Target: Earth Science Reviews

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

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Abstract

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

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

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

1. Introduction

1.1. Overview

The Miocene has been referred to as the “making of the modern world” (Potter and Szatmari, 2009) with major uplift of modern mountain chains, the initiation of bipolar glaciations, the origin of modern ocean currents, the aridification of the continental interiors, the overall cooling trend of the global climate and the reduction in atmospheric CO_2 levels (Beerling and Royer, 2011; Potter and

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

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

Both approaches have their benefits and caveats. The direct comparison of GCM climate parameters with those reconstructed from palaeobotanical sites need to take into account error margins. Both from the technique used to reconstruct the climate estimates from the fossil vegetation and from the boundary condition and physics uncertainties that are a challenge to fully explore with GCMs. The data sets currently available with palaeoclimate estimates are also limited in size and geographic distribution due to the large amount of time required in generating this data (Utescher et al., 2011b). By reconstructing a biome and comparing it to model generated biomes a simple and relatively quick comparison can be achieved (Salzmann et al., 2008; Haywood et al. 2009; Pope et al., 2011). However, biomes reconstructed from palaeobotanical sites need to be directly comparable to model output, this can be achieved by using the classification scheme of the chosen model. This raises the issue that biome models, such as BIOME4, have been developed using modern biomes and how comparable these are to fossil biomes has yet to be fully explored. Despite this indicates the technique has been successfully applied to the Pleistocene (Prentice et al., 1998), the Pliocene (Salzmann et al., 2008; Pope et al., 2011) and the Miocene (Micheels et al., 2007; Pound et al., 2011). All of this means that fossil vegetation can be used to examine climate from a single locality, providing a valuable pin – point view of the ambient conditions during deposition. To a regional or global view of climate using larger datasets of fossil vegetation distribution and finally, combining the data with GCMs to look at dynamic climate and vegetation patterns through time.

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

Within this paper we present a 617 site palaeobotanical dataset for the Middle and Late Miocene. This is the most comprehensive dataset of its kind suitable for use in palaeoclimate and palaeoecology studies. Within the paper the dataset is used to explore the climate that is reconstructed from the fossil vegetation and this is compared to the various CO_2 proxies in an attempt to better understand Miocene climate and CO_2 evolution. The vegetation has been reconstructed using the 27 biome scheme of the BIOME4 vegetation model (Fig. 1), which makes it suitable for data – model comparison studies. Such studies are beyond the scope of this paper, which focuses on a review of available palaeobotanical data. However, future modelling studies on the Miocene can use the data presented in this paper to evaluate the predictive ability of GCMs to simulate Miocene climate. The presented data can also be used to generate global vegetation maps in combination with vegetation models to explore the impacts of Miocene vegetation on climate (Pound et al., 2011; Salzmann et al., 2008).

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

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

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

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

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

1.4. Orography during the Miocene

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

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

1.4. CO_2 proxies

Miocene CO_2 levels are reconstructed using numerous techniques and each differs in both atmospheric concentration and in trend through time. Reconstructions are based on alkenones (Pagani et al., 2005; 2010), boron isotopes (Pearson and Palmer, 2000), B/Ca ratio (Tripati et al., 2009), pedogenic carbonates (Ekart et al., 1999; Retallack, 2009) and stomatal indices (Beerling et al., 2009; Kürschner et al., 1996; 2008; Stults et al., In press). Through the Middle Miocene to the end of the Miocene the alkenone based reconstructions place atmospheric CO_2 levels between 190 – 360 ppmv reaching a peak at around 6 - 7 Ma of ca. 360 ppmv (Pagani et al., 2005; 2010). The reconstructed atmospheric CO_2 concentrations from boron isotopes show a range from 137 – 305 ppmv with a peak in CO_2 at ca. 16 Ma and ca. 6 Ma (Pearson and Palmer, 2000). The stomatal indices reconstructions are very different to those based on boron isotopes and alkenones. A range over the Middle to end Miocene of 270 – 564 ppmv has been reconstructed, with a peak at ca. 16 Ma of between 460 – 564 ppmv (Beerling et al., 2009; Kürschner et al., 2008). These records then show a fall in atmospheric CO_2 concentration to between 270 – 370 ppmv for the rest of the Miocene (Beerling et al., 2009; Kürschner et al., 1996; 2008; Stults et al., In press). The B/Ca ratio shows a peak of 433 ppmv at 15 Ma and then drops to concentrations of between 206 – 304 ppmv by 10 Ma

(Tripati et al., 2009). The pedogenic carbonate reconstructions could be described as more erratic, fluctuating from very low to as high as 1170 ppmv (Ekart et al., 1999). More recent work on pedogenic carbonates, across the Middle Miocene, has shown a peak in concentration at 15.6 Ma of 852 ppmv (Retallack, 2009). This then drops rapidly to 116 ppmv at 14.6 Ma and rises to 433 ppmv by 12.8 Ma (Retallack, 2009). Overall, the apparent low atmospheric levels of Miocene CO_2 have led to disagreements over how much Miocene climate was influenced by this greenhouse gas (Kürschner et al., 2008; Mosbrugger et al., 2005; Pagani et al., 2005; Shevenell et al., 2004;).

2. Methods

2.1. Constructing the vegetation database

Using TEVIS (Tertiary Environments Vegetation Information System) (Salzmann et al., 2008; Pound et al., 2011), which is a Microsoft Access and ArcGIS 9 based database, 617 Middle to Late Miocene vegetation sites (Fig. 2, 3) have been collected from the literature and recorded in an internally consistent manner. Using the author's interpretation the reconstructed palaeovegetation has been translated into biomes using the classification scheme of the BIOME4 mechanistic vegetation model (Kaplan, 2001). TEVIS not only records the vegetation of the palaeobotanical site but also the latitude and longitude, sedimentology, method used to date the sample and a quality indicator – to ascertain the resolution of the chronology. Where available, numerical climatic parameters such as mean annual temperature and precipitation are also recorded in TEVIS. Extracting climatic parameters from fossil assemblages can be achieved by a number of techniques and the majority of the estimates in the TEVIS database come from either the co-existence approach (Bruch et al., 2006) or CLAMP (Wolfe, 1979; 1993; Spicer, 2007; Spicer et al., 2009). The co-existence approach uses the climatic tolerances of a fossil plant's nearest living relative as a guide to the climate tolerances of the fossil taxa (Mosbrugger and Utescher, 1997). When this is done for a whole assemblage a climatic envelope is generated where all the fossil plants could have co-existed; providing an estimate of climatic parameters (Mosbrugger and Utescher, 1997). CLAMP uses 31 leaf physiognomic (structure) characteristics, that have been shown to be related to the environment to which the leaf architecture is exposed (Spicer, 2007; Spicer et al., 2009), to estimate the climatic parameters of fossil leaf assemblages (Wolfe, 1993).

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

2.2 Bioclimatic zones

To gain a better insight into the latitudinal temperature gradients of the Middle to Late Miocene the latitudinal vegetation distribution can be compared to the pre - industrial potential vegetation distribution. The pre - industrial potential natural vegetation shows progressively colder biomes from the equator, as latitude increases. In simple terms this reflects the latitudinal temperature gradient, which is highest at the equator and lowest at the poles. This requires a simplified scheme to provide an understandable view of the latitudinal temperature gradients for the Langhian, Seravallian, Tortonian and Messinian stages. To facilitate this each fossil site, within TEVIS, is assigned to one of seven megabiomes and one of six bioclimatic zones (Table 1), as well as assigning each fossil site to one of the 28 biomes of the BIOME4 classification (Salzmann et al., 2009). The bioclimatic zone classifications are based on the seven megabiome classification scheme presented in Salzmann et al., (2009). Megabiomes are broader categories grouping numerous biomes. The six bioclimatic zones are; tropical, subtropical/warm-temperate, temperate, boreal, tundra and ice. These classifications reflect a simplified qualitative view of the temperature range of the 28 biomes used in the BIOME4 model. However certain biomes can be included in multiple bioclimatic zones, for example the temperate deciduous broadleaf savanna biome. This biome is referred to as a temperate vegetation type (Gnibidenko et al., 1999) and a warm – temperate vegetation type (Thomasson, 2005). To avoid complications from biomes that are more climatically controlled by seasonality and precipitation than they are by temperature, only forest, woodland or tundra biomes were used in the construction of the bioclimatic zone gradients (Table 1).

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

Using the latitudinal transects in Figure 4 the maximum pole - ward extent of each bioclimatic zone has been plotted, for each of the four studied time slices. These have been compared to the maximum pole ward extent of pre - industrial potential natural vegetation generated using the BIOME4 model (Kaplan, 2001), driven by observed climate (Fig. 1). The methodology does not provide numerical climate data to reconstruct the latitudinal temperature gradient, but does compare the maximum pole ward extent of bioclimatic zones. The method shows the relative change in the qualitative bioclimatic zones over time and provides an insight into how different the latitudinal temperature gradient would have been during the studied geological stages.

3. Results: Global vegetation change from Langhian to Messinian

3.1. Global biome distributions through time

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

The plotted biomes, from the 634 fossil vegetation sites in TEVIS, provide an insight into Middle to Late Miocene vegetation and climate. The Langhian stage is represented by 184 fossil sites (Fig. 6A), the Seravallian by 205 sites (Fig. 6B), the Tortonian by 326 sites (Fig. 7A) and the Messinian by 252 sites (Fig. 7B). Some of these sites cover multiple time stages whilst others may be better dated and correspond to an interval smaller than the assigned geological stage. The ages assigned to the geological stages follows Gradstein et al. (2004). There is excellent data coverage, for all stages, in temperate and tropical Eurasia. North and South America also have good data coverage. Whilst the high northern latitudes, Africa and central Australia have poor data coverage. All the data points are presented in the supplementary information with their modern day latitude – longitude, age range, biome and megabiome code and references (Appendices A and B).

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

3.1.1. Northern North America

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

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

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

3.1.2. Western North America

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

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

By the Tortonian palaeobotanical evidence suggests that the extensive warm – temperate evergreen broadleaf and mixed forest of the Langhian, that began to fragment in the Seravallian, had become even more restricted. During the Tortonian the warm – temperate evergreen broadleaf and mixed forest was present between 43°N and 48°N (Sites T13 – T17, T19 & T26) and along the coast between 31°N and 33°N (Sites T30 – T32) (Fig. 7A). A drill hole in Willamette Valley, Oregon, USA (Site T17) yielded a rich palynomorph assemblage derived from the warm – temperate evergreen broadleaf and mixed forest biome, the assemblage contains *Carya, Castanea, Cedrus*, *Fagus, Liquidambar, Nyssa, Platanus, Pterocarya, Sequoia* and *Ulmus* (Roberts and Whitehead, 1984). Climate estimates from the warm – temperate evergreen broadleaf and mixed forest biome suggests it existed under an MAT of 11 - 19°C and a MAP of 617.5 – 1250mm (Table 2). The lower MAP estimate of 617.5mm seems rather too low to support the warm – temperate evergreen broadleaf and mixed forest biome but this reflects an unusual setting of one palaeobotanical site (Site T30) which may have been a forest supported by summer fog (Axelrod, 2000). Separating the two areas of warm – temperate evergreen broadleaf and mixed forests during the Tortonian there was a mixture of temperate deciduous broadleaf forest, temperate deciduous broadleaf savanna and temperate sclerophyll woodland and shrubland. Further south there was temperate xerophytic shrubland (Sites 22, 24, 29, 31 & 33). These biomes are estimated to have had a MAT comparable to the warm – temperate evergreen broadleaf and mixed forest but with a lower MAP (Table 2). North of 48°N there was a temperate deciduous broadleaf forest (Sites T11 – T13) and temperate evergreen needleleaf forest (Site T10) further north. At Skonun Point (Site 9) a pollen assemblage reminiscent of the high latitude Langhian cool - temperate mixed forest biome with abundant *Alnus, Pinus*, *Quercus* and Taxodiaceae (Martin and Rouse, 1966; White et al., 1994) represents the southernmost evidence for the biome seen in Alaska (Sites T1 & T7) during this stage.

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

3.1.3 Central North America

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

3.1.4 Eastern North America

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

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

3.1.5 Central America and the Caribbean

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

3.1.6 Northern South America

In the northern half of South America, all palaeobotanical sites indicate a tropical evergreen broadleaf forest during the Langhian (Fig. 6A). In the Seravallian the tropical evergreen broadleaf forest continued to exist with an estimated MAP of 1750±250mm at La Venta (Kay and Madden, 1997). However, in the west three sites (Sites S37 – S39) record a tropical deciduous broadleaf forest and woodland suggesting a lower rainfall than at La Venta. During the Tortonian more open biomes became abundant(Fig. 7A) with tropical savanna between 5°S and 12°S (Sites T61, T66 & T67) and tropical deciduous broadleaf forest and woodland further south (Sites T71 & T72). This southern forest is estimated to have had a MAT of between 16.1 – 23.5°C and a MAP of 550±180mm (Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2002). During the Messinian a mixture of tropical evergreen broadleaf forest and tropical savanna existed in this region (Fig. 7B). At Pislepampa, Bolivia (Site M41) the tropical evergreen broadleaf forest is estimated to have grown under a MAT of 20±5°C and a MAP of 1250±250mm (Graham et al., 2001).

3.1.7 Southern South America

The western side of southern South America between 26°S and 35°S contained arid type biomes during the Langhian (Fig. 6B). There may have been an Atacama desert present (Site L41) with temperate xerophytic shrubland and temperate sclerophyll woodland and shrubland further south. On the east side south of 35°S there was a mixture of warm – temperate evergreen broadleaf and mixed forest and temperate grassland (Sites L46 – L51). At 55°S a warm – temperate evergreen broadleaf and mixed forest inhabited Tierra del Fuego (Site L53) and the Falkland Islands (Site L52) during the Langhian (Fig. 6A). The palaeobotanical bearing deposits on the Falklands have not been well dated (Macphail and Cantrill, 2006). The better dated deposits on Tierra del Fuego are of a comparable biome type suggesting they may be coeval, however the Falkland Island site has still been included in the younger datasets until its age has been confirmed. The Forest Beds of the Falkland Islands show a flora dominated by *Dacrydium*, *Lagarostrobos*, *Nothofagus* and *Podocarpus,* this forest community had a MAT of 12±1°C and a MAP of around 1200mm (Macphail and Cantrill, 2006). There is very little difference in the biome types of southern South America between the Langhian and the Seravallian; this is mostly due to the uncertainty in the dating of sites in this region.

By the Tortonian there were more humid biomes to the south of the Atacama Desert (Fig. 7A). Tropical evergreen broadleaf forest inhabited mountain slopes and areas with adequate moisture (Sites T74 & T75), whilst tropical savanna dominated the lowlands (Sites T76 - T78). Between 31°S and 44°S, a mixture of temperate sclerophyll woodland and shrubland, temperate xerophytic shrubland and isolated coastal warm – temperate evergreen broadleaf and mixed forests were present (Fig. 7A). These warm – temperate evergreen broadleaf and mixed forests were replaced by temperate deciduous broadleaf savanna during the Messinian. Other than the loss of the warm – temperate evergreen broadleaf and mixed forests there is very little difference between the Tortonian and the Messinian and this is due to dating restrictions. There is evidence for glaciers being present at 47°S (Site M62) during the Messinian (Mercer and Sutter, 1982).

3.1.8. North Atlantic Islands

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

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

3.1.9. Europe

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

On the Iberian Peninsula during the Langhian warm – temperate evergreen broadleaf and mixed forest dominated the landscape (Fig. 6A). At Rubielos de Mora, Spain (Site L62) a pollen and macro-fossil assemblage shows that the warm – temperate evergreen broadleaf and mixed forest was chiefly composed of *Acer*, *Betula, Carya, Corylus, Fraxinus, Glyptostrobus, Juglans*, *Quercus, Salix* and *Sequoia* (Ramis and Marron, 1994). On the southern coast of the Iberian Peninsula there was an arid region of temperate xerophytic shrubland (Sites L63 – L66) and on the eastern coast there was an area of temperate deciduous broadleaf savanna (Site L61). To the north and east of the Pyrenees palaeobotanical evidence shows the presence of a warm – temperate evergreen broadleaf and mixed forest throughout Europe between the latitudes of 36°N and 53°N and the longitudes of 1°W and 47°E (Fig. 6A). This warm – temperate evergreen broadleaf and mixed forest is estimated to have grown under a MAT of 13.6 - 21°C and a MAP of 823 – 2500mm, in Turkey the MAT is estimated to have been slightly higher with a range of 16. 5 – 21.3°C (Table 2.) (Akgün and Akyol, 1999; Akgün et al., 2007; Kayseri and Akgün, 2010). The only exception to this widespread warm – temperate evergreen broadleaf and mixed forest was a small area of temperate sclerophyll woodland and shrubland in southern Germany (Sites L82 – L83), this is estimated to have had an MAT comparable to the warm – temperate evergreen broadleaf and mixed forest but a lower MAP (Table. 2) (Böhme et al., 2007).

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

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

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

During the Messinian the vegetation patterns that had developed in the Tortonian continued (Fig. 7B). The warm – temperate evergreen broadleaf and mixed forest continued to dominate Europe up to 23°E, with a reconstructed MAT of 9 – 19.8°C and a MAP of 700 – 1759mm (Table 2) (Bruch et al., 2006). Evidence from the Iberian Peninsula is limited, though it still shows the presence of temperate xerophytic shrubland along the southern coast and warm – temperate evergreen broadleaf and mixed forests in the Pyrenees (Fig. 7B). Some palaeobotanical sites show evidence for areas of temperate deciduous broadleaf forest (Sites M76 &M106), temperate evergreen needleleaf forest (Sites M101 & M102) and temperate xerophytic shrubland (Site M94). These had MAT comparable to the warm – temperate evergreen broadleaf and mixed forests of around 15°C but with lower MAP, below 1000mm (Table 2). East of 23°E there was a mixture of warm – temperate evergreen broadleaf and mixed forests and temperate deciduous broadleaf savanna, similar to the Tortonian (Fig. 7A).

3.1.10. North Africa and the Middle-East

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

3.1.11. Equatorial Africa

Data for this region is restricted to a narrow band between 1°S and 12°N and records the changes between tropical closed and tropical open vegetation. During the Langhian the west side of the Niger Delta was dominated by tropical evergreen broadleaf forest (Site L105), whilst pollen assemblages from the Niger Delta record the existence of regional tropical savanna (Fig. 6A). In the east of this region tropical deciduous broadleaf woodland is recorded at 12°N (Site L108) and tropical evergreen broadleaf forest at 0.2°S (Site L109). South of the tropical evergreen broadleaf forest a younger site; Fort Ternan and Sondu, Kenya (Sites L110 & L111) shows evidence for tropical savanna. The Seravallian is only represented by four sites for this region which shows a vegetation pattern comparable to the Langhian (Sites S137 – S140). At Kabasuro, Kenya the MAT of the tropical evergreen broadleaf forest is estimated to be around 21.9°C (Jacobs and Kabuye, 1989; Jacobs and Deino, 1996).

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

3.1.12 Southern Africa

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

3.1.13 West Asia

During the Langhian a latitudinal south to north drying and cooling trend existed for this region. Between 41°N and 46°N a warm – temperate evergreen broadleaf and mixed forest inhabited the region, with a composition of mainly *Betula, Carpinus, Carya, Fagus, Juglans, Liquidambar, Magnolia, Quercus, Pinus* and *Zelkova* (Liu and Leopold, 1994; Sun and Zhang, 2008). North of the warm – temperate evergreen broadleaf and mixed forest at 48°N a temperate deciduous broadleaf forest was present and north of this between 56°N and 57°N temperate deciduous broadleaf savanna, with an estimated MAT of 9±1°C and a MAP of around 700mm (Gnibidenko et al., 1999) existed (Fig. 6A). The pattern is still present in the Seravallian, though the warm – temperate evergreen broadleaf and mixed forest was restricted to 41°N (Fig. 6B). By the Tortonian the warm – temperate evergreen broadleaf and mixed forests were replaced by temperate deciduous broadleaf savanna from 45°N to 57°N. From Travolzhansky, Russia (Site T206), a pollen flora shows that the temperate deciduous broadleaf savanna was composed of *Alnus, Betula, Carpinus, Carya,* Compositae, Gramineae, *Picea*, *Quercus, Tsuga* and *Ulmus* (Volkova et al., 1986). By the Messinian the region had desert at 38°N (Site M159). North of the desert, between 45°N and 53°N, there existed a region of temperate deciduous broadleaf forest and temperate deciduous broadleaf savanna (Fig. 7B). Further north at 68°N a cool-temperate mixed forest was present (Fig. 7B) containing taxa such as; *Ilex*, Juglandaceae, Myrtaceae, *Nyssa* and Taxodiaceae (Belkin, 1964).

3.1.14 Northeast Asia

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

3.1.15 Eastern Asia

During the Langhian this region was principally vegetated by the warm – temperate evergreen broadleaf and mixed forest from 21°N to 56°N (Fig. 6A). This biome contained a diverse assemblage of both gymnosperms and angiosperms including *Carya, Castanea, Corylus, Engelhardtia, Keteleeria,* *Liquidambar, Metasequoia, Pinus, Quercus, Sequoia, Taxodium* and *Zelkova* (Liu and Leopold, 1994; Kong, 2000). Climatic estimates for this biome, north of 36°N, indicate a MAT of 12±3°C and a MAP of around 1000mm (Table. 2) (Liu and Leopold, 1994; Tao, 1997; Sun et al., 2002). Along the coast between 31°N and 33°N a tropical evergreen broadleaf forest exisited (Sites L146 – L148). West of 111°E a drier region vegetated by a mixture of temperate deciduous broadleaf forest, temperate evergreen needleleaf open woodland and temperate evergreen needleleaf forest existed during the Langhian (Fig. 6A). During the Seravallian the warm – temperate evergreen broadleaf and mixed forest continued to dominate the region, between 22°N and 50°N (Fig. 6B). Tropical evergreen broadleaf forest was still present between 31°N and 33°N (Sites S168 – S170), as was the drier region west of 111°E (Fig. 6B). Drying in this region had continued from the Langhian and at 90°E a pollen assemblage from Quaidam, China (Site S149) shows that a temperate xerophytic shrubland inhabited this region from around 14 Ma.

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

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

3.1.16 The Indian subcontinent

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

3.1.17 South-east Asia

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

3.1.18 Australia and New Zealand

For the Langhian data is only available for east Australia. In the North a tropical evergreen broadleaf forest (Site L169) existed to as far south as 28°S, below 28°S a warm – temperate evergreen broadleaf and mixed forest inhabited the region (Fig. 6A). This warm – temperate evergreen broadleaf and mixed forest grew under a MAT of around 19°C and a MAP of between 1500 and 2200mm (Kershaw, 1997; Holdgate et al., 2007). New Zealand was also dominated by the warm – temperate evergreen broadleaf and mixed forest with isolated regions of drier temperate sclerophyll woodland and shrubland, during the Langhian (Fig. 6A). During the Seravallian data only exists to confirm the presence of a warm – temperate evergreen broadleaf and mixed forest in south – east Australia (Fig. 6B), growing under a climate similar to that of the Langhian (Table 2). New Zealand also shows a biome distribution comparable to that of the Langhian (Fig. 6B). By the Tortonian a dramatic drying of Australia had begun. The main biome on the continent was now the temperate sclerophyll woodland and shrubland (Fig. 7A), estimated from Lake Tay (Site T307) to have grown under a MAP of between 600 and 1500mm (Macphail, 1997). There were still isolated patches of warm – temperate evergreen broadleaf and mixed forests in the south-east of the continent (Site T312) with a MAP of at least 1500mm and areas of temperate deciduous broadleaf savanna (Site T311). Along the northeast coast a temperate evergreen needleleaf forest existed (Fig. 7A). New Zealand continued to be dominated by a warm – temperate evergreen broadleaf and mixed forest, but evidence exists to suggest cool – temperate mixed forests may have inhabited higher altitudes (Fig. 7A). During the Messinian the drying and the expansion of the temperate sclerophyll woodland and shrubland continued (Fig. 7B). No palaeobotanical data shows the existence of major areas of warm – temperate evergreen broadleaf and mixed forest during the Messinian, though this biome was still dominant on New Zealand (Fig. 7B).

3.1.19 Antarctica and the surrounding Islands

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

3.2. Latitudinal temperature gradients derived from megabiome distribution

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

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

3.2. Latitudinal temperature gradients derived from megabiome distribution

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

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

4. Discussion

4.1. Middle to Late Miocene vegetation evolution and CO_2

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

During the Langhian (15.97 – 13.65 Ma), the period of time referred to as the Mid – Miocene Climatic Optimum (MMCO) was ending. The MMCO was a significant warm interval recorded in the deep sea records (Flower and Kennett, 1994; Zachos et al., 2008). The MMCO and the Langhian also correspond to a peak in atmospheric CO_2 concentration, stomatal indices indicate atmospheric concentrations of between 460 and 564 ppmv (Kürschner et al., 2008; Beerling et al., 2009) whilst estimates from boron isotopes suggest 300 ppmv (Pearson and Palmer, 2000) and alkenone based estimates place it at a more modest 220 ppmv (Pagani et al., 2005). Although the 300 ppmv recorded in the boron isotopic record does not appear to be “high”, it does represent a peak in that particular CO_2 reconstruction. The alkenone record does not present the MMCO as a period of elevated CO_2 within the rest of the Miocene (Pagani et al., 1999). These elevated levels of CO_2, in all the records except the alkenone based reconstruction, and the warming recognised in the benthic oxygen isotope curve during the Langhian are reflected in the biome pattern; cool – temperate forests at the high northern latitudes, extensive warm – temperate evergreen broadleaf and mixed forests in the middle latitudes, a broader tropical zone and tundra on Antarctica (Fig. 6A).

During the Seravallian (13.65 – 11.61 Ma) the biome pattern is still similar to that of the Langhian however changes had occurred. The benthic oxygen isotope curve shows from about 14 to around 10 Ma either the bottom water temperature was dropping or significant land ice was developing or a combination of the two (Flower and Kennett, 1994; Zachos et al., 2008). The CO_2 proxies also record falling atmospheric concentrations to; 300 – 330 ppmv from the stomatal indices (Kürschner et al., 2008; Beerling et al., 2009); 268 – 290 ppmv from boron isotopes (Pearson and Palmer, 2000) and alkenone estimates of 194 – 252 ppmv concentration (Pagani et al., 2005). The biome distribution still shows cool – temperate mixed forest at the high northern latitudes, though not as high as it was during the Langhian. Whilst in the middle latitudes the warm-temperate evergreen broadleaf and mixed forest had begun to be replaced by drier and cooler biomes (Fig. 6B). In the tropics too, drier biomes had begun to spread and on Antarctica tundra was no longer present (Fig. 6B).

The biome pattern of the Tortonian (11.61 – 7.25 Ma) is markedly different from that of the Seravallian. In terms of the benthic oxygen isotopic record the Late Miocene shows relative stability, after the warming of the MMCO and the cooling seen in the late Langhian and Seravallian, with isotopic levels reflecting an increased (ice free) bottom water temperature range of 0 to +2°C (Zachos et al., 2008). The CO_2 reconstructions give mixed estimates of the atmospheric concentration of this greenhouse gas during the Tortonian. The stomatal indices show an increase of CO_2 from the Seravallian to 350 – 370 ppmv (Kürschner et al., 1996; Stultz et al., In Press), whilst the boron isotopes record a fall in CO_2 from the Seravallian to between 212 – 236 ppmv (Pearson and Palmer, 2000) and the alkenone based reconstructions show that CO_2 concentrations fluctuated between 190 – 330 ppmv with a general increasing trend towards the end of the Tortonian (Pagani et al., 2005; 2010). The biome pattern of the Tortonian reflects a cooler and drier world than that of the Seravallian. Cold evergreen needleleaf forests are found at the high northern latitudes for the first time during the Middle to Late Miocene (Fig. 7A). In the middle latitudes the warm – temperate evergreen broadleaf and mixed forest continued to be restricted and replaced by drier and cooler biomes (Fig. 7A). In the tropics the major change from the Seravallian was the appearance of tropical savanna in South America. The changes in biome distribution from the Seravallian to the Tortonian would appear to agree with the boron isotope reconstructed CO_2 trend more than the stomatal indices. However, the distribution of Tortonian palaeobotanical data compares best against GCM simulated vegetation that is driven by climate under higher atmospheric levels of CO_2 than both these reconstructions suggest (Micheels et al., 2007; 2009; Pound et al., 2011).

During the Messinian (7.25 – 5.33 Ma) the biome distribution was similar to that of the Tortonian. The benthic oxygen isotope records also resemble the Tortonian records, with increased amplitude between the peaks and troughs of the record (Zachos et al., 2008). CO_2 reconstructions are also comparable to the Tortonian with stomatal indices showing atmospheric concentrations of 270 – 360 ppmv (Kürschner et al., 1996), boron isotopes indicating levels of between 268 – 305 ppmv (Pearson and Palmer, 2000) and alkenone based reconstructions showing atmospheric concentrations of 230 – 360 ppmv (Pagani et al., 2005; 2010). Although biome distribution was similar to the Tortonian, during the Messinian, some important regional changes had occurred. Warm – temperate evergreen broadleaf and mixed forest was no longer present in western North America or Australia (Fig. 7B), indicating progressing aridification. Further evidence for a global drying comes from the expansion of desert in North Africa and central Asia (Fig. 7B). Again during the Messinian both the stomatal indices and boron isotope reconstructions differ. The stomatal indices show a decrease from the Tortonian whilst the boron isotopes increase. The global distribution of biomes appears to support the stomatal indices more than the boron isotope based reconstructions due to regional extinctions of warm – temperate evergreen broadleaf and mixed forests, an expansion of deserts and temperate biomes not reaching as far north (Fig. 7B)

So far the alkenone records have not been mentioned with regard to the observed changes in global biome distribution. This is because the atmospheric CO_2 levels reconstructed from alkenones show very little trend from the Langhian to the end of the Messinian. According to the alkenone based reconstructions the atmospheric concentration of CO_2 fluctuated from as low as 190 ppmv to as high as 360 ppmv (Pagani et al., 2005; 2010). This would suggest that either the alkenone based CO_2 reconstruction requires further study, or that the changes in global biome distribution were not related to changes in the atmospheric CO_2 levels. This would contradict the two other main CO_2

reconstructions, which show that the cooling and drying trend seen in the palaeobotanical record from the Langhian through to the Messinian is accompanied by falling atmospheric concentrations of CO_2 and by the pattern in the bottom water oxygen isotopes (Zachos et al., 2008).

4.2. Middle to Late Miocene latitudinal gradients

In the Langhian stage the latitudinal vegetation gradient shows a significantly flatter equator to pole vegetation gradient in both hemispheres, than pre - industrial (Fig. 8A, 9A). This, coupled with the distribution of biomes (Fig. 6A) must reflect a significantly warmer planet associated with elevated atmospheric CO_2 levels, seen in the stomatal indices and boron isotope reconstructions, associated with the end of the MMCO. The high northern latitudes had a MAT around 14°C higher than the pre – industrial (White and Ager, 1994), whilst the MAT of the temperate zone may have been around 9°C warmer than the pre – industrial (Table 2). Estimates of climate parameters from the tropics, for the Langhian, are limited at the moment but from the global distribution of tropical evergreen broadleaf forests the tropics likely occupied a greater latitudinal extent and may not have had a significantly different MAT from pre – industrial. By the Seravallian the latitudinal vegetation gradient had changed significantly in the southern hemisphere due to a global cooling and the full glaciation of Antarctica indicated by the absence of vegetation evidence and the presence of glacial deposits (Fig. 6B). The northern hemisphere gradient still reflects a significantly warmer world, whilst the latitudinal vegetation distribution of the southern hemisphere was more similar to the pre – industrial. This cooling continued into the Late Miocene and with it the latitudinal distribution of biomes continued to become more pre – industrial like (Fig. 8, 9).

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

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

4.3. Data model comparisons of the Middle and Late Miocene

The geological record is increasingly being cited as providing possible analogues to future anthropogenic driven climate change (Zeebe, 2011). Although it is hard to apply the term analogue to any period of geological time due to the dynamic nature of planet Earth, there are lessons that can be learnt about how climate changes and its longer term impacts (Haywood et al., 2011). Possibly more important than providing an “analogue to future climate change” is the geological records ability to provide test-beds to evaluate the predictive ability of GCMs (Haywood et al., 2011; Salzmann et al. 2009; Valdes, 2011).

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

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

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

5. Conclusions

The palaeobotanical changes from the Langhian to the Messinian reflect a global cooling and drying of the planet, linked to falling atmospheric CO_2 concentrations. The biome distribution of the studied 10 Ma period reflects a warmer and wetter world, when compared to the pre – industrial era.

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

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

- By the Messinian the global distribution of biomes reflects a significant cooling from the Langhian. Cold evergreen needleleaf forests occupied the high latitudes and an expanse of drier and cooler biomes had replaced much of the warm – temperate mixed forests in the middle latitudes.
- The distribution of biomes and the change in distribution through time reflects the changes in CO_2 reconstructed by the stomatal indices and boron isotopes more than the alkenone reconstruction.
- The latitudinal bioclimatic gradients show that the Langhian gradient was significantly flatter than the pre – industrial. By the Seravallian the southern hemisphere bioclimatic gradient was more modern whilst the northern hemisphere bioclimatic gradient was still flatter.
- This comprehensive biome dataset is now suitable for further palaeoclimate studies including the incorporation into and assessment of GCM simulations of the Miocene climate.
- The latitudinal bioclimatic gradients presented within this paper provide an initial view of the information the terrestrial realm maybe able to contribute to the understanding of the evolution of the latitudinal temperature gradient through time.

6. Acknowledgements

This work forms part of the first author's PhD funded by the Natural Environment Research Council (UK) and the British Geological Survey University Funding Initiative (PhD studentship NE/G523563/1). Thanks are expressed to Aisling Dolan, Luciana Genio, Wang Hao, Claire MacDonald and Marion Maury for their kind assistance in translating the literature. Such a vast data set would not have been possible without access to the John Williams Index of Palaeopalynology (JWIP) currently housed at the Natural History Museum, London. James B. Riding publishes with the approval of the Executive Director, British Geological Survey (NERC).

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Supplementary Material

The following supplementary material is available for this article:

Appendix A Location, biome code, megabiome code and reference for the palaeobotanical sites for Fig. 2 and Fig. 3

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

Figure captions

Figure 1. The pre - industrial potential natural vegetation simulated by the mechanistic vegetation model BIOME4 (Kaplan, 2001). From Salzmann et al. (2009).

Figure 2. Distribution of Langhian (A) and Seravallian (B) palaeobotanical locations. The references for the locations are listed in Appendices A and B.

Figure 3. Distribution of Tortonian (A) and Messinian (B) palaeobotanical locations. The references for the locations are listed in Appendices A and B.

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

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

Figure 6. The vegetation distribution of the Langhian (A) and Seravallian (B) from palaeobotanical data, translated into the 28 biome scheme of the BIOME4 model.

Figure 7. The vegetation distribution of the Tortonian (A) and Messinian (B) from palaeobotanical data, translated into the 28 biome scheme of the BIOME4 model.

Figure 8. West Pacific transect (WPT) of maximum poleward distribution of bioclimatic zones for the Langhian (A), Seravallian (B), Tortonian (C) and Messinian (D). 1) Ice, 2) Tundra, 3) Boreal, 4) Temperate, 5) Warm-temperate, 6) Tropical. Blue squares are pre - industrial potential natural vegetation, red squares represent poleward - most fossil evidence for that vegetation zone.

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

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

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