

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

2

3 Matthew J. Pound^{1,3*}, Alan M. Haywood¹, Ulrich Salzmann², James B. Riding³, Daniel J. Lunt⁴, Stephen

4 J. Hunter¹

5

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

10

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 CO₂ which range
36 from Last Glacial Maximum to mid-20th Century levels.

37

38 Keywords

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

40

41 1. Introduction

42

43 1.1 Preamble

44 As a result of anthropogenic emissions of greenhouse gases 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*

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). ~~#-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 periodan 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 Palaeocene (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

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 CO₂ 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 CO₂ 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 CO₂ variations
110 (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005), though new CO₂ estimates,
111 such as those derived from stomatal indices, are more consistent with the co-evolution of Miocene
112 climate and CO₂ (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 CO₂ 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 CO₂ 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:

—

178

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 $f(\Phi)$. 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.

Formatted: Font: Italic

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,

Formatted: Font: Italic

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

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

Formatted: Font: Italic

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;

Formatted: Font: Italic

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

Formatted: Font: Italic

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.

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 $4.5 \pm 1.5^\circ\text{C}$, $4 \pm 1^\circ\text{C}$ and
300 $10 \pm 10^\circ\text{C}$ (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 needleleaf 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

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.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

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 occurred 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 $12.5 \pm 1.5^\circ\text{C}$ 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 $12.5 \pm 2.5^\circ\text{C}$, 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 sclerophyll
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 $13.4 \pm 7.8^\circ\text{C}$ 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 $7\text{-}8^\circ\text{C}$ 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 $15 \pm 4^\circ\text{C}$ 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 $13.3\pm 5^{\circ}\text{C}$ and $15\pm 9^{\circ}\text{C}$ 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 $14.85\pm 0.95^{\circ}\text{C}$ – $16.8\pm 1.2^{\circ}\text{C}$ 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 Pannonian 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 sclerophyll woodland and shrubland (Site 75). The modern Sahara was
425 greatly reduced, if not absent altogether (Fig. 6). Temperate sclerophyll 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

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 $17.9 \pm 1.2^\circ\text{C}$ 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 sclerophyll
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 sclerophyll 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 ($23.5^{\circ}\text{S} - 23.5^{\circ}\text{N}$) 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 sclerophyll 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 $19.8 \pm 3.7^\circ\text{C} - 21.5 \pm 2.5^\circ\text{C}$ 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 sclerophyll 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 CO₂ 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 sclerophyll 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 sclerophyll 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 CO₂, 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

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 sclerophyll 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 CO₂ 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 CO₂ 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 CO₂ 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; Tripathi *et al.*, 2009). This has led to the suggestion that Tortonian climate

842 was decoupled from CO₂ (Shevenell *et al.*, 2004; Pagani *et al.*, 2005; Mosbrugger *et al.*, 2005).
843 However recent work by Tripathi *et al.* (2009) has shown that climate is highly sensitive to ρ CO₂ and
844 for the last 20 Ma major climatic changes were synchronous with changes in ρ CO₂. Ruddiman (2010)
845 recently suggested that one of the possibilities for apparent low CO₂ levels over the past 22 Ma,
846 whilst climate has fluctuated considerably, could be the incorrect calculation of CO₂ from proxies.
847 Recently CO₂ estimates for the Pliocene have been recalculated using the alkenone proxy, which
848 placed atmospheric CO₂ 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 CO₂ 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 CO₂ levels
853 (Kürschner *et al.*, 1996; Pearson and Palmer, 2000). Although current estimates of CO₂ 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 ($\Delta+4.5^{\circ}\text{C}$ 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

878 Acknowledgements

879 This work forms part of the first author's PhD funded by the Natural Environment Research Council
880 (UK) and the British Geological Survey University Funding Initiative (PhD studentship
881 NE/G523563/1). Thanks are expressed to Aisling Dolan, Luciana Genio, Wang Hao, Claire MacDonald
882 and Marion Maury for their kind assistance in translating literature. James B. Riding publishes with
883 the approval of the Executive Director, British Geological Survey (NERC).

884

885 References

886 | [Ackert, R.P., Jr., Kurz, M.D., 2004. Age and uplift rates of Sirius Group sediments in the Dominion](#)
887 | [Range, Antarctica, from surface exposure dating and geomorphology. Global and Planetary](#)
888 | [Change 42, 207–225.](#)

889 Agrasar, E.L., 2003. New fossil crocodylians from the Middle/Upper Miocene of Tunisia. *Annales*
890 *de Paléontologie* 89, 103-110.

891 Alonso, R.N., Jordan, T.E., Tabbutt, K.T., Vandervoort, D.S., 1991. Giant evaporite belts of the
892 Neogene central Andes. *Geology* 19, 401-404.

893 [Ashworth, A.C., Cantrill, D.J., 2004. Neogene vegetation of the Meyer Desert Formation \(Sirius](#)
894 [Group\) Transantarctic Mountains, Antarctica. *Palaeogeography, Palaeoclimatology,*](#)
895 [*Palaeoecology* 213, 65-82.](#)

896 [Ashworth, A.C., Lewis, A.R., Marchant, D.R., Askin, R.A., Cantrill, D.J., Francis, J.E., Leng, M.J.,](#)
897 [Newton, A.E., Raine, J.L., Williams, M., Wolfe, A.P., 2007. The Neogene biota of the](#)
898 [Transantarctic Mountains In: Cooper, A., Raymond, C., the 10th ISAES Editorial Team \(Eds.\),](#)
899 [Online Proceedings of the ISAES X. USGS Open-File Report 2007-1047, Extended Abstract 071, p.](#)
900 [4.](#)

901 Axelrod, D.I., 2000. A Miocene (10-12Ma) Evergreen Laurel-Oak forest from Carmel Valley,
902 California. *University of California Publications: Geological Sciences* 145, 1-34.

903 Baghai, N.L., Jorstad, R.B., 1995. Paleontology, paleoclimatology and paleoecology of the late
904 middle Miocene Musselshell Creek flora, Clearwater County, Idaho; a preliminary study of a new
905 fossil flora. *Palaios* 10, 424-436.

906 Berner, R.A., Kothavala, Z., 2001. GEOCARB III: a revised model of atmospheric CO₂ over
907 Phanerozoic time. *American Journal of Science* 304, 397-437.

908 Beuchler, W.K., Dunn, M.T., Rember, W.C., 2007. Late Miocene Pickett Creek flora of Owyhee
909 County, Idaho. *Contributions from the Museum of Paleontology, The University of Michigan* 31,
910 305-362.

911 Böhme, M., Ilg, A., Winkhofer, M., 2008. Late Miocene "washhouse" climate in Europe. Earth
912 and Planetary Science Letters 275, 393-401.

913 Bonan, G.B., Pollard, D., Thompson, S.L., 1992. Effects of boreal forest vegetation on global
914 climate. Nature 359, 716-718.

915 Bonfils C.J., Lewden, D., Taylor K.E., 1998. Summary documentation of the PMIP models: main
916 document directory. PMIP Documentation (PCMDI Report). Available at: <http://pmip.lsce.ipsl.fr/>

917 Boulter, M.C., Manum, S.B., 1997. A lost continent in a temperate Arctic. Endeavor 21, 105-108.

918 Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I., Ivanov, D.A., 2006. Late Miocene
919 climate in the circum-Alpine realm — a quantitative analysis of terrestrial palaeofloras.
920 Palaeogeography, Palaeoclimatology, Palaeoecology 238, 270–280.

921 Cattle, H., Crossley, J., 1995. Modelling Arctic climate change. Philosophical Transaction of the
922 Royal Society of London A 352, 201-213.

923 Clarke, J.D.A., 2006. Antiquity of aridity in the Chilean Atacama Desert. Geomorphology 73, 101-
924 114.

925 Cohen, J., 1960. A coefficient of agreement for nominal scales. Educational and Psychological
926 Measurement 2, 37–46.

927 Congalton, R.G., Green, K., 1999. Assessing the accuracy of remotely sensed data: Principles and
928 practices. Lewis Publishers. 137pp.

929 Cox, P.M., Betts, R.A., Bunton, C. B., Essery, R. L. H., Rowntree, P. R., Smith, J., 1999: The impact
930 of new land surface physics on the GCM simulation of climate and climate sensitivity. Climate
931 Dynamics 15, 183–203.

932 [Dingle, R.V., Lavelle, M., 1998. Antarctic Peninsular cryosphere: Early Oligocene \(c. 30 Ma\)](#)
933 [initiation and a revised glacial chronology. Journal of the Geological Society 55, 433–437.](#)

934 Dorf, E., 1938. A Late Tertiary flora from Southwestern Idaho. Contributions to Paleontology
935 from the Carnegie Institution of Washington 476, 75-128.

936 Edwards, J.M., Slingo, A., 1996. Studies with a flexible new radiation code. 1: choosing a
937 configuration for a large-scale model. Quarterly Journal of the Royal Meteorological Society 122,
938 689–719.

939 Ekart, D.D., Cerling, T.E., Montanez, I.P., Tabor, N.J., 1999. A 400 million year carbon isotope
940 record of pedogenic carbonate: Implications for paleoatmospheric carbon dioxide. American
941 Journal of Science 299, 805-827.

942 English, J.M., Johnston, S.T., 2004. The Laramide Orogeny: What Were the Driving Forces?
943 International Geology Review 46, 833-838.

944 Erdei, B., Dolezych, M., Hably, L., 2009. The buried Miocene forest at Bükkábrány, Hungary.
945 Review of Palaeobotany and Palynology 155, 69-79.

946 Figueiral, I., Mosbrugger, V., Rowe, N.P., Ashraf, A.R., Utescher, T., Jones, T.P., 1999. The
947 Miocene peat-forming vegetation of northwestern Germany: an analysis of wood remains and
948 comparison with previous palynological interpretations. Review of Palaeobotany and Palynology
949 104, 239-266.

950 Flowers, R.M., Wernicke, B.P., Farley, K.A., 2008. Unroofing, incision, and uplift history of the
951 southwestern Colorado Plateau from apatite (U – Th)/He thermochronometry. Geological
952 Society of America Bulletin 120, 571-587.

953 François, L., Ghislain, M., Otto, D., Micheels, A., 2006. Late Miocene vegetation reconstruction
954 with the CARAIB model. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 302-320.

955 Frederiksen, N.O., 1984. Stratigraphy, paleoclimate and paleobiogeographic significance of
956 Tertiary sporomorphs from Massachusetts. U.S. Geological Survey Professional Paper 1308, 1-
957 25.

958 Garcia, M.J., Bistrichi, C.A., Saad, A.R., Campanha, V.A., Oliveira, P.E.d., 2008. Stratigraphy and
959 palaeoenvironments of the Tanque Basin, Southeastern Brazil. *Revista Brasileira de*
960 *Paleontologia* 11, 147-168.

961 Gladstone, G., Flecker, R., Valdes, P., Lunt, D., Markwick, P., 2007. The Mediterranean hydrologic
962 budget from a Late Miocene global climate simulation. *Palaeogeography, Palaeoclimatology,*
963 *Palaeoecology* 251, 254–267.

964 Graham, A., 1975. Late Cenozoic Evolution of Tropical Lowland Vegetation in Veracruz, Mexico.
965 *Evolution* 29, 723-735.

966 Gregory, D., Kershaw, R., Inness, P.M., 1997. Parametrisation of momentum transport by
967 convection II: tests in single column and general circulation models. *Quarterly Journal of the*
968 *Royal Meteorological Society* 123, 1153–1183.

969 Gregory-Wodzicki, K.M., 2000. Uplift history of the Central and Northern Andes: A review.
970 *Geological Society of America Bulletin* 112, 1091-1105.

971 Gregory-Wodzicki, K.M., 2002. A late Miocene subtropical-dry flora from the northern Altiplano,
972 Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 180, 331-348.

973 Greller, A.M., Rachele, L.D., 1983. Climatic limits of exotic genera in the Legler palynoflora,
974 Miocene, New Jersey, USA. *Review of Palaeobotany and Palynology* 40, 149-163.

975 Guo, Z.T., Ruddiman, W.F., Hao, Q.Z., Wu, H.B., Qiao, Y.S., Zhu, R.X., Peng, S.Z., Wei, J.J., Yuan,
976 B.Y., Liu, T.S., 2002. Onset of Asian desertification by 22 Myr ago inferred from loess deposits in
977 China. *Nature* 416, 159-163.

978 Harrison, S.P., Prentice, I.C. 2003 Climate and CO₂ controls on global vegetation distribution at
979 the last glacial maximum: analysis based on palaeovegetation data, biome modelling and
980 palaeoclimate simulations. *Global Change Biology* 9, 983–1004.

981 Harrison, T.M., Yin, A., 2004. Timing and processes of Himalayan and Tibetan uplift. *Himalayan*
982 *Journal of Sciences* 2, 152-153.

983 [Harwood, D.M., 1986. Recycled marine microfossils from basal debris-ice in ice-free valleys of](#)
984 [southern Victoria Land, Antarctica. *Antarctic Journal of the United States* 21, 101– 103.](#)

985 Haxeltine, A., Prentice, I.C., 1996. BIOME3: an equilibrium terrestrial biosphere model based on
986 ecophysiological constrains, resource availability, and competition among plant functional types.
987 *Global Biogeochemical Cycles* 10, 693–709.

988 Haywood, A.M., Valdes, P.J., 2006. Vegetation cover in a warmer world simulated using a
989 dynamic global vegetation model for the Mid-Pliocene. *Palaeogeography, Palaeoclimatology,*
990 *Palaeoecology* 237, 412-427.

991 Hoffmann, W.A., Jackson, R.B., 2000. Vegetation–climate feedbacks in the conversion of tropical
992 savanna to grassland. *Journal of Climate* 13, 1593-1602.

993 Ivanov, D., Ashraf, A.R., Mosbrugger, V., Palamarev, E., 2002. Palynological evidence for Miocene
994 climate change in the Forecarpathian Basin (Central Paratethys, NW Bulgaria). *Palaeogeography,*
995 *Palaeoclimatology, Palaeoecology* 178, 19-37.

996 Jacobs, B.F., Deino, A.L., 1996. Test of climate-leaf physiognomy regression models, their
997 application to two Miocene floras from Kenya, and 40Ar/39Ar dating of the Late Miocene
998 Kapturo site. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123, 259-271.

999 Jakobsson, J., Backam, J., Rudels, B., Nycander, J., Frank, M., Mayer, L., Jokat, W., Sangiorgi, F.,
1000 O'Regan, M., Brinkhuis, H., King, J., Moran, K., 2007. The early Miocene onset of a ventilated
1001 circulation regime in the Arctic Ocean. *Nature* 447, 986–990.

1002 Jenness, J., Wynne, J.J., 2005. Cohen's Kappa and classification table metrics 2.0: an ArcView 3x
1003 extension for accuracy assessment of spatially explicit models. U.S. Geological Survey Open-File
1004 Report OF 2005-1363, 1-86.

1005 Jiménez-Moreno, G., Fauquette, S., Suc, J.-P., 2008. Vegetation, climate and palaeoaltitude
1006 reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria,
1007 Central Europe. *Journal of Biogeography* 35, 1638-1649.

1008 Kageyama, M., Peyron, O., Pinot, S., Tarasov, P., Guiot, J., Jousaume, S., Ramstein, G., 2001. The
1009 Last Glacial Maximum climate over Europe and western Siberia : a PMIP comparison between
1010 models and data. *Climate Dynamics* 17, 23-43.

1011 Kaplan, J.O. (2001) Geophysical applications of vegetation modeling. Unpublished PhD thesis,
1012 Lund University, Lund, Sweden.

1013 Kohfeld, K.E., Harrison, S.P., 2000. How well can we simulate past climates? Evaluating the
1014 models using global palaeoenvironmental datasets. *Quaternary Science Reviews* 19, 321-346.

1015 Kohn, M.J., Fremd, T.J., 2008. Miocene tectonics and climate forcing of biodiversity, western
1016 United States. *Geology* 36, 783-786.

1017 Koreneva, E.V., Zaklinskaya, E.D., Bratseva, G.M., 1976. Palynology studies of sites 336, 338, 345,
1018 346, and 348, DSDP Leg 38. *Initial Reports of the Deep Sea Drilling Project* 38, 1169-1193.

1019 Kürschner, W.M., Kvaček, Z., Dilcher, D.L. 2008. The impact of Miocene atmospheric carbon
1020 dioxide fluctuations on climate and the evolution of terrestrial ecosystems. *Proceedings of the*
1021 *National Academy of Sciences* 105, 449-453.

1022 Kürschner, W.M., van der Burgh, J., Visscher, H., Dilcher, D.L., 1996. Oak leaves as biosensors of
1023 Late Neogene and Early Pleistocene paleoatmospheric CO₂ concentrations. *Marine*
1024 *Micropaleontology* 27, 299-312.

1025 Kvacsek, Z., Manchester, S.R., Zetter, R., Pingen, M., 2002. Fruits and seeds of *Craigia bronnii*
1026 (Malvaceae - Tilioideae) and associated flower buds from the late Miocene Inden Formation,
1027 Lower Rhine Basin, Germany. *Review of Palaeobotany and Palynology* 119, 311-324.

1028 Lambert, W.D., 1994. The fauna and paleoecology of the Late Miocene Moss Acres Racetrack
1029 site, Marion County, Florida. Unpublished PhD thesis, University of Florida, Gainesville, USA.

1030 Lambert, W.D., 1997. The osteology and paleoecology of the giant otter *Enhydritherium*
1031 *terraenovae*. *Journal of Vertebrate Paleontology* 17, 738-749.

1032 [Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hedenäs, L., Hemming, S.R., Johnson, J.V., Leng,](#)
1033 [M.J., Machlus, M.L., Newton, A.E., Raine, J.L., Willenbring, J.K., Williams, M., Wolfe, A.P., 2008.](#)
1034 [Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proceedings of the*](#)
1035 [National Academy of Sciences 105, 10676-10680.](#)

1036 Lohmann, G., Butzin, M., Micheels, A., Bickert, T., Mosbrugger, V., 2006. Effect of vegetation on
1037 the Late Miocene ocean circulation: *Climate of the Past Discussions* 2, 605-631.

1038 Lunt, D.J., Flecker, R., Valdes, P.J., Salzmann, U., Gladstone, R., Haywood, A.M., 2008. A
1039 methodology for targeting palaeo proxy data acquisition: A case study for the terrestrial late
1040 Miocene. *Earth and Planetary Science Letters* 271, 53-62.

1041 Macphail, M.K., 1997. Late Neogene climates in Australia: Fossil pollen and spore based
1042 estimates in retrospect and prospect. *Australian Journal of Botany* 45, 425-464.

1043 Maier-Reimer, E., Mikolajewicz, U., T. Crowley. 1990. Ocean general circulation model sensitivity
1044 experiment with an open Central American isthmus, *Paleoceanography* 5, 349-366.

Formatted: Font: + Body

1045 [Marensi, S.A., Casadio, S., Santillana, S.N., 2010. Record of Late Miocene glacial deposits on Isla](#)
1046 [Marambio \(Seymour Island\), Antarctic Peninsula. *Antarctic Science* 22, 193-198.](#)

1047 Markwick, P.J., 2007. The Paleogeographic and paleoclimatic significance of climate proxies for
1048 data-model comparisons. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.),
1049 Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and
1050 Biological Proxies. The Micropaleontological Society Special Publications. The Geological Society,
1051 London, pp. 251–312.

1052 Martin, H.A., Mcminn, A., 1994. Late Cenozoic vegetation history of north-western Australia,
1053 from the palynology of a deep sea core (ODP Site 765). *Australian Journal of Botany* 42, 95-102.

1054 Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A.,
1055 Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007.
1056 Global climate projections. *Climate Change 2007: the physical science basis. Contribution of*
1057 *Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate*
1058 *Change* (S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L.
1059 Miller eds.), pp. 747–845. Cambridge University Press, Cambridge.

1060 Micheels, A., 2003. Late Miocene climate modelling with ECHAM4/ML—the effects of the
1061 palaeovegetation on the Tortonian climate. Unpublished PhD Thesis, University of Tübingen,
1062 Germany.

1063 Micheels, A., Bruch, A.A., Uhl, D., Utescher, T., Mosbrugger, V., 2007. A Late Miocene climate
1064 model simulation with ECHAM4/ML and its quantitative validation with terrestrial proxy data.
1065 *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 251-270.

1066 Mosbrugger, V., Utescher, T., 1997. The coexistence approach – a method for quantitative
1067 reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Paleogeography,*
1068 *Palaeoclimatology, Palaeoecology* 134, 61–86.

1069 Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of
1070 Central Europe. *Proceedings of the National Academy of Sciences* 102, 14964-14969.

1071 Moucha, R., Forte, A.M., Rowley, D.B., Mitrovica, J.X., Simmons, N.A., Grand, S.P., 2009. Deep
1072 mantle forces and the uplift of the Colorado Plateau. *Geophysical Research Letters* 36, 1-6.

1073 Nikitin, V.P., 2007. Paleogene and Neogene strata in Northeastern Asia: paleocarpological
1074 background: *Russian Geology and Geophysics* 48, 675-682.

1075 Noblet, N.I. de, Prentice, I.C., Joussaume, S., Texier, D., Botta, A., Haxeltine, A., 1996. Possible
1076 role of atmosphere-biosphere interactions in triggering the last glaciation. *Geophysical Research*
1077 *Letters* 23, 3191-3194.

1078 Pagani, M., Liu, Z., LaRiviere, J., Ravelo, A.C., 2010. High Earth-system climate sensitivity
1079 determined from Pliocene carbon dioxide concentrations. *Nature Geoscience* 3, 27-30.

1080 Pagani, M., Zachos, J.C., Freeman, K.H., Tipple, B., Bohaty, S., 2005. Marked decline in
1081 atmospheric carbon dioxide concentrations during the Paleogene. *Science* 309, 600-603.

1082 Pearson, P.N., Palmer, M.R. 2000. Atmospheric carbon dioxide concentrations over the past 60
1083 million years. *Nature* 406, 695-699.

1084 Pearson, P.N., van Dongen, B.E., Nicholas, C.J., Pancost, R.D., Schouten, S., Singano, J.M., Wade,
1085 B.S., 2007. Stable warm tropical climate through the Eocene Epoch. *Geology* 35, 211-214.

1086 Pickford, M., 2000. Crocodiles from the Beglia Formation, Middle/Late Miocene boundary,
1087 Tunisia, and their significance for saharan palaeoclimatology. *Annales de Paléontologie* 86, 59-
1088 67.

1089 Pickford, M., Wanas, H., Soliman, H., 2006. Indications for a humid climate in the Western Desert
1090 of Egypt 11-10 Myr ago: evidence from Galagidae (Primates, Mammalia). *Comptes Rendus*
1091 *Palevol* 5, 935-943.

1092 Pope, V.D., Gallani, M.L., Rowntree, P.R., Stratton, R.A., 2000. The impact of new physical
1093 parametrizations in the Hadley Centre climate model: HadAM3. *Climate Dynamics* 16, 123–146.

1094 Quade, J., Cerling T.E., Bowman, J.R., 1989. Development of Asian monsoon revealed by marked
1095 ecological shift during the latest Miocene in Northern Pakistan. *Nature* 342, 163-166.

1096 Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C.,
1097 Kaplan, A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air
1098 temperature since the late nineteenth century. *Journal of Geophysical Research* 108, 4407.

1099 Reinink-Smith, L.M., Leopold, E.B., 2005. Warm climate in the Late Miocene of the south coast of
1100 Alaska and the occurrence of Podocarpaceae pollen. *Palynology* 29, 205-262.

1101 Retallack, G.J., Tanaka, S., Tate, T., 2002. Late Miocene advent of tall grassland paleosols in
1102 Oregon. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183, 329-354.

1103 Ruddiman, W.F., 2010. A paleoclimatic enigma? *Science* 328, 838-839.

1104 Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., Hill, D.J., 2008. A new global biome
1105 reconstruction and data-model comparison for the Middle Pliocene: *Global Ecology and*
1106 *Biogeography* 17, 432-447.

1107 Salzmann, U., Haywood, A.M., Lunt, D.J., 2009. The past is a guide to the future? Comparing
1108 Middle Pliocene vegetation with predicted biome distributions for the twenty-first century.
1109 *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering*
1110 *Sciences* 367, 189-204.

1111 Schuster, M., Durringer, P., Ghienne, J.-F., Vignaud, P., Mackaye, H.T., Likies, A., Brunet, M., 2006.
1112 The age of the Sahara Desert. *Science* 311, 821.

1113 Shevenell, A.E., Kennett, J.P., Lea, D.W., 2004. Middle Miocene Southern Ocean Cooling and
1114 Antarctic Cryosphere Expansion. *Science* 305, 1766-1770.

1115 Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. *Science* 247,
1116 1322-1325.

1117 [Smellie, J.L., McArthur, J.M., McIntosh, W.C., Esser, R., 2006. Late Neogene interglacial events in](#)
1118 [the James Ross Island region, northern Antarctic Peninsula, dated by Ar/Ar and Sr-isotope](#)
1119 [stratigraphy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 242, 169–187.](#)

1120 Smith, H.V., 1941. A Miocene Flora from Thorn Creek, Idaho. *American Midland Naturalist* 25,
1121 473-522.

1122 Spencer, J.E., 1996. Uplift of the Colorado Plateau due to lithosphere attenuation during
1123 Laramide low angle subduction. *Journal of Geophysical Research - Solid Earth* 101, 13595–13609

1124 Spicer, R.A., 2007. Recent and future developments of CLAMP: Building on the legacy of Jack A.
1125 Wolfe. *Courier Forschungsinstitut Senckenberg* 258, 109-118.

1126 Spicer, R.A., Harris, N.B.W., Widdowson, M., Herman, A.B., Guo, S., Valdes, P.J., Wolfe, J.A.,
1127 Kelley, S.P., 2003. Constant elevation of Southern Tibet over the past 15 million years. *Nature*
1128 412, 622-624.

1129 Spicer, R.A., Valdes, P.J., Spicer, T.E.V., Craggs, H.J., Srivastava, G., Mehrotra, R.C., Yang, J., 2009.
1130 New developments in CLAMP: Calibration using global gridded meteorological data.
1131 *Palaeogeography, Palaeoclimatology and Palaeoecology* 283, 91-98.

1132 Sturm, M., Racine, C., Tape, K., 2001. Climate change: Increasing shrub abundance in the Arctic:
1133 *Nature* 411, 546-547.

1134 Sun, J., Zhang, Z., Zhang, L., 2009. New evidence on the age of the Taklimakan Desert. *Geology*
1135 37, 159-162.

1136 Syabryaj, S., Utescher, T., Molchanoff, S., Bruch, A.A., 2007. Vegetation and palaeoclimate in the
1137 Miocene of Ukraine. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 153-168.

1138 Texier, D., de Noblet, N., Harrison, S.P., Haxeltine, A., Jolly, D., Joussaume, S., Laarif, F., Prentice,
1139 I.C., Tarasov, P., 1997. Quantifying the role of biosphere-atmosphere feedbacks in climate
1140 change: coupled model simulations for 6000 years BP and comparison with paleodata for
1141 northern Eurasia and Africa. *Climate Dynamics* 13, 865–882.

1142 Tripathi, A.K., Roberts, C.D., Eagle, R.A., 2009. Coupling of CO₂ and ice sheet stability over major
1143 climate transitions of the last 20 million years. *Science* 326, 1394-1397.

1144 Valdes, P.J., 2000. South American palaeoclimate model simulations: how reliable are the
1145 models? *Journal of Quaternary Science* 15, 357-368.

1146 Vignaud, P., Düringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L.,
1147 Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez,
1148 N., Mourer-Chauvire, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., Brunet, M.,
1149 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad.
1150 *Nature* 418, 152-155.

1151 [Warny, S., Askin, R.A., Hannah, M.J., Mohr, B.A.R., Raine, J.I., Harwood, D.M., Florindo, F., Team,](#)
1152 [S.S., 2009. Palynomorphs from a sediment core reveal a sudden remarkably warm Antarctica](#)
1153 [during the middle Miocene. *Geology* 37, 955-958.](#)

1154 Webb, S.D., Perrigo, S.C., 1984. Late Cenozoic Vertebrates from Honduras and El Salvador.
1155 *Journal of Vertebrate Paleontology* 4, 237-254.

1156 White, J.M., Ager, T.A., Adam, D.P., Leopold, E.B., Liu, G., Jetté, H., Schweger, C.E., 1997. An 18
1157 million year record of vegetation and climate change in northwestern Canada and Alaska:
1158 tectonic and global climatic correlates. *Palaeogeography, Palaeoclimatology, Palaeoecology* 130,
1159 293-306.

- 1160 Williams, M., Haywood, A.M., Taylor, S.P., Valdes, P.J., Sellwood, B.W., Hillenbrand, C.D., 2005.
1161 Evaluating the efficacy of planktonic foraminifer calcite $\delta_{18}\text{O}$ data for sea surface temperature
1162 reconstruction for the Late Miocene. *Geobios* 38, 843–863.
- 1163 Wolfe, J.A., 1979. Temperature parameters of humid to mesic forests of Eastern Asia and
1164 relation to the forests of other regions of the Northern Hemisphere and Australasia. U.S.
1165 Geological Survey Professional Papers 1106, 1-37.
- 1166 Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S.
1167 Geological Survey Bulletins 2040, 1-71.
- 1168 Wolfe, J.A., 1994a. Tertiary climatic changes at middle latitudes of western North America.
1169 *Palaeogeography, Palaeoclimatology, Palaeoecology* 108, 195–205.
- 1170 Wolfe, J.A., 1994b. An analysis of Neogene climates in Beringia. *Palaeogeography,*
1171 *Palaeoclimatology, Palaeoecology* 108, 207-216.
- 1172 Woodruff, F., Savin, S.M., 1989. Miocene Deepwater Oceanography. *Paleoceanography* 4, 87-
1173 140.
- 1174 Xia, K., Su, T., Liu, Y.-S., Xing, Y.-W., Jacques, F.M.B., Zhou, Z.-K., 2009. Quantitative climate
1175 reconstructions of the late Miocene Xiaolongtan megaf flora from Yunnan, southwest China.
1176 *Palaeogeography, Palaeoclimatology, Palaeoecology* 276, 80-86.

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 CO₂ 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.