A Tortonian (Late Miocene, 11.61-7.25 Ma) global vegetation reconstruction

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Abstract

For the Tortonian ~~Stage~~ Age of the Miocene ~~epoch~~ Epoch (11.6-7.25 Ma) we present a global palaeobotanical and palaeoecologically-based vegetation dataset, combined with a best-fit Late Miocene climate-vegetation model experiment to create an advanced global data-model hybrid biome reconstruction. This new reconstruction can be used both for the purposes of validating future palaeoclimate model simulations or as a land cover dataset to initialise palaeoclimate modelling experiments. Our Tortonian reconstruction shows significant changes in the distribution of vegetation compared to modern natural vegetation. For example in contrast to the modern scenario in the Northern Hemisphere, boreal forests reached 80°N and temperate forests were present above 60°N. Warm-temperate forests covered much of Europe, coastal North America and South-East Asia.

Our reconstruction shows a spread of temperate savanna in central USA, the Middle East and on the Tibetan Plateau. Evidence for arid deserts is sparse, with the exception of the Atacama region (South America). Areas that exhibit arid desert today in the Tortonian were instead covered by shrublands, grasslands, savannas and woodlands. The extent of tropical forests in South America was likely reduced but expanded in the Indian sub-continent and East Africa. This pattern of global vegetation in the Late Miocene suggests a warmer and wetter world, which is supported by the pattern of climate anomalies predicted by our best-fit palaeoclimate-vegetation model experiment. Global mean annual temperature may have been as much as 4.5°C higher than present day with many regions experiencing higher than modern amounts of precipitation over the annual cycle. The pattern of temperature and precipitation change reconstructed palaeobotanically, and predicted within our climate model experiment, infers a global forcing agent on Tortonian climate (e.g. such as elevated concentrations of greenhouse gases) to explain the observed and modelled climate anomalies. This is in contrast to current proxy records of Tortonian atmospheric CO_2 which range from Last Glacial Maximum to mid-20th Century levels.

Keywords

General Circulation Model, Palynology, Vegetation, Tortonian, Late Miocene, Palaeoecological

1. Introduction

1.1 Preamble

As a result of anthropogenic emissions of greenhouse ga~~s~~ses it has been predicted that by the end of the 21st Century average global surface temperatures will have increased by ~~up~~ 1.8 to 4°C (Meehl *et* *al.*, 2007). These predictions are generated by ~~Global~~ General Circulation Models (GCM) simulating the present day with projected increases of greenhouse gases from anthropogenic sources. To assess how well GCMs perform under significantly different climates than the present day, it has become common to use the geological record as a laboratory (Valdes, 2000; Micheels *et al.*, 2007; Salzmann *et al.*, 2009). Earth history presents many intervals that were significantly warmer than present, to be able to successfully simulate these with GCMs it is important to have a reasonable grasp of the boundary conditions, for each interval. One important boundary condition is the vegetation. Vegetation affects the global climate in ~~many~~ a number of ways ~~such as~~including; altering the surface albedo (Bonan *et al.*, 1992; de Noblet *et al.*, 1996; Hoffmann and Jackson, 2000) and changes in evapotranspiration from the conversion of forests into grasslands leading to reduced regional precipitation (Shukla *et al.*, 1990). ~~It~~ Vegetation is also strongly affected by the ambient climate, which principally influences its distribution. This makes vegetation, not only an important boundary condition, but a method to assess GCM predictions where direct measurements are not possible. Palaeobotanical remains such as pollen, wood and leaves are a widely utilised proxy for reconstructing past continental climates, and are used in the assessment of the predictive abilities of ~~Global Circulation Models (~~GCMs~~)~~ (Kohfield and Harrison, 2000; Valdes, 2000; Kageyama *et al.*, 2001).

We present herein a new vegetation reconstruction for the Tortonian ~~Stage~~ Age suitable for use in both assessing GCM simulations and as a boundary condition for experiments. This reconstruction uses a novel combination of merging palaeobotanical data and outputs from a state-of-the-art GCM-vegetation model experiment, to produce an advanced global biome distribution map of Tortonian vegetation. The reconstructed distribution provides insights into Tortonian climate, which will help inform future modelling studies. Previous global maps of Tortonian vegetation have been generated using unpublished data sets (François *et al.*, 2006) or vegetation reconstructed from a small (<50) number of palaeobotanical sites (Micheels, 2003; Micheels *et al.*, 2007). These reconstructions have also been based on a modern geography, instead of the appropriate Tortonian palaeogeography, and have classified Tortonian vegetation into a small (maximum 14) number of biome types. The reconstruction presented here builds and improves on these by presenting a 240-site palaeoecological dataset, combined with a state of the art GCM driven vegetation model experiment, to form a global vegetation reconstruction based on a 27 biome classification scheme.

1.2. An overview of the Tortonian

The Tortonian Stage of the Late Miocene (11.61-7.25 Ma) is ~~a period~~an interval generally considered to have been warmer than today (Wolfe, 1994a; Bruch *et al.*, 2006; Micheels *et al.*, 2007) with modest changes in continental position and orography. These changes include the presence of a Central American seaway, a marine encroachment from the south into Argentina, a large extension of Eurasia into the Arctic Sea to approximately 80°N, the large Pannonian Lake in central Europe and a wider Indonesian seaway (Markwick, 2007). By 10 Ma ago aspects of ocean circulation were becoming comparable to the modern (Woodruff and Savin, 1989; Lohmann *et al.*, 2006), though Miocene circulation was affected by the open Central American seaway which allowed an eastwards flow of Pacific waters into the Atlantic Ocean, preventing deep water formation in the North Atlantic (Maier-Reimer *et al.*, 1990; Lohmann *et al.*, 2006; Lunt *et al.*, 2008). The Miocene also represented a crucial period of uplift and the generation of arid regions (Harrison and Yin, 2004; Kohn and Fremd, 2008). The uplift of the Himalayas from a relatively low Tibetan Plateau (1-3 km) in the Late Oligocene to an average height of 4-5 km in the Late Miocene (~9 Ma) had effects on global atmospheric circulation, weathering rates and the Asian Monsoon (Quade *et al.*, 1989; Guo *et al.*, 2002; Spicer *et al.*, 2003; Harrison and Yin, 2004; Sun *et al.*, 2009). The Andes may have been at half their modern height by 10.7 Ma (~1800 m) and have since been uplifting at 0.2-0.3 mm per year (Gregory-Wodzicki, 2000). The Rocky Mountains of western North America are a product of several orogenic events, the most recent of which was the Laramide Orogeny which is dated to the Late Cretaceous to Pal~~a~~eocene (English and Johnston, 2004). Subsequent to this major event the Colorado Plateau has been uplifted by nearly 2 km since the Cretaceous (Spencer, 1996). Estimates on the exact timing of the uplift and the rate are still unresolved but recent work focusing on the Colorado Plateau suggests a change in the dynamic topography of 400-1100 m has occurred in the last 30 Ma (Flowers *et al.*, 2008; Moucha *et al.*, 2009). The Alps in the Early to Middle Miocene were merely islands between the Paratethys and Western Tethys Seas being at an estimated height of <1800 m, then major uplift occurred after 14 Ma until present (Jiménez-Moreno *et al.*, 2008).

Atmospheric Carbon dioxide levels for the Tortonian have been estimated, using boron isotopes (Pearson and Palmer, 2000), alkenones (Pagani *et al.*, 2005), stomatal indices (Kürschner *et al.*, 1996; 2008), pedogenic carbonate (Ekart *et al.*, 1999) and the GEOCARB mass balance model (Berner and Kothavala, 2001). All of these techniques estimate Tortonian CO_2 to range between Last Glacial Maximum, pre-industrial (Pearson and Palmer, 2000; Pagani *et al.*, 2005) and mid-20th Century levels (Kürschner *et al.*, 1996; Ekart *et al.*, 1999 Berner and Kothavala, 2001; Kürschner *et al.*, 2008), although pedogenic carbonates used to estimate CO_2 go as high as 1170 ppmv at 10 Ma (Ekart *et al.*, 1999). It is possible that Miocene climate change was not related to atmospheric CO_2 variations (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005), though new CO_2 estimates, such as those derived from stomatal indices, are more consistent with the co-evolution of Miocene climate and CO_2 (Kürschner *et al.*, 2008).

2. Methods

2.1. Constructing the vegetation database

Using TEVIS (Tertiary Environments Vegetation Information System) (Salzmann *et al.*, 2008), which is a Microsoft Access and ArcGIS 9 based database, 223 Tortonian vegetation sites (Fig. 1) have been collected and recorded in an internally consistent manner. Using the author's interpretation of palaeobotanical sites, taken from the published literature, the recorded Tortonian sites have been translated into the classification scheme of the BIOME4 mechanistic model of vegetation (Kaplan, 2001). TEVIS not only records the vegetation of the palaeobotanical site but also the latitude and longitude, sedimentology, method used to date the sample and a quality indicator – to ascertain the resolution of the chronology. Where available, numerical climatic parameters such as mean annual temperature and precipitation are also recorded in TEVIS. This facilitates quantitative data-model comparison. Extracting climatic parameters from fossil assemblages can be achieved by a number of techniques and the majority of the estimates in the TEVIS database come from either the co-existence approach (Mosbrugger and Utescher, 1997 and the NECLIME working group) or Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1979; 1993; Spicer, 2007; Spicer *et al.*, 2009). The co-existence approach uses the climatic tolerances of a fossil plant's nearest living relative as a guide to the climate tolerances of the fossil taxa. When this is done for a whole assemblage a climatic envelope is generated where all the fossil plants could have co-existed; providing an estimate of climatic parameters (Mosbrugger and Utescher, 1997). CLAMP uses 31 leaf physiognomic (structure) characteristics, that have been shown to be related to the environment to which the leaf architecture is exposed (Spicer, 2007; Spicer *et al.*, 2009), to estimate the climatic parameters of fossil leaf assemblages (Wolfe, 1993).

It has been possible to confidently assign all literature-based vegetation reconstructions to a corresponding BIOME4 classification (Fig. 2). However, it should be noted that although the BIOME4 classification represents biomes of the modern world these are not identical, in species composition, to those of the Tortonian and in some regions the Tortonian biome has no modern analogue.

2.2. Construction of the animal database

To provide additional information on Tortonian vegetation where palaeobotanical information is absent we have constructed, using the same Microsoft Access and ArcGIS platform successfully employed for TEVIS, a new database termed MAD (Miocene Animal Database). This database records palaeo-rotated vertebrate fossil sites and the author's inferred habitat as well as taxonomic data. The author's inferred habitat is also converted, where possible, into a BIOME4 scheme vegetation type. However there are limitations in using vertebrate assemblages to infer vegetation, such as the respective scale of the inferred habitat and the reconstructed biome~~,~~ and this will require further investigation. MAD also records information about the sedimentary facies, age and dating method, specimen completeness and any taphonomic information provided. The sites collected in MAD are critical to increase our vegetation data coverage in regions where plant fossils are not preserved. MAD contains 70 vertebrate locations and has provided 17 additional biome data points and provided valuable coverage in regions such as the Middle East and Central America (Fig. 3).

2.3. Description of the HadAM3 GCM and BIOME4 models

A suite of Late Miocene atmosphere-only General Circulation Model (AGCM) runs have been carried out using the Hadley Centre Atmospheric Model Version 3 (HadAM3; Pope *et al.*, 2000) and the climatologies used to run the mechanistic vegetation model BIOME4 (Kaplan 2001). A brief outline of the model and boundary conditions used in the simulations can be found below. A fuller description of the modelling methodology can be found in Lunt *et al.* (2008).

HadAM3 has a horizontal resolution of 2.5° latitude × 3.75° longitude, this equates to a spatial resolution of 278 × 417 km at the equator. The model has 19 vertical layers, a time step of 30 minutes and includes the Edwards and Slingo (1996) radiation scheme, the Gregory *et al.* (1997) convection scheme, a sea ice model that is largely the same as in HadAM2 (Cattle and Crossley, 1995) and MOSES (Cox *et al.*, 1999) a land surface scheme capable of simulating freezing and melting of soil moisture (Pope *et al.*, 2000). HadAM3 has been successfully applied to numerous palaeoclimate intervals of the pre-Quaternary (e.g. Haywood and Valdes, 2006; Lunt *et al.*, 2008).

The Late Miocene palaeogeography, orography and ice sheet extent were derived from Markwick (2007). Crucially this gives a significant decrease in altitude of the Tibetan Plateau relative to the present day, as well as the western cordillera of North and South America. The land surface scheme was set to globally homogeneous values (in this case shrubland). Shrubland was chosen to initialise the model as its physical characteristics are least biasing in terms of climate prediction. Atmospheric CO_2 levels were set at 395 ppmv which is at the higher end of available estimates yet it should be noted that given prescribed sea surface temperatures in this model the exact CO_2 value chosen does not have a large effect on the climate predicted by the model.

In the absence of sufficient proxy sea surface temperatures (SSTs), we derive our Late Miocene SST distribution from a pre-industrial surface temperature distribution, $T^*_{pre\text{-}industrial}$, in the following way:

Where m is the number of the month (January=1), Φ is the latitude, and A, B, and C are defined in Lunt *et al.* (2008; Table 1). $T^*_{pre\text{-}industrial}$ is derived from the means from years 1870–1900 of the Hadley Centre sea surface temperature (SST) and sea ice climatologies (HadISST, Rayner *et al.*, 2003). This formulation allows the sensitivity of the global warming, the amount of polar warmth, the seasonality of the polar warmth, and the form of the latitudinal gradient of warming, to be tested using just 4 key parameters; A, B, C, and f(Φ).We address the inherent uncertainty associated with the prescribed boundary conditions by carrying out a suite of seven Late Miocene simulations, with different values of A, B, C and f (Lunt *et al.*, 2008, table 1). The resulting distributions, from this calculation, are illustrated in and summarised in Lunt *et al.* (2008; Fig.2, table 2). The prescribed SSTs all have a lower equator to pole temperature gradient than the pre-industrial, in agreement with proxy data (e.g. Williams *et al.*, 2005; Pearson *et al.*, 2007), with a maximum change in Northern Hemisphere winter. This is also consistent with the idea that the current strength of the thermohaline circulation developed through the Miocene (e.g. Jakobsson *et al.*, 2007). These seven distributions are identical to those contemplated by Gladstone *et al.* (2007) in relation to the hydrological budget in the Mediterranean of the Late Miocene. For all simulations, where the value of $SST_{LateMiocene}$ is below the freezing point of ocean water, T_{freeze}, sea ice is allowed to form. In these instances, the SST is set to T_{freeze}, and the surface temperature is no longer prescribed but is computed by the sea ice component of HadAM3. Certain coastal SSTs had to be extrapolated due to the difference between the modern and Late Miocene land–sea masks, but this is a minor effect.

BIOME4 (Kaplan, 2001) is a mechanistic equilibrium vegetation model which predicts global biome distribution from monthly averages of temperature, precipitation, cloudiness and absolute minimum temperature. Biomes are predicted based on the bioclimatic tolerances of 12 Plant Functional Types (PFT) ranging from cushion forbs to tropical evergreen trees. At the core of the model is a coupled carbon-water flux scheme which maximises Net Primary Productivity (NPP) for any given PFT through the determination of Leaf Area Index (LAI). This is calculated on a daily simulation of the soil water balance, canopy conductance, photosynthesis and respiration. The woody PFT that achieves the highest annual NPP at its maximised LAI for a given grid square is considered dominant. This however is not the case for grass-tree areas such as savannas; here a weighted NPP is calculated and inferred fire risks are both used to determine the forest-grassland boundary. The model then orders all the PFTs that could exist under ambient conditions in a grid cell based on NPP, LAI and mean annual soil moisture. It then uses semi-empirical rules to decide on which of the 27 biomes should be plotted in the cell (Kaplan 2001). For the Late Miocene simulations BIOME4 was run in anomaly mode. This is a standard technique that removes known systematic errors in the climate prediction of HadAM3 and has been employed in numerous modern and palaeoclimate/palaeoecological studies (e.g. Haxeltine and Prentice, 1996; Texier *et al.*, 1997; Salzmann *et al.*, 2008).

2.4. Coupling of the data and model

To provide a global vegetation reconstruction it is necessary to fill the regions with limited palaeoecological data (Fig. 1; Fig. 3) with vegetation. In this study the technique of Salzmann *et al.* (2008), using a state-of-the-art model simulation and merging this with the palaeoecological data is employed. Before the process of merging the data and model into a hybrid reconstruction of global Tortonian vegetation it was first necessary to determine which Late Miocene HadAM3 experiment was best suited for this purpose. The original HadAM3 experiments presented in Lunt *et al.* (2008; Mioc1-Mioc7) were all used to produce BIOME4 vegetation predictions. Mioc1-Mioc7 represent seven HadAM3 experiments with different SST gradient profiles, generated with the equation described in section 2.3. The resulting BIOME4 estimates were compared to the Tortonian data collected in TEVIS and MAD, using ArcGIS9 software. Before comparison could begin the palaeoecological data ~~was~~ were first palaeo-rotated to its Tortonian latitude and longitude (using the palaeo-rotation codes of Paul Markwick ensuring consistency between our data and the Tortonian palaeogeography used in HadAM3). To aid comparison and selection, Cohen's Kappa statistic (Cohen, 1960) was used to highlight the statistically most comparable BIOME4 model simulation (Table 1). Cohen's Kappa statistic measures the agreement between two sets of categorizations while taking into account chance agreements between categories, where 0 means the agreement is no better than chance and 1 shows a perfect fit (Cohen, 1960; Jenness and Wynne, 2005). BIOME4 simulations Mioc1 – Mioc7 were compared using both the full and mega biome classification schemes of the BIOME4 model. The use of the broader mega biome scheme, following Harrison and Prentice (2003) and Salzmann *et al.* (2009), was necessary due to avoid the Kappa statistic becoming meaningless due to some categories containing a low number of sample points for the full biome scheme. Of the experiments, Mioc5 compared most favourably to the palaeobotanical and palaeoecological data (i.e. achieved the highest Kappa score using the mega biome scheme) and this experiment was therefore chosen for use in the construction of the data-model hybrid. Mioc5 represents a reduced equator to pole gradient in the Northern Hemisphere, with SSTs around 9°C warmer at 60°N (compared to the pre-industrial). The equator to pole gradient in the Southern Hemisphere is slightly reduced when compared to the pre-industrial gradient but with SSTs 3 - 4°C higher. Equatorial SSTs are 1°C warmer than in the pre-industrial (Table 1).

The strategy used to join the databased vegetation with model predicted vegetation is summarised in Fig. 4 and based on the techniques used in Salzmann *et al.* (2008). The merger was undertaken on a grid by grid basis; examining each model predicted grid cell and, if necessary, correcting it using available palaeobotanical data. This is most visible in Fig. 5, which shows the consistency of the data – model comparison and the degree of correction. Areas with low or no palaeobotanical data are left unchanged as model predicted vegetation.

3. Results

3.1. Global Tortonian vegetation reconstruction

The plotted biomes, based on 240 TEVIS and MAD data points, provide an insight into Late Miocene vegetation and climate. There is good data coverage in western USA, Europe, India, southeast Asia and western South America, allowing a confident vegetation reconstruction for these regions. This allows for a confident robust vegetation-reconstruction for these regions. Data coverage also allows a confident reconstruction of Alaska, central Africa, parts of Asia and southern Australia. However, data coverage is not uniform and thus areas lacking adequate coverage rely on modelled vegetation for the reconstruction. These areas include most of the high latitude Northern Hemisphere including much of Canada and northeast USA, Greenland, Scandinavia and Russia. Other areas of poor coverage also include eastern South America, southern Africa and northern Australia.

The Tortonian vegetation reconstruction from both the palaeobotanical data and the BIOME4 model prediction show a warmer and moister world (Fig.6A). The following section describes and highlights regional vegetation patterns from the Tortonian world. Numbers in parentheses refer to palaeobotanical site location numbers (Fig. 1) and numbers within parentheses with an “M” relate to mammal site location numbers (Fig. 3). All references for specific sites, and the biome code assigned to each has been made available as supplementary information (Appendices 1, 2). Climatic data ~~is~~ are also presented below in the form of Mean Annual Temperature (MAT) in °C and Mean Annual Precipitation (MAP) in mm per year. The climatic data is also presented in Table 2.

3.1.1. Polar and boreal regions

During the Tortonian the polar and boreal regions (>60°N, >60°S) were dominated by cold evergreen coniferous forests and temperate grasslands. In Eurasia and Greenland there is also an extension of temperate deciduous broadleaved forests from the temperate region. Antarctica is not vegetated in this reconstruction, which is in agreement with the extinction of tundra from Antarctica during the Middle Miocene (Lewis *et al.*, 2008). The ANDRILL AND-2A core, drilled in McMurdo Sound, yielded a palynological assemblage showing the presence of tundra vegetation between 15.7-15.5 Ma. Following this warm period the content of palynomorphs decreases sharply until they are absent before the start of the Tortonian (Warny *et al.*, 2009). On Seymour Island and James Ross Island, Antarctic Peninsula the Hobbs Glacier formation has been dated as Late Miocene (Dingle and Lavelle, 1998; Marenssi *et al.*, 2010).This marine diamictite is considered to have been deposited close to a glacier terminus suggesting the West Antarctic Ice Sheet was almost at its present extent on the Antarctic Peninsula, though with evidence for interglacial events (Smellie *et al.*, 2006; Marenssi *et al.*, 2010). Previously tundra vegetation had been reported from the Pliocene of the Transantarctic Mountains (Ashworth and Cantrill, 2004). The dating of these deposits was based on the assemblage of reworked marine diatoms (Harwood, 1986), more recent work has suggested an age >5.1 Ma and likely much older (Ackert and Kurz, 2004; Ashworth *et al.*, 2007). The growing body of evidence from Antarctica suggests that by the Tortonian the continent was largely glaciated.

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The polar and boreal realms are not well constrained in the Tortonian reconstruction. A scarcity of Tortonian palaeobotanical data in Canada, Scandinavia and northern Russia (Fig. 6A), combined with an extension of the continent into the modern Arctic Ocean north of Scandinavia and the Novosibirsk Islands extending to Svalbard in the palaeogeography means much of the high latitude biomes are model-defined. Likewise Antarctica is defined as having near-modern ice sheet cover in the model boundary conditions, meaning that the BIOME4 model would not predict vegetation on the Antarctic continent. There are some locations that provide evidence of vegetation at the high latitudes during the Tortonian. In Alaska, around the Cook Inlet and Nenana Coal Field (Sites 1-5) there was a cool mixed forest to 61°N and a mix of cool needleleaf and cold evergreen needleleaf forest further north. Three of the five sites give a mean annual temperature of 4.5±1.5°C, 4±1°C and 10±10°C (Wolfe, 1994b; White *et al.*, 1997; Reinink-Smith and Leopold, 2005); this is 4-10°C warmer than present. The palaeobotanical data and model agreed well on the position of the cold evergreen needleleaf forests but differed on the position of the cool mixed forest. In the BIOME4 model simulation the area with cool mixed forest palaeobotanical data is reconstructed to have temperate deciduous broadleaved forest and warm-temperate evergreen and mixed forest biomes. This discrepancy between the BIOME4 predictions and the palaeobotanical data is related to the SST profile used in the model boundary conditions.

In the North Atlantic (Sites 72-73), ocean cores provide evidence of terrestrial biomes during the Tortonian. DSDP 338 provides evidence of a temperate forest dominated by coniferous trees at 67°N offshore Norway (Koreneva *et al.*, 2005). ODP Leg 151 contains a pollen assemblage showing the presence of a swampy taiga at 77°N on the Hovgård Ridge (Boulter and Manum, 1997). In Russia there is evidence of the evergreen taiga forest at 70°N (Site 139) and a temperate evergreen forest at 59°N (Site 141). The model successfully predicts the presence of the cold evergreen needleleaf forest at 77°N, but does not predict the presence of the temperate evergreen needleaf forest seen at DSDP 338. Whether this relates to problems in the model prescribed SSTs or is due to the sample coming from an oceanic core rather than a terrestrial deposit will need to be explored in future work. Khapchan (Site 140) was described by Nikitin (2007) as a northeastern Turgayan Flora (warm-temperate mixed forest) and contains a diverse seed assemblage of 130 taxa containing; *Alnus*, *Betula*, *Brasenia*, Cyperaceae, Ericaceae Myricaceae, *Rosa*, *Rubus*, *Tubela*, Vitaceae and *Weigela*, (Nikitin, 2007). This site represents a Turgayan Flora near the transition period in northeastern Asia, from the Oligocene-Miocene Turgayan flora to the Pliocene-recent flora (Nikitin, 2007). Nikitin (2007) classified it as a Turgayan flora despite the absence of *Taxodium* and the minor amount of broadleaved taxa. This may mean that in terms of the biome classification of the BIOME4 model the flora at Khapchan no longer represents a warm-temperate mixed forest, which the Turgayan Flora is considered to be. This will require future investigations to establish a suitable BIOME4 classification for a northeastern Turgayan Flora and therefore it is omitted from the present reconstruction.

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As data ~~is~~ are scarce for the boreal and polar realms, these regions rely heavily on the BIOME4 model for the Tortonian reconstruction. Across North America, BIOME4 predicts a direct transition from boreal taiga to temperate grasslands at 60°N in central Canada and 68°N in western Canada (Fig. 6A). In northernmost North America, BIOME4 predicts a mixture of temperate grassland, boreal taiga and temperate xerophytic shrubland. In northeast Russia, the model predicts extensive temperate grasslands from 66°N to 78°N with temperate deciduous broadleaved forest reaching 78°N between the longitudes of 25°E and 36°E. This then changes to cool needleleaf forest at 78°N, whereas, for most of the polar boreal region temperate grassland is predicted to change directly into boreal taiga forest, much as it does in North America (Fig. 6A). There are also minor areas of cool mixed forest, cool needleleaf forests and temperate xerophytic shrubland within the extensive temperate grassland region, these same minor biomes are also found on the west coast. At 60°N the BIOME4 model predicts the presence of warm-temperate forest on the east coast of Eurasia (Fig. 6A). In eastern Russia and the Kamchatka Peninsula the boreal taiga is predicted by BIOME4 to have had a much lower southern extent at 55°N and changes directly to temperate grassland. BIOME4 shows the presence of boreal forest mixed with some areas of temperate grassland and in the northernmost area, a small region of deciduous boreal taiga. Along the southern coast of the Kamchatka Peninsula, the model predicts a mix of cool mixed and cool needleleaf forest (Fig. 6A).

Currently there are no published palaeobotanical sites for the Tortonian of Greenland. The BIOME4 model predicts a large expanse of temperate grassland in the northwest and central areas with temperate forests in the south and east. In the far northeast and northwest, small areas of temperate xerophytic shrubland are predicted to have existed (Fig. 6A). In the boundary conditions of the GCM experiment, based on the palaeogeography (Markwick, 2007), the east Greenland highlands are covered by an ice-sheet and thus were not vegetated. Despite the lack of data on Greenland, good data coverage on Iceland (Sites 68-71) shows a warm-temperate to temperate climate during the Tortonian. This provides some evidence to support temperate forest on Greenland at this latitude during the Tortonian. All the areas on Greenland defined by the BIOME4 model are generated from the climate of the best fit GCM experiment and a single ~~data~~ datum point could confirm or change these regions. There are no model-predicted biomes for Antarctica because the palaeogeography used in the model boundary conditions ~~have~~ has a modern Antarctic ice sheet.

3.1.2 Temperate zones

The BIOME4 model predicts a considerable extension of the temperate zone into what is present boreal and polar regions. Data coverage in the temperate zone (23.5-60°N/°S) is good. Notable areas of absence are the Appalachians in the eastern USA, north Mexico, Australia and southernmost South America. Broadly the reconstruction shows a spread of warm-temperate evergreen broadleaved and mixed forest into Europe, Southeast Asia, eastern USA and areas of western USA and an expansion of temperate deciduous broadleaved savanna in Eurasia and central USA.

On the west of the Rocky Mountains, a mixture of forest, woodland and savanna occured until 38°N, below this the area was dominated by temperate xerophytic shrubland with some coastal forests. At 55°N on what is now the Queen Charlotte Islands, Canada, there was a warm-temperate evergreen mixed forest (Site 6). To the south of this there was temperate needleleaf forest (Site 7) near the coast and temperate deciduous broadleaved forest further inland (Site 8). South of this at between 43°N and 48°N, many locations show the presence of a warm-temperate evergreen and mixed forest (Sites 9-12, 14 and 19-21). The forest at Musselshell Creek (Baghai and Jorstad, 1995) had a MAT of 12.5±1.5°C and a MAP of 1250 mm (Site 14), this is 7°C warmer than at present and nearly 500 mm/yr wetter. South of this is temperate broadleaved savanna near the coast at Kimble Homestead (Site 13), which is estimated to have a MAT of 12.5±2.5°C, comparable to the warm-temperate evergreen and mixed forest but, with a MAP of 900±100 mm (Retallack *et al.*, 2002). Further inland there was a mix of temperate broadleaved deciduous forest (Site 15) and temperate sc~~h~~lerophyll woodland and shrubland (Sites 16, 17). The former having a MAT of 14°C and a MAP of 635±180 mm (Dorf, 1938) and the latter estimated to have a MAT of 13.4±7.8°C and a MAP of 762 mm (Smith, 1941; Beuchler *et al.*, 2007). For this area the climate data provided by the palaeobotanical locations suggests an increase in MAT of 7-8°C and an increase in MAP of 50-200 mm/yr compared to modern information. The model disagrees with the palaeobotanical data within this region on the amount of MAP, causing the model to predict much drier biomes. The Rocky Mountains are shown to have had some areas of cool mixed forest (Site 18) and areas of temperate needleleaf open woodland (Fig. 6). South of 38°N, an open area of temperate xerophytic shrubland is predicted by the BIOME4 model and supported by numerous palaeobotanical locations (Sites 23, 25-27). This open area extended down to the tropical zone, apart from a coastal forest with a warm-temperate evergreen and mixed character (Sites 22, 24) at 31-33°N (Fig. 6). This is estimated to have had a MAT of 15±4°C and a MAP of 679±62.5 mm (Axelrod, 2000); although the level of precipitation seems low to support this type of forest, Axelrod (2000) compared it to cloud forests of Pacific Islands, suggesting it may have required extensive summer fogs. The modelled biomes and the palaeobotanical data agree well with the distribution and extent of the temperate xerophytic shrubland and the presence of coastal warm-temperate forest.

East of the open temperate xerophytic shrubland, the BIOME4 model and the palaeoecological data agree on the presence of a mixture of temperate needleleaf forest and temperate deciduous broadleaved savanna (Sites 28-31 and M1). Along the Gulf Coast there was a mixture of warm-temperate evergreen and mixed forest (Site 37) and tropical semi-deciduous broadleaved forest (Site 36). In Florida, mammalian fossils and pollen at the Moss Acres Racetrack site (Lambert, 1994; Lambert, 1997) show the presence of a temperate to warm-temperate, deciduous broadleaved savanna (Sites M2-M3). On the east coast of the USA there was a warm-temperate evergreen mixed forest until 46°N (Sites 32-35). Further inland where the palaeobotanical data ~~is~~ are absent, the BIOME4 model predicts a mixture of temperate deciduous broadleaved forests, temperate deciduous broadleaved savanna and temperate grasslands (Fig. 6). The warm-temperate evergreen and mixed forest on the east coast, this biome at Martha's Vineyard and preserved in the Legler Lignite is predicted to have a MAT of between 13.3±5°C and 15±9°C with a MAP of 1270 mm (Greller and Rachele, 1983; Frederiksen, 1984; Axelrod, 2000).

In Europe the palaeobotanical data indicate a vast swathe of warm-temperate evergreen and mixed forest with subtropical elements, from 8°W to 51°E and from 38°N to 60°N (Sites 79-99, 103-110, 119). Within this biome, which is considered most comparable to the warm-temperate forests of southeast China, climate estimates for the Tortonian from the fossil remains are predicted to have had a MAT of 14.85±0.95°C – 16.8±1.2°C and a MAP of between 988.5±9.5 mm and 1242.5±55.5 mm (Figueiral *et al.*, 1999; Ivanov *et al.*, 2002; Kvacek *et al.*, 2002; Bruch *et al.*, 2006; Syabryaj *et al.*, 2007; Erdei *et al.*, 2009). This is around 6.3°C warmer than at present (the range of difference is -2.4°C – +8.5°C) and the difference in MAP is between 159 mm to 740 mm when compared to modern data. Areas of difference to this apparently homogenous biome are the Iberian Peninsula and the land to the south of the Pannonian Lake in Turkey. In this region, the warm-temperate evergreen and mixed forest opened up into a region of temperate deciduous broadleaved savanna (Site 111; 115-116) and BIOME4 predicted temperate needleleaf forest. Further east the vegetation returned to warm-temperate evergreen and mixed forest (Sites 117-118). Continuing east from here there was a region of temperate deciduous broadleaved savanna (Sites M13-M14), and BIOME4 predicted temperate needleleaf forest extending to 62°E (Fig. 6). The model and palaeobotanical data agrees well for Europe around the Panonnian Lake however, the model makes western Europe anomalously dry.

The Iberian Peninsula also had drier open vegetation than the rest of Europe. On the south coast there was a region of tropical xerophytic shrubland (Site 76), and along the west coast there was a small amount of temperate sc~~h~~lerophyll woodland and shrubland (Site 75). The modern Sahara was greatly reduced, if not absent altogether (Fig. 6). Temperate sc~~h~~lerophyll woodland and shrubland (Sites 77-78) and tropical savanna (Site M7) inhabited coastal regions of northwest Africa (Tunisia, Morocco and Algeria). Further inland there is no vegetation data and the BIOME4 model predicts tropical xerophytic shrubland and small areas of desert (Fig. 6). The mix of predominantly tropical xerophytic shrubland and desert continued east across the modern Sahara region until 21°E, from here until the east coast of the Arabian Peninsula there was extensive tropical xerophytic shrubland and an absence of desert. The area around the modern Nile delta had tropical savanna along the coast (Site 112). The BIOME4 model agrees with the palaeobotanical data in that the Iberian Peninsula has more open vegetation than the rest of Europe. However, there is some disagreement as to which biome types are present. The BIOME4 model also fails to predict the coastal vegetation of North Africa; this may be a problem with the model or a question of scale. The palaeobotanical data may reflect vegetation restricted to the coast whereas the model has predicted the overall biome for the grid cell; this will require further study.

Along the east coast of the Pannonian Lake, the BIOME4 model predicts a mixture of temperate xerophytic shrubland and temperate needleleaf forests (Fig. 6A). These temperate needleleaf forests are predicted by BIOME4 to continue, in isolated patches, until 81°E. These forest patches are within an extensive temperate deciduous broadleaved savanna (Sites 137-138, 144, M15) which existed from 35°N to 58°N in Asia. At the northern extent of the savanna area it is bordered by temperate deciduous woodland which inhabited some of the boreal realm during the Tortonian (Fig. 6). At its southern limit, the BIOME4 model predicts the temperate savanna blended into temperate needleleaf forest and temperate needleleaf parkland. The palaeobotanical data shows that the model simulation for this region produces a biome pattern with anomalously high levels of forest.

South of the Himalayas on the Indian subcontinent a band of warm-temperate evergreen and mixed forest ran longitudinally between 28°N and 33°N (Sites 169, 177). Below this there was a mixture of tropical evergreen broadleaved forest, tropical deciduous forest and tropical savanna (Sites 170-175), and these biome types continued into the tropical zone (Fig. 6). In China and southeast Asia, the warm-temperate forests continued in the longitudinal band between 23.5°N and 33°N (Sites 182, 185). Fossils from the Xiolongtan coal mine in China are estimated to have lived with a MAT of 17.9±1.2°C with a MAP of 1427±212 mm (Xia *et al.*, 2009), this is nearly modern levels for this region. As this band of warm-temperate evergreen and mixed forest reached the east coast of Asia it followed it north, reaching 48°N (Sites 147-148, 156, 158-159, 161). In Japan, many fossil sites indicate this forest biome also existed there (Sites 162-163, 166-168). Throughout India and southeast Asia the model compares very well to the palaeobotanical data and only required slight alterations to create the hybrid reconstruction.

On the Himalayan Plateau and further north a patchwork of temperate xerophytic shrubland (Site 152), temperate deciduous broadleaved savanna (Sites 142, 145-146, 149-151, 153-155, 198, M16), temperate deciduous broadleaved forest (Site 143) was present during the Tortonian. At the northern limit of the temperate zone, BIOME4 predicted cool needleleaf forest existed at this time (Fig. 6). This mixture of biome types continued north until it bordered an extensive temperate grassland predicted by BIOME4. In north central Asia the transition from temperate biomes to the cold evergreen needleleaf forest biome occurred as far south as 55°N (Fig. 6); currently there is no available data to confirm this transition. This region in the BIOME4 simulation is heavily influenced by the orography which is the reason for minor differences with the palaeobotanical data. For the majority of this region the model predicted temperate grassland or temperate deciduous broadleaved forest, whereas the palaeobotanical data reflected a temperate deciduous broadleaved savanna.

In South America, the temperate zone contains many sites along the western side and sparse data along the east. On the east coast BIOME4 predicts a continuation of tropical vegetation into the temperate zone, this is mainly tropical xerophytic shrubland with some areas of semi-deciduous to deciduous tropical forest (Fig. 6). At Taubate, Brazil (Site 57) pollen provides evidence of a subtropical to warm-temperate forest along the coast (Garcia *et al.*, 2008). On the west side of the South American temperate zone, tropical xerophytic shrubland changed to tropical savanna (Sites 60-61, M5) and a proto-Atacama desert (Site 58) at 24-26°S. South of this, an area of temperate xerophytic shrubland occupied a narrow band (Site 62) before changing into temperate sc~~h~~lerophyll woodland and shrubland (Site 63). South of this area there is scarce data, apart from an area of temperate xerophytic shrubland (Sites 64-66) between 39°S and 46°S. For the rest of southern South America, BIOME4 predicts a mixture of warm-temperate to cool-temperate forests (Fig. 6). The palaeoecological data and BIOME4 model compare well for temperate South America. Model-predicted biomes that required altering for the hybrid reconstruction were either too dry or too wet. This seemingly contradictory statement is probably related to the orography; both within the model boundary conditions and the orography the palaeoecological data existed at.

The temperate zone of southern Africa is small and poorly-covered by data. The temperate zone is predicted, by BIOME4, to start with a continuation of the tropical xerophytic shrubland until 28°S to 31°S where tropical semi-deciduous and deciduous forests are predicted to begin. The data points come below this area, from western South Africa and they show the presence of a temperate needleleaf forest (Sites 135-136). For the South African Cape, BIOME4 predicts a warm-temperate evergreen and mixed forest (Fig. 6). The model-predicted biomes around the South African Cape were too dry to match the limited palaeobotanical data for the area. This shows there is some problem in the amount of precipitation generated by the model for this region.

In Australia, the temperate zone was dominated by temperate sc~~h~~lerophyll woodland and shrubland during the Tortonian (Sites 211-213, 215-216). Location 212 at Lake Tay predicts this biome to have a MAP of 1375±125 mm (Macphail, 1997), which was an increase of around 1100 mm/yr when compared to modern data. A small area of temperate grassland was present in southeast Australia (Site 214) and BIOME4 predicts coastal warm-temperate evergreen and mixed forest and temperate needleleaf forest along the east coast (Fig. 6). In central Australia, the model also predicts an area of tropical grassland. On New Zealand, many data points agree with the BIOME 4 prediction of warm-temperate evergreen and mixed forest (Sites 218-220). Overall the palaeobotanical data and model-generated biomes for temperate Australia compare well in places, but broadly the model predicts biomes that are too dry.

3.2.3. Tropical zones

The tropical zones (23.5°S – 23.5°N) have good data coverage. Notable exceptions are southern Africa, Central America, eastern South America and northern Australia. In general there is an opening up of the tropical forests of South America, an expansion of tropical vegetation into the Sahara Desert in Africa, extensive tropical forests in India and southeast Asia and open biomes in Australia.

In Central America, palaeobotanical data show the presence of a warm-temperate evergreen and mixed forest (Site 38) at Jalapa, Mexico (Graham, 1975) where a warm oak-liquidambar forest bordered mangroves. Further south, near Gracias, Honduras (Site M4) an assemblage of mammals shows that a tropical savanna occupied the region during the Tortonian (Webb and Perrigo, 1984). Apart from these sites the rest of Central America is predicted by BIOME4 (Fig. 6). In the north, tropical xerophytic shrubland and temperate sc~~h~~lerophyll woodland and shrubland continued into the tropical zone from the temperate zone. Below 20°N a patchwork mixture of tropical savanna, tropical deciduous woodland and tropical semi-evergreen forest is predicted to have existed. At the Panama Seaway, BIOME4 predicts a tropical evergreen broadleaved forest (Fig. 6). The limited palaeoecological data for Central America make a comprehensive data-model comparison difficult, but based on the available evidence the model appears to simulate vegetation here well.

Crossing this seaway into South America, a broad expanse of predominantly tropical evergreen broadleaved forest (Sites 41, 44, 46-47, 49, 51-52), with some isolated areas of tropical deciduous woodland (Sites 42-43, 45) and along the edges of this forest BIOME4 predicts tropical semi-evergreen forest and tropical deciduous woodland existed. This forest opened up into tropical savanna (Sites 50, 53-54) which continued east across South America to between 46°W-38°W where, in an absence of data, BIOME4 predicts tropical xerophytic shrubland (Fig. 6). Some evidence for tropical evergreen broadleaved forest along the coast is present on Outeiro Island, Brazil (Site 48). Near 23.5°S on the east side of South America there is a lack of data and BIOME4 predicts an area of tropical deciduous woodland within the extensive tropical savanna. In eastern South America, at this latitude there is evidence for tropical deciduous woodland (Sites 55-56). This eastern tropical deciduous forest biome is estimated to have a MAT of 19.8±3.7°C – 21.5±2.5°C and a MAP of 550±180 mm at Upper Jakokkota (Gregory-Wodzicki, 2002). This is an increase of 9-10°C when compared to the modern, but a reduction in MAP of about 570 mm. The BIOME4 model generated biomes and palaeobotanical data for tropical South America compare very well. The majority of the palaeobotanical data ~~is~~ are grouped in the west and this shows the extent of the tropical forest successfully predicted by the model to be. It also clearly indicates the areas with tropical savanna and tropical deciduous forest predicted by the model and supported by the palaeobotanical data. In the east of tropical South America there is only a single, coastal, data point. This pollen record however shows the model is anomalously dry in this region and the model generated biomes required modification for the hybrid reconstruction.

The tropical zone of Africa, south of the Sahara was an extensive tropical xerophytic shrubland during the Tortonian (Fig. 6). This turned into tropical savanna at between 15-20°N (Sites 123, M8), except on the Arabian Peninsula where xerophytic shrubland is the dominant biome with minor amounts of tropical grasslands along rivers and the coast (Site 120). In West Africa, tropical forests began at 16°N (Sites 121-122) but were mainly restricted to coastal grid squares and tropical savanna is found as far south as 6°N (Site 128). In central Africa, the tropical forests occupied a region comparable to the modern forests. Data for this comes from the Niger Delta in the west (Sites 129-130) and Kenya in the east (Sites 131-132) with BIOME4 supporting the data and showing the extent of the forest (Fig. 6). Climatic estimates for the tropical forest in Kenya give a MAT of 21.7±2°C and a MAP of 1045±200 mm (Jacobs and Deino, 1996); this is comparable to modern levels. Around Ethiopia and Sudan, an area of tropical evergreen forest was present (Site 124) surrounded by tropical savanna (Site 127) and tropical grassland (Sites 125-126). Apart from the sites mentioned, there is an absence of other data points for tropical Africa and so the reconstruction relies on BIOME4. Between 1°S and 6°S, the tropical forests opened up into tropical savanna with isolated patches of tropical deciduous woodland. At around 19°S this gave way to tropical xerophytic shrubland and a small Namib Desert. Along the east coast of Africa BIOME4 predicts tropical xerophytic shrubland (Fig. 6). From the palaeoecological data available for tropical Africa it is clear that the data and model compare closely. Modifications to the model-predicted biomes was mainly restricted to the savanna-xerophytic shrubland boundary which mammalian sites showed was too far south by the distance of a grid cell.

In tropical India, palaeobotanical data ~~is~~ are confined to the south and northeast of the subcontinent and indicate~~s~~ the presence of a tropical evergreen broadleaved forest (Sites 179-181, 195-197, 199-201). Away from these regions the vegetation is predicted by BIOME4 (Fig. 6). The biomes predicted show a mixture of tropical evergreen, semi-evergreen and deciduous forests along the coast and tropical savanna inland. Moving east, data from Vietnam show the warm-temperate evergreen and mixed forest as far south as 18°N (Sites 185-191). This forest opened up to tropical savanna (Site M17) and tropical grassland (Site 194) along the west of the southeast Asian peninsula. On the east side, a mixture of warm-temperate evergreen and mixed forest (Sites 203-204) and tropical evergreen broadleaved forest (Site 205) existed. Below 11°N, an absence of data means the vegetation is predicted by BIOME4. From 11°N to 5°N, the model predicts an area of semi-evergreen tropical forest with isolated tropical savanna, below 5°N BIOME4 predicts the presence of tropical evergreen broadleaved forest (Fig. 6). This is supported by a pollen assemblage from Brunei (Site 207). As in the temperate zone, the model predicted tropical zone of India and southeast Asia compares well to palaeoecological data requiring only minor modifications for the hybrid reconstruction.

Palaeobotanical sites for the Australian tropical zone are exceedingly sparse. ODP 765 (Site 208), located immediately off the west coast, suggests the presence of a temperate sc~~h~~lerophyll woodland with an estimated MAP of 1050±450 mm (Martin and McMinn, 1994; MacPhail, 1997). On the east coast, there was a coastal temperate needleleaf forest (Site 210), which continued south into the temperate zone. The rest of tropical Australia is predicted by BIOME4 to be coastal tropical savanna and tropical xerophytic shrubland until the temperate zone (Fig. 6). Limited data for the tropical zone of Australia means the hybrid reconstruction relies on the model defined biomes. The available palaeobotanical data shows that, as with the temperate zone of Australia, the tropical zone is too dry in places.

4. Discussion

4.1. Tortonian vegetation and climate

The Tortonian palaeoecological data show agreement with the predictions of the BIOME4 model, with higher than pre-industrial SSTs and atmospheric CO_2 levels at 395 ppmv. The reconstruction of Tortonian biome distribution shows significant differences compared to the present-day potential natural vegetation, in the high latitudes and temperate realms (Fig. 6B). Differences are also seen in the tropics but these involve the change in distribution of modern tropical biomes, rather than the movement of biomes into regions where they do not exist today. Of these significant vegetation shifts, the northwards shift of boreal taiga, temperate deciduous forest and temperate grasslands are the most pronounced. Potential natural (i.e. without human influence) present day biome distribution (Fig. 2) shows the boreal forests (cold evergreen needleleaf and cold deciduous forests of BIOME4) have a southern limit of ca. 45°N in east Eurasia and a northern limit of ca. 70°N in northern Russia and Canada (Kaplan, 2001). During the Tortonian, the evergreen boreal forests reached at least 77°N (Site 72) and in the reconstruction it extends to 80°N. Reconstructing the southern limit is difficult due to a lack of data from the polar region. In Alaska it is at 61°N (Site 5) and minimally at 70°N in Russia (Site 139). In the hybrid reconstruction, the BIOME4 model indicates the lowest occurrence of the boreal taiga forests is in east Eurasia at 55°N. This dramatic shift of the boreal taiga by up to 10° indicates significant high latitude warming relative to today. Accompanying this northward shift of the boreal taiga was a loss of tundra biomes (Fig. 6B). The northward shift of the boreal forests has been shown to be a vegetation–climate positive feedback; with the treeline moving north altering the surface albedo and carbon budget of the high latitudes (de Noblet *et al.* 1996; Sturm *et al.* 2001). Inclusion of this Tortonian vegetation reconstruction, as a boundary condition in future modelling studies, may help to increase high northern latitude MATs and the simulation of a reduced pole to equator gradient. In this study the HadAM3-driven BIOME4 vegetation model was able to predict the northward shift of forest biomes but this required a significant increase in SSTs (Table 1). These high SSTs could also be responsible for making model-predicted biomes for areas of western Europe, western USA, Australia, South Africa and eastern

South America too dry, when compared to the biomes reconstructed from the palaeoecological data. Although higher SSTs will create a more active hydrological cycle, the Mioc5 AGCM experiment has a global MAP increase of only 126.7 mm/year relative to the pre-industrial scenario. From the number of regions showing model-generated biomes that are too dry compared to palaeobotanical data, the increase in global precipitation is either not enough or is occurring in the wrong regions. These discrepancies in regions that current experiments make to dry will form part of future model simulations. These future simulations will include the Tortonian vegetation reconstruction presented here as a boundary condition instead of the global shrublands used by Lunt *et al.* (2008).

Following the cold taiga forests northwards were the temperate forests and temperate grassland biomes (Fig. 6). The extensive temperate grasslands predicted by BIOME4 are not supported by any palaeobotanical data points. The data and BIOME4 model predictions agree on the presence of a warm-temperate evergreen and mixed forest in Europe bordering the Pannonian Lake, however in western Europe BIOME4 predicts a much more fragmentary biome pattern than indicated by palaeobotany. In places, the model predicts temperate evergreen needleleaf forests and tropical xerophytic shrublands. This suggests the model interprets western Europe as too dry, and is most likely related to the increased MATs from the higher SSTs. This is because there is only a slight difference in the modelled MAP between the Late Miocene and the pre-industrial model experiments (Fig. 7). Considering the differences in climate between the Late Miocene model and those derived from palaeobotanical data for this biome; the model predicts slightly higher MATs (within the range of the fossil data) and a MAP comparable to that estimated from the data (Table 2). The climatic data suggests the Tortonian MAT in Europe was at least 5-8°C warmer than the pre-industrial age and received around 400 mm/year more precipitation. This warm-wet climate across Europe during the Tortonian is in agreement with studies using other proxies (Bohme *et al.*, 2008).

The palaeobotanical data and BIOME4 predictions for the western USA differ. In this region, the model predicts a mixture of temperate grassland, temperate xerophytic shrubland and temperate needleleaf forest. The palaeobotanical data also suggests a mixture of biomes; warm-temperate evergreen and mixed forest, temperate deciduous broadleaved savanna, temperate sc~~h~~lerophyll woodland and shrubland and temperate deciduous broadleaved forest. The differences between BIOME4 and the data relates to the orography. It is a common problem for model-data discrepancies in mountainous regions due to both the model resolution and preservation bias of the fossil record (Salzmann *et al.*, 2008). In the BIOME4 model, each 2.5° x 3.75° grid cell has its biome calculated based on the climate generated by the AGCM and the average altitude of the cell. In comparison, the palaeobotanical data comes from a single locality. This ~~area~~ locality is within an area of deposition, typically lowland areas such as valley bottoms. This means that the palaeobotanical evidence for mountain regions is often biased towards valley and low altitude habitats and not the regional vegetation. This hampers a meaningful data-model comparison within mountainous regions (Salzmann *et al.*, 2008).

In the reconstruction, there is a relatively small Sahara Desert, mainly based on the BIOME4 reconstruction. The model predicts an expansion of tropical xerophytic shrubland across most of the modern Sahara and the Arabian Peninsula; desert areas were restricted to the north and northeast of the modern Sahara region (Fig. 6B). The palaeobotanical and mammalian evidence shows that along the Mediterranean coast, a mixture of temperate sc~~h~~lerophyll woodland and shrubland and tropical savanna existed. Tropical grasslands are reconstructed for the east coast of the Arabian Peninsula and tropical savanna was present along the modern southern margin of the Sahara desert. Evidence for desert conditions in North Africa comes from sedimentological evidence in Chad. Here wind-blown sandstones conformably underlie a mammal-bearing horizon dated as 7.4-6 Ma (Vignaud *et al.*, 2002; Schuster *et al.*, 2006). Across the Sahara region there are however vertebrate fossil sites that suggest more vegetated conditions. Fossil bushbabies (*Galago farafraensis*) from Egypt provide evidence of a habitat with trees and an estimated rainfall of 500-1200 mm/year (Pickford *et al.*, 2006); crocodiles from Tunisia also indicate more humid conditions (Pickford, 2000; Agrasar, 2003).

In South America, southeast Asia and tropical Africa the palaeobotanical data and BIOME4 predictions are consistent (Fig. 5). However in the Amazonian basin and Africa south of the equator, the absence of palaeobotanical data means the reconstruction relies entirely on BIOME4 (Fig. 5). In East Africa south of the equator the model predicts tropical xerophytic shrubland, this is the same biome predicted for this region in the Piacenzian (Salzmann *et al.*, 2008). The difference between this Tortonian reconstruction and the Piacenzian reconstruction is the presence of palaeobotanical data in this region during the Piacenzian, allowing the reconstruction of tropical savanna rather than tropical xerophytic shrubland. The difference for the Piacenzian between the AGCM and palaeobotanical data was placed on the modelling of rainfall patterns possibly related to the Somali Jet (Salzmann *et al.*, 2008). If this is a problem in the model then the same error may exist in the Tortonian simulations, further palaeobotanical exploration in the Horn of Africa and south along the east side may help to prove or disprove the Tortonian vegetation reconstruction.

Of the available Tortonian AGCM experiments from Lunt *et al.* (2008), Mioc5 compared most favourably to the 240 palaeoecological data points. Statistically Mioc4 compared more favourably in the full biome scheme, but this model predicted a desert in the Amazonian Basin. Mioc5 achieved a higher Kappa score for the mega biome scheme and did not predict the desert in Amazonian Basin. Choosing the experiment with the best megabiome score increases our confidence in the statistical test applied since; having a large number of categories with a low sample in each is less robust than having fewer categories with more samples in each. A minimum of 50 samples per category should be used, and 75-100 samples for more than 12 categories (Congalton and Green, 1999; Jenness and Wynne, 2005). This is difficult for palaeontological studies where sample sizes are restricted by many factors such as deposition, taphonomy, preservation and limited exposure. This makes the mega biome Kappa scores more statistically robust than that for the full biome classification. Combining the palaeoecological data with the Mioc5-driven BIOME4 vegetation model required some model defined areas to be modified (Fig. 5). These include western USA, western temperate South America, western Europe, central Asia, South Africa and Australia. All these regions are in the temperate zone which may indicate the SST gradient used in the experiment was unsuitable. Some of the regions are also heavily influenced by orography which, as previously discussed, confounds palaeoecological data and model comparisons. Areas that compared favourably included eastern and central USA, tropical South America, central Europe, tropical Africa and southeast Asia. These areas also include regions in the temperate zone but mainly those in the tropics, showing that the SSTs for the tropical zone were correctly defined. The limited palaeoecological data available in the polar zone provides evidence that the prescribed SSTs for this climatic zone were well-defined, perhaps even too warm around Alaska where the Mioc5 driven BIOME4 model predicts temperate to warm-temperate biomes. Palaeobotanical data for this region shows the presence of a cool mixed forest, a biome that is colder than those predicted by the model. Overall, the prescribed SST gradient for the Mioc5 GCM experiment that generated the model-defined biome distribution best matches the available palaeoecological data. However, the areas of data-model discrepancy show that further work is required to correctly simulate the Tortonian climate.

4.2. A comparison of the vegetation of the Late Miocene and the Pliocene

Examining trends in vegetation patterns of a warmer world, the Tortonian reconstruction presented here is compared with the vegetation of the Piacenzian (3.6-2.6 Ma), created using the same methodology (Salzmann *et al.*, 2008). Both reconstructions show boreal forests migrating towards the poles, followed by temperate forests and grasslands. The spread of warm-temperate evergreen mixed forests in Europe and southeast Asia are evident in both reconstructions, though this biome spreads more in North America in the Late Miocene than in the Piacenzian. Both reconstructions show a reduction in the extent of the Sahara Desert, though more-so in the Late Miocene. Both reconstructions show an opening up of the tropical forest in South America when compared to present day potential vegetation. In temperate South America however the reconstructions differ, with the Late Miocene having drier conditions than those of the Piacenzian. In tropical Africa the biome distribution is comparable with slightly more tropical evergreen broadleaved forest in the Tortonian. Below the equator, the Piacenzian reconstruction benefits from better data coverage and thus the reconstructed biomes differ. Similar biomes are predicted in both reconstructions for Asia behind the Himalayan Front. In the Piacenzian a mixture of temperate grasslands, temperate xerophytic shrubland and temperate forests existed, whilst in the Tortonian temperate savanna dominates with patches of temperate forests and temperate xerophytic shrublands. South of the Himalayan Front, both reconstructions show a mixture of warm-temperate forest, tropical forests and tropical savanna in Southeast Asia. In Australia both reconstructions show much wetter vegetation than that of the present-day potential vegetation; the main difference is where the woodland and forest biomes are distributed. In the Piacenzian forests woodland and savanna are distributed in the east of the continent, whereas in the Tortonian a large area of temperate sc~~h~~lerophyll woodland and shrubland is present across the south of the continent (Salzmann *et al.*, 2008).

Both reconstructions, despite the difference in age, show similar patterns of biome changes relating to both being warmer worlds than present. The reconstructions show a spread of boreal forests polewards followed by temperate biomes. Both show an expansion of warm-temperate forests with subtropical taxa in the temperate realms of Eurasia and both show a reduction of deserts. Different continental configuration, orography and ice-sheet extent are most likely to account for differences between the two reconstructions. These broad patterns are also seen in future GCM simulations (Salzmann *et al.*, 2009).

4.3. Comparison to previously published Tortonian vegetation reconstructions

The Tortonian reconstruction presented here, using a 27 biome classification of 240 palaeoecological sites and a state-of-the-art AGCM shows similarities and differences to previously published

Tortonian vegetation reconstructions (François *et al.*, 2006; Micheels *et al.*, 2007). Both of these studies used an AGCM with a resolution of 3.75°x3.75°. In François *et al.* (2006) a modern palaeogeography was populated with vegetation based on an unpublished palaeobotanical database and predicted vegetation from BIOME1 (Prentice *et al.*, 1992). This 14 biome reconstruction shows the same spread of boreal forests in the high latitudes. However in North America, Iceland, and east Eurasia, the boreal forests extended southwards into regions with palaeoecological data showing the presence of other biomes (Fig. 6). In the temperate region both the reconstructions presented here, and that of François *et al.* (2006), indicate a spread of warm-temperate evergreen mixed forests [temperate broadleaved evergreen forest in François *et al.* (2006)] in Europe and the eastern USA. For the rest of North America, the Tortonian reconstructions differ, with palaeobotanical evidence suggesting temperate savanna where François *et al.*, (2006) predicted tropical seasonal forest and temperate forests (Fig. 6). In Eurasia, both reconstructions predict a patchwork of vegetation on the Himalayan Plateau, François *et al.*, (2006) predicted grassland, semi-desert and minor savanna leading directly into boreal forests at ca. 45°N. The reconstruction herein (Fig. 6) shows predominantly temperate savanna with minor areas of temperate xerophytic shrubland, temperate deciduous broadleaved forest and temperate evergreen needleleaf forest. This then changed to temperate grassland at 45°N before a transition to boreal forest at ca. 55°N. In South America, the reconstruction of François *et al.* (2006) predicted tropical rain forest extending into the temperate realm to about 40°S and a tropical seasonal forest occupying the Atacama Desert. The palaeoecological evidence presented here indicates that the temperate zone of South America was a mixture of temperate xerophytic shrubland and tropical savanna with a reduced Atacama Desert (Fig. 6). These discrepancies in South America may relate to differences in geography, because a seaway was present in much of modern Argentina (Fig. 6). Differences also occurred in tropical South America where palaeobotanical evidence suggests an opening up of the modern rainforest to create an area of tropical savanna, whereas François *et al.* (2006) presented an extensive area of tropical forest. In Africa, the reconstructions appear comparable except in the Sahara where BIOME4 predicts small areas of desert and in southern Africa where BIOME4 predicts a mixture of tropical savanna and tropical xerophytic shrubland. Again the reconstructions compare favourably in southeast Asia, both predicting tropical forests. On Australia the reconstructions differ again though this may be more related to different classification schemes; as temperate sc~~h~~lerophyll woodland and shrubland is not represented in the scheme used by François *et al.* (2006). Overall, some of the differences between the reconstruction of François *et al.* (2006) and the one presented here may be related to differences in CO_2, geography and the use of a smaller number of biomes.

The reconstruction of Micheels *et al.*, (2007) is again on a modern land-sea mask, and was based on a 36 site proxy dataset (Micheels, 2003) translated into 13 biomes. Comparing the reconstruction presented here and that of Micheels *et al.* (2007) there are similarities in the poleward shift of boreal forests. However in Micheels *et al.*, (2007), the boreal forest consistently changed into cool conifer forests; in the reconstruction here this is only observed in Alaska (Fig. 6). Continuing into the temperate realms, the two reconstructions differ significantly in North America. In the west, palaeobotanical data indicate warm-temperate mixed forests at a slightly higher latitude than reconstructed in Micheels *et al.* (2007). At the latitude of the warm mixed forest of Micheels *et al.* (2007), palaeobotanical data show the presence of coastal warm-temperate mixed forest but temperate xerophytic shrubland further inland (Fig. 6); these differences may be related to spatial resolution. In the central USA, palaeobotany provides evidence of temperate savanna mixed with BIOME4-predicted temperate needleleaf forests; in Micheels *et al.* (2007) this region is completely forested. The eastern coast of the USA compares favourably in both reconstructions.

The Iberian Peninsula in this reconstruction shows a higher vegetational diversity than in Micheels *et al.* (2007) (Fig. 6). Moving east across Europe, both reconstructions are comparable, although the reconstruction presented here has a greater expanse of warm-temperate forest. This forest occupied significantly less area in southeast Asia; this is comparable to the reconstruction of Micheels *et al.* (2007). On the Himalayan Plateau and north of it, the reconstruction herein shows more vegetational variation, this is due to using a larger biome scheme. The reconstruction of Micheels *et al.* (2007) also presented a polar desert on the Tibetan Plateau, which is not recognised here.

The most significant difference between the Tortonian reconstruction herein (Fig. 6) and the reconstruction of Micheels *et al.* (2007) is in South America and Australia. In South America, the reconstruction of Micheels *et al.* (2007) shows latitudinal bands of tropical rain forest, tropical seasonal forest and warm mixed forest to 23.5°S, whereas palaeobotanical data shows tropical savanna separating areas of tropical forest (Fig. 6). In temperate South America, the reconstructions differ mainly in the absence of the Atacama Desert in Micheels *et al.* (2007), whereas sedimentological evidence shows that it was present (Alonso *et al.*, 1991; Clarke, 2006). In Australia, Micheels *et al.* (2007) interpreted vegetation in longitudinal bands becoming more humid to the northeast. In the present reconstruction, the palaeobotanical data show a dominance of temperate sc~~h~~lerophyll woodland and shrubland along the south of the continent and the predictions of BIOME4 indicate that the vegetation became moister to the southeast (Fig. 6).

In Africa, the present reconstruction and that of Micheels *et al.* (2007) are comparable. The vegetation distributions differ mainly in the areas predicted by BIOME4 in the reconstruction presented herein. Micheels *et al.* (2007) reconstructed the Tortonian Sahara as a mixture of warm grassland and savanna. In this reconstruction, BIOME4 predicts most of the Sahara Desert to be tropical xerophytic shrubland with isolated areas of desert (Fig. 6). BIOME4 also predicts a mixture of savanna and xerophytic shrubland in southern Africa (Fig.6); in the reconstruction of Micheels *et al.*, (2007) savanna changed to warm mixed forest towards the Cape. The differences between the present reconstruction and that of Micheels *et al.* (2007) could be related to the use of a Tortonian land-sea mask and a larger palaeoecological data set in the study presented here.

This study has refined previous Tortonian vegetation reconstructions. Previous work used limited palaeoecological data which was not cited (François *et al.*, 2006; Micheels *et al.*, 2007). Here we present a 240 point palaeobotanical and vertebrate-based data set for the Tortonian in a format which is readily compatible with a state-of-the-art mechanistic vegetation model. This allows it to be easily used for data-model comparisons, and permits it to be used as a boundary condition in future modelling studies. The methodology used to generate the global vegetation reconstruction also uses a novel approach, previously only applied to the Piacenzian (Salzmann *et al.* 2008). The 240 point palaeoecological data set has been merged with a "best-fit" Tortonian model generated biome distribution map. This has meant that areas lacking palaeoecological data have been filled with vegetation that most closely suits the climate that fits best with regions with a large amount of palaeoecological data. This is instead of inferring biome distribution or filling gaps with modern vegetation. Hence an advanced Tortonian biome distribution map has been constructed, which will be used in future modelling studies.

4.4 Tortonian vegetation, climate and CO_2 levels

The distribution of Tortonian biomes, reconstructed using palaeoecological data and model-predicted vegetation shows evidence for a warmer world than at present (Fig. 6). This is also supported by estimates of climate from palaeobotanical data presented in Table 2. The AGCM-generated temperature difference with the pre-industrial in Fig. 7A, shows that the warming of the Tortonian relative to pre-industrial was a global phenomenon. Exceptions to this are due to differences in the land-sea distribution. This global warming requires a forcing agent that can operate at all latitudes, an increase in CO_2 relative to the pre-industrial would be the most likely cause. This is not the only study that has shown these changes in the vegetation during the Tortonian relate to a warmer world (François *et al.*, 2006; Micheels *et al.*, 2007). However estimates of CO_2 levels for the Tortonian are between the Last Glacial Maximum and mid 20th Century concentrations (Kürschner *et al.*, 1996, 2008; Berner and Kothavala, 2001; Pearson and Palmer, 2004; Pagani *et al.*, 2005; Tripati *et al.*, 2009). This has led to the suggestion that Tortonian climate was decoupled from CO_2 (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005). However recent work by Tripati *et al.* (2009) has shown that climate is highly sensitive to $_{p}CO_2$ and for the last 20 Ma major climatic changes were synchronous with changes in $_{p}CO_2$. Ruddiman (2010) recently suggested that one of the possibilities for apparent low CO_2 levels over the past 22 Ma, whilst climate has fluctuated considerably, could be the incorrect calculation of CO_2 from proxies. Recently CO_2 estimates for the Pliocene have been recalculated using the alkenone proxy, which placed atmospheric CO_2 levels for 4.5 Ma at between 370-420 ppmv (Pagani *et al.*, 2010). Previous alkenone estimates for the latest Miocene (5.37Ma) range from 247-340 ppmv (Pagani *et al.*, 2005). Taking the upper estimates for both alkenone records requires an increase in atmospheric CO_2 of 80 ppmv across the Miocene-Pliocene boundary. Whilst using the lower estimates requires an increase of 123 ppmv over a period of 0.87 Ma, this is not compatible with other estimates of CO_2 levels (Kürschner *et al.*, 1996; Pearson and Palmer, 2000). Although current estimates of CO_2 for the Tortonian do not match the warming relative to pre-industrial seen in the palaeoecological data, it would appear to be the most likely driving force for a global increase in MAT.

5. Conclusions

Our Tortonian vegetation reconstruction created using palaeoecological data and a mechanistic vegetation model forced by HadAM3 shows that this interval was warmer and wetter than present. The Tortonian vegetation distribution shows significant differences to the modern. Such as a spread of boreal forests and temperate biomes too much higher latitudes than today. The expansion of warm-temperate evergreen mixed forests in Europe, southeast Asia and parts of North America. The replacement of arid desert regions by shrubland, grasslands, savanna and woodland. An expansion of temperate savanna in Central USA, the Middle East and on and north of the Himalayan Plateau.

This comprehensive dataset for the Tortonian will be used both to assess future palaeoclimate modelling studies and as a land cover mask to initialise future Tortonian experiments. It is hoped this will be the starting point for a more detailed understanding of the Late Miocene using a combined data-model methodology.

The level and nature of warming (Δ+4.5°C compared to pre-industrial) reconstructed by our palaeoecological data and modelling study requires a climatic forcing mechanism operating on a global scale (i.e. CO_2). However, published Tortonian atmospheric CO_2 levels from a variety of proxies range between the Last Glacial Maximum, pre-industrial and mid-20th Century levels. Before Miocene climate is assumed to be decoupled from atmospheric CO_2, it is first necessary to reconcile this miss-match between terrestrial proxy and climate model evidence with available techniques used to reconstruct palaeo-atmospheric CO_2.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1 Reference and biome code to palaeoecological sites for Fig. 1 and Fig. 3

Appendix S2 Literature used for the Tortonian biome reconstruction

Captions

Figure 1. Distribution of Tortonian palaeobotanical locations. The references for the 223 locations are listed in Appendices S1 and S2.

Figure 2. The present day potential natural vegetation simulated by the mechanistic vegetation model BIOME4 (Kaplan, 2001). This was simulated using the boundary conditions of the Palaeoclimate Modelling Intercomparison Project (PMIP) with present sea surface temperatures and a CO_2 concentration of 324 ppmv (Bonfils *et al.*, 1998).

Figure 3. Distribution of the Tortonian mammalian fossil sites. The references are listed in Appendices S1 and S2.

Figure 4. Flow diagram explaining the data-model comparison approach. Adapted from Salzmann *et al.* (2008).

Figure 5. A map of the Tortonian world illustrating the degree of consistency between the HadAM3/BIOME4-predicted vegetation and the palaeoecological data. The map also shows the degree to which the model predicted vegetation was corrected by the palaeoecological data. “Small change” represents a relatively minor change in biome type (e.g. tropical evergreen broadleaf forest

to tropical semi-evergreen broadleaf forest) and a “Large change” represents a significant change in biome type (e.g. tropical xerophytic shrubland to warm-temperate evergreen broadleaf and mixed forest).

Figure 6. The vegetation and palaeogeography of the Tortonian. A) The combined palaeobotanical and mammalian data sites (circles), translated into the BIOME4 scheme, overlaying the Mioc5 model predicted biome distribution. B) The merger of data and model creating the hybrid Tortonian vegetation reconstruction.

Figure 7. Climate maps for the Mioc5 AGCM experiment minus the present day, shown on modern geography. A) Mean annual temperature (°C), B) Mean annual precipitation (mm/day). Both plots show the difference with the pre-industrial.

Table 1. Cohen’s Kappa statistic for the data – model comparison using both the 27 biome scheme and 7 megabiome scheme. Also shown are the sea surface temperatures along a latitudinal profile at 30°W, prescribed to the AGCM from Lunt *et al.* (2008).

Table 2. Climate data derived from palaeobotanical evidence. Mean annual temperature (°C) and mean annual precipitation (mm/year) is presented for various regions of the world subdivided by biome type. Mean annual temperature and mean annual precipitation estimates are derived from CLAMP (Wolfe, 1979; Spicer, 2007), NLR (Mosbrugger and Utescher, 1997) and other techniques described in the source literature. Site numbers refer to Figure 1. References for the sites and the climatic data from them can be found in the appendixes S1 and S2.