverage.

3.2.3 Continental positions

We use the Late Miocene land-sea definitions of Markwick (2007), aggregated up to the GCM resolution. Notable changes in continental positions are the more southerly position of the Australian continent, the closed Bering Straits, the extension of Eurasia into the Arctic, and the open Panama Gateway and Indonesian Seaway for the Late Miocene.

5 3.2.4 Soil type

Some of the palaeoenvironmental conditions are largely unknown for the Miocene period, such as the soil type which is typically unknown outside of some regions in North America and Kenya (Retallack, 2004; Retallack et al., 1990, 1995, 2002a, b), and so for these we use an average homogenous value derived from the CTRL simulation. Soil parameters have been shown to have significant influence on soil hydrology (Osborne et al., 2004), and therefore our choice of soil type could bias the simulated vegetation distribution and modify the simulated climate. Future experiments will be conducted to assess the extent to which the soil type could affect the results presented here.

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Late Miocene palaeobathymetry is assumed to be the same as for the CTRL, except for the land-sea mask itself, which results in a wider Indonesian Seaway and an open Panama Gateway. The algorithm used to generate the Late Miocene bathymetry assumes that the depth of all Late Miocene ocean grid boxes (that would be land today in the CTRL simulation) is the average of all neighbouring ocean grid boxes.

As palaeomagnetic studies for plate tectonic reconstruction are difficult to apply to the Indonesian islands (Gourlan et al., 2008), the evolution of their palaeogeography remains uncertain. It is generally believed that the restriction of the Indonesian Seaway has occurred in the past 20 Ma, with timing estimates for different water mass restrictions from Early Miocene to early Late Miocene (van Andel et al., 1975; Edwards, 1975), or even Pliocene (Kennett et al., 1985; Cane and Molnar, 2001; Srinivasan and Sinha, 1998). The Late Miocene seaway in our simulations is >2000 m at its deepest, as for the CTRL.

The closure of the Panama gateway in the Pliocene is the most recent major modification to oceanic gateways (Keigwin, 1982; Duque-Caro, 1990). The shoaling of the region is believed to have commenced in the Middle Miocene (Keller and Barron, 1983; Duque-Caro, 1990; Droxler et al., 1998) but determining potential depth of the sill during the Late Miocene is problematic; a depth of 200–500 m at 6 Ma is suggested by Collins et al. (1996) and <100 m depth by the early Pliocene by Keigwin (1982). Duque-Caro (1990) suggests that in the earliest Late Miocene sill depth was ~1000 m, and 150–500 m between 8.6–7 Ma, <150 m at 7–6.3 Ma and <50 m at the latest Miocene. Given our large timeslab, possible sill depths for the Late Miocene range from 1000 m to <50 m; our bathymetric algorithm produces a depth of 995 m which lies within the range of estimates.

The choice of bathymetry has been shown to have large regional impacts (e.g. the Greenland-Scotland Ridge: Robinson et al., 2011), but the uncertainty associated with palaeobathymetric reconstruction is large and therefore future work will seek to assess

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the climatic uncertainty associated with the choice of palaeobathymetry through climate sensitivity studies.

3.2.6 Atmospheric CO₂ concentration

We carry out two Late Miocene simulations, with two different values of atmospheric CO_2 concentration. Firstly, a value of 280 ppm was used, the same as CTRL, the difference in climate between these two simulations indicates the role of the palaeogeographic changes that we have made on the simulated climate. Secondly, a value of 400 ppm was used in order to test the sensitivity of the results to uncertainties in the CO_2 concentration; the difference between the 400 ppm simulation and the 280 ppm simulation indicates the role of CO_2 in determining the simulated Late Miocene climate. These values are well within the range of uncertainty of Late Miocene CO_2 concentrations based on the available proxy data, shown in Fig. 1 (Freeman and Hayes, 1992; Pagani et al., 1999a, b; Pearson and Palmer, 2000; Demicco et al., 2003; Kurschner et al., 1996, 2008; Retallack, 2001; Tripati et al., 2009). The Late Miocene simulation with a 280 ppm CO_2 concentration is hereafter referred to as LM280 and the simulation with a CO_2 concentration of 400 ppm is referred to as LM400.

3.3 Model-data comparison methodology

There are many difficulties associated with developing a methodology for a model-data comparison and in the interpretation of any results. We have considered uncertainties associated with model and data reconstructions that are often overlooked. These include uncertainties associated with the reference climatologies; poor temporal constraint leading to data location uncertainty; data transportation issues and palaeorotation uncertainty.

The methodology for estimating error ranges for each data record is as follows. First, we estimate the modern calibration error for each proxy type, if this is not already given in the original source, by assuming the same calibration error as the next most

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similar proxy reconstruction method (for example, by assuming that the physiognometric/morphology reconstructions have the same uncertainty as defined for CLAMP; see Table 1 for full details).

Secondly, we translate the individual proxy data locations back to their estimated 5 palaeolocations as dictated by their age control, with the uncertainty in age resulting in a number of possible locations for each data point. We use the same palaeorotation as Markwick (2007) to ensure consistency with the Late Miocene palaeogeography used in HadCM3L. As we do not include Iceland as land in our model, we exclude the Icelandic data from our analysis, reducing the original number of datapoints from 1109 to 1104.

Thirdly, we consider it unreasonable to expect our climate model to be able to reconstruct the exact climate at a single grid cell given the model uncertainties outlined in Sect. 2.3.4, and because comparisons made between the BIOME4 model and maps of potential natural vegetation have shown that greater reliance should be placed on broad-scale patterns rather than individual grid cells (Prentice et al., 1992), we assume that all adjacent grid cells to that underlying the palaeodata could potentially be consistent with that data. Taking this approach to the model-data comparison also allows for uncertainties in the true location of the data due to either data transportation or incorrect assumptions in the palaeorotations applied.

Because HadCM3L does not completely reproduce the modern reference climatology in the CTRL simulation it is assumed that the relative differences simulated by the model are more robust than the absolute values, and results are presented as the anomaly between the Late Miocene simulations and the modern control simulation. When comparisons are made between the model results and the palaeorecord, bias corrections are applied to the simulation results (the anomalies between the modern control simulation and the modern reference climate). As the CTRL simulation is designed to represent the modern potential natural climate and not the climate of the 20th century, we are unable to use the ideal bias correction factors given in Eq. (2),

 $Model_{HadCM3L} = Model_{HadCM3L} + (Observation_{20thC} - Model_{HadCM3L20thC})$ (2)

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Therefore, the modern potential natural climate estimates from Eq. (1) are used, as detailed in Eq. (3),

$$Model_{HadCM3L} = Model_{HadCM3L} + (Modern potential natural climate - CTRL)$$
 (3)

Where bias corrections have been applied to the model simulations, these are denoted by the subscript "c", e.g. LM280_c. When these corrections are applied to the modern control simulation CTRL, Eq. (3) reduces to,

$$CTRL_c = Modern potential natural climate$$
 (4)

Whilst it is possible to make bias corrections to the climatology, we are unable to do the same for TRIFFID modelled vegetation cover because of the interactive coupling within the climate model. The standard anomaly method is however applied when forcing the BIOME4 model (e.g. Haxeltine and Prentice, 1996; Texier et al., 1997), applying a correction factor equal to the anomaly between the CTRL model climate and the modern climate, although it should be noted that this correction is based on the modern instrumental record and does not include our estimates of uncertainty of that record for a modern potential natural climate. In order to simplify the model-data comparison, the 28 biomes of the BIOME4 model are combined into 9 megabiomes: Tropical Forest, Temperate Forest, Warm-Temperate Forest, Grassland and Dry Shrubland, Savannah and Dry Woodland, Tundra, Boreal Forest, Desert and Land Ice.

In order to acknowledge the uncertainties in the data reconstructions and model results, both are treated as a range of possible values rather than the mean of possible values. The term "overlap" is defined as consistency between model and data if their uncertainty ranges overlap (see Fig. 3a). Overlap between model and data does not necessarily imply "good" agreement because the uncertainty ranges may be large, but rather that where model and data overlap it is not possible to determine that they are different. In the figures and discussion that follow, the differences between model and data uncertainties are defined as the minimum possible difference given the range of possible values for both; if the true values for each were at the extremes of their

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respective uncertainties, then the differences between the two would be much larger (see Fig. 3b).

4 Description of the simulated Late Miocene climate

Here, model results are described in terms of anomalies; the difference between the Late Miocene (LM280 or LM400) and the modern (CTRL) climates. We also conduct a model-model comparison of the present work with respect to previous Miocene GCM simulations, although direct comparison is difficult where different palaeogeographies, model complexity and ocean model setup have been used (Table 2). Comparison between results from different vegetation models is even more difficult because of the different plant functional type and biome classification systems used. The Late Miocene simulations have been used to drive the interactive vegetation model TRIFFID which is coupled to the climate in the GCM, but also offline by the BIOME4 model and therefore it is possible to make some general comparison between the results of the two vegetation models.

4.1 Global

The annual and seasonal (DJF – December/January/February, JJA – June/July/August) mean air temperature and precipitation anomalies between our Late Miocene and CTRL experiments are shown in Figs. 4a–c and 5a–c. The magnitudes of the global anomalies are modest for LM280-CTRL (the impact of changing palaeogeography alone), with the mean annual temperature (MAT) only 0.3°C higher and the mean annual precipitation (MAP) only 4.5 mm a⁻¹ higher. The Micheels et al. (2011) model results obtain a larger MAT difference of 1.5°C between their same-CO₂ Tortonian and control simulations. However these results are not really comparable to ours because of the palaeogeographic differences between our studies, and the fact that they used a prescribed Late Miocene vegetation in

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their Tortonian simulations. It could also be that the influence of palaeogeographic change is dependent on the background $\rm CO_2$ (Micheels et al. (2011) assume a $\rm CO_2$ concentration of 360 ppmv for both simulations compared to our 280 ppmv). The magnitudes of the global anomalies are higher for LM400-CTRL (the impact of changing palaeogeography and $\rm CO_2$ concentration), with the MAT 2.88 °C higher and the MAP 46.6 mm a⁻¹ higher.

4.2 Regional

Regions of palaeogeographic change in the Late Miocene simulations, either due to ice removal or lower mountains, generally experience significant increases in temperature (Fig. 4a–c). These changes are consistent with the lapse rate cooling effect and have been found in other modelling studies of ice removal (Lunt et al., 2004; Tonazzio et al., 2004) and mountain uplift (Foster et al., 2010). However, since we have performed a number of palaeoenvironmental changes simultaneously, these simulations represent a combination of all of these changes.

4.2.1 High latitudes

Over Greenland we find a mean annual warming of the interior due to palaeogeographic change of more than 10 °C as shown in Fig. 4a, with a maximum warming of 8 °C and 21 °C for DJF and JJA respectively (Fig. 4b–c). Lapse rate corrected temperature calculations reveal these temperatures to be ~3–5 °C cooler than would be expected due solely to topographic lowering. In LM280, the DJF precipitation over most of Greenland is very low (<0.5 mm day⁻¹; Fig. 5c) and the ice-free land surface remains largely snow-free resulting in a lower land surface albedo for LM280 than CTRL in both DJF and JJA, consistent with the small imposed Late Miocene Greenland ice sheet in the GCM (Fig. 2). A reduction in the albedo should also lead to warming of this region. Several modelling studies report warming across the whole of Greenland, and further afield, as a result of the complete melting of the Greenland ice sheet (Crowley

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and Baum, 1995; Tonazzio et al., 2004; Lunt et al., 2004), whereas our study shows large areas of cooling in the North Atlantic. This could be due to the impact of an open Panama gateway (e.g. Lunt et al., 2008b), differences in runoff from a less-glaciated Greenland and from the Late Miocene Arctic Eurasian landmass, or it could also be 5 caused by vegetation-climate feedback mechanisms, potentially affected by the high latitude cold bias in our GCM. Although there is little significant difference in the high latitude vegetation cover predicted by the TRIFFID model for the palaeogeographic changes we have made (Fig. 6a compared to Fig. 6b), there are large changes in vegetation predicted for the CO₂ increase (Fig. 6b compared to Fig. 6c). The unglaciated areas of Greenland and the high latitudes of North America and Eurasia are modelled as vegetated by TRIFFID with the dominant PFT being C₃ grasses for LM280 (Fig. 6b), altering to shrub for LM400 (Fig. 6c). Figures 4f and 5f show that the largest climatic changes as a result of higher CO₂ are seen in the winter months of the high northern latitudes. Both vegetation models (TRIFFID and BIOME4) agree that the higher CO₂ LM400 simulation has more trees at the high northern latitudes, in Asia and in North America, than the lower CO₂ LM280 simulation, for which grasses are predicted.

The Antarctic orographic differences result in temperature anomalies between LM280 and CTRL that are broadly consistent with the lapse rate cooling effect, but, opposite to the Greenland case in that the changes are slightly greater than lapse rate corrected temperature calculations suggest. The high southern latitudes are generally simulated as being significantly warmer and having significantly more precipitation in LM280 than CTRL, and these changes are more pronounced in JJA (Southern Hemisphere winter) than DJF (Southern Hemisphere summer). The Southern Ocean has significantly less sea ice in both LM280 and LM400 than in CTRL (not shown), and we infer that the reduction in the ice-albedo feedback mechanism amplifies the warming associated with topographic lowering.

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The model results suggest that palaeogeographic changes alter the seasonality of the Late Miocene climate of the south-western European countries, which is generally simulated to be warmer (with some grid boxes up to 6 degrees warmer) and drier in the summer months (Figs. 4b and 5b) and cooler and wetter in the winter months (Figs. 4c and 5c) for LM280 compared to the CTRL. Conversely, a reduction in seasonal temperature range is seen in LM280 compared to CTRL in the region from the Paratethys across into central-eastern Asia, and both DJF and JJA are modelled as wetter in LM280 than in CTRL. These changes are consistent with simulations of the closure of the Paratethys (e.g. Ramstein et al., 1997). There is a shift in the distribution of modelled PFTs in Central Asia from a mix of shrubs, trees and grasses in LM280 to bare soil in CTRL, causing large changes in surface albedo (not shown). There are large differences in the predicted vegetation in this locality for LM400 compared to LM280 with the majority of Eurasia being forested under the LM400 scenario (Fig. 6c). There is evidence in this region for dynamic changes in vegetation and mammal communities across the Late Miocene, with the rise and fall of the Pikermian palaeobiome (see Eronen et al., 2009 and references therein).

We calculate lapse rate corrected temperatures for this region and suggest that topographic changes in the Tibetan Plateau are largely responsible for the LM280 warming seen here in DJF. In JJA however, the temperatures are ~3 °C cooler than lapse rate corrections would suggest. Our study indicates a decrease in JJA precipitation across the northern Indian Ocean and the Indian Subcontinent, indicating a weakened monsoon, and this is consistent with many modelling studies (Ramstein et al., 1997; Steppuhn et al., 2006; Lunt et al., 2008a; Zhongshi et al., 2007a, b). However, the Tortonian vegetation reconstructions for the Indian subcontinent are composed of tropical forests and savanna; which suggests an increase in precipitation relative to today (Pound et al., 2011). These reconstructions are consistent with some modelling studies (e.g. Lunt et al., 2008a; Micheels et al., 2011), which simulate large increases in precipitation in

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this region. It is not clear what the probable cause of these differences in our results for this region might be.

Away from the Tibetan Plateau, Southern Asia is cooler in LM280 than CTRL, in disagreement with many modelling uplift studies that suggest this region could have been ~5 °C warmer with lower orography (Ruddiman et al., 1997; Kutzbach and Behling, 2004) and Late Miocene climate simulations (Knorr et al., 2011; Micheels et al., 2011). We suggest that either the changes we have made to the Indonesian Seaway may play an important role in the climate of Southern Asia, or that this region is very sensitive other palaeoenvironmental differences. However, our modelled Southern Asia vegetation changes are generally consistent with other modelling work (Kutzbach and Behling, 2004; Lunt et al., 2010).

4.2.3 Americas

In Northwestern America, there are cooler temperatures and an increase in precipitation simulated for LM280 compared to CTRL (Figs. 4 and 5). Correspondingly the PFT distribution changes from wooded vegetation in the Late Miocene simulations to deserts in CTRL, and this result is robust to the $\rm CO_2$ concentration assumed (Fig. 6). Alaska and northwest Canada are warmer and wetter in the Late Miocene simulations than CTRL. Vegetation changes here are small if only palaeogeographic changes are considered (Fig. 6a and b), but much larger under a higher Late Miocene $\rm CO_2$ assumption (Fig. 6a and c).

Over Central America the Late Miocene configuration simulates colder drier air than CTRL, with a large reduction in JJA precipitation (Fig. 5). In this region C_4 grasses and bare soil are simulated for the Late Miocene, replaced by trees in CTRL, and this finding is robust to the CO_2 concentration assumed for the Late Miocene (Fig. 6). Both vegetation models agree that in modern Central America, an open Panama Gateway results in the desertification of the southern tip of North America and the north tip of South America, for both CO_2 concentration assumptions, and therefore we are confident that this vegetation change is due to the palaeogeographic changes made.

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In South America, temperature changes between the Late Miocene simulations and the CTRL are small, and those seen in Fig. 4c are generally associated with the differences in the land-sea mask of the two simulations. There is some warming in the region of Andean uplift for the Late Miocene compared to CTRL. The largest climatic changes in this region though are for precipitation, which shows an increase in seasonality with wetter winters (JJA) and drier summers (DJF). Vegetation changes here are also notable (Fig. 6). The Patagonian region is simulated as dominated by the needleleaf tree PFT in LM280 and LM400, changing to desert in CTRL. The Amazon Rainforest is much reduced in our Late Miocene simulations compared to CTRL, replaced by C₄ grass and bare soil PFTs. As similar vegetation distributions occur in LM280 and LM400, we are confident that the vegetation changes are due to the palaeogeographic alterations made. There is very little difference in the vegetation predictions for the tropics between the two CO₂ scenarios by TRIFFID, however, BIOME4 predicts quite large differences between the two CO₂ scenarios, such that the tropical forests of the lower CO₂ scenario are replaced by grasslands and dry shrublands, and this trend is seen in South America, but also in Africa and in SE Asia.

4.2.4 Africa/Middle East

Widespread year-round drying, an increase in seasonality and the expansion of the Sahara Desert occurs in North Africa in the Late Miocene simulations compared to CTRL (Figs. 4, 5 and 6). The presence of the Sahara desert itself can contribute to cooling at high latitudes and the aridification/cooling of North Africa (Micheels et al., 2009b). Evidence of rooting systems in the Saharan region during the Late Miocene suggests the presence of some vegetation (Duringer et al., 2007) but it is suggested that this vegetation was probably seasonal in nature, with the landscape alternating between being sand-covered and vegetated due to the presence of large lakes (Duringer et al., 2007; Vignaud et al., 2002). The large area of drying we see extending from the mid-Pacific Ocean into North Africa, are in direct contrast to the Lunt et al. (2008a) study which shows large increases in precipitation in these regions. In the Micheels

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et al. (2007) work, the prescribed vegetation assumed in the Sahara (grasslands and savannahs) in their TORT simulations is responsible for up to 6 °C of warming, and increases in precipitation in North Africa.

All of the areas predicted to be bare soil are by TRIFFID are predicted to be slightly more vegetated by BIOME4.

4.2.5 Australia

Australia is drier in winter for the Late Miocene simulations compared to CTRL; the band of increased precipitation for DJF (Fig. 5f) is most likely an artefact of the different land-sea masks in the two simulations. The palaeorecord provides evidence for the drying of central Australia as a result of continental drift (Truswell, 1993; McGowran et al., 2004) which is perhaps consistent with our simulated precipitation results.

The TRIFFID model results clearly show vegetation changes as Australia shifts northwards between the Late Miocene and CTRL simulations. In the Late Miocene experiments, Australia is dominated by C_4 grass and bare soil PFTs, largely replaced by the broadleaf tree PFT in the CTRL (Fig. 6). However the interpretation of the TRIFFID results, and analysis of the role of palaeogeography or CO_2 in this region are hampered by the inconsistencies between the vegetation modelled by TRIFFID and the modern Australian vegetation distribution.

5 Model-data comparison results and discussion

In this section we compare our simulations with the Late Miocene terrestrial proxy data reconstructions (hereafter referred to as LMdata), to assess the extent to which solely changing the palaeogeography to that appropriate for the Late Miocene results in a better consistency to this dataset, and to determine the sensitivity of those results to the uncertainty in the palaeoCO₂ record.

We compare LMdata, categorised into the two stages of the Messinian and the Tortonian, with the climatologies of: (a) the bias corrected CTRL simulation, equivalent to

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our modern potential natural climate estimates; (b) the bias corrected LM280 simulation; and (c) the bias corrected LM400 simulation. The extent to which comparison (b) is better than comparison (a) indicates the importance of palaeogeographic changes in determining Late Miocene climate. The extent to which comparison (c) is better than comparison (b) indicates the importance of CO₂ uncertainties in determining Late Miocene climate.

The numerical results from the model-data comparisons are given in Tables 3 and 4, and shown in Figs. 7 to 16.

5.1 Mean annual temperature

5.1.1 Late Miocene data compared to modern potential natural climate estimates

The differences in MAT we find between the Late Miocene palaeodata and our modern climate estimates are shown in Fig. 7. The comparison shows that, where we are confident that the MATs suggested by the palaeodata are different to our modern climate MAT estimates, they are significantly warmer; no datapoint is suggesting cooler temperatures in the Late Miocene. There are 156 overlaps from a total of 479 datapoints (see Table 3). There is a clear difference in the microfaunal MAT reconstructions between the Tortonian and the Messinian (Fig. 7f compared to Fig. 7c). These results suggest that the Mediterranean Basin was much warmer in the Tortonian than today, but by the Messinian we are unable to confidently say that the MAT was any different to today. The same signal is perhaps apparent in the macroflora data in south-western Europe and in South America (Fig. 7e compared to Fig. 7b) and in the microflora data in south-western Europe (Fig. 7d compared to Fig. 7a).

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5.1.2 Late Miocene data compared to the Late Miocene simulations

Figure 8 and Table 3 show how well our LM280c simulation compares to the Late Miocene MAT data reconstructions. Figure 8 clearly demonstrates that we are unable to generate the warm MATs suggested by the data for either the Messinian or the Tortonian by just changing the palaeogeography alone, and this finding is robust to the choice of proxy with microflora, macroflora and microfaunal proxies indicating the same results (Table 3: 136 overlaps from 479 datapoints).

The LM400_c simulation, which includes both a palaeogeographic change and a CO₂ change, provides a better match to the data overall (Fig. 9, Table 4: 297 overlaps from 479 datapoints), with overlap between the modelled MATs and all but one of the Tortonian faunal-based MAT reconstructions (Fig. 9f). It is also noticeable that the model-data comparison for the Messinian aged microflora datapoints results in many more overlaps than the similar comparison with Tortonian aged data (Fig. 9a compared to Fig. 9d). Despite these improvements in the model-data comparison, there are still many datapoints which indicate warmer MATs than the LM400_c simulation is able to model.

The summary Fig. 10a and b show that there are regions where the palaeogeographic changes have resulted in improvements in the model-data comparison (e.g. north-western America, mid-western Europe) and regions where the changes have resulted in deteriorations (e.g. northern and southern extents of the European data, south-east Asia, Australia). Table 3 details that the palaeogeographic changes result in a simulation that overlaps less with the MAT data than the modern potential natural climate estimates overlap (a reduction of 20 overlaps, or 4%), but that overall the modelled MATs are closer to the data reconstructions (13% better) due to improvements in the distance to overlap, mostly seen in the model-data comparison of Tortonian-aged datapoints.

Figure 10c and d demonstrate the impact that CO₂ uncertainty has on the modeldata comparison. They clearly show that the MATs of LM400c are an improvement in their match to the data reconstructions than the MATs of $LM280_c$ (Table 4: 232 data-points are closer to model-data overlap in the $LM400_c$ than the $LM280_c$ – an improvement of 48% overall, and a 34% improvement in the number of overlaps). However, the data are very spatially biased towards Europe, and Fig. 10c and d also show that outside of Europe and mid-eastern Asia, the model-data comparison actually deteriorates as a result of the increased CO_2 concentration.

These results suggest that changing the palaeogeography to that appropriate for the Late Miocene and increasing the $\rm CO_2$ concentration from that of the modern potential natural climate together results in a model simulation that is able to reproduce much of the warm European MATs (Fig. 9), but that it is unable to entirely reproduce the warm MATs indicated by the Late Miocene data elsewhere.

5.2 Mean annual precipitation

5.2.1 Late Miocene data compared to modern potential natural climate estimates

The comparison between the Late Miocene data and the modern climate estimates for precipitation are shown in Fig. 11. The MAP data reconstructions suggest that where we are confident that the climate of the Late Miocene is different to a potential natural modern one, the MAPs are wetter; none of the datapoints suggest drier MAPs in the Late Miocene. There are a large number of overlaps between the Late Miocene MAP data and the modern MAP estimates (Table 3; 1037 overlaps from a total of 1253 datapoints). The faunal Tortonian data reconstruct a much wetter climate in Europe (Fig. 11f), whereas the Messinian data reconstructions in this region are largely similar to today (Fig. 11c). A similar pattern is perhaps seen in the microflora and macroflora MAP reconstructions in this area (Fig. 11d compared to Fig. 11a; Fig. 11e compared to Fig. 11b).

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5.2.2 Late Miocene data compared to the Late Miocene simulations

The LM280_c simulation compares well to the reconstructed MAPs (Fig. 12; Table 3: 1152 overlaps from 1253 datapoints), and of the macroflora reconstructions, just 2 datapoints do not overlap (Fig. 12b and e; Table 3). The 101 datapoints which 5 do not overlap with the modelled MAPs are wetter than the model predicts.

There is a significant improvement in the model-data comparison for MAPs when compared with the modern climate comparison (Fig. 12 compared to Fig. 11; Table 3: 210 improvements versus just 27 deteriorations) suggesting that changing the palaeogeography alone takes the modelled MAPs closer to the reconstructed MAPs.

Although the LM400 simulation predicts generally an increase in the MAP as compared to the LM280 simulation (Fig. 5d-f), both the simulations result in MAP predictions that are within the uncertainty of the Late Miocene MAP reconstructions, and therefore little change is seen in the model-data comparison for this variable between the two simulations (Fig. 13 compared to Fig. 12; Table 4: 1152 overlaps for LM280_c compared with 1158 for LM400_c). This suggests that the palaeogeographic changes we have made are the driving force behind the modelled precipitation changes observed, and that the CO₂ concentration plays only a minor role. However, Fig. 14 demonstrates that many of the datapoints overlap both the LM280c modelled MAPs and those of our modern potential natural climate. In fact, Fig. 14c and d demonstrates that many of the datapoints in western Europe are further from overlap with the LM400. modelled MAPs than they are with the LM280c modelled MAPs, indicating that higher CO₂ may actually worsen model-data comparison in this region.

5.3.1 Tortonian data compared to the modern potential natural control simulation

Figure 15a and d show the comparison between the biomes derived from the modern control simulation CTRL_c and the Tortonian data. There are some large vegetation shifts are documented at the biome level (Pound et al., 2011), and when aggregated to megabiome level, the vegetation shifts between the Tortonian and today are still noticeable, and in fact there are only 96 overlaps from a total of 225 datapoints (Table 3). There are many regions where there are significant differences in the megabiomes predicted for the Tortonian and today, including north-west America and north-east Asia, Greenland and northern Europe, the Mediterranean Basin, central Asia, southern and south-eastern Asia, South America, South Africa and in Australia.

5.3.2 Tortonian data compared to the Late Miocene simulations

Figure 15b and e show the comparison between the megabiomes of the Tortonian data and those predicted by the $LM280_c$ simulation. As discussed in Sect. 4.2.3, the BIOME4 model predicts quite a significant change in the vegetation of Central America, but unfortunately there are no datapoints in this region to verify that change. The $LM280_c$ simulates a change from the modern tropical forests of central Africa to grasslands and dry shrubland, but, again, there are no datapoints in this region in order to verify this change. The $LM280_c$ simulation also results in a shift from the modern Boreal forest to tundra in north-eastern Asia but the datapoints in this region do not support this change. Compared to the $CTRL_c$ simulation, the $LM280_c$ simulation does not improve the model-data comparison for most datapoints, and in fact overall the comparison worsens very slightly (Fig. 16a; Table 3: 15 improvements versus 19 deteriorations, a worsening of 2 %).

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Figure 15c and f show the comparison between the megabiomes of the Tortonian data and the LM400 $_{\rm c}$ simulation. The megabiomes are in agreement for many of the datapoints of northwest America and north and east Asia that disagreed with the CTRL $_{\rm c}$ simulation (Fig. 15f). There are 121 agreements between the megabiomes reconstructed by the data and the LM400 $_{\rm c}$ simulation, from 225 datapoints in total. The 104 datapoints that disagree with this simulation are located mainly in central, southern and south-eastern Asia, and the land surrounding the Mediterranean Basin. When compared to the LM280 $_{\rm c}$ simulation, the model-data comparison worsens in South America in particular (Fig. 16b). Overall though, the LM400 $_{\rm c}$ simulation offers a 13% improvement over the LM280 $_{\rm c}$ (Table 4).

5.4 Discussion

We ask the question to what extent the different palaeogeography of the Late Miocene can explain the differences in the climate documented in the palaeorecord, and how important the uncertainty in the atmospheric CO₂ concentration is.

The results from the model-data comparison for the mean annual temperature are difficult to interpret. Table 3 details that a large number of improvements and a large number of deteriorations exist as a result of the palaeogeographic changes made. The Messinian data generally suggests that the palaeogeographic changes are not able to improve the model-data comparison as compared to the modern potential natural climate estimates but the Tortonian data generally suggests the opposite. However, overall there are more datapoints closer to overlap with the Late Miocene simulation LM280_c than the modern potential natural climate estimates, but that the total number of overlaps reduces as a result of palaeogeographic change (Fig. 17). However, Fig. 17 demonstrates that the atmospheric CO₂ concentration is very important in determining the mean annual temperatures of the Late Miocene, with large improvements seen for both the Messinian and Tortonian model-data comparison as a result of increasing the assumed CO₂ concentration. Furthermore, the higher CO₂ assumption combined with the palaeogeographic changes made in the LM400_c simulation offers

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a significant improvement in the model-data comparison when compared to the modern potential natural climate estimates with nearly twice as many overlaps with the datapoints (Table 4).

Figure 17 shows that the different Late Miocene palaeogeography is important in 5 determining the different mean annual precipitation for both the Messinian and the Tortonian stages, because all of the proxy reconstructions considered show an improvement in the model-data comparison for the Late Miocene simulation as compared to the modern potential climate estimates (Table 3). Figure 17 however suggests that the uncertainty in the atmospheric CO₂ concentration is not important in determining the different mean annual precipitation documented for the Late Miocene, as only very small differences are found between the results of LM400c and LM280c (Table 4).

The Tortonian megabiome results show very little difference in the model-data comparison with the Late Miocene simulation LM280_c as compared to the model-data comparison with the control simulation CTRL_c. There is also an improvement in the megabiome model-data comparison for the higher CO₂ simulation as compared to the lower CO₂ simulation, again suggesting that atmospheric CO₂ concentration is an important consideration.

Our modelling results are in general agreement with those of other similar studies (Knorr et al., 2011; Micheels et al., 2011) in that palaeogeographic changes for the Late Miocene causes regions of warming in the areas of tectonic change, and regions of cooling, particularly in the North Atlantic. A recent study has found that vegetation changes are very important in determining the Late Miocene climate, perhaps three times more important than the palaeogeographic changes (Knorr et al., 2011). They find reasonable agreement between their Late Miocene model simulation with preindustrial atmospheric CO2 concentrations and the palaeorecord, thereby reconciling a warmer climate with low CO₂ concentrations. We do not find the same results with our GCM. Although there are many differences, the main difference between our study and that of Knorr et al. (2011) is that we use an interactive vegetation model dynamically linked to our GCM, whereas a Miocene vegetation reconstruction based on palaeodata

is imposed in their work. The benefit of a coupled GCM-vegetation model is that the simulated vegetation distribution will be in equilibrium with the modelled climate, but the disadvantage is that the simulated vegetation will not match the palaeodata if the climate is incorrectly modelled. Based on our results, we hypothesise that the vegetation reconstruction imposed in the Knorr et al. (2011) study is not in equilibrium with their simulated climate and that a higher-than-preindustrial level of CO₂ is required in order for the vegetation distributions recorded in the palaeorecord to have occurred. The relative impacts of vegetation changes versus CO₂ changes will be explored in future work.

The megabiome model-data comparison results for LM400_c show that some of the documented extreme changes in vegetation are captured by the BIOME4 model when forced by this simulation. BIOME4/LM400_c predicts temperate forests in what is now the circumboreal region, consistent with Denk et al. (2005) and Worobiec and Lesiak (1998); and grasslands in the Arabian peninsula, consistent with Kingston and Hill (1999). However, despite the improvements that we find in the model-data comparison for changing palaeogeography and for changing the CO₂ assumption, there are still significant model-data inconsistencies, particularly in eastern Asia for the mean annual temperature in both the Messinian and the Tortonian (as with the model-data comparison of Knorr et al. (2011)). Further verification of this discrepancy is provided by the inconsistency in both the Tortonian mean annual temperature and the Tortonian megabiome reconstructions in this region, however there is consistency between the Late Miocene simulations and the data reconstructions for the Asian MAPs. We therefore suggest that future work with this GCM should concentrate on the sensitivity of the climate in this region to the various tectonic changes independently in order to isolate the impact that each change has.

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Summary 6.1

We have simulated two potential Late Miocene climates using the fully coupled atmosphere-ocean-vegetation GCM model HadCM3L-TRIFFID. Both simulations assume a palaeogeography appropriate for the Late Miocene, but one has preindustrial levels of CO₂ at 280 ppm and the other a slightly higher CO₂ concentration at 400 ppm. We compare the 280 ppm Late Miocene simulation against a modern control simulation with the same preindustrial level of CO2 in order to investigate the potential role of palaeogeography in determining the simulated Late Miocene climate. We also compare the two Late Miocene climate simulations to investigate the role of CO₂ in determining the simulated climates.

The global anomaly between the two 280 ppm climatologies is close to zero for both mean annual temperature and precipitation, but there are significant regional differences. Our Late Miocene palaeogeographic changes have been found to alter the climate: for example, there is a large area of cooler drier air that spreads across the North Atlantic Ocean into Eurasia for the Late Miocene, the lapse rate effect on temperature results in regional warming in areas of topographic lowering for the Late Miocene, and significant reductions in Late Miocene monsoonal precipitation are modelled.

A database containing 1109 terrestrial proxy records for the Late Miocene has been compiled from the literature. From these data we infer a substantially warmer and wetter Late Miocene climate as compared to a potential modern natural climate. We have made quantitative comparisons of these data and Tortonian biome data (Pound et al., 2011), to both our Late Miocene simulations and our modern potential natural climate estimates, in order to investigate the extent to which palaeogeographic changes alone can explain Late Miocene climate and to examine the importance of the uncertainty in the CO₂ palaeorecord.

We have used proxy data from a variety of different reconstruction methods, and overlap between different methods of climate reconstruction used on the same proxy Discussion Paper

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data will indicate reliability, but ideally overlap between entirely independent proxies is desirable. We therefore also recommend, where possible, the expansion and better temporal constraint of the multiproxy palaeorecord for the Late Miocene, in particular for the regions where the model-data inconsistencies are largest, and a more robust and consistent assessment of uncertainties in all proxy records. We have tried to account as much as possible for uncertainties in the proxy reconstructions so we have some confidence that the reconstructed signals are robust. However, we cannot rule out significant errors in our palaeogeographic reconstruction and/or the model itself. We will conduct future modelling with the same coupled atmosphere-ocean-vegetation GCM in order to establish sensitivity to our choice of palaeogeographic configuration on the simulated climate, and also the relative roles of CO₂ concentration versus vegetation distribution.

7 Conclusions

Despite the uncertainties in proxy data reconstructions and the limited distribution and spatial/temporal bias of the palaeorecord, we do find significant evidence to suggest that the palaeogeography does have an important role in determining aspects of the Late Miocene climate, particularly for the mean annual precipitation for both the Messinian and the Tortonian. The megabiome model-data comparisons show some improvements as a result of the palaeogeographic alterations on the west coast of North America, in Australasia, south-east Europe and eastern Asia. We find significantly better model-data consistency for the higher CO_2 Late Miocene simulation than for the lower CO_2 simulation for the both Messinian and Tortonian mean annual temperatures but only modest differences for the mean annual precipitation of both stages. We therefore conclude that the mean annual precipitation differences are driven by the palaeogeographic changes that we have made but that the temperature differences are strongly influenced by the CO_2 concentration.

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Table 1. Calibration errors for climate reconstructions of proxy data.

		Cal				
Method	MAT	MAP	CMT	WMT	MAMLT	Reference
	(°C)	$(mm a^{-1})$	(°C)	(°C)	(°C)	
Climatic Amplitude Approach	3.4	257				Fauquette et al. (2006)
Coexistence Approach	2	200	as MAT	as MAT		Mosbrugger and Utescher (1997); This study
Small mammal species composition		350–400				van Dam (2006)
Herpetofaunal composition		250–275				Bohme et al. (2008)
Mammal tooth-crown height		388				Eronen et al. (2010)
CLAMP	1–3		1.5–3	1–4		Wolfe (1994); Teodorides et al. (2011)
Leaf morphology	1.98	57.97	3.55	2.92		Jacobs and Deino (1996)
Rodent species composition	0.004-4.8					Montuire et al. (2006)
Palaeosol Analysis		141				Retallack et al. (2002)
CLAMP Multiple regression analysis	0.7	180				Gregory-Wodziscki (2000)
Physiognometric/morphology reconstructions	as CLAMP		as CLAMP	as CLAMP		This study
Nearest living relative, autecology	as Climatic Amplitude Approach	as Climatic Amplitude Approach				This study

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Table 2. Details of published Miocene simulations.

Ref	Miocene Period	Model Name	Atmospheric Model Resolution	Ocean Model Type	Oceanic Model Resolution	Land-sea Mask	Ice Sheet Configuration	Orography	Vegetation	Modern CO ₂	Miocene CO ₂	Same CO ₂ for Modern and Miocene?	Reference
1	Early	CCM1	4.5 × 7.5°	None		Miocene	All ice-free	Miocene	N/A	Mo	Mo	Yes	Barron (19850)
2	Early	GENESIS	7.5 × 4.5°	Slab		Miocene	All ice-free	Miocene	Modern + Miocene	Мо	Мо	Yes	Dutton and Barron (1997)
3	Late	LDM 5.3	2 × 5.6°	None		Miocene	No Greenland	Miocene	Modern	345	345	Yes	Fluteau et al. (1999)
4	Late	ECHAM4	3.75 × 3.75°	Slab		Modern	No Greenland	Miocene	Miocene	353	353	Yes	Francois et al. (2006)
5	Early	GENESIS	3.7 × 3.7°	Slab		Modern	No Greenland	Miocene	N/A	990 330,	990	Yes (future)	Kutzbach and Behling (2004)
6	Late	CCM0	4.5 × 7.5°	None		Modern	Modern	Half + No mountains	N/A	330	330	Yes	Kutzbach et al. (1989)
7	Late	HadAM3	2.5 × 3.75°	None		Miocene	Reduced Modern Greenland	Miocene	Homogenous	280	395	No	Lunt et al. (2008a)
8	Late	E CHAM4	3.75 × 3.75°	Slab		Modern	No Greenland	Miocene	Miocene	353	353	Yes	Micheels et al. (2007a)
9	Late	Planet Simulator	5.6 × 5.6°	Slab		Modern	No Greenland	Miocene	Miocene	280, 360, 700	280, 360, 700+	Yes	Micheels et al. (2009)
10	Late	COSMOS	3.75 × 3.75°	Dynamic	3°3°	Miocene	No Greenland	Miocene	Miocene	360	360	Yes	Micheels et al. (2011)
11	All	CCM0 + CCM1	4.5 × 7.5°	Slab		Modern	Modern + Last Glacial	No + Half Himalayas	Modern	330	600, 1000	No	Prell and Kutzbach (1992)
12	Late	LDM 5.3	2 × 5.6°	Slab		Miocene	No Greenland	Miocene	N/A	Modern	Modern	Yes	Ramstein et al. (1997)
13	Late	CCM0	4.5 × 7.5°	None		Modern	Modern	Half + No mountains	N/A	330	330	Yes	Ruddiman and Kutzbach (1989)
14	Early	CCM1	4.5 × 7.5°	Slab		Modern	Modern	Half + No mountains	N/A	330	330, 660	Yes	Ruddiman et al. (1997)
15	Late	E CHAM4	3.75 × 3.75°	Slab		Modern	No Greenland	Miocene	Modern	353	353	Yes	Stepphun et al. (2006)
16	Late	ECHAM4	3.75 × 3.75°	Slab		Modern	No Greenland	Miocene	Modern	353	700	No	Stepphun et al. (2007)
17	Middle	CAM v3.1/CLM v3.0	3.75 × 3.75°	Slab		Miocene	No Greenland	Miocene	Miocene	379	180, 355, 700	No	Tong et al. (2009)
18	Middle	CAM v3.1/CLM v3.0	3.75 × 3.75°	Slab		Miocene	No Greenland + West Antarctic	Miocene	Miocene	355	180, 355, 700	No	You et al. (2009)
19	All	IAP	4 × 5°	None		Modern	Middle Pliocene	Miocene	Modern	345	345	Yes	Zhongshi et al. (2007a)
20	All	IAP	4 × 5°	None		Modern	Middle Pliocene	Miocene	Modern	345	345	Yes	Zhongshi et al. (2007b)
21	Middle	Planet Simulator	5.6 × 5.6°	Slab		Miocene	All ice-free	Miocene + Modern	Miocene + Modern	280	200, 280, 500	Yes	Henrot et al. (2010)
22	Late	ECHAM5-MPIOM	3.75 × 3.75°	Dynamic	3 × 3°	Miocene	No Greenland	Miocene	Miocene	280	280	Yes	Knorr et al. (2011)
23	Late	HadCM3L+TRIFFID	2.5 × 3.75°	Dynamic	2.5 × 3.75°	Miocene	Reduced Modern	Miocene	Dynamic	280	280	Yes	(This study)

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Table 3. Results from the model-data comparison for modern and Late Miocene palaeogeography.

Variable	Epoch	CTRL _c - LMdata datapoints in agree- ment	LM280 _c - LMdata datapoints in agree- ment	Total num- ber of LMdata datapoints	Number of LM280 _c improve- ments over CTRL _c All data (overlaps)	Number of LM280 _c deterio- rations over CTRL _c All data (overlaps)	Global LM280 _c improve- ment over CTRL _c All data (overlaps)	Percentage Improve- ment LM280 _c over CTRL _c All data (overlaps)
MAT (Macroflora)		12	9	40	11(3)	23(6)	-12(-3)	-30(-8)
MAT (Microflora)	Messinian	71	53	187	92(34)	76(52)	16(-18)	9(-10)
MAT (Fauna)	Messinan	9	9	9	0(0)	0(0)	0(0)	0(0)
MAT (Macroflora)		18	19	101	50(8)	40(7)	10(1)	10(1)
MAT (Microflora)	Tortonian	33	32	122	73(13)	30(14)	43(-1)	35(-1)
MAT (Fauna)		13	14	20	6(1)	1(0)	5(1)	25(5)
MAT (All)	Late Miocene	156	136	479	232(59)	170(79)	62(-20)	13(-4)
MAP (Macroflora)		35	38	38	3(3)	0(0)	3(3)	8(8)
MAP (Microflora)	Messinian	128	172	181	52(47)	4(3)	48(44)	27(24)
MAP (Fauna)		262	276	298	36(17)	3(3)	33(14)	11(5)
MAP (Macroflora)	Tortonian	79	85	89	10(8)	2(2)	8(6)	9(7)
MAP (Microflora)		98	97	115	16(5)	7(6)	9(-1)	8(-1)
MAP (Fauna)		435	484	532	93(56)	11(7)	82(49)	15(9)
MAP (All)	Late Miocene	1037	1152	1253	210(136)	27(21)	183(115)	15(9)
Megabiome	Tortonian	96	92	225	N/A(15)	N/A(19)	N/A(-4)	N/A(-2)

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Table 4. Results from the model-data comparison for high and low CO_2 concentration assumptions.

Variable	Epoch	LM280 _c -LMdata datapoints in agree- ment	LM400 _c -LMdata datapoints in agree- ment	Total number of LMdata datapoints	Number of LM400 _c improve- ments over LM280 _c All data	Number of LM400 _c deterio- rations over LM280 _c All data	Global LM400 _c improve- ment over LM280 _c All data (overlaps)	Percentage Improve- ment LM400 _c over LM280 _c All data
					(overlaps)	(overlaps)		(overlaps)
MAT (Macroflora) MAT (Microflora) MAT (Fauna)	Messinian	9 53 9	24 105 9	40 187 9	25(17) 123(0) 0(0)	8(2) 23(12) 0(0)	17(15) 100(-12) 0(0)	43(38) 53(-6) 0(0)
MAT (Macroflora) MAT (Microflora) MAT (Fauna)	Tortonian	19 32 14	63 77 19	101 122 20	74(53) 77(58) 6(5)	17(9) 25(13) 0(0)	57(44) 52(45) 6(5)	56(44) 43(37) 30(25)
MAT (All)	Late Miocene	136	297	479	305(197)	73(36)	232(161)	48(34)
MAP (Macroflora) MAP (Microflora) MAP (Fauna)	Messinian	38 172 276	38 174 277	38 181 298	0(0) 6(2) 17(3)	0(0) 3(0) 7(2)	0(0) 3(2) 10(1)	0(0) 2(1) 3(0)
MAP (Macroflora) MAP (Microflora) MAP (Fauna)	Tortonian	85 97 484	87 97 485	89 115 532	4(2) 15(1) 24(5)	0(0) 4(1) 28(4)	4(2) 11(0) -4(1)	4(2) 10(0) -1(0)
MAP (All)	Late Miocene	1152	1158	1253	66(13)	42(7)	24(6)	2(0)
Megabiome	Tortonian	92	121	225	N/A(38)	N/A(9)	N/A(29)	N/A(13)

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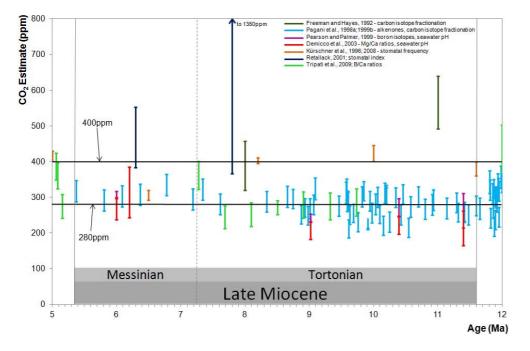


Fig. 1. Atmospheric CO₂ reconstructions for the Late Miocene.

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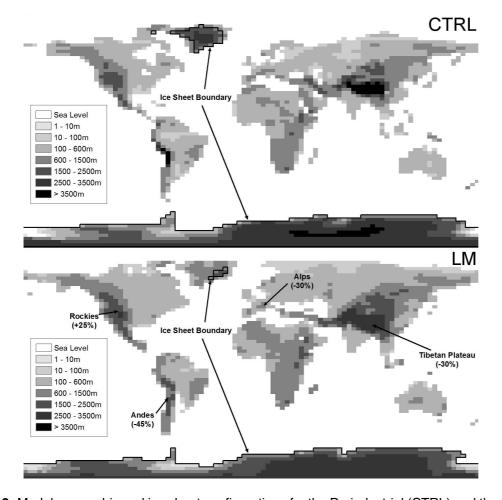


Fig. 2. Model orographic and ice sheet configurations for the Preindustrial (CTRL) and the Late Miocene (LM). The LM panel shows the percentage differences in high topography between CTRL and LM.

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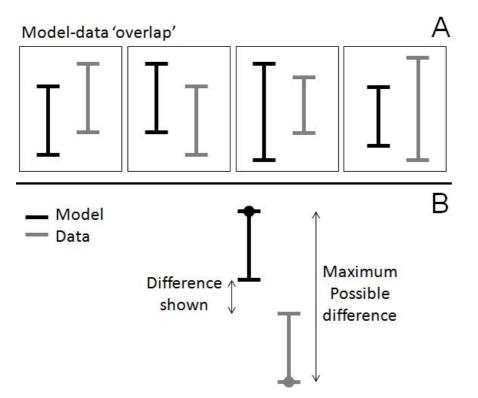


Fig. 3. Model-data comparison definitions. Panel **(A)** shows the definition for "overlap" used in the model-data comparison: all four instances shown are considered as an overlap. Panel **(B)** shows that although we define model-data mismatch as the minimum possible distance to overlap, the maximum possible differences could be much greater if the true values for both the model and the data were to lie at the extremes of the uncertainty ranges.

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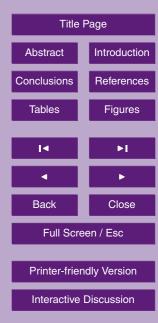




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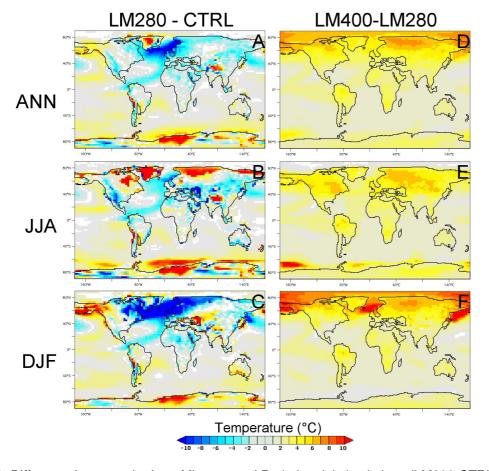


Fig. 4. Difference between the Late Miocene and Preindustrial simulations (LM280-CTRL: left side) and between the Late Miocene CO₂ simulations (LM400-LM280: right side) for mean air temperature. Only significant differences are shown using a 95 % confidence interval Student's *t*-Test, white areas are not significant.

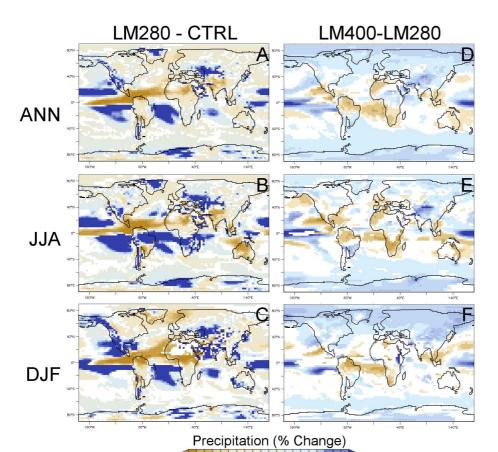


Fig. 5. Difference between the Late Miocene and Preindustrial simulations (LM280-CTRL: left side) and between the Late Miocene CO_2 simulations (LM400-LM280: right side) for mean precipitation. Only significant differences are shown using a 95 % confidence interval Student's t-Test, white areas are not significant.

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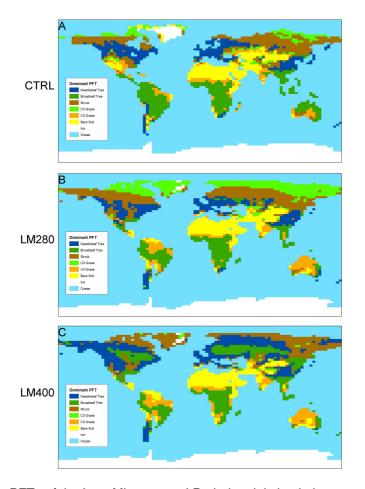


Fig. 6. Dominant PFTs of the Late Miocene and Preindustrial simulations, as predicted by the TRIFFID dynamic vegetation model.

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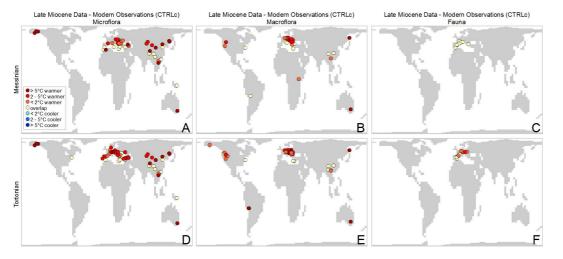
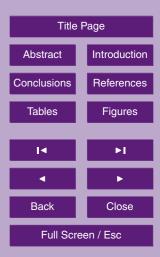


Fig. 7. Results from the model-data comparison for mean annual temperature, Late Miocene data – modern potential natural climate estimates.

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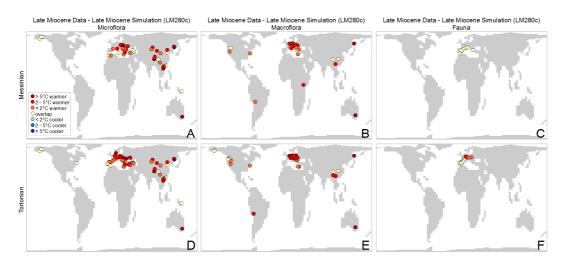


Fig. 8. Results from the model-data comparison for mean annual temperature, Late Miocene data $- LM280_c$.

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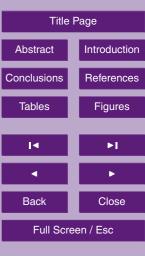
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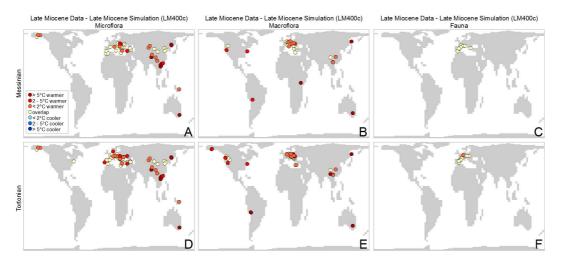


Fig. 9. Results from the model-data comparison for mean annual temperature, Late Miocene data - LM400_c.

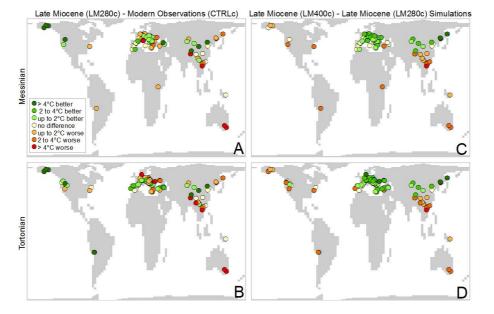


Fig. 10. Improvements in the model-data comparison for mean annual temperature. The left-hand column (\mathbf{A}, \mathbf{B}) shows the improvement that the Late Miocene palaeogeography makes to the model-data comparison. The righthand colum (\mathbf{C}, \mathbf{D}) shows the improvement that higher CO_2 makes to the model-data comparison. Green circles indicate an improvement, red circles indicate a deterioration. The datapoints showing "no difference" are plotted underneath the other datapoints in order to highlight the differences.

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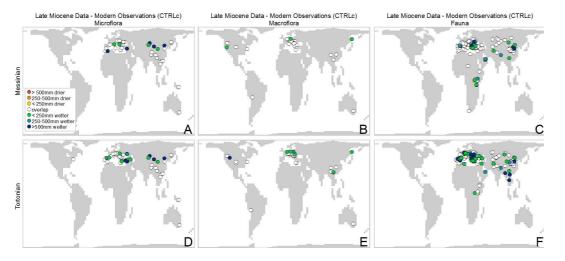


Fig. 11. Results from the model-data comparison for mean annual precipitation, Late Miocene data – modern potential natural climate estimates.

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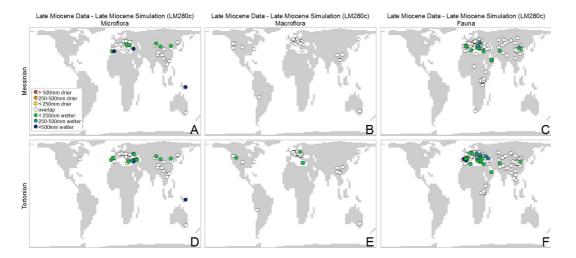


Fig. 12. Results from the model-data comparison for mean annual precipitation, Late Miocene $data - LM280_c$.

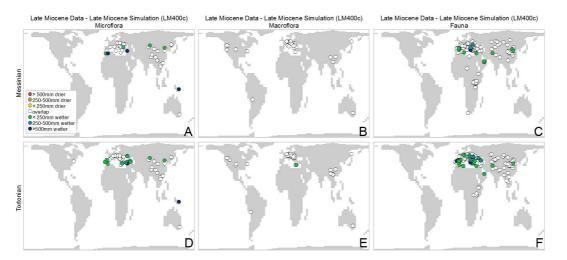


Fig. 13. Results from the model-data comparison for mean annual precipitation, Late Miocene data $- \, \text{LM400}_{\text{c}}$.

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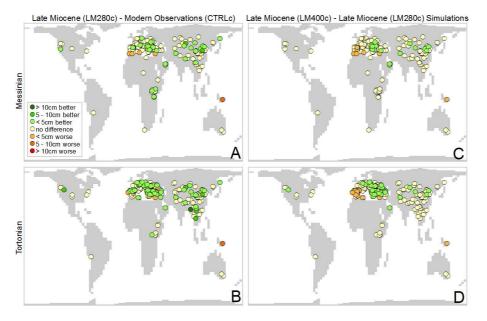


Fig. 14. Improvements in the model-data comparison for mean annual precipitation. The lefthand column (A, B) shows the improvement that the Late Miocene palaeogeography makes to the model-data comparison. The righthand colum (C, D) shows the improvement that higher CO_2 makes to the model-data comparison. Green circles indicate an improvement, red circles indicate a deterioration. The datapoints showing "no difference" are plotted underneath the other datapoints in order to highlight the differences.

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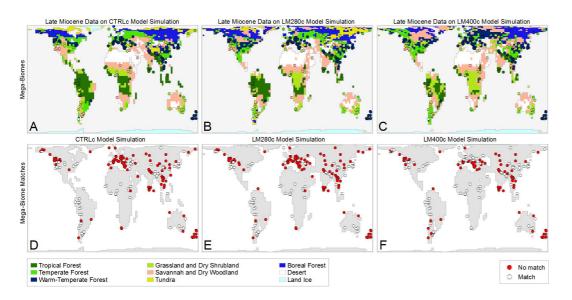


Fig. 15. Results from the model-data comparison for Tortonian megabiomes: Late Miocene data on CTRL_c, LM280_c, and LM400_c.

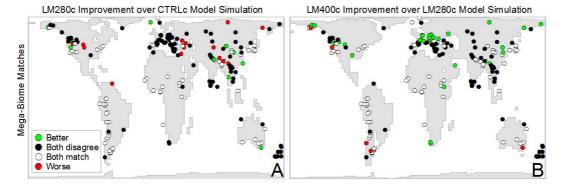


Fig. 16. Improvements in the model-data comparison for Tortonian megabiomes. Panel **(A)** shows the improvement that the Late Miocene palaeogeography makes to the model-data comparison. Panel **(B)** shows the improvement that higher CO₂ makes to the model-data comparison. Green circles indicate an improvement, red circles indicate a deterioration.

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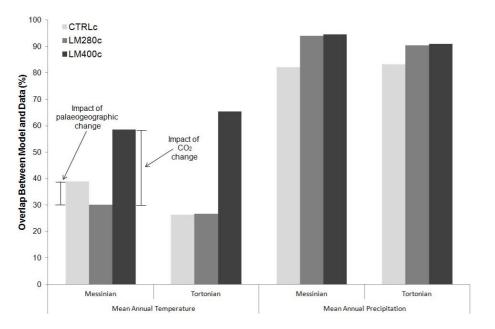


Fig. 17. Model-Data comparison summary.

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