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1 Global vegetation dynamics and latitudinal temperature gradients during the mid to Late Miocene
2 (15.97 - 5.33 Ma)

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12

13 Abstract

14 A 617 site palaeobotanical dataset for the mid to Late Miocene is presented. This dataset is
15 internally consistent and provides a comprehensive overview of vegetational change from 15.97 to
16 5.33 Ma. The palaeobotanical dataset has been translated into the BIOME4 classification scheme to
17 enable direct comparison with climate model outputs. The vegetation change throughout the
18 Langhian, Seravallian, Tortonian and Messinian is discussed. The data shows that the Langhian,
19 which includes the end of the Mid – Miocene Climatic Optimum, represents a world significantly
20 warmer than today. The high northern latitudes were characterised by cool – temperate forests, the
21 mid – latitudes by warm – temperate mixed forests, the tropics by tropical evergreen broadleaf
22 forests and Antarctica by tundra shrub vegetation. Cool – temperate mixed forest existed during the

23 Seravallian in the high northern latitudes, a reduction in warm – temperate mixed forests in the mid
24 latitudes and a loss of tundra on Antarctica was noted. Tortonian vegetation distribution indicates
25 that further cooling had occurred since the Seravallian. The major changes in vegetation include the
26 first evidence for cold taiga forest in the high northern latitudes, and a further reduction of warm –
27 temperate mixed forests were the major changes in vegetation. By the Messinian, this cooling trend
28 had eliminated warm – temperate mixed forests from the western USA and Australia and had
29 formed mid – latitude deserts. Despite the cooling trend throughout the Mid to Late Miocene, the
30 vegetation distribution of all four reconstructed stages reflect the vegetation of a world warmer
31 than the pre – industrial conditions. The latitudinal distribution of bioclimatic zones suggests that
32 the latitudinal temperature gradient for the Langhian would have been significantly shallower than
33 at present and has gradually, but asymmetrically, become more modern towards the end of the
34 Miocene. First the southern hemisphere distribution of bioclimatic zones became more modern,
35 probably due to the climatic effects of a fully glaciated Antarctica. The northern hemisphere
36 bioclimatic zone gradient continued to be shallower than modern throughout the Miocene and
37 slowly became more modern by the Messinian.

38 Keywords: Miocene; vegetation; climate; global change; latitudinal gradient; biome

39

40 1. Introduction

41

42 1.1. Overview

43 The Miocene has been referred to as the “making of the modern world” (Potter and Szatmari, 2009)
44 with major uplift of modern mountain chains, the initiation of bipolar glaciations, the origin of
45 modern ocean currents, the aridification of the continental interiors, the overall cooling trend of the
46 global climate and the reduction in atmospheric CO₂ levels (Beerling and Royer, 2011; Potter and

47 Szatmari, 2009; Zachos et al., 2008). The interplay of elements of the Earth system has created a
48 complex story of evolving global climate. Understanding this climate requires the use of climate
49 proxies. Vegetation represents an excellent climate proxy as it is widely preserved in the geological
50 record in the form of wood, leaves, seeds, pollen and spores. Vegetation can also be reconstructed
51 from organic carbon isotopes and paleosols (Retallack, 2007; Widodo et al., 2009).

52 Vegetation is a well established climate proxy that has been used to assess the predictive abilities of
53 Global Climate Models (GCMs) (Kohfield and Harrison, 2000; Valdes, 2000). The global distribution of
54 vegetation is mainly controlled by temperature and precipitation, as well as, soil type, seasonality,
55 fire and biogeographic history (Schulze et al., 2010). Estimates of temperature and precipitation can
56 be reconstructed from palaeobotanical sites using techniques such as the co – existence approach
57 (Mosbrugger and Utescher, 1997) and Climate Leaf Analysis Multivariate Program (CLAMP) (Spicer et
58 al., 2009; Wolfe, 1979). The estimates can then be compared directly to the climate produced by a
59 GCM. Alternatively, a fossil vegetation datum can be translated into a biome (Fig. 1); a community of
60 plants and animals co – existing under a particular climate (Cramer, 2002). The fossil biomes can
61 then be compared to a model predicted biome distribution using biome models, such as BIOME4,
62 that are driven by the climate generated by a GCM (Prentice et al., 1992; 1998; Kaplan, 2001).

63 Both approaches have their benefits and caveats. The direct comparison of GCM climate parameters
64 with those reconstructed from palaeobotanical sites need to take into account error margins. Both
65 from the technique used to reconstruct the climate estimates from the fossil vegetation and from
66 the boundary condition and physics uncertainties that are a challenge to fully explore with GCMs.
67 The data sets currently available with palaeoclimate estimates are also limited in size and geographic
68 distribution due to the large amount of time required in generating this data (Utescher et al.,
69 2011b). By reconstructing a biome and comparing it to model generated biomes a simple and
70 relatively quick comparison can be achieved (Salzmann et al., 2008; Haywood et al. 2009; Pope et al.,
71 2011). However, biomes reconstructed from palaeobotanical sites need to be directly comparable to

72 model output, this can be achieved by using the classification scheme of the chosen model. This
73 raises the issue that biome models, such as BIOME4, have been developed using modern biomes and
74 how comparable these are to fossil biomes has yet to be fully explored. Despite this indicates the
75 technique has been successfully applied to the Pleistocene (Prentice et al., 1998), the Pliocene
76 (Salzmann et al., 2008; Pope et al., 2011) and the Miocene (Micheels et al., 2007; Pound et al., 2011).
77 All of this means that fossil vegetation can be used to examine climate from a single locality,
78 providing a valuable pin – point view of the ambient conditions during deposition. To a regional or
79 global view of climate using larger datasets of fossil vegetation distribution and finally, combining
80 the data with GCMs to look at dynamic climate and vegetation patterns through time.

81 Previous work on the Miocene vegetation has mainly been conducted on a regional (e.g. Favre et al.,
82 2007) to continental scale (Utescher et al., 2011b). Global studies of vegetation have been based on
83 small numbers of data sites either by extrapolation (Wolfe, 1985) or by combination with a
84 vegetation model (Micheels et al., 2007). Wolfe (1985) presented a broad overview of the evolution
85 of global Miocene vegetation based on the data available at the time. This study showed that the
86 Miocene was warmer, particularly the first half of the time period where limited sites suggested cool
87 mixed forests bordered the Arctic (Wolfe, 1985). More recently regional studies have provided
88 improved insight into Africa (Jacobs et al., 2010), Asia (Wang, 1994; Yao et al., 2011), Australia
89 (Macphail, 2007), Europe (Bruch et al., 2006; Favre et al., 2007; Jiménez-Moreno and Suc, 2007;
90 Utescher et al., 2007), North America (Retallack, 2007) and South America (Barreda et al., 2007).

91 Within this paper we present a 617 site palaeobotanical dataset for the Middle and Late Miocene.
92 This is the most comprehensive dataset of its kind suitable for use in palaeoclimate and
93 palaeoecology studies. Within the paper the dataset is used to explore the climate that is
94 reconstructed from the fossil vegetation and this is compared to the various CO₂ proxies in an
95 attempt to better understand Miocene climate and CO₂ evolution. The vegetation has been
96 reconstructed using the 27 biome scheme of the BIOME4 vegetation model (Fig. 1), which makes it

97 suitable for data – model comparison studies. Such studies are beyond the scope of this paper,
98 which focuses on a review of available palaeobotanical data. However, future modelling studies on
99 the Miocene can use the data presented in this paper to evaluate the predictive ability of GCMs to
100 simulate Miocene climate. The presented data can also be used to generate global vegetation maps
101 in combination with vegetation models to explore the impacts of Miocene vegetation on climate
102 (Pound et al., 2011; Salzmann et al., 2008).

103 The aim of this work is to examine how much warmer than pre – industrial the Miocene was. The
104 global distribution of biomes is one technique used to explore this aim. Using the distribution of
105 vegetation, the latitudinal temperature gradients for the Middle to Late Miocene are also
106 reconstructed. For the pre – industrial era the latitudinal temperature gradients were relatively
107 steep: warm temperatures at the equator cooling rapidly to the poles. For warmer intervals in the
108 geological record it has been proposed that the latitudinal temperature gradient was much
109 shallower (Ballantyne et al., 2010).

110

111 1.2. Continental configuration and ocean circulation during the Middle to Late Miocene

112 The continental distribution in the Middle to Late Miocene was similar to today. Palaeogeographical
113 differences between the present day and the Middle to Late Miocene world included; North and
114 South America were separated until the Pliocene, there was more landmass in the Arctic circle, the
115 Paratethys Sea was still present in Eastern Europe, more land in Southeast Asia and a seaway in
116 southern South America present until ca. 9 Ma (Aceñolaza and Sprechmann, 2002; Markwick, 2007;
117 Potter and Szatmari, 2009).

118 The Miocene also bore witness to the onset of modern oceanic currents. During the Paleogene, a
119 circum – equatorial current dominated oceanic currents (Potter and Szatmari, 2009). By the latest
120 Oligocene (Ca. 25 Ma) the Australian tectonic plate had collided with the Eurasian plate, by the late

121 Early Miocene this had blocked deep water exchange between the Pacific and Indian Oceans and
122 restricted deep water movement along the circum – equatorial current (Kuhnt et al., 2004; Potter
123 and Szatmari, 2009). By the Middle Miocene the Arabian plate - Eurasian plate collision had closed
124 this Early Paleogene seaway to such an extent that it allowed only intermittent water exchange until
125 a complete closure at 11 – 10 Ma (Rögl, 1999; Allen and Armstrong, 2008; Potter and Szatmari,
126 2009). The final seal on the circum – equatorial current was the collision of North and South America
127 at 12.8 Ma (Coates et al., 2004), stifling exchange between the Atlantic and Pacific Oceans. Before
128 12.8 Ma, deep water could exchange between the Pacific and Atlantic Oceans. After 12.8 Ma the
129 Central American Seaway gradually shallowed, until its final closure at 3.5 – 2.7 Ma (Coates et al.,
130 2004; Webb, 2006).

131

132 1.4. Orography during the Miocene

133 The Miocene was a key interval for mountain construction with uplifting of all the world's major
134 orographic regions. The Tibetan Plateau and the Himalayas uplifted at an increased rate during the
135 Middle and Late Miocene as suggested by a rise in sediment flux into the Indian Ocean after 15 Ma
136 (Rea, 1992; Potter and Szatmari, 2009). At 15 Ma the mean maximum altitude of the region was
137 between 3775m and 6570m (Spicer et al., 2003; Currie et al., 2005), at 11 – 9 Ma the mean
138 maximum altitude for the region is estimated to have been between 3200m and 6630m (Garziona et
139 al., 2000a; Garziona et al., 2000b; Harrison and Yin, 2004) and areas over 7000m existed by 5 Ma
140 (Rowley et al., 2001; Molnar et al., 2010). The Alps have been raised steadily since the Middle
141 Miocene from 1600 to 3000m above sea level at 16 – 14 Ma, to 2500 – 3500m at around 8 Ma
142 (Kuhlemann, 2001; Jiménez-Moreno et al., 2008). The Andes are also estimated to have had a steady
143 uplift of 0.2 - 0.3mm/year from around 1800m at 10.7 Ma (Gregory-Wodzicki, 2000). The Rocky
144 Mountains of western North America are a product of several mountain building events, the most
145 recent of which was the Laramide Orogeny which is dated as the Late Cretaceous to Paleocene

146 (English and Johnston, 2004). After this major event the Colorado Plateau has been uplifted by
147 nearly 2000 m since the Cretaceous (Spencer, 1996). Estimates on the exact timing of the uplift and
148 the rate are still unresolved but recent work focusing on the Colorado Plateau suggests a change in
149 the dynamic topography of 400–1100 m has occurred in the last 30 Ma (Flowers et al., 2008;
150 Moucha et al., 2009). Estimates from Nevada between 16 – 15 Ma shows this region was 2000 –
151 3000m above sea level and then reduced to modern altitude by 13 Ma (Wolfe et al., 1997).

152

153

154 1.4. CO₂ proxies

155 Miocene CO₂ levels are reconstructed using numerous techniques and each differs in both
156 atmospheric concentration and in trend through time. Reconstructions are based on alkenones
157 (Pagani et al., 2005; 2010), boron isotopes (Pearson and Palmer, 2000), B/Ca ratio (Tripathi et al.,
158 2009), pedogenic carbonates (Ekart et al., 1999; Retallack, 2009) and stomatal indices (Beerling et
159 al., 2009; Kürschner et al., 1996; 2008; Stults et al., In press). Through the Middle Miocene to the
160 end of the Miocene the alkenone based reconstructions place atmospheric CO₂ levels between 190 –
161 360 ppmv reaching a peak at around 6 - 7 Ma of ca. 360 ppmv (Pagani et al., 2005; 2010). The
162 reconstructed atmospheric CO₂ concentrations from boron isotopes show a range from 137 – 305
163 ppmv with a peak in CO₂ at ca. 16 Ma and ca. 6 Ma (Pearson and Palmer, 2000). The stomatal indices
164 reconstructions are very different to those based on boron isotopes and alkenones. A range over the
165 Middle to end Miocene of 270 – 564 ppmv has been reconstructed, with a peak at ca. 16 Ma of
166 between 460 – 564 ppmv (Beerling et al., 2009; Kürschner et al., 2008). These records then show a
167 fall in atmospheric CO₂ concentration to between 270 – 370 ppmv for the rest of the Miocene
168 (Beerling et al., 2009; Kürschner et al., 1996; 2008; Stults et al., In press). The B/Ca ratio shows a
169 peak of 433 ppmv at 15 Ma and then drops to concentrations of between 206 – 304 ppmv by 10 Ma

170 (Tripathi et al., 2009). The pedogenic carbonate reconstructions could be described as more erratic,
171 fluctuating from very low to as high as 1170 ppmv (Ekart et al., 1999). More recent work on
172 pedogenic carbonates, across the Middle Miocene, has shown a peak in concentration at 15.6 Ma of
173 852 ppmv (Retallack, 2009). This then drops rapidly to 116 ppmv at 14.6 Ma and rises to 433 ppmv
174 by 12.8 Ma (Retallack, 2009). Overall, the apparent low atmospheric levels of Miocene CO₂ have led
175 to disagreements over how much Miocene climate was influenced by this greenhouse gas
176 (Kürschner et al., 2008; Mosbrugger et al., 2005; Pagani et al., 2005; Shevenell et al., 2004;).

177

178 2. Methods

179

180 2.1. Constructing the vegetation database

181 Using TEVIS (Tertiary Environments Vegetation Information System) (Salzmann et al., 2008; Pound et
182 al., 2011), which is a Microsoft Access and ArcGIS 9 based database, 617 Middle to Late Miocene
183 vegetation sites (Fig. 2, 3) have been collected from the literature and recorded in an internally
184 consistent manner. Using the author's interpretation the reconstructed palaeovegetation has been
185 translated into biomes using the classification scheme of the BIOME4 mechanistic vegetation model
186 (Kaplan, 2001). TEVIS not only records the vegetation of the palaeobotanical site but also the
187 latitude and longitude, sedimentology, method used to date the sample and a quality indicator – to
188 ascertain the resolution of the chronology. Where available, numerical climatic parameters such as
189 mean annual temperature and precipitation are also recorded in TEVIS. Extracting climatic
190 parameters from fossil assemblages can be achieved by a number of techniques and the majority of
191 the estimates in the TEVIS database come from either the co-existence approach (Bruch et al., 2006)
192 or CLAMP (Wolfe, 1979; 1993; Spicer, 2007; Spicer et al., 2009). The co-existence approach uses the
193 climatic tolerances of a fossil plant's nearest living relative as a guide to the climate tolerances of the

194 fossil taxa (Mosbrugger and Utescher, 1997). When this is done for a whole assemblage a climatic
195 envelope is generated where all the fossil plants could have co-existed; providing an estimate of
196 climatic parameters (Mosbrugger and Utescher, 1997). CLAMP uses 31 leaf physiognomic (structure)
197 characteristics, that have been shown to be related to the environment to which the leaf
198 architecture is exposed (Spicer, 2007; Spicer et al., 2009), to estimate the climatic parameters of
199 fossil leaf assemblages (Wolfe, 1993).

200 It has been possible to confidently assign all literature-based vegetation reconstructions to a
201 corresponding BIOME4 classification (Fig. 1). However, it should be noted that although the BIOME4
202 classification represents biomes of the modern world these are not identical, in species composition,
203 to those of the Miocene and in some regions the Miocene biome has no modern analogue. The
204 correspondence between a Miocene biome and a modern analogue becomes more uncertain with
205 increasing age. By the Langhian some biomes, particularly those of the high northern latitudes, begin
206 to show a species assemblage not seen in the modern world. An excellent example of this is the high
207 latitude (>69°N) forests from the Middle Miocene of North America. These forests had a
208 composition of *Fagus*, *Glyptostrobus*, *Liquidambar*, *Metasequoia*, *Picea*, *Pinus*, *Quercus*, *Taxodium*
209 and *Ulmus* (White and Ager, 1994; White et al., 1997; Williams et al., 2008). This is a very different
210 assemblage to the modern flora of boreal and arctic North America (Barbour and Billings, 2000).
211 Despite the taxonomic differences between this Middle Miocene flora and the modern floras of
212 North America, the structure and estimated productivity of this forest is comparable to modern
213 biomes (Williams et al., 2008).

214 2.2 Bioclimatic zones

215 To gain a better insight into the latitudinal temperature gradients of the Middle to Late Miocene the
216 latitudinal vegetation distribution can be compared to the pre - industrial potential vegetation
217 distribution. The pre - industrial potential natural vegetation shows progressively colder biomes
218 from the equator, as latitude increases. In simple terms this reflects the latitudinal temperature

219 gradient, which is highest at the equator and lowest at the poles. This requires a simplified scheme
220 to provide an understandable view of the latitudinal temperature gradients for the Langhian,
221 Seravallian, Tortonian and Messinian stages. To facilitate this each fossil site, within TEVIS, is
222 assigned to one of seven megabiomes and one of six bioclimatic zones (Table 1), as well as assigning
223 each fossil site to one of the 28 biomes of the BIOME4 classification (Salzmann et al., 2009). The
224 bioclimatic zone classifications are based on the seven megabiome classification scheme presented
225 in Salzmann et al., (2009). Megabiomes are broader categories grouping numerous biomes. The six
226 bioclimatic zones are; tropical, subtropical/warm-temperate, temperate, boreal, tundra and ice.
227 These classifications reflect a simplified qualitative view of the temperature range of the 28 biomes
228 used in the BIOME4 model. However certain biomes can be included in multiple bioclimatic zones,
229 for example the temperate deciduous broadleaf savanna biome. This biome is referred to as a
230 temperate vegetation type (Gnibidenko et al., 1999) and a warm – temperate vegetation type
231 (Thomasson, 2005). To avoid complications from biomes that are more climatically controlled by
232 seasonality and precipitation than they are by temperature, only forest, woodland or tundra biomes
233 were used in the construction of the bioclimatic zone gradients (Table 1).

234 Two transects were chosen to reconstruct the latitudinal bioclimatic zonal gradients. The west
235 Pacific transect (WPT) and the west Atlantic transect (WAT) (Fig. 4) were selected due to the good
236 data coverage, not only spatially but also temporally. These transects also avoid most of the major
237 mountain regions (though the Himalayas may have influenced part of the WPT), which minimises the
238 complicating factor of altitude.

239 Using the latitudinal transects in Figure 4 the maximum pole - ward extent of each bioclimatic zone
240 has been plotted, for each of the four studied time slices. These have been compared to the
241 maximum pole ward extent of pre - industrial potential natural vegetation generated using the
242 BIOME4 model (Kaplan, 2001), driven by observed climate (Fig. 1). The methodology does not
243 provide numerical climate data to reconstruct the latitudinal temperature gradient, but does

244 compare the maximum pole ward extent of bioclimatic zones. The method shows the relative
245 change in the qualitative bioclimatic zones over time and provides an insight into how different the
246 latitudinal temperature gradient would have been during the studied geological stages.

247

248 3. Results: Global vegetation change from Langhian to Messinian

249

250 3.1. Global biome distributions through time

251 The vegetation change shown by the 634 palaeobotanical sites indicates a global cooling trend from
252 the Langhian to the Messinian. During the Middle Miocene (Langhian and Seravallian) cool -
253 temperate mixed forests were above 60°N with no evidence for boreal forests. By the Late Miocene
254 (Tortonian and Messinian) boreal forests are abundant above 60°N, though in places temperate
255 biomes are still present. The cooling trend is also indicated by the subtropical/warm temperate
256 megabiome, which is most widely distributed during the Langhian. Through the remaining Miocene
257 it gradually becomes more restricted, being displaced by cooler and/or drier biomes. Linked with this
258 cooling and drying trend is the expansion of deserts. During the Langhian there is evidence for an
259 Atacama Desert in South America, by the Messinian there is evidence for a Sahara (Africa) and
260 Taklimakan (Asia) desert.

261 The plotted biomes, from the 634 fossil vegetation sites in TEVIS, provide an insight into Middle to
262 Late Miocene vegetation and climate. The Langhian stage is represented by 184 fossil sites (Fig. 6A),
263 the Seravallian by 205 sites (Fig. 6B), the Tortonian by 326 sites (Fig. 7A) and the Messinian by 252
264 sites (Fig. 7B). Some of these sites cover multiple time stages whilst others may be better dated and
265 correspond to an interval smaller than the assigned geological stage. The ages assigned to the
266 geological stages follows Gradstein et al. (2004). There is excellent data coverage, for all stages, in
267 temperate and tropical Eurasia. North and South America also have good data coverage. Whilst the

268 high northern latitudes, Africa and central Australia have poor data coverage. All the data points are
269 presented in the supplementary information with their modern day latitude – longitude, age range,
270 biome and megabiome code and references (Appendices A and B).

271 In the following section the global vegetation pattern, distribution and changes from the Middle
272 Miocene to the Messinian will be discussed by regions (Fig. 5). Specific fossil localities will be
273 referred to using the site numbers (Fig. 2,3) in parentheses with a prefix denoting the geological
274 stage it has been assigned to (L = Langhian; S = Seravallian; T = Tortonian; M = Messinian). Climatic
275 data is also presented below in the form of Mean Annual Temperature (MAT) in °C and Mean Annual
276 Precipitation (MAP) in mm per year. The climatic data is also presented in Table 2.

277

278 3.1.1. Northern North America

279 Overall this region changes from a region dominated by cool - temperate forests in the Middle
280 Miocene, to a region dominated by boreal forests in the Messinian. This cooling trend is associated
281 with an increase in biome types but a reduction in taxa diversity and a loss of more thermophilic
282 elements, except in southern coastal Alaska (Reinink-Smith and Leopold, 2005).

283 Presently, in northern North America (above 60°N) reported Middle to Late Miocene fossil floras are
284 restricted to Alaska and north-west Canada. During the Langhian a cool - temperate mixed forest is
285 found on Banks Island (74°N), the Mackenzie Delta (69.5°N) and at numerous sites in Alaska (Sites L1
286 – L6) (Fig. 6A). This cool - temperate mixed forest was taxonomically diverse with *Fagus*,
287 *Glyptostrobus*, *Liquidambar*, *Metasequoia*, *Picea*, *Pinus*, *Quercus*, *Taxodium* and *Ulmus* and has a
288 reconstructed MAT of 8 - 9°C (White and Ager, 1994; White et al., 1997; Williams et al., 2008). This
289 cool - temperate mixed forest still dominated this region during the Seravallian (Sites S1 – S4) (Fig.
290 6B), although CLAMP derived climate estimates suggest a climatic cooling lowered regional MAT to
291 as low as 4°C by 12 Ma (White et al., 1997).

292 By the Tortonian this region showed a more diverse array of biomes (Fig. 7A). The cool - temperate
293 mixed forest which dominated the region during the Middle Miocene was still present between 60°N
294 at Homer (Site T1) and 65°N Coal Creek (Site T7). The Coal Creek flora changed biome type at around
295 9 Ma to a cool evergreen needleleaf forest. This biome is also preserved at Tatlinaka Creek (Site T4)
296 which has a pollen assemblage dominated by *Betula* and *Pinus* spp., with an estimated MAT of 5°C
297 (Wahrhaftig et al., 1969; Leopold and Liu, 1994). During the Tortonian a cold evergreen needleleaf
298 forest was also present in the northern North America region (Site T2, T3 & T6), this can be
299 considered to have been a taxonomically richer form of the present day boreal forests, with a MAT
300 of 4±1°C (Wolfe and Leopold, 1967; Wolfe, 1994). During the Messinian the biome distribution of
301 north-west North America appears to reflect a continued cooling (Fig. 7B). The cool - temperate
302 mixed forest was still present but only up to 59°N (Site M2). North of 60°N the vegetation was a mix
303 of cool evergreen needleleaf forests (Sites M3, M4 & M6) and cold evergreen needleleaf forests
304 (Sites M1 & M5) (Fig. 7B). The cold evergreen needleleaf forest preserved at Lava Camp, Alaska is
305 dominated by *Larix* and *Pinus monticola*, the regional MAT for this biome is reconstructed to be
306 between -10 to +6°C (Matthews Jr. and Oviden, 1990; White et al., 1997).

307

308 3.1.2. Western North America

309

310 During the Langhian this region was dominated by a warm – temperate evergreen broadleaf and
311 mixed forest. Through the Seravallian and Tortonian a drier climate caused the warm-temperate
312 mixed biome to gradually become more restricted and was replaced by drier and more open biomes.
313 By the Messinian the warm-temperate biome was replaced by a north to south pattern of
314 progressively drier biomes.

315

316 During the Langhian western North America was dominated by a warm – temperate evergreen
317 broadleaf and mixed forest biome between 40°N and 54°N (Fig. 6A). At Purple Mountain (Site L23), a
318 late Langhian to early Seravallian locality, the warm – temperate evergreen broadleaf and mixed
319 forest biome is estimated to have had a MAT of 11.5°C and a MAP of 825±65mm (Axelrod, 1995).
320 There is evidence for drier biomes at Pyramid (Site L22) and Tenachapi (Site L24), which have been
321 reconstructed as a temperate deciduous broadleaf forest and temperate xerophytic shrubland,
322 respectively. These biomes located south of 40°N suggest a drier climate regime existed in the south-
323 west of North America. During the Seravallian the vegetation of western North America was much
324 less uniform when compared to the Langhian. Whilst areas of warm – temperate evergreen
325 broadleaf and mixed forest still existed these had become separated by areas of drier and/or cooler
326 biome types (Fig. 6B). At Esmeralda (Site S20) a diverse palaeobotanical fossil assemblage records an
327 oak – juniper woodland (temperate deciduous broadleaf forest) estimated to have grown under a
328 MAP of 406±51mm (Berry, 1927; Axelrod, 1940). At Cougar Point (Site S15) a pollen flora dominated
329 by *Artemisia* and Poaceae shows the existence of a xerophytic shrubland at ca. 12 Ma (Davis and
330 Ellis, 2010).

331 By the Tortonian palaeobotanical evidence suggests that the extensive warm – temperate evergreen
332 broadleaf and mixed forest of the Langhian, that began to fragment in the Seravallian, had become
333 even more restricted. During the Tortonian the warm – temperate evergreen broadleaf and mixed
334 forest was present between 43°N and 48°N (Sites T13 – T17, T19 & T26) and along the coast
335 between 31°N and 33°N (Sites T30 – T32) (Fig. 7A). A drill hole in Willamette Valley, Oregon, USA
336 (Site T17) yielded a rich palynomorph assemblage derived from the warm – temperate evergreen
337 broadleaf and mixed forest biome, the assemblage contains *Carya*, *Castanea*, *Cedrus*, *Fagus*,
338 *Liquidambar*, *Nyssa*, *Platanus*, *Pterocarya*, *Sequoia* and *Ulmus* (Roberts and Whitehead, 1984).
339 Climate estimates from the warm – temperate evergreen broadleaf and mixed forest biome suggests
340 it existed under an MAT of 11 - 19°C and a MAP of 617.5 – 1250mm (Table 2). The lower MAP
341 estimate of 617.5mm seems rather too low to support the warm – temperate evergreen broadleaf

342 and mixed forest biome but this reflects an unusual setting of one palaeobotanical site (Site T30)
343 which may have been a forest supported by summer fog (Axelrod, 2000). Separating the two areas
344 of warm – temperate evergreen broadleaf and mixed forests during the Tortonian there was a
345 mixture of temperate deciduous broadleaf forest, temperate deciduous broadleaf savanna and
346 temperate sclerophyll woodland and shrubland. Further south there was temperate xerophytic
347 shrubland (Sites 22, 24, 29, 31 & 33). These biomes are estimated to have had a MAT comparable to
348 the warm – temperate evergreen broadleaf and mixed forest but with a lower MAP (Table 2). North
349 of 48°N there was a temperate deciduous broadleaf forest (Sites T11 – T13) and temperate
350 evergreen needleleaf forest (Site T10) further north. At Skonun Point (Site 9) a pollen assemblage
351 reminiscent of the high latitude Langhian cool - temperate mixed forest biome with abundant *Alnus*,
352 *Pinus*, *Quercus* and *Taxodiaceae* (Martin and Rouse, 1966; White et al., 1994) represents the
353 southernmost evidence for the biome seen in Alaska (Sites T1 & T7) during this stage.

354 By the Messinian the warm – temperate evergreen broadleaf and mixed forest was gone from
355 western North America. The drier biomes, that had been gradually replacing the warm – temperate
356 evergreen broadleaf and mixed forests, were present continuously from 31°N to 48°N. On Queen
357 Charlotte Island the cool - temperate mixed forests (Sites M7 & M8), present during the Tortonian,
358 still inhabited the region – suggesting little change in MAT between the Tortonian and Messinian.
359 Further south at 48°N evidence exists for a temperate deciduous broadleaf forest (Sites M9, M10 &
360 M12) with similarities to the modern eastern American deciduous forests (Sparks et al., 1972). South
361 of this a mixture of temperate xerophytic shrubland (M11, M13 & M15) and temperate sclerophyll
362 woodland and shrubland (Site M14) inhabited what would have been a much drier region than
363 existed during the Langhian.

364

365 3.1.3 Central North America

366 Palaeobotanical evidence for the Langhian is limited for this region. Kleinfelder Farm, Canada (Site
367 L25) shows the presence of temperate grassland at 49°N, 107°W. Gabel et al (1998) suggested that
368 the region has been vegetated with savanna and grasslands since at least the Middle Miocene. There
369 is evidence for a temperate deciduous broadleaf savanna (Sites S35 & S36) in this region during the
370 Seravallian, Tortonian (Sites T35 – T38) and Messinian (Sites M18 – M20). At Minium Quarry, USA a
371 diverse fossil assemblage records a temperate deciduous broadleaf savanna estimated to have had a
372 MAT of 19°C and a MAP of 875±125mm (Thomasson et al., 1990).

373

374 3.1.4 Eastern North America

375 Three sites (L26 - L28) show that during the Langhian the vegetation of eastern North America
376 consisted of warm – temperate evergreen broadleaf and mixed forest from at least 29°N to, at least,
377 39°N. Martha’s Vineyard (Site L26) a pollen bearing locality dated to the Middle Miocene has been
378 estimated to have deposited under a MAT of 13.3±5°C (Frederiksen, 1984; Axelrod, 2000). The warm
379 – temperate evergreen broadleaf and mixed forest continued to be the dominant biome during the
380 Seravallian (S27 – S31). During the Tortonian the warm – temperate evergreen broadleaf and mixed
381 forest continued to be dominant (Fig. 7A) but there is also evidence for tropical semi-evergreen
382 forest in Louisiana during this time (Site T40), that was rich in ferns and palm trees (Wrenn et al.,
383 2003). Further inland, at 86°W the Pipe Creek sinkhole (Site T41) contains diverse macrofloral fossils
384 with common *Platanus* leaves and a pollen assemblage dominated by Juglandaceae and Pinaceae;
385 this has been interpreted to represent a temperate deciduous broadleaf savanna (Farlow et al.,
386 2001; Shunk, 2009). During the Tortonian the warm – temperate evergreen broadleaf and mixed
387 forest that dominated the eastern USA is estimated to have had a MAT of 15±9°N and a MAP of
388 1270mm. Palaeobotanical evidence can only confirm the warm – temperate evergreen broadleaf
389 and mixed forest between 36°N and 38°N during the Messinian (Fig. 7B). At Gray Fossil Site (Site

390 M21) a palynological assemblage records the presence of a temperate deciduous broadleaf forest
391 dominated by *Carya*, *Pinus* and *Quercus* (DeSantis and Wallace, 2008).

392

393 3.1.5 Central America and the Caribbean

394 Palaeobotanical evidence from Central America and the Caribbean is limited. During the Langhian
395 stage, two sites (Sites L30 – L31) located between 17°N and 7°N provide evidence for a tropical
396 climate in Central America. A third site (Site L29) records a temperate deciduous broadleaf forest
397 which is interpreted to have been derived from altitude to explain the presence of a temperate
398 biome in the tropics (Lenhardt et al., 2006). Further south at the Panama Canal (Site L31) a leaf flora
399 records the presence of a tropical semi-evergreen broadleaf forest with a MAT of $15.5 \pm 4.9^\circ\text{C}$ and
400 MAP of $658.2 \pm 483.8\text{mm}$ (Retallack and Kirby, 2007). During the Seravallian the well dated site of
401 Panolta (Site S32) shows the presence of a tropical evergreen broadleaf forest at 18°N (Castañeda-
402 Posadas et al., 2009). Again there is evidence of quite diverse palaeoaltitude in this region with a
403 pollen spectrum at Jalapa (Site S33) reflecting a warm *Liquidambar* - *Quercus* forest rather than a
404 tropical rainforest (Graham, 1975). During the Tortonian and Messinian there also was a warm –
405 temperate evergreen broadleaf and mixed forest (with palms) preserved as a palynological
406 assemblage at Location B, Guatemala (Graham, 1998). On the islands of Haiti and Cuba tropical
407 deciduous broadleaf woodland and a tropical evergreen broadleaf forest are present, respectively
408 (Site T51 & T52). These contrast with the prominence of warm – temperate evergreen broadleaf and
409 mixed forest preserved on mainland Central America at similar latitudes.

410

411 3.1.6 Northern South America

412 In the northern half of South America, all palaeobotanical sites indicate a tropical evergreen
413 broadleaf forest during the Langhian (Fig. 6A). In the Seravallian the tropical evergreen broadleaf

414 forest continued to exist with an estimated MAP of 1750 ± 250 mm at La Venta (Kay and Madden,
415 1997). However, in the west three sites (Sites S37 – S39) record a tropical deciduous broadleaf forest
416 and woodland suggesting a lower rainfall than at La Venta. During the Tortonian more open biomes
417 became abundant (Fig. 7A) with tropical savanna between 5°S and 12°S (Sites T61, T66 & T67) and
418 tropical deciduous broadleaf forest and woodland further south (Sites T71 & T72). This southern
419 forest is estimated to have had a MAT of between $16.1 - 23.5^{\circ}\text{C}$ and a MAP of 550 ± 180 mm
420 (Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2002). During the Messinian a mixture of tropical
421 evergreen broadleaf forest and tropical savanna existed in this region (Fig. 7B). At Pislepampa,
422 Bolivia (Site M41) the tropical evergreen broadleaf forest is estimated to have grown under a MAT of
423 $20\pm 5^{\circ}\text{C}$ and a MAP of 1250 ± 250 mm (Graham et al., 2001).

424

425 3.1.7 Southern South America

426 The western side of southern South America between 26°S and 35°S contained arid type biomes
427 during the Langhian (Fig. 6B). There may have been an Atacama desert present (Site L41) with
428 temperate xerophytic shrubland and temperate sclerophyll woodland and shrubland further south.
429 On the east side south of 35°S there was a mixture of warm – temperate evergreen broadleaf and
430 mixed forest and temperate grassland (Sites L46 – L51). At 55°S a warm – temperate evergreen
431 broadleaf and mixed forest inhabited Tierra del Fuego (Site L53) and the Falkland Islands (Site L52)
432 during the Langhian (Fig. 6A). The palaeobotanical bearing deposits on the Falklands have not been
433 well dated (Macphail and Cantrill, 2006). The better dated deposits on Tierra del Fuego are of a
434 comparable biome type suggesting they may be coeval, however the Falkland Island site has still
435 been included in the younger datasets until its age has been confirmed. The Forest Beds of the
436 Falkland Islands show a flora dominated by *Dacrydium*, *Lagarostrobos*, *Nothofagus* and *Podocarpus*,
437 this forest community had a MAT of $12\pm 1^{\circ}\text{C}$ and a MAP of around 1200mm (Macphail and Cantrill,

438 2006). There is very little difference in the biome types of southern South America between the
439 Langhian and the Seravallian; this is mostly due to the uncertainty in the dating of sites in this region.
440 By the Tortonian there were more humid biomes to the south of the Atacama Desert (Fig. 7A).
441 Tropical evergreen broadleaf forest inhabited mountain slopes and areas with adequate moisture
442 (Sites T74 & T75), whilst tropical savanna dominated the lowlands (Sites T76 - T78). Between 31°S
443 and 44°S, a mixture of temperate sclerophyll woodland and shrubland, temperate xerophytic
444 shrubland and isolated coastal warm – temperate evergreen broadleaf and mixed forests were
445 present (Fig. 7A). These warm – temperate evergreen broadleaf and mixed forests were replaced by
446 temperate deciduous broadleaf savanna during the Messinian. Other than the loss of the warm –
447 temperate evergreen broadleaf and mixed forests there is very little difference between the
448 Tortonian and the Messinian and this is due to dating restrictions. There is evidence for glaciers
449 being present at 47°S (Site M62) during the Messinian (Mercer and Sutter, 1982).

450

451 3.1.8. North Atlantic Islands

452 For the Langhian and Seravallian the only vegetation evidence for this region comes from Iceland
453 (Fig. 6A,B). During the Middle Miocene Iceland was inhabited by a warm – temperate evergreen
454 broadleaf and mixed forest with taxa such as *Betulaceae*, *Glyptostrobus*, *Fagus*, *Fraxinus*, *Magnolia*,
455 *Sequoia* and *Ulmus* (Grimsson et al., 2007). During the Tortonian Iceland continued to have warm –
456 temperate evergreen broadleaf and mixed forests until 9 – 10 Ma when temperate deciduous
457 broadleaved forests and cool - temperate mixed forests become the main biome type of the island.
458 The early Tortonian warm – temperate evergreen broadleaf and mixed forest grew under a MAT of
459 $7.7\pm 0.1^{\circ}\text{C}$ and a MAP of $1075\pm 0.5\text{mm}$ (Denk et al., 2005). Other evidence for the North Atlantic
460 comes from Ocean Drilling Project (ODP) and Deep Sea Drilling Project (DSDP) sites. Off the southern
461 tip of Greenland a pollen assemblage has been recovered showing the existence of warm –

462 temperate evergreen broadleaf and mixed forests on Greenland during the Tortonian (Site T95).
463 North of Iceland, between 67°N and 69°N pollen assemblages provide evidence of a cool - temperate
464 mixed forest on either Greenland, northern Eurasia or both (Sites T100 & T102). Further north at
465 78°N a cold evergreen needleleaf forest was present (Site T101). By the Messinian the warm –
466 temperate evergreen broadleaf and mixed forests were gone from the region, the last fossil
467 evidence being from offshore southern Greenland at 6.5 Ma (Site M66). Between 58°N and 68°N
468 pollen recovered from marine cores shows that the predominant biome of this region was cool -
469 temperate mixed forest with cold evergreen needleleaf forest at 78°N (Fig. 7B).

470

471 3.1.9. Europe

472 From the Langhian to the Messinian the vegetation of Europe shows a gradual response to a cooling
473 and drying climate. The dominance of warm – temperate evergreen broadleaf and mixed forests
474 present throughout the Langhian begins to be broken up by areas of cooler and drier biomes. This
475 pattern is particularly evident in the east of Europe where temperate deciduous broadleaf savanna
476 becomes a major biome during the Late Miocene breaking up the extensive warm – temperate
477 evergreen broadleaf and mixed forest (Akgün and Akyol, 1999).

478 On the Iberian Peninsula during the Langhian warm – temperate evergreen broadleaf and mixed
479 forest dominated the landscape (Fig. 6A). At Rubielos de Mora, Spain (Site L62) a pollen and macro-
480 fossil assemblage shows that the warm – temperate evergreen broadleaf and mixed forest was
481 chiefly composed of *Acer*, *Betula*, *Carya*, *Corylus*, *Fraxinus*, *Glyptostrobus*, *Juglans*, *Quercus*, *Salix* and
482 *Sequoia* (Ramis and Marron, 1994). On the southern coast of the Iberian Peninsula there was an arid
483 region of temperate xerophytic shrubland (Sites L63 – L66) and on the eastern coast there was an
484 area of temperate deciduous broadleaf savanna (Site L61). To the north and east of the Pyrenees
485 palaeobotanical evidence shows the presence of a warm – temperate evergreen broadleaf and

486 mixed forest throughout Europe between the latitudes of 36°N and 53°N and the longitudes of 1°W
487 and 47°E (Fig. 6A). This warm – temperate evergreen broadleaf and mixed forest is estimated to
488 have grown under a MAT of 13.6 - 21°C and a MAP of 823 – 2500mm, in Turkey the MAT is
489 estimated to have been slightly higher with a range of 16. 5 – 21.3°C (Table 2.) (Akgün and Akyol,
490 1999; Akgün et al., 2007; Kayseri and Akgün, 2010). The only exception to this widespread warm –
491 temperate evergreen broadleaf and mixed forest was a small area of temperate sclerophyll
492 woodland and shrubland in southern Germany (Sites L82 – L83), this is estimated to have had an
493 MAT comparable to the warm – temperate evergreen broadleaf and mixed forest but a lower MAP
494 (Table. 2) (Böhme et al., 2007).

495 During the Seravallian the warm – temperate evergreen broadleaf and mixed forest biome
496 continued to dominate Europe but some areas had begun to develop drier biomes (Fig. 6B). On the
497 Iberian Peninsula a vegetation pattern similar to that of the Langhian existed (Fig. 6A), with the
498 exception of evidence for a temperate sclerophyll woodland in central Spain (Site S64). In southern
499 France there is evidence for temperate deciduous broadleaf savanna (Sites S80 & S91) as well warm
500 – temperate evergreen broadleaf and mixed forest. Further disruption to the warm – temperate
501 evergreen broadleaf and mixed forest occurs in southern Germany where temperate deciduous
502 broadleaf forest occurred (Fig. 6B), and east of 28°E where more open areas of temperate deciduous
503 broadleaf savanna (Sites S118, S124 & S127) occupied drier regions. The warm – temperate
504 evergreen broadleaf and mixed forest during the Seravallian is estimated to have grown under a
505 MAT and MAP comparable to that of the Langhian (Table 2.). The temperate deciduous broadleaf
506 savanna found east of 28°E is estimated to have had a MAT of $9.5\pm 4.9^{\circ}\text{C}$ and a MAP of $951\pm 216\text{mm}$
507 (Syabryaj et al., 2007), showing that not only was this biome drier than the dominant warm –
508 temperate evergreen broadleaf and mixed forests but also colder.

509 The expansion of colder and drier biomes continued into the Tortonian, although large areas of
510 warm – temperate evergreen broadleaf and mixed forest still dominated much of Europe (Fig. 7A).

511 The Iberian Peninsula during the Tortonian had a vegetation pattern similar to that of the Seravallian
512 (Fig. 7A). Climate estimates from the Tagus Basin, Portugal suggests the MAT of the warm –
513 temperate evergreen broadleaf and mixed forests was around 11°C. The warm – temperate
514 evergreen broadleaf and mixed forests were still dominant across Europe until 23°E, where more
515 open biomes began to intermingle with the warm – temperate evergreen broadleaf and mixed
516 forest (Fig. 7A). The warm – temperate evergreen broadleaf and mixed forests were typically
517 composed of *Abies*, *Betula*, *Cedrus*, *Craigia*, *Engelhardia*, *Keteleeria*, *Liquidambar*, *Myrica* *Pinus*,
518 *Quercus* and *Taxodium* as well as other taxa and occasionally palms (Nagy, 1967; Blanc et al., 1974;
519 Kvacek et al., 2002). Reconstructed climate of this warm – temperate evergreen broadleaf and
520 mixed forest for the Tortonian provides a MAT range of 11.6 – 18.4°C and a MAP of around 1153mm
521 (Table 2) (Bruch et al., 2006). West of 23°E a small area of cool - temperate mixed forests of *Fagus*,
522 *Liquidambar* and *Quercus* inhabited a small area of southern Germany, possibly indicating an area of
523 palaeo-altitude (Gregor et al., 1989). East of 23°E a mixture of warm – temperate evergreen
524 broadleaf and mixed forests, temperate evergreen needleleaf forests and temperate deciduous
525 broadleaf savanna was found (Fig. 7A). In Turkey, the warm – temperate evergreen broadleaf and
526 mixed forest inhabited a region warmer than that in the rest of Europe with a reconstructed MAT of
527 15.6 – 21.3°C and a MAP of 823 – 1574mm (Table 2) (Akgün et al., 2007). The temperate deciduous
528 broadleaf savanna of Turkey has a comparable reconstructed climate (Table 2).

529 During the Messinian the vegetation patterns that had developed in the Tortonian continued (Fig.
530 7B). The warm – temperate evergreen broadleaf and mixed forest continued to dominate Europe up
531 to 23°E, with a reconstructed MAT of 9 – 19.8°C and a MAP of 700 – 1759mm (Table 2) (Bruch et al.,
532 2006). Evidence from the Iberian Peninsula is limited, though it still shows the presence of
533 temperate xerophytic shrubland along the southern coast and warm – temperate evergreen
534 broadleaf and mixed forests in the Pyrenees (Fig. 7B). Some palaeobotanical sites show evidence for
535 areas of temperate deciduous broadleaf forest (Sites M76 & M106), temperate evergreen needleleaf
536 forest (Sites M101 & M102) and temperate xerophytic shrubland (Site M94). These had MAT

537 comparable to the warm – temperate evergreen broadleaf and mixed forests of around 15°C but
538 with lower MAP, below 1000mm (Table 2). East of 23°E there was a mixture of warm – temperate
539 evergreen broadleaf and mixed forests and temperate deciduous broadleaf savanna, similar to the
540 Tortonian (Fig. 7A).

541

542 3.1.10. North Africa and the Middle-East

543 Evidence for the Langhian and Seravallian is very scarce for this region. The only evidence comes
544 from Enfidha, Tunisia (Site L77; S91) and Jabal Barakah, UAE (Site L104). At Enfidha, a warm –
545 temperate evergreen broadleaf and mixed forest dominated by *Carya* and Myricaceae inhabited this
546 region (Planderová, 1971). At Jabal Barakah, a high proportion of grass pollen, as well as, *Alchornea*,
547 *Celtis*, Myrtilaceae and Palm indicate a tropical deciduous broadleaf woodland with mangroves along
548 the coast (Whybrow and McClure, 1980; Jacobs et al., 2010). By the Tortonian numerous sites show
549 the existence of tropical savanna, tropical grassland, tropical xerophytic shrubland and temperate
550 sclerophyll woodland and shrubland throughout North Africa and the Middle-East (Fig. 7A). This
551 pattern continues into the Messinian with the addition of evidence for desert conditions starting at
552 around 7 Ma (Site M144). Although the origin of these deposits has come under contest (Kroepelin,
553 2006; Swezey, 2006; Schuster et al., 2006) and wider sedimentary evidence shows that the Sahara
554 region was predominantly fluvial in deposition before the major onset of northern hemisphere
555 glaciations (Swezey, 2009).

556

557 3.1.11. Equatorial Africa

558 Data for this region is restricted to a narrow band between 1°S and 12°N and records the changes
559 between tropical closed and tropical open vegetation. During the Langhian the west side of the
560 Niger Delta was dominated by tropical evergreen broadleaf forest (Site L105), whilst pollen

561 assemblages from the Niger Delta record the existence of regional tropical savanna (Fig. 6A). In the
562 east of this region tropical deciduous broadleaf woodland is recorded at 12°N (Site L108) and
563 tropical evergreen broadleaf forest at 0.2°S (Site L109). South of the tropical evergreen broadleaf
564 forest a younger site; Fort Ternan and Sondu, Kenya (Sites L110 & L111) shows evidence for tropical
565 savanna. The Seravallian is only represented by four sites for this region which shows a vegetation
566 pattern comparable to the Langhian (Sites S137 – S140). At Kabasuro, Kenya the MAT of the tropical
567 evergreen broadleaf forest is estimated to be around 21.9°C (Jacobs and Kabuye, 1989; Jacobs and
568 Deino, 1996).

569 During the Tortonian, in western Equatorial Africa tropical evergreen broadleaf forest dominated
570 from 16°W to 8°E, up to 12°N. At 6°N, 8°E pollen from Oku Lake shows the presence of tropical
571 savanna dominated by Cyperaceae and Poaceae (Médus et al., 1988). Drill cores from the Niger
572 Delta show a predominance of tropical evergreen broadleaf forests growing along its source rivers
573 until 7.6 Ma when there was a shift to tropical savanna suggesting a possible drying of the region
574 (Sites T188 – T190). In east equatorial Africa a mixture of tropical evergreen broadleaf forest (Sites
575 T196 & T200), tropical savanna (Sites 199) and tropical grassland (Sites T197 & T198) inhabited the
576 region. By the Messinian, tropical evergreen broadleaf forest continued to inhabit the western part
577 of equatorial Africa from 16°W to 4°W, the Niger Delta was inhabited by tropical savanna during the
578 Messinian (Fig. 7B). In east equatorial Africa a pattern similar to the Tortonian existed except south
579 of 1°N, here tropical deciduous broadleaf woodland (Sites M149 & M150) with a MAT of $21.7 \pm 2.5^\circ\text{C}$
580 and a MAP of $1045 \pm 200\text{mm}$ (Jacobs and Deino, 1996; Bonnefille, 2010) was present close to tropical
581 evergreen broadleaf forest (Site M151).

582

583 3.1.12 Southern Africa

584 As with much of Africa data is scarce for southern Africa and only allows the difference between
585 Middle and Late Miocene to be determined. During the Middle Miocene (Langhian and Seravallian)
586 the vegetation of South Africa was tropical (Fig. 6A,B). Evidence exists for tropical savanna (Sites
587 L113; S143) and tropical semi-evergreen broadleaf forest (Sites L112; S142). By the Late Miocene
588 (Tortonian and Messinian) the vegetation of South Africa suggests a cooler climate with temperate
589 evergreen needleleaf forest along the western coast. Offshore Namibia, DSDP Site 530A contains a
590 pollen assemblage showing the presence of tropical xerophytic shrubland in modern day Namibia
591 during the Late Miocene (van Zinderen Bakker Sr., 1980). Other evidence suggests that the Namib
592 Desert may have been present since the Early Miocene (Senut et al., 2009).

593

594 3.1.13 West Asia

595 During the Langhian a latitudinal south to north drying and cooling trend existed for this region.
596 Between 41°N and 46°N a warm – temperate evergreen broadleaf and mixed forest inhabited the
597 region, with a composition of mainly *Betula*, *Carpinus*, *Carya*, *Fagus*, *Juglans*, *Liquidambar*,
598 *Magnolia*, *Quercus*, *Pinus* and *Zelkova* (Liu and Leopold, 1994; Sun and Zhang, 2008). North of the
599 warm – temperate evergreen broadleaf and mixed forest at 48°N a temperate deciduous broadleaf
600 forest was present and north of this between 56°N and 57°N temperate deciduous broadleaf
601 savanna, with an estimated MAT of 9±1°C and a MAP of around 700mm (Gnibidenko et al., 1999)
602 existed (Fig. 6A). The pattern is still present in the Seravallian, though the warm – temperate
603 evergreen broadleaf and mixed forest was restricted to 41°N (Fig. 6B). By the Tortonian the warm –
604 temperate evergreen broadleaf and mixed forests were replaced by temperate deciduous broadleaf
605 savanna from 45°N to 57°N. From Travolzhansky, Russia (Site T206), a pollen flora shows that the
606 temperate deciduous broadleaf savanna was composed of *Alnus*, *Betula*, *Carpinus*, *Carya*,
607 Compositae, Gramineae, *Picea*, *Quercus*, *Tsuga* and *Ulmus* (Volkova et al., 1986). By the Messinian
608 the region had desert at 38°N (Site M159). North of the desert, between 45°N and 53°N, there

609 existed a region of temperate deciduous broadleaf forest and temperate deciduous broadleaf
610 savanna (Fig. 7B). Further north at 68°N a cool-temperate mixed forest was present (Fig. 7B)
611 containing taxa such as; *Ilex*, Juglandaceae, Myrtaceae, *Nyssa* and Taxodiaceae (Belkin, 1964).

612

613 3.1.14 Northeast Asia

614 During the Langhian this region was vegetated with cool - temperate biomes (Fig. 6A). The main
615 biome was a cool - temperate mixed forest (Sites L125, L128, L129 & L131), these forests were
616 dominated by conifers but contained angiosperms such as *Alnus*, *Betula*, *Juglans*, *Quercus* and *Tilia*
617 (Baranova et al., 1970; Lavrushin and Alekseev, 2005). Also present during the Langhian were cool
618 evergreen needleleaf forests dominated by *Larix* and other gymnosperms, but containing some
619 angiosperms (Site L130). During the Seravallian the cool – temperate mixed forest continued to be
620 the dominant biome between 61°N and 77°N with no evidence for other biomes being present (Fig.
621 6B). By the Tortonian the main biome in the northeast Asian region was cold evergreen needleleaf
622 forest between 61°N and 70°N (Fig. 7A). South of the cold evergreen needleleaf forest a cool –
623 temperate evergreen needleleaf and mixed forest inhabited the coast (Site T215). This forest was
624 mainly composed of Fagaceae, *Larix*, *Picea* and Taxodiaceae (Nikitin, 2007). During the Messinian the
625 cold evergreen needleleaf forest continued to dominate the northeast Asian region (Sites M163,
626 M164, M166 & M167) with smaller amounts of cool – temperate evergreen needleleaf and mixed
627 forest along the coast (Fig. 7B).

628

629 3.1.15 Eastern Asia

630 During the Langhian this region was principally vegetated by the warm – temperate evergreen
631 broadleaf and mixed forest from 21°N to 56°N (Fig. 6A). This biome contained a diverse assemblage
632 of both gymnosperms and angiosperms including *Carya*, *Castanea*, *Corylus*, *Engelhardtia*, *Keteleeria*,

633 *Liquidambar, Metasequoia, Pinus, Quercus, Sequoia, Taxodium* and *Zelkova* (Liu and Leopold, 1994;
634 Kong, 2000). Climatic estimates for this biome, north of 36°N, indicate a MAT of 12±3°C and a MAP
635 of around 1000mm (Table. 2) (Liu and Leopold, 1994; Tao, 1997; Sun et al., 2002). Along the coast
636 between 31°N and 33°N a tropical evergreen broadleaf forest existed (Sites L146 – L148). West of
637 111°E a drier region vegetated by a mixture of temperate deciduous broadleaf forest, temperate
638 evergreen needleleaf open woodland and temperate evergreen needleleaf forest existed during the
639 Langhian (Fig. 6A). During the Seravallian the warm – temperate evergreen broadleaf and mixed
640 forest continued to dominate the region, between 22°N and 50°N (Fig. 6B). Tropical evergreen
641 broadleaf forest was still present between 31°N and 33°N (Sites S168 – S170), as was the drier region
642 west of 111°E (Fig. 6B). Drying in this region had continued from the Langhian and at 90°E a pollen
643 assemblage from Quaidam, China (Site S149) shows that a temperate xerophytic shrubland
644 inhabited this region from around 14 Ma.

645 By the Tortonian the warm – temperate evergreen broadleaf and mixed forest was still present from
646 20°N to 48°N but had become more restricted in its distribution longitudinally (Fig. 7A). Climatic
647 estimates for the warm – temperate evergreen broadleaf and mixed forest, at 23°N, show it grew
648 under a MAT of 17.9±1.2°C with a MAP of 1427±212mm (Xia et al., 2009). The drier biomes, present
649 in the Middle Miocene as far east as 111°E, now spread as far east as 118°E (Fig. 7A). The major dry
650 biome was a temperate deciduous broadleaf savanna, which was present from 28°N to 55°N
651 throughout inland eastern Asia. Within this extensive temperate deciduous broadleaf savanna there
652 were isolated areas of more humid warm – temperate evergreen broadleaf and mixed forest and
653 drier regions of temperate xerophytic shrubland (Fig. 7A). At Sikouzi, China (Sites T227 – T230) a high
654 resolution pollen sequence shows that in this region the vegetation changes from temperate
655 evergreen needleleaf open woodland at 11.35 Ma to temperate xerophytic shrubland, this then
656 changes again at 8.3 Ma to a more humid temperate deciduous broadleaf savanna and finally
657 changes back to temperate xerophytic shrubland at 8.05 Ma (Jiang and Ding, 2008).

658 By the Messinian the dominant biome in eastern Asia was the temperate deciduous broadleaf
659 savanna (Fig. 7B). The warm – temperate evergreen broadleaf and mixed forest was restricted to the
660 coast to as far north as 39°N (Site M179) and possibly as far north as 50°N (Sites M168 – M169),
661 though these sites would only represent the earliest Messinian (Ca. 7 Ma). Further west, away from
662 the coastal warm – temperate evergreen broadleaf and mixed forests, within the more extensive
663 temperate deciduous broadleaf savanna isolated areas of temperate xerophytic shrubland existed
664 (Site M171).

665

666 3.1.16 The Indian subcontinent

667 For the Langhian all palaeobotanical evidence shows that the Indian subcontinent was vegetated by
668 a tropical evergreen broadleaf forest (Fig. 6A). This dominance of tropical evergreen broadleaf
669 forest, on the Indian subcontinent, continued into the Seravallian (Fig. 6B). The Langhian and
670 Seravallian tropical evergreen broadleaf forests were composed mainly of *Bursera*, *Dialium*
671 *Dipterocarpus*, *Dracontomelum*, *Sterculia* and abundant ferns (Prasad, 1993; Sarkar and Singh,
672 1994). By the Tortonian the tropical evergreen broadleaf forests continued to be dominant on the
673 southern tip of the Indian subcontinent, however in the north more biomes were present (Fig. 7A).
674 On the Himalayan Front a mixture of tropical evergreen broadleaf forest (Sites T258, T262, T264,
675 T266 & T267), tropical semi – evergreen broadleaf forest (Site T263), warm – temperate evergreen
676 broadleaf and mixed forest (Sites T256, T260, T261 & T268), temperate evergreen needleleaf forest
677 (Site T257) and temperate grassland existed at around 8 Ma (Site T265). This mixture of biomes in
678 such close proximity probably reflects the regional topography at the time, with tropical forests on
679 the lowlands and the warm – temperate and temperate biomes at altitude. This diversity of biomes
680 continued into the Messinian along the Himalayan Front, but with the tropical forests 2° further
681 south than during the Tortonian (Fig. 7B). Tropical evergreen broadleaf forests continued to
682 dominate the Indian subcontinent Peninsula (Site M202 – M208).

683

684 3.1.17 South-east Asia

685 During the Langhian the vegetation of south-east Asia was tropical evergreen broadleaf forest (Fig.
686 6A). The tropical evergreen broadleaf forest continued to dominate south-east Asia during the
687 Seravallian, but isolated areas of tropical savanna (Site S186) and tropical deciduous broadleaf forest
688 and woodland (Site S189) shows that some drying of the region had occurred. By the Tortonian the
689 once extensive tropical evergreen broadleaf forest had become more disjointed with regions of
690 tropical deciduous broadleaf forest and woodland, tropical grassland and warm – temperate
691 evergreen broadleaf and mixed forest occupying much of the region between 12°N and 20°N (Fig.
692 7A). This pattern is also seen in the Messinian though this may be related to uncertainties in dating
693 of some of the sites.

694

695 3.1.18 Australia and New Zealand

696 For the Langhian data is only available for east Australia. In the North a tropical evergreen broadleaf
697 forest (Site L169) existed to as far south as 28°S, below 28°S a warm – temperate evergreen
698 broadleaf and mixed forest inhabited the region (Fig. 6A). This warm – temperate evergreen
699 broadleaf and mixed forest grew under a MAT of around 19°C and a MAP of between 1500 and
700 2200mm (Kershaw, 1997; Holdgate et al., 2007). New Zealand was also dominated by the warm –
701 temperate evergreen broadleaf and mixed forest with isolated regions of drier temperate sclerophyll
702 woodland and shrubland, during the Langhian (Fig. 6A). During the Seravallian data only exists to
703 confirm the presence of a warm – temperate evergreen broadleaf and mixed forest in south – east
704 Australia (Fig. 6B), growing under a climate similar to that of the Langhian (Table 2). New Zealand
705 also shows a biome distribution comparable to that of the Langhian (Fig. 6B). By the Tortonian a
706 dramatic drying of Australia had begun. The main biome on the continent was now the temperate

707 sclerophyll woodland and shrubland (Fig. 7A), estimated from Lake Tay (Site T307) to have grown
708 under a MAP of between 600 and 1500mm (Macphail, 1997). There were still isolated patches of
709 warm – temperate evergreen broadleaf and mixed forests in the south-east of the continent (Site
710 T312) with a MAP of at least 1500mm and areas of temperate deciduous broadleaf savanna (Site
711 T311). Along the northeast coast a temperate evergreen needleleaf forest existed (Fig. 7A). New
712 Zealand continued to be dominated by a warm – temperate evergreen broadleaf and mixed forest,
713 but evidence exists to suggest cool – temperate mixed forests may have inhabited higher altitudes
714 (Fig. 7A). During the Messinian the drying and the expansion of the temperate sclerophyll woodland
715 and shrubland continued (Fig. 7B). No palaeobotanical data shows the existence of major areas of
716 warm – temperate evergreen broadleaf and mixed forest during the Messinian, though this biome
717 was still dominant on New Zealand (Fig. 7B).

718

719 3.1.19 Antarctica and the surrounding Islands

720 During the Langhian low- and high- shrub tundra and prostrate dwarf – shrub tundra were present
721 on the fringes of Antarctica (Fig. 6A). ODP Site 696 (Site L54) contains evidence that South Georgia
722 and the South Sandwich Islands (62°S) were vegetated by a temperate deciduous broadleaf forest
723 rich in ferns, Podocarpaceae and *Nothofagus* (Mohr, 2001). By the Seravallian vegetation was extinct
724 on Antarctica (Lewis et al., 2008). Except for isolated communities of limited tundra on the Antarctic
725 Peninsula, which may have survived until 12.8 Ma (Site S57) (Anderson et al., 2011). By around 12
726 Ma glaciers may have been at their present extent, shown by glacial deposits on the James Ross
727 Peninsula (Dingle and Lavelle, 1998; Marensi et al., 2010). Although vegetation was gone from
728 Antarctica after the Langhian the islands in the Southern Ocean provide some insight into the
729 climate during the Late Miocene. On Heard Island (Site T326; M252) a temperate grassland existed
730 with a composition comparable to that seen on islands 10° latitude to the north in the present day.

731

732 3.2. Latitudinal temperature gradients derived from megabiome distribution

733 From the pattern of megabiomes and bioclimatic zones (Table 1) an easily accessible view of the
734 latitudinal temperature gradient throughout the Middle to Late Miocene can be achieved. Although
735 no estimate of absolute temperatures or temperature change can be currently applied, the pattern
736 shows that throughout the Middle to Late Miocene the world was warmer than at present day. The
737 pattern of bioclimatic zones (Fig. 8, 9) shows that the latitudinal temperature gradient was much
738 shallower in the Langhian and became progressively steeper throughout the remaining Miocene.
739 However the gradient did not change uniformly in both the northern and southern hemispheres.
740 From the vegetation data it appears that the southern hemisphere latitudinal temperature gradient
741 became more modern like by the Seravallian (Fig. 8, 9). Conversely the northern hemisphere
742 latitudinal temperature gradient appears to have become more modern at a slower pace; vegetation
743 was still at higher latitudes during the Messinian than it is at present day (Fig. 8, 9).

744 During the Langhian the latitudinal distribution of bioclimatic zones indicates a latitudinal
745 temperature gradient very different from the modern world (Fig. 8A, 9A). Along both the west
746 Pacific transect (WPT) (Fig. 8) and the west Atlantic transect (WAT) (Fig. 9) all the bioclimatic zones,
747 in both hemispheres, are at higher than modern latitude. This is also the case in the Seravallian,
748 although not by much in the southern hemisphere (Fig. 8B, 9B). By the Tortonian, the southern
749 hemisphere latitudinal distribution of bioclimatic zones appears comparable to modern (Fig. 8C, 9C).
750 The northern hemisphere however still shows vegetation at higher latitudes than in the modern
751 potential natural vegetation especially along the WAT (Fig. 9C). During the Messinian the WPT shows
752 a latitudinal vegetation gradient very comparable to that of the present day potential natural
753 vegetation (Fig. 8D), however along the WAT, in the northern hemisphere, the Messinian latitudinal
754 vegetation distribution was still higher than that of the present day (Fig. 9D).

755

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777 vegetation (Fig. 8D), however along the WAT, in the northern hemisphere, the Messinian latitudinal
778 vegetation distribution was still higher than that of the present day (Fig. 9D).

779

780 4. Discussion

781

782 4.1. Middle to Late Miocene vegetation evolution and CO₂

783 From 617 palaeobotanical sites, translated into the 28 biome scheme of the BIOME4 model, it can
784 be seen that there is a global cooling and drying trend from the Langhian to the Messinian. This is in
785 accordance with numerous other studies (Zachos et al., 2008; Utescher et al., 2011a).

786 During the Langhian (15.97 – 13.65 Ma), the period of time referred to as the Mid – Miocene
787 Climatic Optimum (MMCO) was ending. The MMCO was a significant warm interval recorded in the
788 deep sea records (Flower and Kennett, 1994; Zachos et al., 2008). The MMCO and the Langhian also
789 correspond to a peak in atmospheric CO₂ concentration, stomatal indices indicate atmospheric
790 concentrations of between 460 and 564 ppmv (Kürschner et al., 2008; Beerling et al., 2009) whilst
791 estimates from boron isotopes suggest 300 ppmv (Pearson and Palmer, 2000) and alkenone based
792 estimates place it at a more modest 220 ppmv (Pagani et al., 2005). Although the 300 ppmv
793 recorded in the boron isotopic record does not appear to be “high”, it does represent a peak in that
794 particular CO₂ reconstruction. The alkenone record does not present the MMCO as a period of
795 elevated CO₂ within the rest of the Miocene (Pagani et al., 1999). These elevated levels of CO₂, in all
796 the records except the alkenone based reconstruction, and the warming recognised in the benthic
797 oxygen isotope curve during the Langhian are reflected in the biome pattern; cool – temperate
798 forests at the high northern latitudes, extensive warm – temperate evergreen broadleaf and mixed
799 forests in the middle latitudes, a broader tropical zone and tundra on Antarctica (Fig. 6A).

800 During the Seravallian (13.65 – 11.61 Ma) the biome pattern is still similar to that of the Langhian
801 however changes had occurred. The benthic oxygen isotope curve shows from about 14 to around
802 10 Ma either the bottom water temperature was dropping or significant land ice was developing or a

803 combination of the two (Flower and Kennett, 1994; Zachos et al., 2008). The CO₂ proxies also record
804 falling atmospheric concentrations to; 300 – 330 ppmv from the stomatal indices (Kürschner et al.,
805 2008; Beerling et al., 2009); 268 – 290 ppmv from boron isotopes (Pearson and Palmer, 2000) and
806 alkenone estimates of 194 – 252 ppmv concentration (Pagani et al., 2005). The biome distribution
807 still shows cool – temperate mixed forest at the high northern latitudes, though not as high as it was
808 during the Langhian. Whilst in the middle latitudes the warm-temperate evergreen broadleaf and
809 mixed forest had begun to be replaced by drier and cooler biomes (Fig. 6B). In the tropics too, drier
810 biomes had begun to spread and on Antarctica tundra was no longer present (Fig. 6B).

811 The biome pattern of the Tortonian (11.61 – 7.25 Ma) is markedly different from that of the
812 Seravallian. In terms of the benthic oxygen isotopic record the Late Miocene shows relative stability,
813 after the warming of the MMCO and the cooling seen in the late Langhian and Seravallian, with
814 isotopic levels reflecting an increased (ice free) bottom water temperature range of 0 to +2°C
815 (Zachos et al., 2008). The CO₂ reconstructions give mixed estimates of the atmospheric
816 concentration of this greenhouse gas during the Tortonian. The stomatal indices show an increase of
817 CO₂ from the Seravallian to 350 – 370 ppmv (Kürschner et al., 1996; Stultz et al., In Press), whilst the
818 boron isotopes record a fall in CO₂ from the Seravallian to between 212 – 236 ppmv (Pearson and
819 Palmer, 2000) and the alkenone based reconstructions show that CO₂ concentrations fluctuated
820 between 190 – 330 ppmv with a general increasing trend towards the end of the Tortonian (Pagani
821 et al., 2005; 2010). The biome pattern of the Tortonian reflects a cooler and drier world than that of
822 the Seravallian. Cold evergreen needleleaf forests are found at the high northern latitudes for the
823 first time during the Middle to Late Miocene (Fig. 7A). In the middle latitudes the warm – temperate
824 evergreen broadleaf and mixed forest continued to be restricted and replaced by drier and cooler
825 biomes (Fig. 7A). In the tropics the major change from the Seravallian was the appearance of tropical
826 savanna in South America. The changes in biome distribution from the Seravallian to the Tortonian
827 would appear to agree with the boron isotope reconstructed CO₂ trend more than the stomatal
828 indices. However, the distribution of Tortonian palaeobotanical data compares best against GCM

829 simulated vegetation that is driven by climate under higher atmospheric levels of CO₂ than both
830 these reconstructions suggest (Micheels et al., 2007; 2009; Pound et al., 2011).

831 During the Messinian (7.25 – 5.33 Ma) the biome distribution was similar to that of the Tortonian.
832 The benthic oxygen isotope records also resemble the Tortonian records, with increased amplitude
833 between the peaks and troughs of the record (Zachos et al., 2008). CO₂ reconstructions are also
834 comparable to the Tortonian with stomatal indices showing atmospheric concentrations of 270 –
835 360 ppmv (Kürschner et al., 1996), boron isotopes indicating levels of between 268 – 305 ppmv
836 (Pearson and Palmer, 2000) and alkenone based reconstructions showing atmospheric
837 concentrations of 230 – 360 ppmv (Pagani et al., 2005; 2010). Although biome distribution was
838 similar to the Tortonian, during the Messinian, some important regional changes had occurred.

839 Warm – temperate evergreen broadleaf and mixed forest was no longer present in western North
840 America or Australia (Fig. 7B), indicating progressing aridification. Further evidence for a global
841 drying comes from the expansion of desert in North Africa and central Asia (Fig. 7B). Again during
842 the Messinian both the stomatal indices and boron isotope reconstructions differ. The stomatal
843 indices show a decrease from the Tortonian whilst the boron isotopes increase. The global
844 distribution of biomes appears to support the stomatal indices more than the boron isotope based
845 reconstructions due to regional extinctions of warm – temperate evergreen broadleaf and mixed
846 forests, an expansion of deserts and temperate biomes not reaching as far north (Fig. 7B)

847 So far the alkenone records have not been mentioned with regard to the observed changes in global
848 biome distribution. This is because the atmospheric CO₂ levels reconstructed from alkenones show
849 very little trend from the Langhian to the end of the Messinian. According to the alkenone based
850 reconstructions the atmospheric concentration of CO₂ fluctuated from as low as 190 ppmv to as high
851 as 360 ppmv (Pagani et al., 2005; 2010). This would suggest that either the alkenone based CO₂
852 reconstruction requires further study, or that the changes in global biome distribution were not
853 related to changes in the atmospheric CO₂ levels. This would contradict the two other main CO₂

854 reconstructions, which show that the cooling and drying trend seen in the palaeobotanical record
855 from the Langhian through to the Messinian is accompanied by falling atmospheric concentrations
856 of CO₂ and by the pattern in the bottom water oxygen isotopes (Zachos et al., 2008).

857

858 4.2. Middle to Late Miocene latitudinal gradients

859 In the Langhian stage the latitudinal vegetation gradient shows a significantly flatter equator to pole
860 vegetation gradient in both hemispheres, than pre - industrial (Fig. 8A, 9A). This, coupled with the
861 distribution of biomes (Fig. 6A) must reflect a significantly warmer planet associated with elevated
862 atmospheric CO₂ levels, seen in the stomatal indices and boron isotope reconstructions, associated
863 with the end of the MMCO. The high northern latitudes had a MAT around 14°C higher than the pre
864 – industrial (White and Ager, 1994), whilst the MAT of the temperate zone may have been around
865 9°C warmer than the pre – industrial (Table 2). Estimates of climate parameters from the tropics, for
866 the Langhian, are limited at the moment but from the global distribution of tropical evergreen
867 broadleaf forests the tropics likely occupied a greater latitudinal extent and may not have had a
868 significantly different MAT from pre – industrial. By the Seravallian the latitudinal vegetation
869 gradient had changed significantly in the southern hemisphere due to a global cooling and the full
870 glaciation of Antarctica indicated by the absence of vegetation evidence and the presence of glacial
871 deposits (Fig. 6B). The northern hemisphere gradient still reflects a significantly warmer world,
872 whilst the latitudinal vegetation distribution of the southern hemisphere was more similar to the pre
873 – industrial. This cooling continued into the Late Miocene and with it the latitudinal distribution of
874 biomes continued to become more pre – industrial like (Fig. 8, 9).

875 For the Tortonian the available palaeobotanical data suggests the latitudinal distribution of
876 vegetation in the southern hemisphere was almost identical to the pre – industrial. However MAT
877 estimates from Upper Jakokkota, Bolivia suggest that this site was around 9°C warmer in the

878 Tortonian than during the pre – industrial (Gregory-Wodzicki, 2002). This significant difference in
879 MAT may, in part, be explained by the uplift of the Andes, which is estimated to have proceeded at a
880 rate of 0.2 – 0.3 mm/year (Gregory-Wodzicki, 2000). The vegetation gradient of the northern
881 hemisphere continued, in the Tortonian, to be greater than during the pre – industrial. MAT
882 estimates for the Tortonian suggests the high northern latitudes may have been up to 10°C warmer
883 than pre – industrial and Europe may have been 5 - 8°C warmer than pre – industrial (Table 2).
884 Recent work in the Netherlands has reconstructed a MAT for Europe of 18 - 21°C for the Tortonian
885 (Donders et al., 2009). A combined technique of merging palaeobotanical data and a GCM suggests
886 that globally the Tortonian may have been around 4.5°C warmer than the pre – industrial (Pound et
887 al., 2011). Estimates of cold month mean temperature, using the co – existence approach, suggests
888 the high latitudes of Asia were 9 - 40°C warmer in the Tortonian than the pre – industrial and the
889 warm month mean temperature was 7 - 20°C warmer than pre – industrial (Utescher et al., 2011b).
890 The latitudinal vegetation distribution of the Messinian was very comparable to the pre – industrial.
891 The southern hemisphere as in the Tortonian, was essentially pre – industrial in latitudinal
892 distribution of biomes. Whilst the northern hemisphere continued to be warmer than the pre –
893 industrial shown by the latitudinal distribution of biomes. In the high northern latitudes MAT may
894 have been 5 - 6°C higher than pre – industrial, whilst Europe may have been between 1 - 11°C
895 warmer than pre – industrial (Table 2).

896

897 4.3. Data model comparisons of the Middle and Late Miocene

898 The geological record is increasingly being cited as providing possible analogues to future
899 anthropogenic driven climate change (Zeebe, 2011). Although it is hard to apply the term analogue
900 to any period of geological time due to the dynamic nature of planet Earth, there are lessons that
901 can be learnt about how climate changes and its longer term impacts (Haywood et al., 2011).
902 Possibly more important than providing an “analogue to future climate change” is the geological

903 records ability to provide test-beds to evaluate the predictive ability of GCMs (Haywood et al., 2011;
904 Salzmann et al. 2009; Valdes, 2011).

905 Fossil vegetation not only provides a means to assess the accuracy of GCM simulations but can be
906 used as a boundary condition as well (Herold et al., 2010; Micheels et al., 2007; 2011; Pound et al.,
907 2011, Salzmann et al., 2008). By applying a relevant vegetation reconstruction to a modelling study it
908 is possible to investigate the impact of vegetation on the climate (Dutton and Barron, 1997; Lunt et
909 al., 2009) as well as simulating a time period more accurately (Haywood and Valdes, 2006).

910 Recent palaeoclimate data - model comparisons on the Miocene have largely focussed on Eurasia
911 (François et al., 2011), have used limited proxy datasets of numerical climate data (Herold et al.,
912 2010; Micheels et al., 2011) or have used large qualitative proxy datasets (Pound et al., 2011). A
913 major area of focus has been the Tortonian, which was a warmer and wetter world without major
914 differences in required GCM boundary conditions (Lunt et al., 2008; Micheels et al., 2007; Pound et
915 al., 2011). The distribution of biomes (Fig. 7A) and the reconstructed bioclimatic latitudinal gradient
916 (Fig. 8C; 9C) both confirm this view of a warmer and wetter world. By combining vegetation models,
917 such as BIOME4 (Kaplan, 2001), with GCMs it is possible to generate a global pattern of vegetation
918 based on the simulated climate. Comparison of such a model generated global vegetation map with
919 a 240 palaeoecological dataset showed that many areas of the world were predicted to be too dry,
920 when compared to the proxy data (Pound et al., 2011). Direct comparison of GCM simulated climate
921 with reconstructed MAT and MAP figures from palaeo – proxies also shows inconsistencies in
922 simulated temperature and precipitation, between the model and the data (François et al., 2011;
923 Micheels et al., 2011). Conversely simulations of the Late Miocene have also been used to highlight
924 areas where the modelling community would like more proxy data to evaluate large uncertainties
925 between GCM experiments (Lunt et al., 2008).

926 The MMCO has also been subject to increasing amounts of modelling studies due to the increased
927 global temperatures of this time period, inferred from the reconstructed bottom water

928 temperatures (Herold et al., 2010; 2011; You et al., 2009; Zachos et al., 2008). In a study using an
929 atmosphere only GCM You et al., (2009) simulated the MMCO and generated a global MAT of
930 between 17.8 - 19°C. This is comparable to the predicted global MAT of the Tortonian from a study
931 that also used an atmosphere only GCM (Lunt et al., 2008; Pound et al., 2011). This seemingly low
932 global MAT for the MMCO could be related to the boundary conditions used in the model (You et al.,
933 2009). In another study Herold et al. (2010) simulated the period of 20 – 14 Ma, designed to
934 incorporate the MMCO, and found that the model simulated climate was too cold and arid, when
935 compared to numerical proxy data. The vegetation used in both these simulations was modified
936 from Wolfe (1985), further modification of this vegetation using the data presented in Figure 6A
937 could help to more accurately simulate the MMCO.

938

939 5. Conclusions

940 The palaeobotanical changes from the Langhian to the Messinian reflect a global cooling and drying
941 of the planet, linked to falling atmospheric CO₂ concentrations. The biome distribution of the studied
942 10 Ma period reflects a warmer and wetter world, when compared to the pre – industrial era.

- 943 • The Langhian shows the warmest biome distribution with cool – temperate mixed forests at
944 the high northern latitudes, extensive warm – temperate mixed forests in the middle
945 latitudes and tundra on Antarctica.
- 946 • Significant cooling had occurred by the Seravallian and vegetation was no longer present on
947 Antarctica. The warm – temperate evergreen broadleaf and mixed forests were partly
948 replaced by cooler and drier temperate biomes.
- 949 • This cooling of global climate continued into the Tortonian with the first sign of cold
950 evergreen needleleaf forests in the high northern latitudes. Within the mid – latitudes the
951 warm – temperate evergreen broadleaf and mixed forest continued to be replaced by cooler

952 and drier biomes. Whilst tropical savanna expanded in northern South America at the
953 expense of tropical evergreen broadleaf forest.

- 954 • By the Messinian the global distribution of biomes reflects a significant cooling from the
955 Langhian. Cold evergreen needleleaf forests occupied the high latitudes and an expanse of
956 drier and cooler biomes had replaced much of the warm – temperate mixed forests in the
957 middle latitudes.
- 958 • The distribution of biomes and the change in distribution through time reflects the changes
959 in CO₂ reconstructed by the stomatal indices and boron isotopes more than the alkenone
960 reconstruction.
- 961 • The latitudinal bioclimatic gradients show that the Langhian gradient was significantly flatter
962 than the pre – industrial. By the Seravallian the southern hemisphere bioclimatic gradient
963 was more modern whilst the northern hemisphere bioclimatic gradient was still flatter.
- 964 • This comprehensive biome dataset is now suitable for further palaeoclimate studies
965 including the incorporation into and assessment of GCM simulations of the Miocene climate.
- 966 • The latitudinal bioclimatic gradients presented within this paper provide an initial view of
967 the information the terrestrial realm maybe able to contribute to the understanding of the
968 evolution of the latitudinal temperature gradient through time.

969

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978

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1393

1394 Supplementary Material

1395 The following supplementary material is available for this article:

1396

1397 Appendix A Location, biome code, megabiome code and reference for the palaeobotanical sites for

1398 Fig. 2 and Fig. 3

1399 Appendix B Literature used for the Langhian, Seravallian, Tortonian and Messinian TEVIS database

1400

1401 Figure captions

1402

1403 Figure 1. The pre - industrial potential natural vegetation simulated by the mechanistic vegetation

1404 model BIOME4 (Kaplan, 2001). From Salzmann et al. (2009).

1405 Figure 2. Distribution of Langhian (A) and Seravallian (B) palaeobotanical locations. The references

1406 for the locations are listed in Appendices A and B.

1407 Figure 3. Distribution of Tortonian (A) and Messinian (B) palaeobotanical locations. The references

1408 for the locations are listed in Appendices A and B.

1409 Figure 4. The location of the latitudinal transects used for reconstructing the latitudinal distribution

1410 of bioclimatic zones.

1411 Figure 5. The distribution of the 20 regions used to discuss the global vegetation changes through

1412 time

1413 Figure 6. The vegetation distribution of the Langhian (A) and Seravallian (B) from palaeobotanical

1414 data, translated into the 28 biome scheme of the BIOME4 model.

1415 Figure 7. The vegetation distribution of the Tortonian (A) and Messinian (B) from palaeobotanical

1416 data, translated into the 28 biome scheme of the BIOME4 model.

1417 Figure 8. West Pacific transect (WPT) of maximum poleward distribution of bioclimatic zones for the

1418 Langhian (A), Seravallian (B), Tortonian (C) and Messinian (D). 1) Ice, 2) Tundra, 3) Boreal, 4)

1419 Temperate, 5) Warm-temperate, 6) Tropical. Blue squares are pre - industrial potential natural

1420 vegetation, red squares represent poleward - most fossil evidence for that vegetation zone.

1421 Figure 9. West Atlantic transect (WAT) of maximum poleward distribution of bioclimatic zones for
1422 the Langhian (A), Seravallian (B), Tortonian (C) and Messinian (D). 1) Ice, 2) Tundra, 3) Boreal, 4)
1423 Temperate, 5) Warm-temperate, 6) Tropical. Blue squares are pre - industrial potential natural
1424 vegetation, red squares represent poleward - most fossil evidence for that vegetation zone.

1425 Table 1. A summary of the BIOME4 vegetation scheme (Kaplan, 2001) and its translation into the
1426 seven megabiome scheme and the six bioclimatic zone scheme. An * denotes that the biome was
1427 suitable to be used in the bioclimatic zone gradients.

1428 Table 2. Climate data derived from palaeobotanical evidence. Mean annual temperature (°C) and
1429 mean annual precipitation (mm/year) are presented for regions of the world (Fig. 5) subdivided by
1430 biome type. Mean annual temperature and mean annual precipitation estimates are derived from
1431 CLAMP (Wolfe, 1979; Spicer, 2007), NLR (Mosbrugger and Utescher, 1997) and other techniques
1432 described in the source literature. Site numbers refer to Fig. 2, 3. References for the sites and the
1433 climatic data from them can be found in Appendices A, B.