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

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3   Matthew J. Pound[1,3*], Alan M. Haywood[1], Ulrich Salzmann[2], James B. Riding[3], Daniel J. Lunt[4], Stephen

4   J. Hunter[1]

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6   1- School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK

7   2- School of Applied Sciences, Northumbria University, Newcastle upon Tyne, NE1 8ST, UK

8   3- British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham NG12 5GG,UK

9   4- School of Geographical Sciences, University of Bristol, Bristol, BS8 1SS, UK

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11   *Contact author: eemjp@see.leeds.ac.uk; Tel:+441133437262 Fax: +441133436716

12

13   Abstract

14   For the Tortonian ~~Stage~~ Age of the Miocene ~~epoch~~ Epoch (11.6-7.25 Ma) we present a global

15   palaeobotanical and palaeoecologically-based vegetation dataset, combined with a best-fit Late

16   Miocene climate-vegetation model experiment to create an advanced global data-model hybrid

17   biome reconstruction. This new reconstruction can be used both for the purposes of validating

18   future palaeoclimate model simulations or as a land cover dataset to initialise palaeoclimate

19   modelling experiments. Our Tortonian reconstruction shows significant changes in the distribution of

20   vegetation compared to modern natural vegetation. For example in contrast to the modern scenario

21   in the Northern Hemisphere, boreal forests reached 80°N and temperate forests were present above

22   60°N. Warm-temperate forests covered much of Europe, coastal North America and South-East Asia.

23 Our reconstruction shows a spread of temperate savanna in central USA, the Middle East and on the

24 Tibetan Plateau. Evidence for arid deserts is sparse, with the exception of the Atacama region

25 (South America). Areas that exhibit arid desert today in the Tortonian were instead covered by

26 shrublands, grasslands, savannas and woodlands. The extent of tropical forests in South America was

27 likely reduced but expanded in the Indian sub-continent and East Africa. This pattern of global

28 vegetation in the Late Miocene suggests a warmer and wetter world, which is supported by the

29 pattern of climate anomalies predicted by our best-fit palaeoclimate-vegetation model experiment.

30 Global mean annual temperature may have been as much as 4.5°C higher than present day with

31 many regions experiencing higher than modern amounts of precipitation over the annual cycle. The

32 pattern of temperature and precipitation change reconstructed palaeobotanically, and predicted

33 within our climate model experiment, infers a global forcing agent on Tortonian climate (e.g. such as

34 elevated concentrations of greenhouse gases) to explain the observed and modelled climate

35 anomalies. This is in contrast to current proxy records of Tortonian atmospheric CO_2 which range

36 from Last Glacial Maximum to mid-20th Century levels.

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38 Keywords

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

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41 1. Introduction

42

43 1.1 Preamble

44 As a result of anthropogenic emissions of greenhouse gasses it has been predicted that by the end of

45 the 21st Century average global surface temperatures will have increased by up 1.8 to 4°C (Meehl *et*

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46 *al.*, 2007). These predictions are generated by ~~Global~~ General Circulation Models (GCM) simulating

47 the present day with projected increases of greenhouse gases from anthropogenic sources. To

48 assess how well GCMs perform under significantly different climates than the present day, it has

49 become common to use the geological record as a laboratory (Valdes, 2000; Micheels *et al.*, 2007;

50 Salzmann *et al.*, 2009). Earth history presents many intervals that were significantly warmer than

51 present, to be able to successfully simulate these with GCMs it is important to have a reasonable

52 grasp of the boundary conditions, for each interval. One important boundary condition is the

53 vegetation. Vegetation affects the global climate in ~~many~~ a number of ways ~~such as~~including;

54 altering the surface albedo (Bonan *et al.*, 1992; de Noblet *et al.*, 1996; Hoffmann and Jackson, 2000)

55 and changes in evapotranspiration from the conversion of forests into grasslands leading to reduced

56 regional precipitation (Shukla *et al.*, 1990). ~~It~~ Vegetation is also strongly affected by the ambient

57 climate, which principally influences its distribution. This makes vegetation, not only an important

58 boundary condition, but a method to assess GCM predictions where direct measurements are not

59 possible. Palaeobotanical remains such as pollen, wood and leaves are a widely utilised proxy for

60 reconstructing past continental climates, and are used in the assessment of the predictive abilities of

61 ~~Global Circulation Models (~~GCMs~~)~~ (Kohfield and Harrison, 2000; Valdes, 2000; Kageyama *et al.*,

62 2001).

63 We present herein a new vegetation reconstruction for the Tortonian ~~Stage~~ Age suitable for use in

64 both assessing GCM simulations and as a boundary condition for experiments. This reconstruction

65 uses a novel combination of merging palaeobotanical data and outputs from a state-of-the-art GCM-

66 vegetation model experiment, to produce an advanced global biome distribution map of Tortonian

67 vegetation. The reconstructed distribution provides insights into Tortonian climate, which will help

68 inform future modelling studies. Previous global maps of Tortonian vegetation have been generated

69 using unpublished data sets (François *et al.*, 2006) or vegetation reconstructed from a small (<50)

70 number of palaeobotanical sites (Micheels, 2003; Micheels *et al.*, 2007). These reconstructions have

71 also been based on a modern geography, instead of the appropriate Tortonian palaeogeography,

72   and have classified Tortonian vegetation into a small (maximum 14) number of biome types. The

73   reconstruction presented here builds and improves on these by presenting a 240-site

74   palaeoecological dataset, combined with a state of the art GCM driven vegetation model

75   experiment, to form a global vegetation reconstruction based on a 27 biome classification scheme.

76   1.2. An overview of the Tortonian

77   The Tortonian Stage of the Late Miocene (11.61-7.25 Ma) is ~~a period~~an interval generally considered

78   to have been warmer than today (Wolfe, 1994a; Bruch *et al.*, 2006; Micheels *et al.*, 2007) with

79   modest changes in continental position and orography. These changes include the presence of a

80   Central American seaway, a marine encroachment from the south into Argentina, a large extension

81   of Eurasia into the Arctic Sea to approximately 80°N, the large Pannonian Lake in central Europe and

82   a wider Indonesian seaway (Markwick, 2007). By 10 Ma ago aspects of ocean circulation were

83   becoming comparable to the modern (Woodruff and Savin, 1989; Lohmann *et al.*, 2006), though

84   Miocene circulation was affected by the open Central American seaway which allowed an eastwards

85   flow of Pacific waters into the Atlantic Ocean, preventing deep water formation in the North Atlantic

86   (Maier-Reimer *et al.*, 1990; Lohmann *et al.*, 2006; Lunt *et al.*, 2008). The Miocene also represented a

87   crucial period of uplift and the generation of arid regions (Harrison and Yin, 2004; Kohn and Fremd,

88   2008). The uplift of the Himalayas from a relatively low Tibetan Plateau (1-3 km) in the Late

89   Oligocene to an average height of 4-5 km in the Late Miocene (~9 Ma) had effects on global

90   atmospheric circulation, weathering rates and the Asian Monsoon (Quade *et al.*, 1989; Guo *et al.*,

91   2002; Spicer *et al.*, 2003; Harrison and Yin, 2004; Sun *et al.*, 2009). The Andes may have been at half

92   their modern height by 10.7 Ma (~1800 m) and have since been uplifting at 0.2-0.3 mm per year

93   (Gregory-Wodzicki, 2000). The Rocky Mountains of western North America are a product of several

94   orogenic events, the most recent of which was the Laramide Orogeny which is dated to the Late

95   Cretaceous to Pal~~a~~eocene (English and Johnston, 2004). Subsequent to this major event the

96   Colorado Plateau has been uplifted by nearly 2 km since the Cretaceous (Spencer, 1996). Estimates

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97   on the exact timing of the uplift and the rate are still unresolved but recent work focusing on the

98   Colorado Plateau suggests a change in the dynamic topography of 400-1100 m has occurred in the

99   last 30 Ma (Flowers *et al.*, 2008; Moucha *et al.*, 2009). The Alps in the Early to Middle Miocene were

100   merely islands between the Paratethys and Western Tethys Seas being at an estimated height of

101   <1800 m, then major uplift occurred after 14 Ma until present (Jiménez-Moreno *et al.*, 2008).

102   Atmospheric Carbon dioxide levels for the Tortonian have been estimated, using boron isotopes

103   (Pearson and Palmer, 2000), alkenones (Pagani *et al.*, 2005), stomatal indices (Kürschner *et al.*, 1996;

104   2008), pedogenic carbonate (Ekart *et al.*, 1999) and the GEOCARB mass balance model (Berner and

105   Kothavala, 2001). All of these techniques estimate Tortonian CO_2 to range between Last Glacial

106   Maximum, pre-industrial (Pearson and Palmer, 2000; Pagani *et al.*, 2005) and mid-20th Century levels

107   (Kürschner *et al.*, 1996; Ekart *et al.*, 1999 Berner and Kothavala, 2001; Kürschner *et al.*, 2008),

108   although pedogenic carbonates used to estimate CO_2 go as high as 1170 ppmv at 10 Ma (Ekart *et al.*,

109   1999). It is possible that Miocene climate change was not related to atmospheric CO_2 variations

110   (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005), though new CO_2 estimates,

111   such as those derived from stomatal indices, are more consistent with the co-evolution of Miocene

112   climate and CO_2 (Kürschner *et al.*, 2008).

113

114   2. Methods

115

116   2.1. Constructing the vegetation database

117   Using TEVIS (Tertiary Environments Vegetation Information System) (Salzmann *et al.*, 2008), which is

118   a Microsoft Access and ArcGIS 9 based database, 223 Tortonian vegetation sites (Fig. 1) have been

119   collected and recorded in an internally consistent manner. Using the author's interpretation of

120   palaeobotanical sites, taken from the published literature, the recorded Tortonian sites have been

121   translated into the classification scheme of the BIOME4 mechanistic model of vegetation (Kaplan,

122   2001). TEVIS not only records the vegetation of the palaeobotanical site but also the latitude and

123   longitude, sedimentology, method used to date the sample and a quality indicator – to ascertain the

124   resolution of the chronology. Where available, numerical climatic parameters such as mean annual

125   temperature and precipitation are also recorded in TEVIS. This facilitates quantitative data-model

126   comparison. Extracting climatic parameters from fossil assemblages can be achieved by a number of

127   techniques and the majority of the estimates in the TEVIS database come from either the co-

128   existence approach (Mosbrugger and Utescher, 1997 and the NECLIME working group) or Climate

129   Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1979; 1993; Spicer, 2007; Spicer *et al.*, 2009).

130   The co-existence approach uses the climatic tolerances of a fossil plant's nearest living relative as a

131   guide to the climate tolerances of the fossil taxa. When this is done for a whole assemblage a

132   climatic envelope is generated where all the fossil plants could have co-existed; providing an

133   estimate of climatic parameters (Mosbrugger and Utescher, 1997). CLAMP uses 31 leaf

134   physiognomic (structure) characteristics, that have been shown to be related to the environment to

135   which the leaf architecture is exposed (Spicer, 2007; Spicer *et al.*, 2009), to estimate the climatic

136   parameters of fossil leaf assemblages (Wolfe, 1993).

137   It has been possible to confidently assign all literature-based vegetation reconstructions to a

138   corresponding BIOME4 classification (Fig. 2). However, it should be noted that although the BIOME4

139   classification represents biomes of the modern world these are not identical, in species composition,

140   to those of the Tortonian and in some regions the Tortonian biome has no modern analogue.

141   2.2. Construction of the animal database

142   To provide additional information on Tortonian vegetation where palaeobotanical information is

143   absent we have constructed, using the same Microsoft Access and ArcGIS platform successfully

144   employed for TEVIS, a new database termed MAD (Miocene Animal Database). This database

145   records palaeo-rotated vertebrate fossil sites and the author's inferred habitat as well as taxonomic

146   data. The author's inferred habitat is also converted, where possible, into a BIOME4 scheme

147   vegetation type. However there are limitations in using vertebrate assemblages to infer vegetation,

148   such as the respective scale of the inferred habitat and the reconstructed biome, and this will

149   require further investigation. MAD also records information about the sedimentary facies, age and

150   dating method, specimen completeness and any taphonomic information provided. The sites

151   collected in MAD are critical to increase our vegetation data coverage in regions where plant fossils

152   are not preserved. MAD contains 70 vertebrate locations and has provided 17 additional biome data

153   points and provided valuable coverage in regions such as the Middle East and Central America (Fig.

154   3).

155   2.3. Description of the HadAM3 GCM and BIOME4 models

156   A suite of Late Miocene atmosphere-only General Circulation Model (AGCM) runs have been carried

157   out using the Hadley Centre Atmospheric Model Version 3 (HadAM3; Pope *et al.*, 2000) and the

158   climatologies used to run the mechanistic vegetation model BIOME4 (Kaplan 2001). A brief outline of

159   the model and boundary conditions used in the simulations can be found below. A fuller description

160   of the modelling methodology can be found in Lunt *et al.* (2008).

161   HadAM3 has a horizontal resolution of 2.5° latitude × 3.75° longitude, this equates to a spatial

162   resolution of 278 × 417 km at the equator. The model has 19 vertical layers, a time step of 30

163   minutes and includes the Edwards and Slingo (1996) radiation scheme, the Gregory *et al.* (1997)

164   convection scheme, a sea ice model that is largely the same as in HadAM2 (Cattle and Crossley,

165   1995) and MOSES (Cox *et al.*, 1999) a land surface scheme capable of simulating freezing and melting

166   of soil moisture (Pope *et al.*, 2000). HadAM3 has been successfully applied to numerous

167   palaeoclimate intervals of the pre-Quaternary (e.g. Haywood and Valdes, 2006; Lunt *et al.*, 2008).

168   The Late Miocene palaeogeography, orography and ice sheet extent were derived from Markwick

169   (2007). Crucially this gives a significant decrease in altitude of the Tibetan Plateau relative to the

170   present day, as well as the western cordillera of North and South America. The land surface scheme

171   was set to globally homogeneous values (in this case shrubland). Shrubland was chosen to initialise

172   the model as its physical characteristics are least biasing in terms of climate prediction. Atmospheric

173   CO_2 levels were set at 395 ppmv which is at the higher end of available estimates yet it should be

174   noted that given prescribed sea surface temperatures in this model the exact CO_2 value chosen does

175   not have a large effect on the climate predicted by the model.

176   In the absence of sufficient proxy sea surface temperatures (SSTs), we derive our Late Miocene SST

177   distribution from a pre-industrial surface temperature distribution, $T^*_{pre-industrial}$, in the following way:

$$\overline{}$$

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179   Where m is the number of the month (January=1), Φ is the latitude, and A, B, and C are defined in

180   Lunt *et al.* (2008; Table 1). $T^*_{pre-industrial}$ is derived from the means from years 1870–1900 of the

181   Hadley Centre sea surface temperature (SST) and sea ice climatologies (HadISST, Rayner *et al.*, 2003).

182   This formulation allows the sensitivity of the global warming, the amount of polar warmth, the

183   seasonality of the polar warmth, and the form of the latitudinal gradient of warming, to be tested

184   using just 4 key parameters; A, B, C, and f(Φ).We address the inherent uncertainty associated with

185   the prescribed boundary conditions by carrying out a suite of seven Late Miocene simulations, with

186   different values of A, B, C and f (Lunt *et al.*, 2008, table 1). The resulting distributions, from this

187   calculation, are illustrated in and summarised in Lunt *et al.* (2008; Fig.2, table 2). The prescribed SSTs

188   all have a lower equator to pole temperature gradient than the pre-industrial, in agreement with

189   proxy data (e.g. Williams *et al.*, 2005; Pearson *et al.*, 2007), with a maximum change in Northern

190   Hemisphere winter. This is also consistent with the idea that the current strength of the

191   thermohaline circulation developed through the Miocene (e.g. Jakobsson *et al.*, 2007). These seven

192   distributions are identical to those contemplated by Gladstone *et al.* (2007) in relation to the

193   hydrological budget in the Mediterranean of the Late Miocene. For all simulations, where the value

194   of $SST_{LateMiocene}$ is below the freezing point of ocean water, T_{freeze}, sea ice is allowed to form. In these

195   instances, the SST is set to T_{freeze}, and the surface temperature is no longer prescribed but is

196   computed by the sea ice component of HadAM3. Certain coastal SSTs had to be extrapolated due to

197   the difference between the modern and Late Miocene land–sea masks, but this is a minor effect.

198   BIOME4 (Kaplan, 2001) is a mechanistic equilibrium vegetation model which predicts global biome

199   distribution from monthly averages of temperature, precipitation, cloudiness and absolute minimum

200   temperature. Biomes are predicted based on the bioclimatic tolerances of 12 Plant Functional Types

201   (PFT) ranging from cushion forbs to tropical evergreen trees. At the core of the model is a coupled

202   carbon-water flux scheme which maximises Net Primary Productivity (NPP) for any given PFT

203   through the determination of Leaf Area Index (LAI). This is calculated on a daily simulation of the soil

204   water balance, canopy conductance, photosynthesis and respiration. The woody PFT that achieves

205   the highest annual NPP at its maximised LAI for a given grid square is considered dominant. This

206   however is not the case for grass-tree areas such as savannas; here a weighted NPP is calculated and

207   inferred fire risks are both used to determine the forest-grassland boundary. The model then orders

208   all the PFTs that could exist under ambient conditions in a grid cell based on NPP, LAI and mean

209   annual soil moisture. It then uses semi-empirical rules to decide on which of the 27 biomes should

210   be plotted in the cell (Kaplan 2001). For the Late Miocene simulations BIOME4 was run in anomaly

211   mode. This is a standard technique that removes known systematic errors in the climate prediction

212   of HadAM3 and has been employed in numerous modern and palaeoclimate/palaeoecological

213   studies (e.g. Haxeltine and Prentice, 1996; Texier *et al.*, 1997; Salzmann *et al.*, 2008).

214

215   2.4. Coupling of the data and model

216   To provide a global vegetation reconstruction it is necessary to fill the regions with limited

217   palaeoecological data (Fig. 1; Fig. 3) with vegetation. In this study the technique of Salzmann *et al.*

218   (2008), using a state-of-the-art model simulation and merging this with the palaeoecological data is

219   employed. Before the process of merging the data and model into a hybrid reconstruction of global

220   Tortonian vegetation it was first necessary to determine which Late Miocene HadAM3 experiment

221   was best suited for this purpose. The original HadAM3 experiments presented in Lunt *et al.* (2008;

222   Mioc1-Mioc7) were all used to produce BIOME4 vegetation predictions. Mioc1-Mioc7 represent

223   seven HadAM3 experiments with different SST gradient profiles, generated with the equation

224   described in section 2.3. The resulting BIOME4 estimates were compared to the Tortonian data

225   collected in TEVIS and MAD, using ArcGIS9 software. Before comparison could begin the

226   palaeoecological data ~~was~~ were first palaeo-rotated to its Tortonian latitude and longitude (using

227   the palaeo-rotation codes of Paul Markwick ensuring consistency between our data and the

228   Tortonian palaeogeography used in HadAM3). To aid comparison and selection, Cohen's Kappa

229   statistic (Cohen, 1960) was used to highlight the statistically most comparable BIOME4 model

230   simulation (Table 1). Cohen's Kappa statistic measures the agreement between two sets of

231   categorizations while taking into account chance agreements between categories, where 0 means

232   the agreement is no better than chance and 1 shows a perfect fit (Cohen, 1960; Jenness and Wynne,

233   2005). BIOME4 simulations Mioc1 – Mioc7 were compared using both the full and mega biome

234   classification schemes of the BIOME4 model. The use of the broader mega biome scheme, following

235   Harrison and Prentice (2003) and Salzmann *et al.* (2009), was necessary due to avoid the Kappa

236   statistic becoming meaningless due to some categories containing a low number of sample points

237   for the full biome scheme. Of the experiments, Mioc5 compared most favourably to the

238   palaeobotanical and palaeoecological data (i.e. achieved the highest Kappa score using the mega

239   biome scheme) and this experiment was therefore chosen for use in the construction of the data-

240   model hybrid. Mioc5 represents a reduced equator to pole gradient in the Northern Hemisphere,

241   with SSTs around 9°C warmer at 60°N (compared to the pre-industrial). The equator to pole gradient

242   in the Southern Hemisphere is slightly reduced when compared to the pre-industrial gradient but

243   with SSTs 3 - 4°C higher. Equatorial SSTs are 1°C warmer than in the pre-industrial (Table 1).

244   The strategy used to join the databased vegetation with model predicted vegetation is summarised

245   in Fig. 4 and based on the techniques used in Salzmann *et al.* (2008). The merger was undertaken on

246   a grid by grid basis; examining each model predicted grid cell and, if necessary, correcting it using

247   available palaeobotanical data. This is most visible in Fig. 5, which shows the consistency of the data

248   – model comparison and the degree of correction. Areas with low or no palaeobotanical data are left

249   unchanged as model predicted vegetation.

250

251   3. Results

252

253   3.1. Global Tortonian vegetation reconstruction

254   The plotted biomes, based on 240 TEVIS and MAD data points, provide an insight into Late Miocene

255   vegetation and climate. There is good data coverage in western USA, Europe, India, southeast Asia

256   and western South America, allowing a confident vegetation reconstruction for these regions. This

257   allows for a confident robust vegetation-reconstruction for these regions. Data coverage also allows

258   a confident reconstruction of Alaska, central Africa, parts of Asia and southern Australia. However,

259   data coverage is not uniform and thus areas lacking adequate coverage rely on modelled vegetation

260   for the reconstruction. These areas include most of the high latitude Northern Hemisphere including

261   much of Canada and northeast USA, Greenland, Scandinavia and Russia. Other areas of poor

262   coverage also include eastern South America, southern Africa and northern Australia.

263   The Tortonian vegetation reconstruction from both the palaeobotanical data and the BIOME4 model

264   prediction show a warmer and moister world (Fig.6A). The following section describes and highlights

265   regional vegetation patterns from the Tortonian world. Numbers in parentheses refer to

266   palaeobotanical site location numbers (Fig. 1) and numbers within parentheses with an "M" relate to

267   mammal site location numbers (Fig. 3). All references for specific sites, and the biome code assigned

268   to each has been made available as supplementary information (Appendices 1, 2). Climatic data ~~is~~

269   are also presented below in the form of Mean Annual Temperature (MAT) in °C and Mean Annual

270   Precipitation (MAP) in mm per year. The climatic data is also presented in Table 2.

271

272   3.1.1. Polar and boreal regions

273   During the Tortonian the polar and boreal regions (>60°N, >60°S) were dominated by cold evergreen

274   coniferous forests and temperate grasslands. In Eurasia and Greenland there is also an extension of

275   temperate deciduous broadleaved forests from the temperate region. Antarctica is not vegetated in

276   this reconstruction, which is in agreement with the extinction of tundra from Antarctica during the

277   Middle Miocene (Lewis *et al.*, 2008). The ANDRILL AND-2A core, drilled in McMurdo Sound, yielded a

278   palynological assemblage showing the presence of tundra vegetation between 15.7-15.5 Ma.

279   Following this warm period the content of palynomorphs decreases sharply until they are absent

280   before the start of the Tortonian (Warny *et al.*, 2009). On Seymour Island and James Ross Island,

281   Antarctic Peninsula the Hobbs Glacier formation has been dated as Late Miocene (Dingle and

282   Lavelle, 1998; Marenssi *et al.*, 2010).This marine diamictite is considered to have been deposited

283   close to a glacier terminus suggesting the West Antarctic Ice Sheet was almost at its present extent

284   on the Antarctic Peninsula, though with evidence for interglacial events (Smellie *et al.*, 2006;

285   Marenssi *et al.*, 2010). Previously tundra vegetation had been reported from the Pliocene of the

286   Transantarctic Mountains (Ashworth and Cantrill, 2004). The dating of these deposits was based on

287   the assemblage of reworked marine diatoms (Harwood, 1986), more recent work has suggested an

288   age >5.1 Ma and likely much older (Ackert and Kurz, 2004; Ashworth *et al.*, 2007). The growing body

289   of evidence from Antarctica suggests that by the Tortonian the continent was largely glaciated.

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290 The polar and boreal realms are not well constrained in the Tortonian reconstruction. A scarcity of

291 Tortonian palaeobotanical data in Canada, Scandinavia and northern Russia (Fig. 6A), combined with

292 an extension of the continent into the modern Arctic Ocean north of Scandinavia and the

293 Novosibirsk Islands extending to Svalbard in the palaeogeography means much of the high latitude

294 biomes are model-defined. Likewise Antarctica is defined as having near-modern ice sheet cover in

295 the model boundary conditions, meaning that the BIOME4 model would not predict vegetation on

296 the Antarctic continent. There are some locations that provide evidence of vegetation at the high

297 latitudes during the Tortonian. In Alaska, around the Cook Inlet and Nenana Coal Field (Sites 1-5)

298 there was a cool mixed forest to 61°N and a mix of cool needleleaf and cold evergreen needleleaf

299 forest further north. Three of the five sites give a mean annual temperature of 4.5±1.5°C, 4±1°C and

300 10±10°C (Wolfe, 1994b; White *et al.*, 1997; Reinink-Smith and Leopold, 2005); this is 4-10°C warmer

301 than present. The palaeobotanical data and model agreed well on the position of the cold evergreen

302 needleleaf forests but differed on the position of the cool mixed forest. In the BIOME4 model

303 simulation the area with cool mixed forest palaeobotanical data is reconstructed to have temperate

304 deciduous broadleaved forest and warm-temperate evergreen and mixed forest biomes. This

305 discrepancy between the BIOME4 predictions and the palaeobotanical data is related to the SST

306 profile used in the model boundary conditions.

307 In the North Atlantic (Sites 72-73), ocean cores provide evidence of terrestrial biomes during the

308 Tortonian. DSDP 338 provides evidence of a temperate forest dominated by coniferous trees at 67°N

309 offshore Norway (Koreneva *et al.*, 2005). ODP Leg 151 contains a pollen assemblage showing the

310 presence of a swampy taiga at 77°N on the Hovgård Ridge (Boulter and Manum, 1997). In Russia

311 there is evidence of the evergreen taiga forest at 70°N (Site 139) and a temperate evergreen forest

312 at 59°N (Site 141). The model successfully predicts the presence of the cold evergreen needleleaf

313 forest at 77°N, but does not predict the presence of the temperate evergreen needleaf forest seen

314 at DSDP 338. Whether this relates to problems in the model prescribed SSTs or is due to the sample

315 coming from an oceanic core rather than a terrestrial deposit will need to be explored in future

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316 work. Khapchan (Site 140) was described by Nikitin (2007) as a northeastern Turgayan Flora (warm-

317 temperate mixed forest) and contains a diverse seed assemblage of 130 taxa containing; *Alnus*,

318 *Betula*, *Brasenia*, Cyperaceae, Ericaceae Myricaceae, *Rosa*, *Rubus*, *Tubela*, Vitaceae and *Weigela*,

319 (Nikitin, 2007). This site represents a Turgayan Flora near the transition period in northeastern Asia,

320 from the Oligocene-Miocene Turgayan flora to the Pliocene-recent flora (Nikitin, 2007). Nikitin

321 (2007) classified it as a Turgayan flora despite the absence of *Taxodium* and the minor amount of

322 broadleaved taxa. This may mean that in terms of the biome classification of the BIOME4 model the

323 flora at Khapchan no longer represents a warm-temperate mixed forest, which the Turgayan Flora is

324 considered to be. This will require future investigations to establish a suitable BIOME4 classification

325 for a northeastern Turgayan Flora and therefore it is omitted from the present reconstruction.

326

327 As data is are scarce for the boreal and polar realms, these regions rely heavily on the BIOME4

328 model for the Tortonian reconstruction. Across North America, BIOME4 predicts a direct transition

329 from boreal taiga to temperate grasslands at 60°N in central Canada and 68°N in western Canada

330 (Fig. 6A). In northernmost North America, BIOME4 predicts a mixture of temperate grassland, boreal

331 taiga and temperate xerophytic shrubland. In northeast Russia, the model predicts extensive

332 temperate grasslands from 66°N to 78°N with temperate deciduous broadleaved forest reaching

333 78°N between the longitudes of 25°E and 36°E. This then changes to cool needleleaf forest at 78°N,

334 whereas, for most of the polar boreal region temperate grassland is predicted to change directly into

335 boreal taiga forest, much as it does in North America (Fig. 6A). There are also minor areas of cool

336 mixed forest, cool needleleaf forests and temperate xerophytic shrubland within the extensive

337 temperate grassland region, these same minor biomes are also found on the west coast. At 60°N the

338 BIOME4 model predicts the presence of warm-temperate forest on the east coast of Eurasia (Fig.

339 6A). In eastern Russia and the Kamchatka Peninsula the boreal taiga is predicted by BIOME4 to have

340 had a much lower southern extent at 55°N and changes directly to temperate grassland. BIOME4

341 shows the presence of boreal forest mixed with some areas of temperate grassland and in the

342 northernmost area, a small region of deciduous boreal taiga. Along the southern coast of the

343 Kamchatka Peninsula, the model predicts a mix of cool mixed and cool needleleaf forest (Fig. 6A).

344 Currently there are no published palaeobotanical sites for the Tortonian of Greenland. The BIOME4

345 model predicts a large expanse of temperate grassland in the northwest and central areas with

346 temperate forests in the south and east. In the far northeast and northwest, small areas of

347 temperate xerophytic shrubland are predicted to have existed (Fig. 6A). In the boundary conditions

348 of the GCM experiment, based on the palaeogeography (Markwick, 2007), the east Greenland

349 highlands are covered by an ice-sheet and thus were not vegetated. Despite the lack of data on

350 Greenland, good data coverage on Iceland (Sites 68-71) shows a warm-temperate to temperate

351 climate during the Tortonian. This provides some evidence to support temperate forest on

352 Greenland at this latitude during the Tortonian. All the areas on Greenland defined by the BIOME4

353 model are generated from the climate of the best fit GCM experiment and a single ~~data~~ datum point

354 could confirm or change these regions. There are no model-predicted biomes for Antarctica because

355 the palaeogeography used in the model boundary conditions ~~have~~ has a modern Antarctic ice sheet.

356

357 3.1.2 Temperate zones

358 The BIOME4 model predicts a considerable extension of the temperate zone into what is present

359 boreal and polar regions. Data coverage in the temperate zone (23.5-60°N/°S) is good. Notable areas

360 of absence are the Appalachians in the eastern USA, north Mexico, Australia and southernmost

361 South America. Broadly the reconstruction shows a spread of warm-temperate evergreen

362 broadleaved and mixed forest into Europe, Southeast Asia, eastern USA and areas of western USA

363 and an expansion of temperate deciduous broadleaved savanna in Eurasia and central USA.

364 On the west of the Rocky Mountains, a mixture of forest, woodland and savanna occured until 38°N,

365 below this the area was dominated by temperate xerophytic shrubland with some coastal forests. At

366 55°N on what is now the Queen Charlotte Islands, Canada, there was a warm-temperate evergreen

367 mixed forest (Site 6). To the south of this there was temperate needleleaf forest (Site 7) near the

368 coast and temperate deciduous broadleaved forest further inland (Site 8). South of this at between

369 43°N and 48°N, many locations show the presence of a warm-temperate evergreen and mixed forest

370 (Sites 9-12, 14 and 19-21). The forest at Musselshell Creek (Baghai and Jorstad, 1995) had a MAT of

371 12.5±1.5°C and a MAP of 1250 mm (Site 14), this is 7°C warmer than at present and nearly 500

372 mm/yr wetter. South of this is temperate broadleaved savanna near the coast at Kimble Homestead

373 (Site 13), which is estimated to have a MAT of 12.5±2.5°C, comparable to the warm-temperate

374 evergreen and mixed forest but, with a MAP of 900±100 mm (Retallack *et al.*, 2002). Further inland

375 there was a mix of temperate broadleaved deciduous forest (Site 15) and temperate schlerophyll

376 woodland and shrubland (Sites 16, 17). The former having a MAT of 14°C and a MAP of 635±180 mm

377 (Dorf, 1938) and the latter estimated to have a MAT of 13.4±7.8°C and a MAP of 762 mm (Smith,

378 1941; Beuchler *et al.*, 2007). For this area the climate data provided by the palaeobotanical locations

379 suggests an increase in MAT of 7-8°C and an increase in MAP of 50-200 mm/yr compared to modern

380 information. The model disagrees with the palaeobotanical data within this region on the amount of

381 MAP, causing the model to predict much drier biomes. The Rocky Mountains are shown to have had

382 some areas of cool mixed forest (Site 18) and areas of temperate needleleaf open woodland (Fig. 6).

383 South of 38°N, an open area of temperate xerophytic shrubland is predicted by the BIOME4 model

384 and supported by numerous palaeobotanical locations (Sites 23, 25-27). This open area extended

385 down to the tropical zone, apart from a coastal forest with a warm-temperate evergreen and mixed

386 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

387 of 679±62.5 mm (Axelrod, 2000); although the level of precipitation seems low to support this type

388 of forest, Axelrod (2000) compared it to cloud forests of Pacific Islands, suggesting it may have

389 required extensive summer fogs. The modelled biomes and the palaeobotanical data agree well with

390   the distribution and extent of the temperate xerophytic shrubland and the presence of coastal

391   warm-temperate forest.

392   East of the open temperate xerophytic shrubland, the BIOME4 model and the palaeoecological data

393   agree on the presence of a mixture of temperate needleleaf forest and temperate deciduous

394   broadleaved savanna (Sites 28-31 and M1). Along the Gulf Coast there was a mixture of warm-

395   temperate evergreen and mixed forest (Site 37) and tropical semi-deciduous broadleaved forest

396   (Site 36). In Florida, mammalian fossils and pollen at the Moss Acres Racetrack site (Lambert, 1994;

397   Lambert, 1997) show the presence of a temperate to warm-temperate, deciduous broadleaved

398   savanna (Sites M2-M3). On the east coast of the USA there was a warm-temperate evergreen mixed

399   forest until 46°N (Sites 32-35). Further inland where the palaeobotanical data is are absent, the

400   BIOME4 model predicts a mixture of temperate deciduous broadleaved forests, temperate

401   deciduous broadleaved savanna and temperate grasslands (Fig. 6). The warm-temperate evergreen

402   and mixed forest on the east coast, this biome at Martha's Vineyard and preserved in the Legler

403   Lignite is predicted to have a MAT of between 13.3±5°C and 15±9°C with a MAP of 1270 mm (Greller

404   and Rachele, 1983; Frederiksen, 1984; Axelrod, 2000).

405   In Europe the palaeobotanical data indicate a vast swathe of warm-temperate evergreen and mixed

406   forest with subtropical elements, from 8°W to 51°E and from 38°N to 60°N (Sites 79-99, 103-110,

407   119). Within this biome, which is considered most comparable to the warm-temperate forests of

408   southeast China, climate estimates for the Tortonian from the fossil remains are predicted to have

409   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

410   (Figueiral *et al.*, 1999; Ivanov *et al.*, 2002; Kvacek *et al.*, 2002; Bruch *et al.*, 2006; Syabryaj *et al.*,

411   2007; Erdei *et al.*, 2009). This is around 6.3°C warmer than at present (the range of difference is -

412   2.4°C – +8.5°C) and the difference in MAP is between 159 mm to 740 mm when compared to

413   modern data. Areas of difference to this apparently homogenous biome are the Iberian Peninsula

414   and the land to the south of the Pannonian Lake in Turkey. In this region, the warm-temperate

415　evergreen and mixed forest opened up into a region of temperate deciduous broadleaved savanna

416　(Site 111; 115-116) and BIOME4 predicted temperate needleleaf forest. Further east the vegetation

417　returned to warm-temperate evergreen and mixed forest (Sites 117-118). Continuing east from here

418　there was a region of temperate deciduous broadleaved savanna (Sites M13-M14), and BIOME4

419　predicted temperate needleleaf forest extending to 62°E (Fig. 6). The model and palaeobotanical

420　data agrees well for Europe around the Panonnian Lake however, the model makes western Europe

421　anomalously dry.

422　The Iberian Peninsula also had drier open vegetation than the rest of Europe. On the south coast

423　there was a region of tropical xerophytic shrubland (Site 76), and along the west coast there was a

424　small amount of temperate schlerophyll woodland and shrubland (Site 75). The modern Sahara was

425　greatly reduced, if not absent altogether (Fig. 6). Temperate schlerophyll woodland and shrubland

426　(Sites 77-78) and tropical savanna (Site M7) inhabited coastal regions of northwest Africa (Tunisia,

427　Morocco and Algeria). Further inland there is no vegetation data and the BIOME4 model predicts

428　tropical xerophytic shrubland and small areas of desert (Fig. 6). The mix of predominantly tropical

429　xerophytic shrubland and desert continued east across the modern Sahara region until 21°E, from

430　here until the east coast of the Arabian Peninsula there was extensive tropical xerophytic shrubland

431　and an absence of desert. The area around the modern Nile delta had tropical savanna along the

432　coast (Site 112). The BIOME4 model agrees with the palaeobotanical data in that the Iberian

433　Peninsula has more open vegetation than the rest of Europe. However, there is some disagreement

434　as to which biome types are present. The BIOME4 model also fails to predict the coastal vegetation

435　of North Africa; this may be a problem with the model or a question of scale. The palaeobotanical

436　data may reflect vegetation restricted to the coast whereas the model has predicted the overall

437　biome for the grid cell; this will require further study.

438　Along the east coast of the Pannonian Lake, the BIOME4 model predicts a mixture of temperate

439　xerophytic shrubland and temperate needleleaf forests (Fig. 6A). These temperate needleleaf forests

18

440   are predicted by BIOME4 to continue, in isolated patches, until 81°E. These forest patches are within

441   an extensive temperate deciduous broadleaved savanna (Sites 137-138, 144, M15) which existed

442   from 35°N to 58°N in Asia. At the northern extent of the savanna area it is bordered by temperate

443   deciduous woodland which inhabited some of the boreal realm during the Tortonian (Fig. 6). At its

444   southern limit, the BIOME4 model predicts the temperate savanna blended into temperate

445   needleleaf forest and temperate needleleaf parkland. The palaeobotanical data shows that the

446   model simulation for this region produces a biome pattern with anomalously high levels of forest.

447   South of the Himalayas on the Indian subcontinent a band of warm-temperate evergreen and mixed

448   forest ran longitudinally between 28°N and 33°N (Sites 169, 177). Below this there was a mixture of

449   tropical evergreen broadleaved forest, tropical deciduous forest and tropical savanna (Sites 170-

450   175), and these biome types continued into the tropical zone (Fig. 6). In China and southeast Asia,

451   the warm-temperate forests continued in the longitudinal band between 23.5°N and 33°N (Sites

452   182, 185). Fossils from the Xiolongtan coal mine in China are estimated to have lived with a MAT of

453   17.9±1.2°C with a MAP of 1427±212 mm (Xia *et al.*, 2009), this is nearly modern levels for this region.

454   As this band of warm-temperate evergreen and mixed forest reached the east coast of Asia it

455   followed it north, reaching 48°N (Sites 147-148, 156, 158-159, 161). In Japan, many fossil sites

456   indicate this forest biome also existed there (Sites 162-163, 166-168). Throughout India and

457   southeast Asia the model compares very well to the palaeobotanical data and only required slight

458   alterations to create the hybrid reconstruction.

459   On the Himalayan Plateau and further north a patchwork of temperate xerophytic shrubland (Site

460   152), temperate deciduous broadleaved savanna (Sites 142, 145-146, 149-151, 153-155, 198, M16),

461   temperate deciduous broadleaved forest (Site 143) was present during the Tortonian. At the

462   northern limit of the temperate zone, BIOME4 predicted cool needleleaf forest existed at this time

463   (Fig. 6). This mixture of biome types continued north until it bordered an extensive temperate

464   grassland predicted by BIOME4. In north central Asia the transition from temperate biomes to the

465 cold evergreen needleleaf forest biome occurred as far south as 55°N (Fig. 6); currently there is no

466 available data to confirm this transition. This region in the BIOME4 simulation is heavily influenced

467 by the orography which is the reason for minor differences with the palaeobotanical data. For the

468 majority of this region the model predicted temperate grassland or temperate deciduous

469 broadleaved forest, whereas the palaeobotanical data reflected a temperate deciduous broadleaved

470 savanna.

471 In South America, the temperate zone contains many sites along the western side and sparse data

472 along the east. On the east coast BIOME4 predicts a continuation of tropical vegetation into the

473 temperate zone, this is mainly tropical xerophytic shrubland with some areas of semi-deciduous to

474 deciduous tropical forest (Fig. 6). At Taubate, Brazil (Site 57) pollen provides evidence of a

475 subtropical to warm-temperate forest along the coast (Garcia *et al.*, 2008). On the west side of the

476 South American temperate zone, tropical xerophytic shrubland changed to tropical savanna (Sites

477 60-61, M5) and a proto-Atacama desert (Site 58) at 24-26°S. South of this, an area of temperate

478 xerophytic shrubland occupied a narrow band (Site 62) before changing into temperate schlerophyll

479 woodland and shrubland (Site 63). South of this area there is scarce data, apart from an area of

480 temperate xerophytic shrubland (Sites 64-66) between 39°S and 46°S. For the rest of southern South

481 America, BIOME4 predicts a mixture of warm-temperate to cool-temperate forests (Fig. 6). The

482 palaeoecological data and BIOME4 model compare well for temperate South America. Model-

483 predicted biomes that required altering for the hybrid reconstruction were either too dry or too wet.

484 This seemingly contradictory statement is probably related to the orography; both within the model

485 boundary conditions and the orography the palaeoecological data existed at.

486 The temperate zone of southern Africa is small and poorly-covered by data. The temperate zone is

487 predicted, by BIOME4, to start with a continuation of the tropical xerophytic shrubland until 28°S to

488 31°S where tropical semi-deciduous and deciduous forests are predicted to begin. The data points

489 come below this area, from western South Africa and they show the presence of a temperate

490   needleleaf forest (Sites 135-136). For the South African Cape, BIOME4 predicts a warm-temperate

491   evergreen and mixed forest (Fig. 6). The model-predicted biomes around the South African Cape

492   were too dry to match the limited palaeobotanical data for the area. This shows there is some

493   problem in the amount of precipitation generated by the model for this region.

494   In Australia, the temperate zone was dominated by temperate schlerophyll woodland and shrubland

495   during the Tortonian (Sites 211-213, 215-216). Location 212 at Lake Tay predicts this biome to have a

496   MAP of 1375±125 mm (Macphail, 1997), which was an increase of around 1100 mm/yr when

497   compared to modern data. A small area of temperate grassland was present in southeast Australia

498   (Site 214) and BIOME4 predicts coastal warm-temperate evergreen and mixed forest and temperate

499   needleleaf forest along the east coast (Fig. 6). In central Australia, the model also predicts an area of

500   tropical grassland. On New Zealand, many data points agree with the BIOME 4 prediction of warm-

501   temperate evergreen and mixed forest (Sites 218-220). Overall the palaeobotanical data and model-

502   generated biomes for temperate Australia compare well in places, but broadly the model predicts

503   biomes that are too dry.

504

505   3.2.3. Tropical zones

506   The tropical zones (23.5°S – 23.5°N) have good data coverage. Notable exceptions are southern

507   Africa, Central America, eastern South America and northern Australia. In general there is an

508   opening up of the tropical forests of South America, an expansion of tropical vegetation into the

509   Sahara Desert in Africa, extensive tropical forests in India and southeast Asia and open biomes in

510   Australia.

511   In Central America, palaeobotanical data show the presence of a warm-temperate evergreen and

512   mixed forest (Site 38) at Jalapa, Mexico (Graham, 1975) where a warm oak-liquidambar forest

513   bordered mangroves. Further south, near Gracias, Honduras (Site M4) an assemblage of mammals

514   shows that a tropical savanna occupied the region during the Tortonian (Webb and Perrigo, 1984).

515   Apart from these sites the rest of Central America is predicted by BIOME4 (Fig. 6). In the north,

516   tropical xerophytic shrubland and temperate schlerophyll woodland and shrubland continued into

517   the tropical zone from the temperate zone. Below 20°N a patchwork mixture of tropical savanna,

518   tropical deciduous woodland and tropical semi-evergreen forest is predicted to have existed. At the

519   Panama Seaway, BIOME4 predicts a tropical evergreen broadleaved forest (Fig. 6). The limited

520   palaeoecological data for Central America make a comprehensive data-model comparison difficult,

521   but based on the available evidence the model appears to simulate vegetation here well.

522   Crossing this seaway into South America, a broad expanse of predominantly tropical evergreen

523   broadleaved forest (Sites 41, 44, 46-47, 49, 51-52), with some isolated areas of tropical deciduous

524   woodland (Sites 42-43, 45) and along the edges of this forest BIOME4 predicts tropical semi-

525   evergreen forest and tropical deciduous woodland existed. This forest opened up into tropical

526   savanna (Sites 50, 53-54) which continued east across South America to between 46°W-38°W where,

527   in an absence of data, BIOME4 predicts tropical xerophytic shrubland (Fig. 6). Some evidence for

528   tropical evergreen broadleaved forest along the coast is present on Outeiro Island, Brazil (Site 48).

529   Near 23.5°S on the east side of South America there is a lack of data and BIOME4 predicts an area of

530   tropical deciduous woodland within the extensive tropical savanna. In eastern South America, at this

531   latitude there is evidence for tropical deciduous woodland (Sites 55-56). This eastern tropical

532   deciduous forest biome is estimated to have a MAT of 19.8±3.7°C – 21.5±2.5°C and a MAP of

533   550±180 mm at Upper Jakokkota (Gregory-Wodzicki, 2002). This is an increase of 9-10°C when

534   compared to the modern, but a reduction in MAP of about 570 mm. The BIOME4 model generated

535   biomes and palaeobotanical data for tropical South America compare very well. The majority of the

536   palaeobotanical data is are grouped in the west and this shows the extent of the tropical forest

537   successfully predicted by the model to be. It also clearly indicates the areas with tropical savanna

538   and tropical deciduous forest predicted by the model and supported by the palaeobotanical data. In

539   the east of tropical South America there is only a single, coastal, data point. This pollen record

540   however shows the model is anomalously dry in this region and the model generated biomes

541   required modification for the hybrid reconstruction.

542   The tropical zone of Africa, south of the Sahara was an extensive tropical xerophytic shrubland

543   during the Tortonian (Fig. 6). This turned into tropical savanna at between 15-20°N (Sites 123, M8),

544   except on the Arabian Peninsula where xerophytic shrubland is the dominant biome with minor

545   amounts of tropical grasslands along rivers and the coast (Site 120). In West Africa, tropical forests

546   began at 16°N (Sites 121-122) but were mainly restricted to coastal grid squares and tropical

547   savanna is found as far south as 6°N (Site 128). In central Africa, the tropical forests occupied a

548   region comparable to the modern forests. Data for this comes from the Niger Delta in the west (Sites

549   129-130) and Kenya in the east (Sites 131-132) with BIOME4 supporting the data and showing the

550   extent of the forest (Fig. 6). Climatic estimates for the tropical forest in Kenya give a MAT of

551   21.7±2°C and a MAP of 1045±200 mm (Jacobs and Deino, 1996); this is comparable to modern levels.

552   Around Ethiopia and Sudan, an area of tropical evergreen forest was present (Site 124) surrounded

553   by tropical savanna (Site 127) and tropical grassland (Sites 125-126). Apart from the sites mentioned,

554   there is an absence of other data points for tropical Africa and so the reconstruction relies on

555   BIOME4. Between 1°S and 6°S, the tropical forests opened up into tropical savanna with isolated

556   patches of tropical deciduous woodland. At around 19°S this gave way to tropical xerophytic

557   shrubland and a small Namib Desert. Along the east coast of Africa BIOME4 predicts tropical

558   xerophytic shrubland (Fig. 6). From the palaeoecological data available for tropical Africa it is clear

559   that the data and model compare closely. Modifications to the model-predicted biomes was mainly

560   restricted to the savanna-xerophytic shrubland boundary which mammalian sites showed was too

561   far south by the distance of a grid cell.

562   In tropical India, palaeobotanical data is are confined to the south and northeast of the subcontinent

563   and indicates the presence of a tropical evergreen broadleaved forest (Sites 179-181, 195-197, 199-

564   201). Away from these regions the vegetation is predicted by BIOME4 (Fig. 6). The biomes predicted

565 show a mixture of tropical evergreen, semi-evergreen and deciduous forests along the coast and

566 tropical savanna inland. Moving east, data from Vietnam show the warm-temperate evergreen and

567 mixed forest as far south as 18°N (Sites 185-191). This forest opened up to tropical savanna (Site

568 M17) and tropical grassland (Site 194) along the west of the southeast Asian peninsula. On the east

569 side, a mixture of warm-temperate evergreen and mixed forest (Sites 203-204) and tropical

570 evergreen broadleaved forest (Site 205) existed. Below 11°N, an absence of data means the

571 vegetation is predicted by BIOME4. From 11°N to 5°N, the model predicts an area of semi-evergreen

572 tropical forest with isolated tropical savanna, below 5°N BIOME4 predicts the presence of tropical

573 evergreen broadleaved forest (Fig. 6). This is supported by a pollen assemblage from Brunei (Site

574 207). As in the temperate zone, the model predicted tropical zone of India and southeast Asia

575 compares well to palaeoecological data requiring only minor modifications for the hybrid

576 reconstruction.

577 Palaeobotanical sites for the Australian tropical zone are exceedingly sparse. ODP 765 (Site 208),

578 located immediately off the west coast, suggests the presence of a temperate schlerophyll woodland

579 with an estimated MAP of 1050±450 mm (Martin and McMinn, 1994; MacPhail, 1997). On the east

580 coast, there was a coastal temperate needleleaf forest (Site 210), which continued south into the

581 temperate zone. The rest of tropical Australia is predicted by BIOME4 to be coastal tropical savanna

582 and tropical xerophytic shrubland until the temperate zone (Fig. 6). Limited data for the tropical

583 zone of Australia means the hybrid reconstruction relies on the model defined biomes. The available

584 palaeobotanical data shows that, as with the temperate zone of Australia, the tropical zone is too

585 dry in places.

586

587 4. Discussion

588

589 4.1. Tortonian vegetation and climate

590 The Tortonian palaeoecological data show agreement with the predictions of the BIOME4 model,

591 with higher than pre-industrial SSTs and atmospheric CO_2 levels at 395 ppmv. The reconstruction of

592 Tortonian biome distribution shows significant differences compared to the present-day potential

593 natural vegetation, in the high latitudes and temperate realms (Fig. 6B). Differences are also seen in

594 the tropics but these involve the change in distribution of modern tropical biomes, rather than the

595 movement of biomes into regions where they do not exist today. Of these significant vegetation

596 shifts, the northwards shift of boreal taiga, temperate deciduous forest and temperate grasslands

597 are the most pronounced. Potential natural (i.e. without human influence) present day biome

598 distribution (Fig. 2) shows the boreal forests (cold evergreen needleleaf and cold deciduous forests

599 of BIOME4) have a southern limit of ca. 45°N in east Eurasia and a northern limit of ca. 70°N in

600 northern Russia and Canada (Kaplan, 2001). During the Tortonian, the evergreen boreal forests

601 reached at least 77°N (Site 72) and in the reconstruction it extends to 80°N. Reconstructing the

602 southern limit is difficult due to a lack of data from the polar region. In Alaska it is at 61°N (Site 5)

603 and minimally at 70°N in Russia (Site 139). In the hybrid reconstruction, the BIOME4 model indicates

604 the lowest occurrence of the boreal taiga forests is in east Eurasia at 55°N. This dramatic shift of the

605 boreal taiga by up to 10° indicates significant high latitude warming relative to today. Accompanying

606 this northward shift of the boreal taiga was a loss of tundra biomes (Fig. 6B). The northward shift of

607 the boreal forests has been shown to be a vegetation–climate positive feedback; with the treeline

608 moving north altering the surface albedo and carbon budget of the high latitudes (de Noblet *et al.*

609 1996; Sturm *et al.* 2001). Inclusion of this Tortonian vegetation reconstruction, as a boundary

610 condition in future modelling studies, may help to increase high northern latitude MATs and the

611 simulation of a reduced pole to equator gradient. In this study the HadAM3-driven BIOME4

612 vegetation model was able to predict the northward shift of forest biomes but this required a

613 significant increase in SSTs (Table 1). These high SSTs could also be responsible for making model-

614 predicted biomes for areas of western Europe, western USA, Australia, South Africa and eastern

615   South America too dry, when compared to the biomes reconstructed from the palaeoecological

616   data. Although higher SSTs will create a more active hydrological cycle, the Mioc5 AGCM experiment

617   has a global MAP increase of only 126.7 mm/year relative to the pre-industrial scenario. From the

618   number of regions showing model-generated biomes that are too dry compared to palaeobotanical

619   data, the increase in global precipitation is either not enough or is occurring in the wrong regions.

620   These discrepancies in regions that current experiments make to dry will form part of future model

621   simulations. These future simulations will include the Tortonian vegetation reconstruction presented

622   here as a boundary condition instead of the global shrublands used by Lunt *et al.* (2008).

623   Following the cold taiga forests northwards were the temperate forests and temperate grassland

624   biomes (Fig. 6). The extensive temperate grasslands predicted by BIOME4 are not supported by any

625   palaeobotanical data points. The data and BIOME4 model predictions agree on the presence of a

626   warm-temperate evergreen and mixed forest in Europe bordering the Pannonian Lake, however in

627   western Europe BIOME4 predicts a much more fragmentary biome pattern than indicated by

628   palaeobotany. In places, the model predicts temperate evergreen needleleaf forests and tropical

629   xerophytic shrublands. This suggests the model interprets western Europe as too dry, and is most

630   likely related to the increased MATs from the higher SSTs. This is because there is only a slight

631   difference in the modelled MAP between the Late Miocene and the pre-industrial model

632   experiments (Fig. 7). Considering the differences in climate between the Late Miocene model and

633   those derived from palaeobotanical data for this biome; the model predicts slightly higher MATs

634   (within the range of the fossil data) and a MAP comparable to that estimated from the data (Table

635   2). The climatic data suggests the Tortonian MAT in Europe was at least 5-8°C warmer than the pre-

636   industrial age and received around 400 mm/year more precipitation. This warm-wet climate across

637   Europe during the Tortonian is in agreement with studies using other proxies (Bohme *et al.*, 2008).

638   The palaeobotanical data and BIOME4 predictions for the western USA differ. In this region, the

639   model predicts a mixture of temperate grassland, temperate xerophytic shrubland and temperate

640 needleleaf forest. The palaeobotanical data also suggests a mixture of biomes; warm-temperate

641 evergreen and mixed forest, temperate deciduous broadleaved savanna, temperate sclerophyll

642 woodland and shrubland and temperate deciduous broadleaved forest. The differences between

643 BIOME4 and the data relates to the orography. It is a common problem for model-data discrepancies

644 in mountainous regions due to both the model resolution and preservation bias of the fossil record

645 (Salzmann *et al.*, 2008). In the BIOME4 model, each 2.5° x 3.75° grid cell has its biome calculated

646 based on the climate generated by the AGCM and the average altitude of the cell. In comparison, the

647 palaeobotanical data comes from a single locality. This ~~area~~ locality is within an area of deposition,

648 typically lowland areas such as valley bottoms. This means that the palaeobotanical evidence for

649 mountain regions is often biased towards valley and low altitude habitats and not the regional

650 vegetation. This hampers a meaningful data-model comparison within mountainous regions

651 (Salzmann *et al.*, 2008).

652 In the reconstruction, there is a relatively small Sahara Desert, mainly based on the BIOME4

653 reconstruction. The model predicts an expansion of tropical xerophytic shrubland across most of the

654 modern Sahara and the Arabian Peninsula; desert areas were restricted to the north and northeast

655 of the modern Sahara region (Fig. 6B). The palaeobotanical and mammalian evidence shows that

656 along the Mediterranean coast, a mixture of temperate sclerophyll woodland and shrubland and

657 tropical savanna existed. Tropical grasslands are reconstructed for the east coast of the Arabian

658 Peninsula and tropical savanna was present along the modern southern margin of the Sahara desert.

659 Evidence for desert conditions in North Africa comes from sedimentological evidence in Chad. Here

660 wind-blown sandstones conformably underlie a mammal-bearing horizon dated as 7.4-6 Ma

661 (Vignaud *et al.*, 2002; Schuster *et al.*, 2006). Across the Sahara region there are however vertebrate

662 fossil sites that suggest more vegetated conditions. Fossil bushbabies (*Galago farafraensis*) from

663 Egypt provide evidence of a habitat with trees and an estimated rainfall of 500-1200 mm/year

664 (Pickford *et al.*, 2006); crocodiles from Tunisia also indicate more humid conditions (Pickford, 2000;

665 Agrasar, 2003).

666 In South America, southeast Asia and tropical Africa the palaeobotanical data and BIOME4

667 predictions are consistent (Fig. 5). However in the Amazonian basin and Africa south of the equator,

668 the absence of palaeobotanical data means the reconstruction relies entirely on BIOME4 (Fig. 5). In

669 East Africa south of the equator the model predicts tropical xerophytic shrubland, this is the same

670 biome predicted for this region in the Piacenzian (Salzmann *et al.*, 2008). The difference between

671 this Tortonian reconstruction and the Piacenzian reconstruction is the presence of palaeobotanical

672 data in this region during the Piacenzian, allowing the reconstruction of tropical savanna rather than

673 tropical xerophytic shrubland. The difference for the Piacenzian between the AGCM and

674 palaeobotanical data was placed on the modelling of rainfall patterns possibly related to the Somali

675 Jet (Salzmann *et al.*, 2008). If this is a problem in the model then the same error may exist in the

676 Tortonian simulations, further palaeobotanical exploration in the Horn of Africa and south along the

677 east side may help to prove or disprove the Tortonian vegetation reconstruction.

678 Of the available Tortonian AGCM experiments from Lunt *et al.* (2008), Mioc5 compared most

679 favourably to the 240 palaeoecological data points. Statistically Mioc4 compared more favourably in

680 the full biome scheme, but this model predicted a desert in the Amazonian Basin. Mioc5 achieved a

681 higher Kappa score for the mega biome scheme and did not predict the desert in Amazonian Basin.

682 Choosing the experiment with the best megabiome score increases our confidence in the statistical

683 test applied since; having a large number of categories with a low sample in each is less robust than

684 having fewer categories with more samples in each. A minimum of 50 samples per category should

685 be used, and 75-100 samples for more than 12 categories (Congalton and Green, 1999; Jenness and

686 Wynne, 2005). This is difficult for palaeontological studies where sample sizes are restricted by many

687 factors such as deposition, taphonomy, preservation and limited exposure. This makes the mega

688 biome Kappa scores more statistically robust than that for the full biome classification. Combining

689 the palaeoecological data with the Mioc5-driven BIOME4 vegetation model required some model

690 defined areas to be modified (Fig. 5). These include western USA, western temperate South America,

691 western Europe, central Asia, South Africa and Australia. All these regions are in the temperate zone

692   which may indicate the SST gradient used in the experiment was unsuitable. Some of the regions are

693   also heavily influenced by orography which, as previously discussed, confounds palaeoecological

694   data and model comparisons. Areas that compared favourably included eastern and central USA,

695   tropical South America, central Europe, tropical Africa and southeast Asia. These areas also include

696   regions in the temperate zone but mainly those in the tropics, showing that the SSTs for the tropical

697   zone were correctly defined. The limited palaeoecological data available in the polar zone provides

698   evidence that the prescribed SSTs for this climatic zone were well-defined, perhaps even too warm

699   around Alaska where the Mioc5 driven BIOME4 model predicts temperate to warm-temperate

700   biomes. Palaeobotanical data for this region shows the presence of a cool mixed forest, a biome that

701   is colder than those predicted by the model. Overall, the prescribed SST gradient for the Mioc5 GCM

702   experiment that generated the model-defined biome distribution best matches the available

703   palaeoecological data. However, the areas of data-model discrepancy show that further work is

704   required to correctly simulate the Tortonian climate.

705

706   4.2. A comparison of the vegetation of the Late Miocene and the Pliocene

707   Examining trends in vegetation patterns of a warmer world, the Tortonian reconstruction presented

708   here is compared with the vegetation of the Piacenzian (3.6-2.6 Ma), created using the same

709   methodology (Salzmann *et al.*, 2008). Both reconstructions show boreal forests migrating towards

710   the poles, followed by temperate forests and grasslands. The spread of warm-temperate evergreen

711   mixed forests in Europe and southeast Asia are evident in both reconstructions, though this biome

712   spreads more in North America in the Late Miocene than in the Piacenzian. Both reconstructions

713   show a reduction in the extent of the Sahara Desert, though more-so in the Late Miocene. Both

714   reconstructions show an opening up of the tropical forest in South America when compared to

715   present day potential vegetation. In temperate South America however the reconstructions differ,

716   with the Late Miocene having drier conditions than those of the Piacenzian. In tropical Africa the

717   biome distribution is comparable with slightly more tropical evergreen broadleaved forest in the

718   Tortonian. Below the equator, the Piacenzian reconstruction benefits from better data coverage and

719   thus the reconstructed biomes differ. Similar biomes are predicted in both reconstructions for Asia

720   behind the Himalayan Front. In the Piacenzian a mixture of temperate grasslands, temperate

721   xerophytic shrubland and temperate forests existed, whilst in the Tortonian temperate savanna

722   dominates with patches of temperate forests and temperate xerophytic shrublands. South of the

723   Himalayan Front, both reconstructions show a mixture of warm-temperate forest, tropical forests

724   and tropical savanna in Southeast Asia. In Australia both reconstructions show much wetter

725   vegetation than that of the present-day potential vegetation; the main difference is where the

726   woodland and forest biomes are distributed. In the Piacenzian forests woodland and savanna are

727   distributed in the east of the continent, whereas in the Tortonian a large area of temperate

728   schlerophyll woodland and shrubland is present across the south of the continent (Salzmann *et al.*,

729   2008).

730   Both reconstructions, despite the difference in age, show similar patterns of biome changes relating

731   to both being warmer worlds than present. The reconstructions show a spread of boreal forests

732   polewards followed by temperate biomes. Both show an expansion of warm-temperate forests with

733   subtropical taxa in the temperate realms of Eurasia and both show a reduction of deserts. Different

734   continental configuration, orography and ice-sheet extent are most likely to account for differences

735   between the two reconstructions. These broad patterns are also seen in future GCM simulations

736   (Salzmann *et al.*, 2009).

737

738   4.3. Comparison to previously published Tortonian vegetation reconstructions

739   The Tortonian reconstruction presented here, using a 27 biome classification of 240 palaeoecological

740   sites and a state-of-the-art AGCM shows similarities and differences to previously published

741   Tortonian vegetation reconstructions (François *et al.*, 2006; Micheels *et al.*, 2007). Both of these

742   studies used an AGCM with a resolution of 3.75°x3.75°. In François *et al.* (2006) a modern

743   palaeogeography was populated with vegetation based on an unpublished palaeobotanical database

744   and predicted vegetation from BIOME1 (Prentice *et al.*, 1992). This 14 biome reconstruction shows

745   the same spread of boreal forests in the high latitudes. However in North America, Iceland, and east

746   Eurasia, the boreal forests extended southwards into regions with palaeoecological data showing the

747   presence of other biomes (Fig. 6). In the temperate region both the reconstructions presented here,

748   and that of François *et al.* (2006), indicate a spread of warm-temperate evergreen mixed forests

749   [temperate broadleaved evergreen forest in François *et al.* (2006)] in Europe and the eastern USA.

750   For the rest of North America, the Tortonian reconstructions differ, with palaeobotanical evidence

751   suggesting temperate savanna where François *et al.*, (2006) predicted tropical seasonal forest and

752   temperate forests (Fig. 6). In Eurasia, both reconstructions predict a patchwork of vegetation on the

753   Himalayan Plateau, François *et al.*, (2006) predicted grassland, semi-desert and minor savanna

754   leading directly into boreal forests at ca. 45°N. The reconstruction herein (Fig. 6) shows

755   predominantly temperate savanna with minor areas of temperate xerophytic shrubland, temperate

756   deciduous broadleaved forest and temperate evergreen needleleaf forest. This then changed to

757   temperate grassland at 45°N before a transition to boreal forest at ca. 55°N. In South America, the

758   reconstruction of François *et al.* (2006) predicted tropical rain forest extending into the temperate

759   realm to about 40°S and a tropical seasonal forest occupying the Atacama Desert. The

760   palaeoecological evidence presented here indicates that the temperate zone of South America was a

761   mixture of temperate xerophytic shrubland and tropical savanna with a reduced Atacama Desert

762   (Fig. 6). These discrepancies in South America may relate to differences in geography, because a

763   seaway was present in much of modern Argentina (Fig. 6). Differences also occurred in tropical

764   South America where palaeobotanical evidence suggests an opening up of the modern rainforest to

765   create an area of tropical savanna, whereas François *et al.* (2006) presented an extensive area of

766   tropical forest. In Africa, the reconstructions appear comparable except in the Sahara where BIOME4

767   predicts small areas of desert and in southern Africa where BIOME4 predicts a mixture of tropical

768   savanna and tropical xerophytic shrubland. Again the reconstructions compare favourably in

769   southeast Asia, both predicting tropical forests. On Australia the reconstructions differ again though

770   this may be more related to different classification schemes; as temperate schlerophyll woodland

771   and shrubland is not represented in the scheme used by François *et al.* (2006). Overall, some of the

772   differences between the reconstruction of François *et al.* (2006) and the one presented here may be

773   related to differences in CO_2, geography and the use of a smaller number of biomes.

774   The reconstruction of Micheels *et al.*, (2007) is again on a modern land-sea mask, and was based on

775   a 36 site proxy dataset (Micheels, 2003) translated into 13 biomes. Comparing the reconstruction

776   presented here and that of Micheels *et al.* (2007) there are similarities in the poleward shift of

777   boreal forests. However in Micheels *et al.*, (2007), the boreal forest consistently changed into cool

778   conifer forests; in the reconstruction here this is only observed in Alaska (Fig. 6). Continuing into the

779   temperate realms, the two reconstructions differ significantly in North America. In the west,

780   palaeobotanical data indicate warm-temperate mixed forests at a slightly higher latitude than

781   reconstructed in Micheels *et al.* (2007). At the latitude of the warm mixed forest of Micheels *et al.*

782   (2007), palaeobotanical data show the presence of coastal warm-temperate mixed forest but

783   temperate xerophytic shrubland further inland (Fig. 6); these differences may be related to spatial

784   resolution. In the central USA, palaeobotany provides evidence of temperate savanna mixed with

785   BIOME4-predicted temperate needleleaf forests; in Micheels *et al.* (2007) this region is completely

786   forested. The eastern coast of the USA compares favourably in both reconstructions.

787   The Iberian Peninsula in this reconstruction shows a higher vegetational diversity than in Micheels *et

788   al.* (2007) (Fig. 6). Moving east across Europe, both reconstructions are comparable, although the

789   reconstruction presented here has a greater expanse of warm-temperate forest. This forest

790   occupied significantly less area in southeast Asia; this is comparable to the reconstruction of

791   Micheels *et al.* (2007). On the Himalayan Plateau and north of it, the reconstruction herein shows

32

792   more vegetational variation, this is due to using a larger biome scheme. The reconstruction of

793   Micheels *et al.* (2007) also presented a polar desert on the Tibetan Plateau, which is not recognised

794   here.

795   The most significant difference between the Tortonian reconstruction herein (Fig. 6) and the

796   reconstruction of Micheels *et al.* (2007) is in South America and Australia. In South America, the

797   reconstruction of Micheels *et al.* (2007) shows latitudinal bands of tropical rain forest, tropical

798   seasonal forest and warm mixed forest to 23.5°S, whereas palaeobotanical data shows tropical

799   savanna separating areas of tropical forest (Fig. 6). In temperate South America, the reconstructions

800   differ mainly in the absence of the Atacama Desert in Micheels *et al.* (2007), whereas

801   sedimentological evidence shows that it was present (Alonso *et al.*, 1991; Clarke, 2006). In Australia,

802   Micheels *et al.* (2007) interpreted vegetation in longitudinal bands becoming more humid to the

803   northeast. In the present reconstruction, the palaeobotanical data show a dominance of temperate

804   schlerophyll woodland and shrubland along the south of the continent and the predictions of

805   BIOME4 indicate that the vegetation became moister to the southeast (Fig. 6).

806   In Africa, the present reconstruction and that of Micheels *et al.* (2007) are comparable. The

807   vegetation distributions differ mainly in the areas predicted by BIOME4 in the reconstruction

808   presented herein. Micheels *et al.* (2007) reconstructed the Tortonian Sahara as a mixture of warm

809   grassland and savanna. In this reconstruction, BIOME4 predicts most of the Sahara Desert to be

810   tropical xerophytic shrubland with isolated areas of desert (Fig. 6). BIOME4 also predicts a mixture of

811   savanna and xerophytic shrubland in southern Africa (Fig.6); in the reconstruction of Micheels *et al.*,

812   (2007) savanna changed to warm mixed forest towards the Cape. The differences between the

813   present reconstruction and that of Micheels *et al.* (2007) could be related to the use of a Tortonian

814   land-sea mask and a larger palaeoecological data set in the study presented here.

815   This study has refined previous Tortonian vegetation reconstructions. Previous work used limited

816   palaeoecological data which was not cited (François *et al.*, 2006; Micheels *et al.*, 2007). Here we

817   present a 240 point palaeobotanical and vertebrate-based data set for the Tortonian in a format

818   which is readily compatible with a state-of-the-art mechanistic vegetation model. This allows it to be

819   easily used for data-model comparisons, and permits it to be used as a boundary condition in future

820   modelling studies. The methodology used to generate the global vegetation reconstruction also uses

821   a novel approach, previously only applied to the Piacenzian (Salzmann *et al.* 2008). The 240 point

822   palaeoecological data set has been merged with a "best-fit" Tortonian model generated biome

823   distribution map. This has meant that areas lacking palaeoecological data have been filled with

824   vegetation that most closely suits the climate that fits best with regions with a large amount of

825   palaeoecological data. This is instead of inferring biome distribution or filling gaps with modern

826   vegetation. Hence an advanced Tortonian biome distribution map has been constructed, which will

827   be used in future modelling studies.

828

829   4.4 Tortonian vegetation, climate and CO_2 levels

830   The distribution of Tortonian biomes, reconstructed using palaeoecological data and model-

831   predicted vegetation shows evidence for a warmer world than at present (Fig. 6). This is also

832   supported by estimates of climate from palaeobotanical data presented in Table 2. The AGCM-

833   generated temperature difference with the pre-industrial in Fig. 7A, shows that the warming of the

834   Tortonian relative to pre-industrial was a global phenomenon. Exceptions to this are due to

835   differences in the land-sea distribution. This global warming requires a forcing agent that can

836   operate at all latitudes, an increase in CO_2 relative to the pre-industrial would be the most likely

837   cause. This is not the only study that has shown these changes in the vegetation during the

838   Tortonian relate to a warmer world (François *et al.*, 2006; Micheels *et al.*, 2007). However estimates

839   of CO_2 levels for the Tortonian are between the Last Glacial Maximum and mid 20th Century

840   concentrations (Kürschner *et al.*, 1996, 2008; Berner and Kothavala, 2001; Pearson and Palmer,

841   2004; Pagani *et al.*, 2005; Tripati *et al.*, 2009). This has led to the suggestion that Tortonian climate

842   was decoupled from CO_2 (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005).

843   However recent work by Tripati *et al.* (2009) has shown that climate is highly sensitive to $_pCO_2$ and

844   for the last 20 Ma major climatic changes were synchronous with changes in $_pCO_2$. Ruddiman (2010)

845   recently suggested that one of the possibilities for apparent low CO_2 levels over the past 22 Ma,

846   whilst climate has fluctuated considerably, could be the incorrect calculation of CO_2 from proxies.

847   Recently CO_2 estimates for the Pliocene have been recalculated using the alkenone proxy, which

848   placed atmospheric CO_2 levels for 4.5 Ma at between 370-420 ppmv (Pagani *et al.*, 2010). Previous

849   alkenone estimates for the latest Miocene (5.37Ma) range from 247-340 ppmv (Pagani *et al.*, 2005).

850   Taking the upper estimates for both alkenone records requires an increase in atmospheric CO_2 of 80

851   ppmv across the Miocene-Pliocene boundary. Whilst using the lower estimates requires an increase

852   of 123 ppmv over a period of 0.87 Ma, this is not compatible with other estimates of CO_2 levels

853   (Kürschner *et al.*, 1996; Pearson and Palmer, 2000). Although current estimates of CO_2 for the

854   Tortonian do not match the warming relative to pre-industrial seen in the palaeoecological data, it

855   would appear to be the most likely driving force for a global increase in MAT.

856

857   5. Conclusions

858

859   Our Tortonian vegetation reconstruction created using palaeoecological data and a mechanistic

860   vegetation model forced by HadAM3 shows that this interval was warmer and wetter than present.

861   The Tortonian vegetation distribution shows significant differences to the modern. Such as a spread

862   of boreal forests and temperate biomes too much higher latitudes than today. The expansion of

863   warm-temperate evergreen mixed forests in Europe, southeast Asia and parts of North America. The

864   replacement of arid desert regions by shrubland, grasslands, savanna and woodland. An expansion

865   of temperate savanna in Central USA, the Middle East and on and north of the Himalayan Plateau.

866   This comprehensive dataset for the Tortonian will be used both to assess future palaeoclimate

867   modelling studies and as a land cover mask to initialise future Tortonian experiments. It is hoped this

868   will be the starting point for a more detailed understanding of the Late Miocene using a combined

869   data-model methodology.

870   The level and nature of warming ($\Delta+4.5°C$ compared to pre-industrial) reconstructed by our

871   palaeoecological data and modelling study requires a climatic forcing mechanism operating on a

872   global scale (i.e. CO_2). However, published Tortonian atmospheric CO_2 levels from a variety of

873   proxies range between the Last Glacial Maximum, pre-industrial and mid-20th Century levels. Before

874   Miocene climate is assumed to be decoupled from atmospheric CO_2, it is first necessary to reconcile

875   this miss-match between terrestrial proxy and climate model evidence with available techniques

876   used to reconstruct palaeo-atmospheric CO_2.

877

884

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1177

1178   Supplementary Material

1179   The following supplementary material is available for this article:

1180

1181   Appendix S1 Reference and biome code to palaeoecological sites for Fig. 1 and Fig. 3

1182   Appendix S2 Literature used for the Tortonian biome reconstruction

1183

1184   Captions

1185

1186   Figure 1. Distribution of Tortonian palaeobotanical locations. The references for the 223 locations

1187   are listed in Appendices S1 and S2.

1188

1189   Figure 2. The present day potential natural vegetation simulated by the mechanistic vegetation

1190   model BIOME4 (Kaplan, 2001). This was simulated using the boundary conditions of the

1191   Palaeoclimate Modelling Intercomparison Project (PMIP) with present sea surface temperatures and

1192   a CO_2 concentration of 324 ppmv (Bonfils *et al.*, 1998).

1193

1194   Figure 3. Distribution of the Tortonian mammalian fossil sites. The references are listed in

1195   Appendices S1 and S2.

1196

1197   Figure 4. Flow diagram explaining the data-model comparison approach. Adapted from Salzmann *et*

1198   *al.* (2008).

1199

1200   Figure 5. A map of the Tortonian world illustrating the degree of consistency between the

1201   HadAM3/BIOME4-predicted vegetation and the palaeoecological data. The map also shows the

1202   degree to which the model predicted vegetation was corrected by the palaeoecological data. "Small

1203   change" represents a relatively minor change in biome type (e.g. tropical evergreen broadleaf forest

1204   to tropical semi-evergreen broadleaf forest) and a "Large change" represents a significant change in

1205   biome type (e.g. tropical xerophytic shrubland to warm-temperate evergreen broadleaf and mixed

1206   forest).

1207

1208   Figure 6. The vegetation and palaeogeography of the Tortonian. A) The combined palaeobotanical

1209   and mammalian data sites (circles), translated into the BIOME4 scheme, overlaying the Mioc5 model

1210   predicted biome distribution. B) The merger of data and model creating the hybrid Tortonian

1211   vegetation reconstruction.

1212

1213   Figure 7. Climate maps for the Mioc5 AGCM experiment minus the present day, shown on modern

1214   geography. A) Mean annual temperature (°C), B) Mean annual precipitation (mm/day). Both plots

1215   show the difference with the pre-industrial.

1216

1217   Table 1. Cohen's Kappa statistic for the data – model comparison using both the 27 biome scheme

1218   and 7 megabiome scheme. Also shown are the sea surface temperatures along a latitudinal profile at

1219   30°W, prescribed to the AGCM from Lunt *et al.* (2008).

1220

1221   Table 2. Climate data derived from palaeobotanical evidence. Mean annual temperature (°C) and

1222   mean annual precipitation (mm/year) is presented for various regions of the world subdivided by

1223   biome type. Mean annual temperature and mean annual precipitation estimates are derived from

1224   CLAMP (Wolfe, 1979; Spicer, 2007), NLR (Mosbrugger and Utescher, 1997) and other techniques

1225   described in the source literature. Site numbers refer to Figure 1. References for the sites and the

1226   climatic data from them can be found in the appendixes S1 and S2.