

New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest

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The aim of this paper is to investigate the longevity and diversity of the Amazonian rainforest and to assess its likely future. Palaeoclimate and palaeoecological records suggest that the Amazon rainforest originated in the late Cretaceous and has been a permanent feature of South America for at least the last 55 million years. The Amazon rainforest has survived the high temperatures of the Early Eocene climate optimum, the gradual Cenozoic cooling, and the drier and lower carbon dioxide levels of the Quaternary glacial periods. Two new theories for the great diversity of the Amazon rainforest are discussed – the canopy density hypothesis and the precessional-forced seasonality hypothesis. We suggest the Amazon rainforest should not be viewed as a geologically ephemeral feature of South America, but rather as a constant feature of the global Cenozoic biosphere. The forest is now, however, entering a set of climatic conditions with no past analogue. The predicted future hotter and more arid tropical climates may have a disastrous effect on the Amazon rainforest.

key words Amazon rainforest Cenozoic Quaternary precession refuge

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Introduction

Tropical rainforests display a biodiversity unmatched by any other vegetation type (e.g. Morley 2000; Willis and McElwain 2002). As such they have stimulated debates concerning both their origin as well as the cause of this unparalleled biodiversity. This paper provides an overview of the long-term history of the Amazon rainforest in the context of both plate tectonics and global climate change. The primary thesis of this study is that the Amazon rainforest has existed since the Cretaceous, and despite huge changes in the global climate, has prevailed relatively intact. This resilience also extends to the Quaternary and its characteristic glacial periods, as increasing evidence indicates the

Pleistocene refuge hypothesis to be incorrect (e.g. Mayle *et al.* 2004). Hence, the Amazon rainforest is not an ephemeral feature of South America; rather it developed during the Cretaceous and has been a permanent feature of this continent for at least the last 55 million years. However, it seems that due to human activity the Amazon rainforest is entering a period with unprecedented disruption and climatic condition with no analogue in the past. Some modelled results suggest that a significant portion of the Amazon rainforest may have turned to savanna by the mid-late twenty-first century (e.g. White *et al.* 1999; Cox *et al.* 2000).

There are a number of definitions of tropical rainforests. Evergreen to partially evergreen forests currently occur in tropical regions receiving more

than 2000 mm of rain annually with less than four consecutive months with less than 100 mm of rain, a mean monthly temperature minimum of 18°C and a small annual variation in temperature. In more broad terms tropical rainforests exist in areas which are 'frost-free', have an abundance of rainfall, and have a dry season less than 4 months long (e.g. Morley 2000; Willis and McElwain 2002). In the present climate regime these conditions only occur within the tropics. However, in earlier geological periods such conditions occurred at much higher latitudes, making 'tropical rainforest' an inappropriate term. Morley (2000) suggests the term 'megathermal moist forests' (MTMF) when discussing the longer term evolution and distribution of tropical rainforest and this together with the simpler 'rainforest' are the terms used in this paper.

Evolution of rainforest-adapted plants

The history of megathermal rainforests is inexorably linked to the history of angiosperms (flowering plants). Angiosperms are the dominant plants in the world today, accounting for between 300 and 400 families and between 250 000 and 300 000 species (Figure 1). It is believed that angiosperms first evolved in the early Cretaceous, ~140 Ma (e.g. Crane *et al.* 1995; Willis and McElwain 2002; Schneider *et al.* 2004), though an earlier origin in the late Permian–early Triassic could be possible depending on how one interprets the recent genetic data (Schneider *et al.* 2004). One interesting question is: did they evolve in the tropics? It has been suggested that angiosperms could have evolved in the mid-latitude uplands (e.g. Axelrod 1970). This might be consistent with the generally semi-arid and arid conditions of the tropical Cretaceous at a time when the middle latitudes were moist and warm (Figure 2). The currently favoured hypothesis, however, based primarily on pollen records, is that angiosperms instead evolved in the tropics (0–30°) and radiated out to colonize high latitude environments over a 30 million year period (e.g. Hickey and Doyle 1977; Barrett and Willis 2001). Based on studies integrating both pollen and macrofossil data (e.g. Lidgard and Crane 1990), five main phases of angiosperm diversification and migration have been suggested (Muller 1981; Morley 2000), with the first four all occurring during the Cretaceous. These key stages also compare well with the most recent phylogenetic reconstructions of angiosperms (Schneider *et al.* 2004).

- 1 Hauterivian to Cenomanian (136–99 Ma). Initial radiation occurred in which weeds and woody shrubs evolved in aseasonal sub-humid low latitudes while early successional vegetation spread through the low and middle latitudes. Localized occurrence of closed canopy forests may have occurred in the middle latitude convergence zones (see Figures 2 and 3). Within this period genetic evidence suggests Eudicots, Asterids and Rosids all evolved (Schneider *et al.* 2004).
- 2 Late Cenomanian (~94 Ma). Ascendancy of angiosperms over all other groups, migration to the polar regions and development of clear latitudinal zonation and increased species diversity.
- 3 Turonian to Santonian (~94–84 Ma). Widespread dispersal due to low sea level and position of tectonic plates. Development of more zonal climate and increased seasonality may have aided the evolution of new families, including a number of key rainforest representatives (e.g. Aquifoliaceae, Palmae, Myrtaceae, Sapindaceae and Zingiberaceae).
- 4 Campanian to Maastrichtian (~83–65 Ma). More zonal climate becomes established, culminating in a wet equatorial zone. Closed canopy rainforests become widespread both in the equatorial convection zone as well as at higher latitudes. Important rainforest families which evolved during this period include Caesalpinoideae, Celastraceae, Euphorbiaceae, Malvaceae, Meliaceae and Olacaceae. By 65 Ma at least 95 per cent of all angiosperm lineages had been established (Schneider *et al.* 2004).
- 5 Paleocene (65–56 Ma). The removal of giant herbivores briefly after the K/T (Cretaceous/Tertiary) boundary event may have allowed MTMF species to expand throughout much of the lower and middle latitudes (Morley 2000). Subsequent fragmentation of the continents through tectonic activity resulted in each of the different continents' rainforests following separate biogeographic trajectories through the Cenozoic.

In essence, therefore, the angiosperm lineages required to form rainforest had evolved by the late Cretaceous and definitely by the beginning of the Cenozoic. Evidence for the existence of South American MTMF during the Palaeocene is limited, but both pollen and leaf physiognomy suggest extensive and diverse MTMF in South America from the early Eocene (Burnham and Johnson 2004). The evidence discussed below suggests that the Amazon rainforest

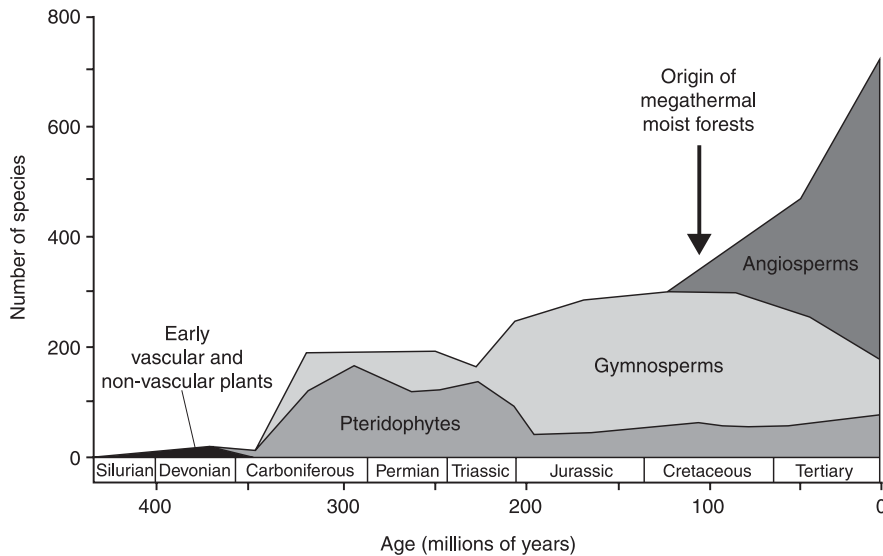


Figure 1 Evidence for the appearance and major expansion of the angiosperms in the Cretaceous. The possible origin of megathermal moist forests is indicated

Source: Adapted from Willis and McElwain (2002)

has remained essentially geographically coherent for at least the last 55 million years, forming a permanent feature of the landscape of South America, even though evolution (and therefore changes in species composition) proceeded apace throughout.

Climate controls on occurrence of megathermal moist forests

There are three main climate factors that control the distribution of different vegetation types in space and time: temperature, precipitation and atmospheric carbon dioxide (CO_2). Each factor is discussed briefly below in the context of megathermal moist forests as understanding these controls is essential if we are to comprehend the distribution of rainforests in the past.

Temperature

A simplified approach to the possible distribution of MTMF in the past with respect to temperature is to assume that it can occur within the frost-free zone. Today, the frost-free zone extends approximately 20°S to 20°N , restricting the present-day rainforest to the tropics. The position of the frost-free zone is primarily related to the current position of the continents and the relatively low atmospheric CO_2 , which result in relatively low average global

temperatures and a steep pole–equator temperature gradient (-30°C to $+30^\circ\text{C}$). However, the average temperature and latitudinal temperature gradient have varied greatly in the past (Hay 1996). In the Mid-Cretaceous, for example, the pole–equator temperature difference was half what it is today (0 to $+30^\circ\text{C}$), extending the frost-free zone to the high latitudes (Figure 3), allowing the potential expansion of MTMFs over most continents (Morley 2000). The magnitude of the pole–equator gradient is primarily controlled by tectonics (Hay 1996). First, the position of land masses over or round each of the poles can allow continental ice and sea ice to build up, as has occurred at both poles during the Neogene (see Figure 4). This ice build-up cannot occur if there is an open ocean over the poles, as ocean currents continually remove cold surface water, replacing it with warmer water from lower latitudes (Hay 1996). Second, ocean gateways play an important part in re-distributing heat around the planet. For example, the opening up of Tasmania–Antarctic Passage (~ 34 Ma) and the Drake Passage (~ 30 Ma) initiated the circum-Polar current that thermally isolated Antarctica and helped initiate its glaciation (Figure 4). The formation of ice on the continent enhances the polar albedo, causing further cooling, leading to a positive feedback on cooling via further ice formation and enhanced albedo. Not

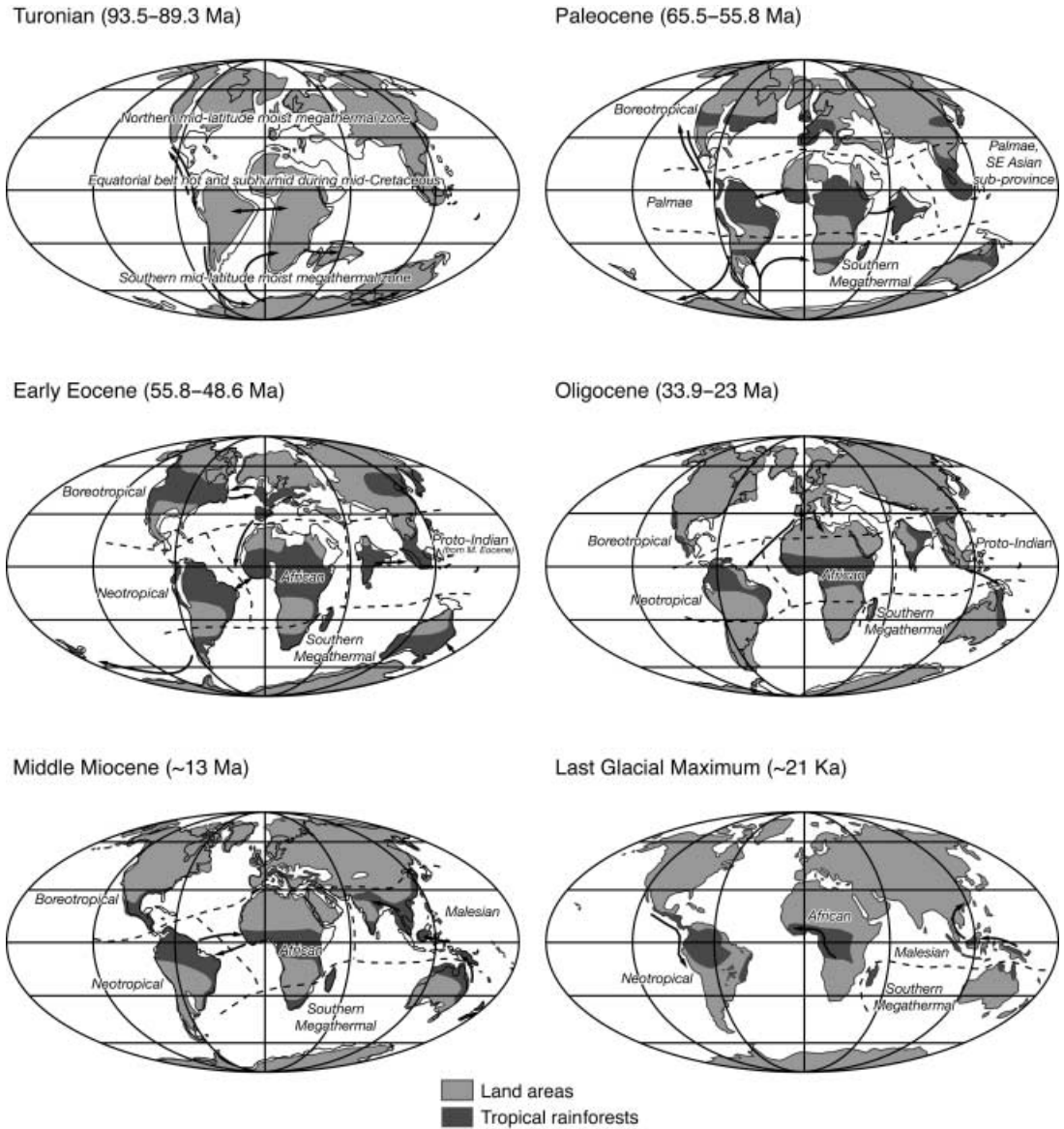


Figure 2 Reconstructions of the exposed land masses and occurrence of megathermal moist forests for six key periods. Arrows indicate possible dispersal of rainforest taxa

Source: Adapted from Morley (2000), Willis and McElwain (2002) and Cowling *et al.* (2001 2004)

only does this effect cause regional cooling, but it also results in global cooling as the planet's net energy balance is shifted. Average global temperatures have been decreasing since the Early Eocene climate optimum (~52 Ma), moving the frost-free

limits equatorward, and eventually into the tropics during much of the Pleistocene.

MTMFs also experience a temperature upper limit. During the Cenomanian, large parts of the tropics were extremely hot and experienced long

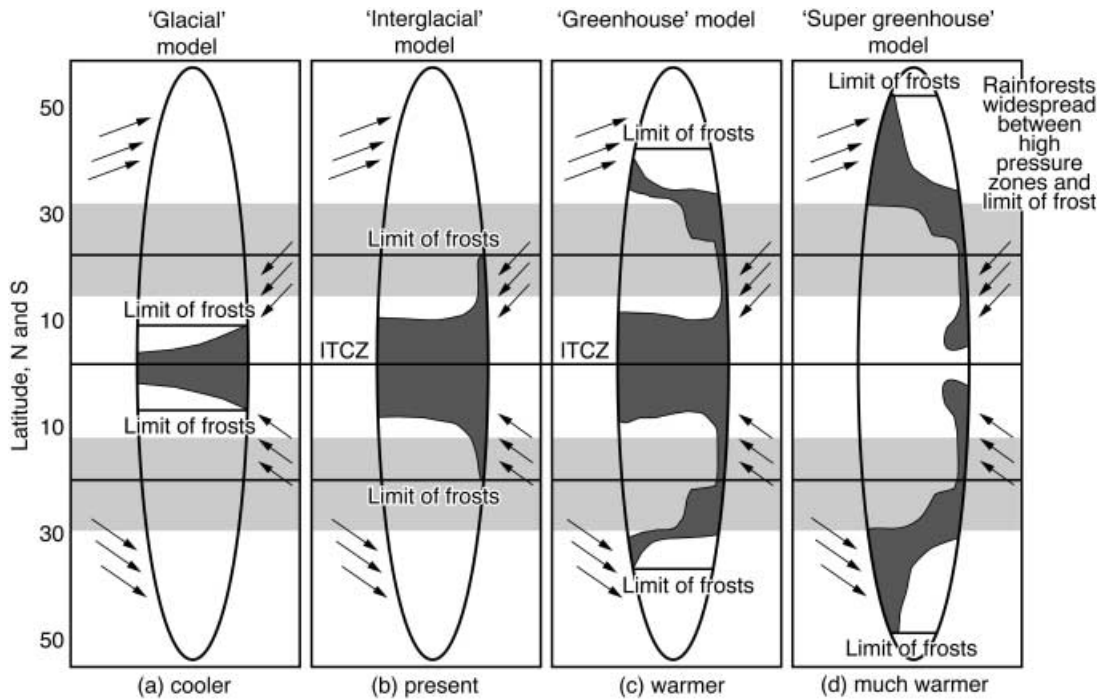


Figure 3 Reconstruction of the possible location of megathermal moist forest during four different climate scenarios. Note the importance of the low latitude ITCZ ‘easterly’ convection driven rainfall and the high latitude ‘westerly’ convergence driven rainfall and the limit of frost-free conditions

Source: Adapted from Morley (2000)

dry seasons. This was due to high global temperatures and the restricted marine influence due to the limited opening of the Atlantic Ocean (Gradstein *et al.* 2004), so limiting moisture supply, which together may have prevented the development of multi-storeyed forests (Figures 2 and 4). It is not until the Paleocene/Early Eocene that tropical temperature reduced slightly and the South Atlantic Ocean opened sufficiently to provide a warm but moist climate to the Amazon Basin. Quaternary temperatures also played another important role in the distribution of rainforest. The lower temperatures during glacial periods have been shown to mitigate the worst effects of aridity and low CO₂. Hence, Cowling *et al.* (2001) suggest the lower glacial temperatures would have allowed trees to still be competitive with grasses, possibly explaining the lack of palaeoclimatic evidence for huge excursions of savanna into the Amazon Basin during the last ice age (Mayle *et al.* 2004). This is discussed in more detail later in this paper.

Precipitation

The global climate system contains two main global regions where rainfall is high enough to support MTMFs. The first is the tropical convection zone (Barry and Chorley 1992). Intense solar radiation in the tropics heats the land and oceans, which in turns warms the lower atmosphere, causing air pressure to drop and air to rise and cool, releasing its stored water as heavy tropical rainfall. Over oceanic regions this convection is usually focused on a tight belt known as the Inter-Tropical Convergence Zone (ITCZ), which approximately girdles the equator but shifts north and south with the seasons in response to the shifting patterns of solar heating. Over continental regions the ITCZ spreads into a more diffuse convective zone, but still shifts north and south with the seasons. The north–south shift in the convection zone results in highly seasonal rainfall in much of Amazonia and thus the usual presence of at least one dry season. There is a supposition that during the Cenomanian this dry

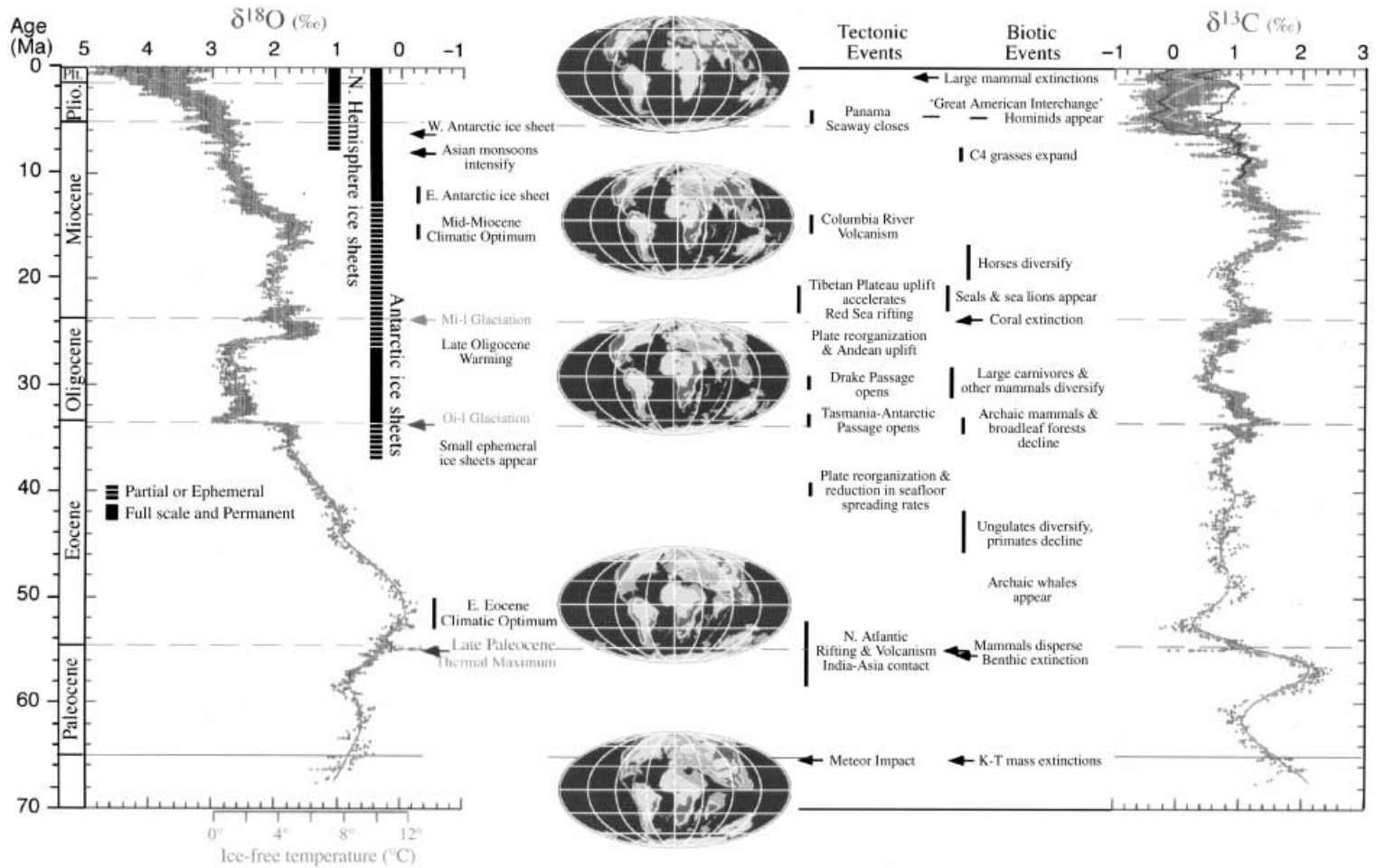


Figure 4 Summary of the major climatic, tectonic and biological events over the last 70 Ma (Zachos *et al.* 2001). The benthic foraminifera oxygen isotope record on the left hand side provides an indication of global temperature trends and also indicates the expansion of both the Antarctic and North Hemisphere ice sheets

season may have been so long, because of both high average temperatures and the restricted marine influence, that rainforests were unable to survive in the equatorial belt.

The other major global high precipitation regions are the mid-latitude convergence zones, where subtropical warm, moist air meets cold, dry polar air, producing a large amount of generally aseasonal rainfall (except at the margins). Under current global climate these convergence zones lie between 40–70°N and 40–70°S. Megathermal moist forests may therefore potentially thrive at very high latitudes within these convergence belts, as long as temperatures remain high and the region frost-free.

Another important element is the role of topography. Orographic and convergence rainfall falls on the windward side of mountain ranges, whereas rain shadows lie on the lee side. In the equatorial belt air masses generally move westward and orographic rainfall falls on the eastern side of mountains, whereas winds in the mid-latitudes generally blow eastward and orographic rainfall occurs on the westward side of a mountain range. A prime example of this is the Andes, on the western edge of the South American continent. Convergence of equatorial air masses forced by the physical barrier of the Andes enhances rainfall in western Amazonia and the eastern flank of the Andes, while orographic rainfall in the mid-latitudes (Chile) falls on the western mountain flanks and is lost rapidly to the ocean, leaving much of Patagonia fairly dry.

The position of the continents can also be very important. For example, the uplift of the Tibetan plateau approximately 20 Ma ago strengthened the SE Asian monsoons, by producing a much stronger convection site during the Northern Hemisphere summer, so pulling even more moist oceanic air across the continent.

Atmospheric carbon dioxide

The third major control on vegetation is the atmospheric concentration of CO₂ (e.g. Cowling 1999; Cowling and Sykes 1999; Levis *et al.* 1999; Cramer *et al.* 2001). This is an essential raw material for photosynthesis, and experimental studies of plants grown under double the current atmospheric levels of CO₂ show that many plants grow faster at higher concentration (e.g. Chambers and Silver 2004). CO₂ is extremely well-mixed in the atmosphere, so has very limited spatial variation at any one point in time, but the total quantity of CO₂ in the atmosphere has varied substantially in the Mesozoic and Cenozoic

(Figure 5). Reconstruction of past atmospheric CO₂ content beyond the Pleistocene ice core records is difficult but has been attempted using carbon budget models (e.g. Berner 1991 1997), fossil stomatal densities (e.g. McElwain 1998), stable carbon isotopes of organic molecules (e.g. Pagani *et al.* 1999) and boron isotopes (e.g. Pearson and Palmer 2000). The general view is that from the Late Triassic to the Early Cretaceous levels of atmospheric CO₂ were four to five times pre-industrial Holocene levels (~280 ppmV). Figure 5 shows modelled and reconstructed atmospheric CO₂ levels for the last 600 Ma. There is some limited evidence that CO₂ levels increased through the Early Cretaceous (Barron *et al.* 1994) coeval with the origin and dispersal of angio-sperms suggesting a possible link; but this is currently just a supposition. Since about 100 Ma, atmospheric CO₂ concentrations appear to have dropped, though there is considerable debate about when and how this occurred. The general consensus is that levels of CO₂ did not approach modern values until the Miocene. Up to this time levels of CO₂ were sufficient to have had little effect on the distribution of MTMFs. It is only when they drop close to or below modern levels that CO₂ is likely to become a physiological constraint on C₃ plants (Cowling and Sykes 1999). The drop in atmospheric CO₂ in the Miocene may have also permitted the evolution of C₄ metabolic pathways (Cerling *et al.* 1997), which allow effective photosynthesis at much lower levels of CO₂ (Ehleringer *et al.* 1997; Retallack 2001). CO₂ becomes an important issue when considering the extent of rainforests during glacial periods as levels of atmospheric CO₂ dropped to 200 ppmV, which would have resulted in considerable stress to plants (Cowling and Sykes 1999; Cowling *et al.* 2001).

Tectonic setting of Amazonia

South America was part of the super continent Pangaea during the Permian, the Triassic and the Jurassic. During the late Jurassic and Early Cretaceous Pangaea started to break up and Gondwana (South America, Africa, India, Antarctica, Australia) progressively became separated from the other continents (Scotese 1997; Gradstein *et al.* 2004). Since the Early Cretaceous the South American continent has drifted only slightly westward and northward. The northward drift resulted in the South America Plate separating from the Antarctic Plate in the mid-Cretaceous (Barron *et al.* 1994). However,

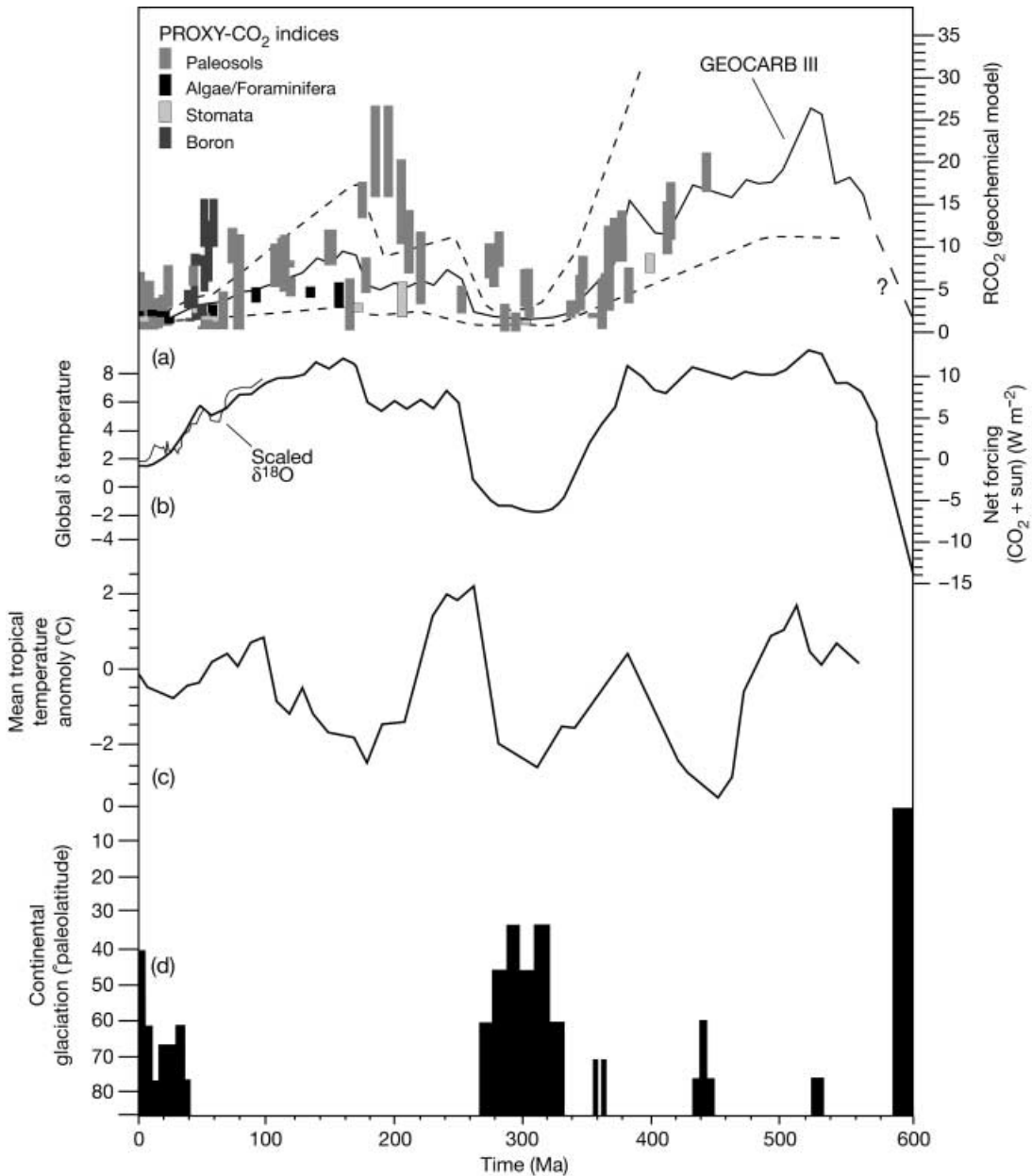


Figure 5 Reconstructions of past atmospheric CO₂ levels over the last 600 Ma using modelling, paleosols, algae and foraminifera carbon isotopes, stomata density and boron isotopes. These are compared with global temperatures, mean tropical temperature variation and the extent of continental glaciation

Source: Adapted from Crowler and Berner (2001)

some southward drift did subsequently occur, causing re-connections between Antarctica and South America throughout the Paleocene and Eocene. South America finally became separated from Antarctica

during the early Oligocene with the opening of the Drake passage and the initiation of the circum-Antarctic current (Figure 4). A significant drop in global atmospheric CO₂ concentrations and the net

loss of heat from Antarctica to the tropics due to the isolating effects of the circum-Antarctic current (DeConto and Pollard 2003) resulted in the onset of permanent glaciation on Antarctica, as demonstrated by a significant enrichment of ocean oxygen isotopes (see Figure 4).

The westward movement of the South American plate was caused by the opening of the South Atlantic during the Cretaceous, causing western South America to override the subducting Nazca (E. Pacific) Plate. This collision resulted in uplift and thus the formation of the Andean Cordillera along the whole western margin. The most intense period of uplift, especially in the northern part of the Andes, occurred during the Late Oligocene (~25 Ma). Not only has this influenced the climate of the continent but it also resulted in changing the drainage pattern of the Amazon Basin. For example, both the Orinoco and Amazon have shifted their positions in response to tectonic changes (Hoorn *et al.* 1995).

The north of the South American plate was also strongly affected by tectonic changes in the Caribbean. During the Early Cretaceous the proto-Caribbean Ocean separated North and South America. It has been postulated that there were land bridges which existed across this water way between the Campanian (84–74 Ma) and Paleocene (66–54 Ma) due to the formation of the Antillean Island Arc. This land bridge was severed after the Paleocene as the Antilles Arc moved northeast. In the Late Cretaceous the Panama–Costa Rica Arc was formed which, by the end of the Eocene, was a continuous feature but had not yet emerged and lay to the west. Through the Cenozoic this Arc has moved eastward, colliding with North and South America. This caused the closure of the Panama Isthmus, which started at about 4.8 Ma and finished about 1.8 Ma (Haug and Tiedemann 1998), producing a land bridge and the ‘Great American Interchange’ of fauna and, to a much lesser extent, flora, as Laurasian and Gondwanan elements mingled and in some cases displaced one another from their ancestral continents.

In summary, the South American plate has been in approximately the same position for the last 100 Ma, with the Amazon Basin always in the tropics. It has remained a single tectonic plate with most of its surface above sea level. For the majority of the Cenozoic, South America has been separated from both North America and Antarctica. The two dominant effects on the climate of South America during this

period have been the uplift of the Andes and changes in global climate (as summarized in Figure 4). The effects of these changes on the extent and diversity of the Amazon rainforest are discussed below.

History of the Amazon rainforest

Based on the discussion of the origins of angiosperms, the history of the Amazon rainforest can be said to have started near the end of the Cretaceous. This is because for much of the middle Cretaceous the tropics were semi-arid and it was only after the opening of the South Atlantic that more humid conditions prevailed. However, the only evidence for rainforest during the late Cretaceous and the Palaeocene is the appearance of moderately high pollen diversity (Burnham and Johnson 2004). However, Morley (2000) argues that the true start of the Amazon rainforest occurred after the K/T impact/extinction event. The meteorite impact which brought to the end the Cretaceous and the dominance of the dinosaurs may have also caused a substantial drop in diversity of fauna and flora in South America (e.g. Wolfe 1990; Morley 2000). However the K/T event did not, according to pollen and macrofossil evidence, produce a comparable mass extinction in plants (Willis and McElwain 2002). It did have a significant effect on the vegetation of both southern North America and northern South America. There is some limited evidence for a mass die-off of vegetation in these areas, initial recolonization by ferns, and then secondary succession of megathermal moist vegetation (e.g. Upchurch and Wolfe 1987). So maybe the combination of wetter climates and the removal of very large generalist herbivores (i.e. dinosaurs) allowed MTMF to spread out and develop throughout the continent (Barrett and Willis 2001). In fact it has been suggested that the small mammals and birds that replaced the herbivore dinosaurs may have enhanced this proliferation due to their greater focus on frugivory and thus seed dispersal (Morley 2000). During the Paleocene in the low latitudes, or ‘Amazonia’, the wet tropical climate may have enabled the development of a diverse MTMF vegetation, while in southern South America the vegetation consisted of a mixture of general megathermal and endemic Southern Hemisphere taxa. Especially noticeable was the considerable diversity of palms throughout both of these South American rainforests. The extent of rainforest in South America during the Paleocene is still contentious, but there

is strong agreement that by the beginning of the Eocene there was extensive rainforest throughout this whole region (Burnham and Johnson 2004).

There is some pollen and genetic evidence of rapid low latitude vegetation species turnover during the Paleocene–Eocene Thermal Maximum (PETM, ~55 Ma), when there is a documented rise in ocean temperatures of at least 5°C (Zachos *et al.* 2001). Terrestrial carbon isotope evidence from Palaeosol carbonates from Spain, China and USA indicates a much larger ¹²C-enrichment in the carbon cycle than occurred in the ocean, –6‰ compared with –3‰ (Bowen *et al.* 2004). Bowen *et al.* (2004) suggest that the difference in terrestrial and ocean records indicates a shift to a much wetter global climate during the PETM. The greatly increased temperatures and moisture availability would have made the PETM an ideal time for rainforest development and, potentially, macroevolutionary changes. Indeed, there is evidence that the occurrence of Palmae was reduced in South America, replaced by dicotyledonous angiosperms several of which have bizarre pollen types that disappear by the Middle Eocene (Morley 2000) and there are several phylogenetic lineages (Schneider *et al.* 2004), both in derived ferns (Pteridoids and Eupolypods) and angiosperms (Asterids and Rosids), which evolve coeval with PETM. MTMF continued to flourish throughout this period and tropical and paratropical rainforest extended as far south as 45°S (Figure 2). Following the PETM there is a gradual cooling throughout the Eocene. South American pollen records show continuation of palms such as *Mauritia* and primitive Palmae through the Oligocene, suggesting the terminal Eocene cooling event had a limited effect on tropical South America compared with other tropical areas (Morley 2000). In contrast, the Oligocene cooling event did have a significant effect on the southern South America MTMF, with its disappearance and the expansion of sub-humid wooded savannas. Tropical South American rainforest was unaffected by this savanna expansion until the Pliocene, when there is the first evidence of grass-dominated vegetation and open woodland expanding into parts of the tropics, particularly with the radiation of C4 grasses after ~8 Ma (Ehleringer *et al.* 1997; Retallack 2001). The significant expansion of grass-dominated savannas into tropical South America occurred about 1 Ma, but even after this savanna expansion the majority of the Amazon Basin remained covered with tropical rainforest. There is one other remnant of the once ubiquitous MTMF of

South America, which is the orographic rainfall maintained Atlantic rainforest of the Brazilian coast.

In summary, from ~65 to 34 Ma rainforest dominated much of the South American continent as far as 45°S. From 34 to 1 Ma tropical rainforest dominated the Amazon region and much of the rest of northern South America. The climate fluctuations of the last million years are dominated by the long glacial–interglacial climate cycle of approximately 100 000 years which allowed grasses to compete with trees in parts of tropical South America.

Amazon rainforest refuge hypothesis refuted?

The 'Pleistocene tropical rainforest refuge hypothesis' has been advanced as one possible explanation for both the immense diversity and species endemism of the Amazon Basin (e.g. Haffer 1969; Haffer and Prance 2001). During each glacial period, it is suggested, lower temperatures and precipitation in the tropics allowed savanna to replace the majority of the tropical rainforest (e.g. Haffer 1969; Prance 1987; van der Hammen and Absy 1994). However, some of the tropical rainforest would have survived in small refugia (Prance 1987). These isolated islands of rainforest would have become hotbeds of evolution by allopatric speciation, producing many new species. At the end of each glacial period the patchwork of rainforest merges back together with higher levels of species diversity and endemism than previously (Prance 1987; van der Hammen and Absy 1994; Haffer and Prance 2001). However, little palaeo-ecological evidence exists for this inferred massive incursion of savanna into the Amazon Basin during the last glacial period (Colinvaux and de Oliveira 2000; Mayle *et al.* 2004). Many lake pollen records show no reduction of rainforest pollen at all (Colinvaux *et al.* 1996; Bush 2002), in fact it is only at ecotonal margins that there is any evidence for savanna expansion (Mayle *et al.* 2004; Burbridge *et al.* 2004). Other evidence for a lack of savanna incursion includes the marine pollen record from the Amazon Fan that shows large changes in the concentrations of pollen over the last 45 ka but almost no variation in the amount of arboreal pollen (Haberle and Maslin 1999). These records suggest that a significant Amazon rainforest still existed during the last glacial period. This interpretation is supported by biomarker work on Amazon Fan sediments which showed a consistency of the carbon isotopic composition of organic

matter and ratios of different phenols received by the Amazon Fan throughout the last glacial–interglacial cycle (Kastner and Goñi 2003). There are two major photosynthetic pathways utilized by plants: C₃ (mainly trees and herbs) and C₄ (mainly tropical grasses) and there is a significant difference in the amount each pathway fractionates carbon isotopes. Hence the lack of variation in carbon isotopes from the Amazon Basin suggests that trees (C₃) still dominated the glacial landscape of the Amazon and there was not the predicted huge influx of tropical grasslands (C₄). Phylogenetic studies of tropical flora and fauna provide conflicting interpretations as to whether there were tropical rainforest refugia (e.g. Fjeldsa and Lovett 1997; Scheider and Moritz 1999; Moritz *et al.* 2000). Some studies, in contrast, have emphasized the greater importance of ‘savanna refuge’ in times of interglacial warming rather than forest refuge during glacial periods (Flagstad *et al.* 2001). Others (Pennington *et al.* 2004) suggest that during the glacial periods closed tropical dry forest ecosystems (i.e. trees) expanded more than savanna vegetation. The additional problem is that it is very difficult palynologically to distinguish between evergreen forest and closed-canopy semi-deciduous dry forest (Pennington *et al.* 2000; Mayle *et al.* 2004). The carbon isotope analysis also cannot distinguish between these forest types, as it only tells you whether trees or grass are present. So currently we can conclude that savanna did not take over Amazonia during the last glacial period, but we are unable to determine exactly what sort of forest existed there, though there is evidence discussed later which suggested it was significantly different.

These latter results are also broadly supported by detailed modelling work using two different types of vegetation models (Cowling *et al.* 2001 2004). Figure 6 shows the results of applying the glacial conditions on the Amazon Basin to the BIOME3 vegetation model (Cowling *et al.* 2001), suggesting a maximum 20 per cent reduction in the area of the Amazon rainforest during the last glacial maximum. Cowling *et al.* (2001) were able to demonstrate that the survival of at least 80 per cent of the Amazon rainforest during the last glacial period could be possible when allowance is given for the *interactions* of three key parameters: temperature, precipitation and atmospheric CO₂. Individually, both low precipitation and atmospheric CO₂ are detrimental to tropical C₃ rainforest and favour C₄ grasslands. However, when the temperature effects are included, many

of the detrimental effects are negated (Cowling *et al.* 2001; Cowling 2004). This is because of two processes operating in the model which should mimic how plants would have responded in reality:

- 1 the decrease in temperature reduces evapotranspirative demand and therefore increases moisture availability for carbon uptake and leaf development and
- 2 temperature decreases result in lower rates of photorespiratory carbon loss in C₃ plants (Brooks and Farquhar 1985), so enhancing carbon use efficiency of trees relative to C₄ grasses.

Allowing for the assumptions inherent in any vegetation/climate model, these results show the importance of considering the combined physiological effects of temperature, CO₂ and precipitation when evaluating the distribution of past vegetation.

Despite the inherent problems of palaeovegetation, phylogenetic and palaeomodelling reconstructions, the current consensus is that Amazon rainforest survived and even flourished during glacial periods (Mayle *et al.* 2004). The work of Cowling *et al.* (2001 2004) suggests that lower temperatures aided trees to compete successfully with grasses in the majority of the Amazon Basin by mitigating the worst effects of aridity and low atmospheric CO₂. What is uncertain is the composition of the glacial Amazon forest in terms of the balance between evergreen and semi-deciduous (partial evergreen) tropical forest.

Rainforest canopy density hypothesis

Many alternative explanations have been put forward for the large species diversity of the Amazon rainforest, and of tropical forests in general. Broadly these can be divided into evolutionary hypotheses (those related to long-term patterns of speciation and extinction) and ecological hypotheses (those that seek to explain how many species can be maintained in the face of the competitive exclusion principle, which suggests that ecosystems should be dominated by a few species). Here we focus principally on the evolutionary question of how so many species have arisen and accumulated through deep time. In addition to the Pleistocene refuge hypothesis there are other suggestions that should be considered. The tropical ‘museum’ theory suggests that a relatively stable climate through the Cenozoic resulted in low extinction rates, allowing species to accumulate over time (Stebbins 1974).

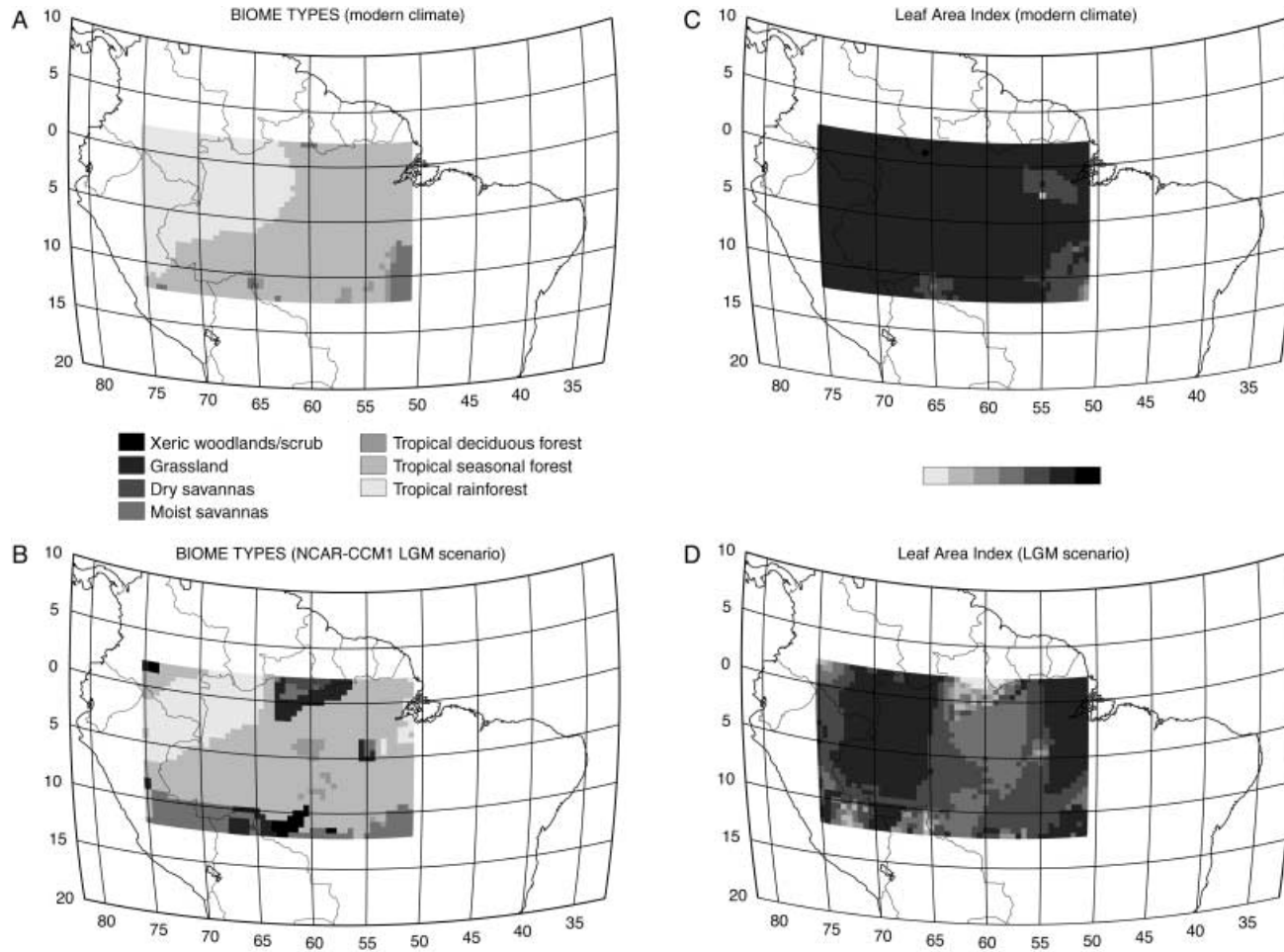


Figure 6 BIOME3 vegetation type reconstructions for both the (A) modern and (B) Last Glacial Maximum (LGM) and Leaf Area Index (LAI) reconstruction for (C) modern and the (D) LGM. Note the minor reduction in rainforest during the LGM but the significant reduction and fragmentation of the LGM LAI.

The LGM scenario uses the NCAR-CCM1 LGM climate output

Source: Adapted from Cowling *et al.* (2001)

This fell out of favour when the variability of tropical Pleistocene climates became clear. Some recent support for the tropical 'museum' hypothesis, however, has been provided by genetic divergence data showing the speciation of some rainforest animals predates the Pleistocene (Glor *et al.* 2001). The results of plant genetic divergence data of seasonally dry tropical forest are less clear-cut, showing pre-Pleistocene diversification in South America and Pleistocene speciation in Central America (Pennington *et al.* 2004). In contrast, there is strong evidence of Pleistocene diversification of *Inga*, a species-rich neotropical tree genus (Richardson *et al.* 1991). A second group of theories suggests that Amazon rainforest diversity could be due to both recent and/or ancient parapatric speciation caused by steep environmental gradients due to variations in soil, topography or latitude (e.g. Gentry 1988; Moritz *et al.* 2000; Buzas *et al.* 2002; Hillebrand 2004).

Added to this body of thought is a new allopatric speciation hypothesis (the 'canopy density hypothesis') suggested by Cowling *et al.* (2001) to replace the Pleistocene rainforest refuge hypothesis. It is suggested that both the vegetation type and structure varied during the last glacial period (Cowling *et al.* 2001; Cowling 2004). Reconstruction of modern and glacial period Leaf Area Index (LAI), a common proxy for canopy density, shows a major difference in uniformity and distribution between the two periods (see Figure 6). The modern rainforest LAI is homogeneous, with very little variation, whereas the glacial reconstruction is heterogeneous, with large variation across very small distances (Cowling 2004). This may be in part a structural response of the rainforest due to the sensitivity of the vegetation to small-scale environmental changes while climatically stressed. That there were climate-induced species-compositional changes within rainforests is undisputed. Haberle and Maslin (1999) showed significant increases in the number of Andean cold-adapted tree species in the glacial pollen record. Pennington *et al.* (2004) report an expansion of dry deciduous forest species during key periods of the Quaternary. In addition Bush *et al.* (2004) showed that though glacial and interglacial periods have compositional stability, there is a continual turnover of species. In fact they found that in the turnover of species during the 8000-year-long transition from ice age to Holocene conditions, although the changes were directional, the rates of community change were no different during this transitional period

than in the preceding 30 000-year period of relative community stability. Hence, pollen and genetic data suggest a dynamic and more varied glacial rainforest than at present. Cowling *et al.* (2001) argued that variations in canopy density could produce 'refugia'. For example, rainforest with high LAI or canopy density would imply a higher degree of specialization and diversity than forest with low LAI (see Figure 7). Both plant and animal species might have difficulty crossing between habitats, restricting gene flow between the two types of forest.

Precessional-forced seasonality hypothesis

We also present here a new additional or alternative hypothesis for the environmental driving force behind the large diversity of the Amazon rainforest. Recent studies have shown that tropical moisture availability is strongly influenced by orbital forcing (Maslin and Burns 2000; Bush *et al.* 2002; Trauth *et al.* 2003; Clement *et al.* 2004; Cruz *et al.* 2005). These studies suggest that of the three main orbital parameters, precession has the largest influence on tropical seasonality and thus rainfall. In fact work by Cruz *et al.* (2005) has shown rainfall in SE Brazil is directly controlled by precession, while modelling work by Clement *et al.* (2004) shows that precipitation changes in the tropics due to variations in precessional-forcing are of similar scale to those caused by glacial-interglacial climate changes (Figure 8).

There are two components of precession: that relating to the elliptical orbit of the Earth and that related to its axis of rotation (Maslin *et al.* 2001). The Earth's *rotational axis* moves around a full circle, or precesses every 27 ka. This is similar to the gyrations of the rotational axis of a toy spinning top. This precession causes the position of the seasons in relation to the Earth-Sun distance to change. The Earth-Sun distance is controlled by the eccentricity of the orbit, which varies from a circle to an ellipse and back again with a cyclicity of 96 ka. When the Earth orbital around the sun is not a perfect circle, the position of the seasons on the orbit directly affects their intensity. Second there is the precession of the Earth's *orbit*, i.e. the movement of the whole orbital plane around the Sun, which has a periodicity of 105 ka and changes the time of year when the Earth is closest to the Sun (perihelion). The combination of these two different precessional components results in the classically quoted

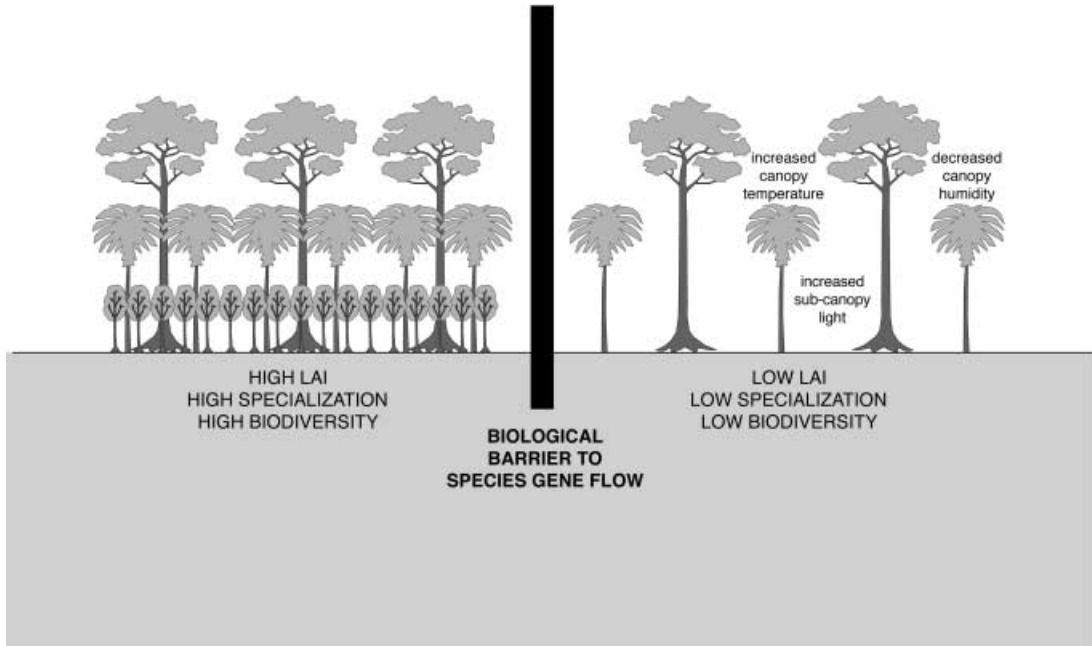
CANOPY-DENSITY HYPOTHESIS OF NEOTROPICAL ALLOPATRY:

Figure 7 Cartoon explaining the biological barrier that would generate refuge in the Canopy density hypothesis suggested by Cowling *et al.* (2001) and Cowling (2004)

precessional periodicities of 23 and 19 ka (Maslin *et al.* 2001). Combining the precession of the axis of rotation plus the precessional changes in orbit produces a period of 23 ka. Combining eccentricity (96 ka) and the precession of the axis of rotation results in a period of 19 ka. These two periodicities combine so that perihelion coincides with the summer season in each hemisphere on average every 21.7 ka, resulting in the precession of the equinoxes (Berger and Loutre 1991). Interestingly, precession has the greatest influence on the tropics. Obliquity (variations in the tilt of the Earth's axis) has no influence at the tropics and eccentricity (shape of the Earth's orbital) merely modulates the extent of the precessional influence (Berger and Loutre 1991).

Until recently it has been assumed that the relatively long periodicities of orbital forcing would mean that it could not influence evolutionary processes. However, because the variation of precession is sinusoidal, most of the variation takes place over a very short period of time. Figure 9 shows that for a randomly chosen period of time, the Sun energy

received at any given time can vary by up to 30 per cent in less than 2500 years. So since the formation of the Amazon rainforest, every 11 000 years there has been a rapid period of climate change involving a change in the annual precipitation of at least 0.5 mm/day, which is just over 180 mm/year (Clement *et al.* 2004) and a major shift in the seasonality. If this variation is then combined with the glacial–interglacial influence on tropical precipitation (Figure 8A), then these shifts can be compounded.

There is also a growing awareness of distinct climate–ecological thresholds. For example, rainforest has been shown to be unable to survive a dry season of longer than 4 months (<100 mm), whatever the rainfall is during the rest of the year (Sternberg 2001; Maslin 2004). In addition Cowling *et al.* (2001), as discussed above, has shown the sensitivity of forest structure to climate variations. So though precessional forcing at its most rapid will occur over a few thousand years, the existence of ecological thresholds may allow for extremely rapid changes in the structure and composition of the Amazon rainforest. Hence precession provides a

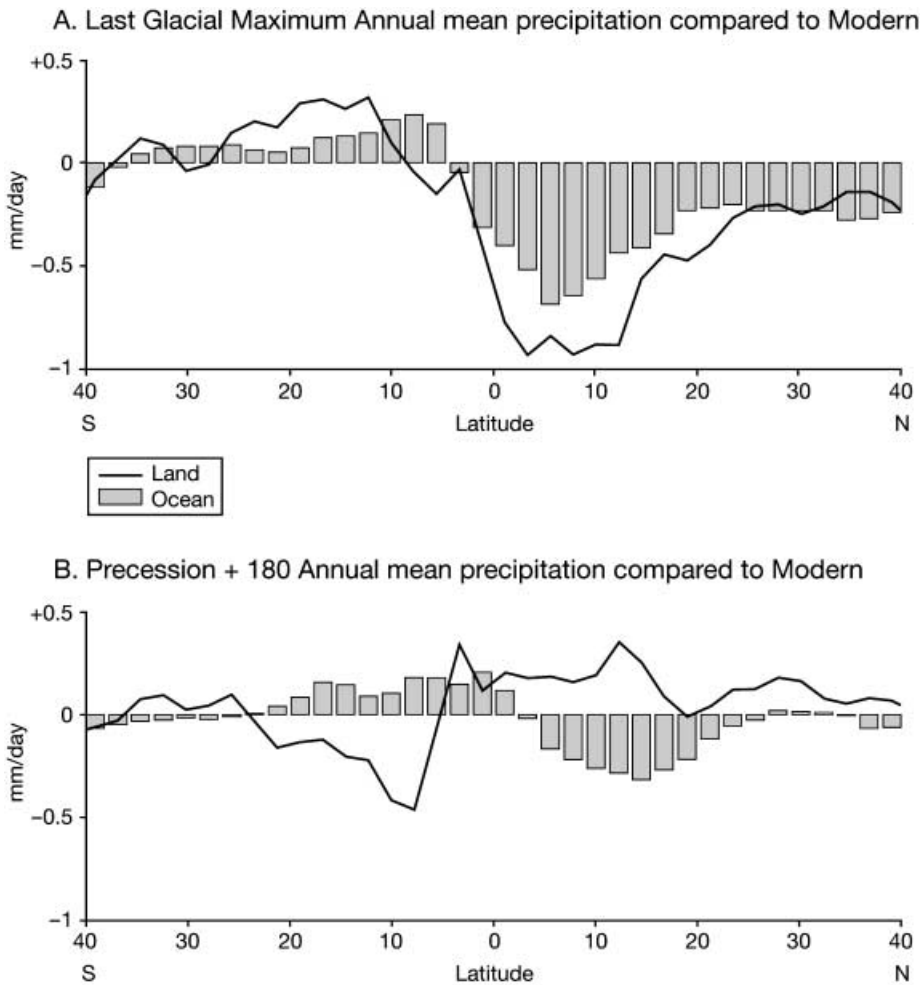


Figure 8 Modelled precipitation differences between (A) Last Glacial Maximum scenario and the present day and (B) 180° opposite precessional with modern precessional values. Note the magnitudes of precipitation shift are similar in both cases

Source: Adapted from Clement *et al.* (2004)

regular forcing which every 11 000 years significantly alters the precipitation regime over the tropics (Cruz *et al.* 2005). Because this forcing has occurred since the inception of the Amazon rainforest it could be the main driving force for rainforest evolution and the cause of its immense diversity.

Future of the Amazon rainforest

Above we have argued that the angiosperm-dominated megathermal moist forests of Amazonia have been a constant feature of the South American continent since the Cretaceous. As such, they have

played a steady role in global biogeochemistry. For example, South American MTMFs forests today account for about 20 Pg C/year of photosynthesis and respiration (Roy *et al.* 2001), accounting for about 20 per cent of terrestrial carbon cycling, and hold about 25 per cent of terrestrial biomass (Malhi *et al.* 2002a). They also have effects on regional and global hydrological cycles. For example, the deep roots permit efficient storage and recycling of precipitation back into evaporation (Kleidon and Heimann 2000), enabling the forests to continue evapotranspiration and photosynthesis during the dry season (Malhi *et al.* 2002a) and providing a

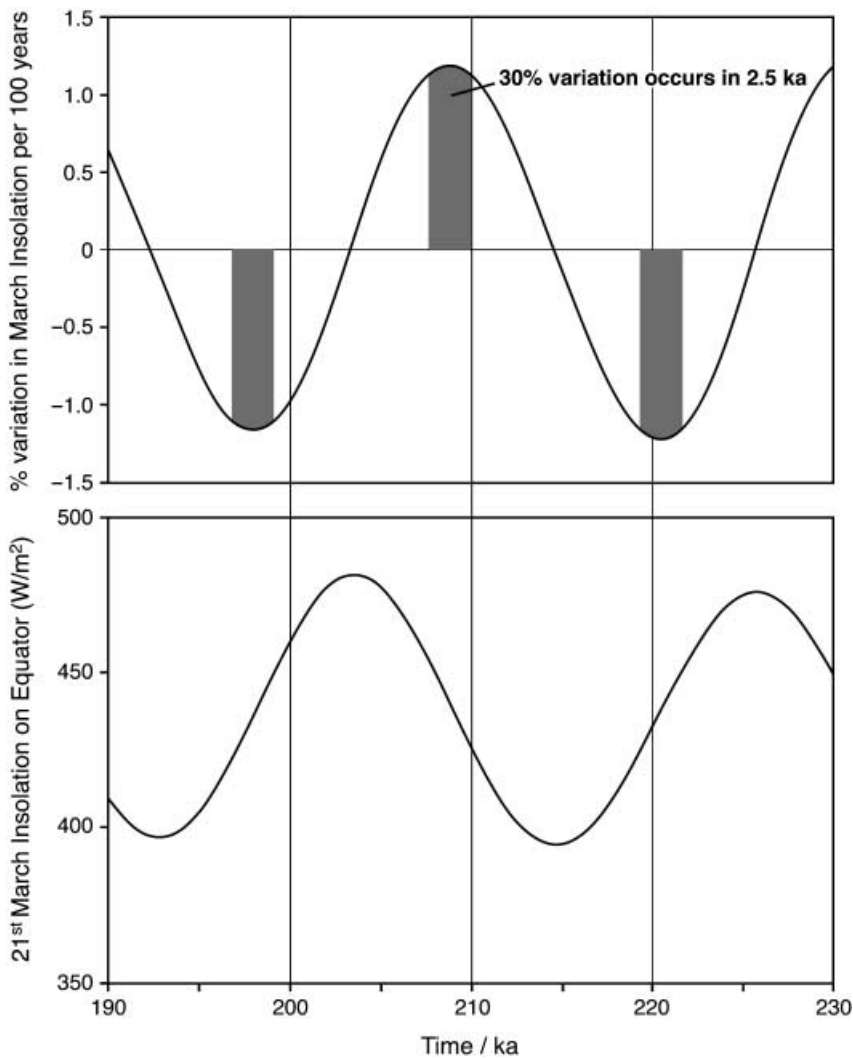


Figure 9 Bottom panel: calculated insolation for 21 March at the Equator between 190 and 230 ka (Laskar 1990) which is controlled primarily by precessional variations. Top panel calculated percentage variation in the 21 March insolation per hundred years. Note that 30 per cent of the total variation of precession occurs in less than 2500 years. So that within a single precessional cycle 60 per cent of the total variation occurs in two short periods of less than 2.5 ka approximately 11 ka apart

significant source of atmospheric moisture in this period. Approximately 50 per cent of Amazonian rainfall is estimated to derive from recycled precipitation (Salati and Nobre 1991), and hence the presence of MTMFs creates a positive hydrological feedback that favours the persistence of MTMFs. Conversely, large-scale deforestation may reduce regional rainfall and increase surface temperatures, leading to retreat of marginal MTMFs in non-

deforested areas (Laurence *et al.* 2001; Laurance 2004; Betts *et al.* 2004). The Amazon Basin is one of the major 'engines' of the global atmospheric and hydrological circulation, and changes in the hydrological regime of Amazonia may change rainfall patterns 'downstream', changing rainfall patterns in mid-latitude regions of North America and Eurasia (Gedney and Valdes 2000; Werth and Avissar 2002).

The South American MTMFs play a further role in regional and global climate through the restriction of cloud condensation nuclei (CCN) associated with smoke and dust (Andreae *et al.* 2004). Most CCN in Amazonia are biogenic products released from vegetation, and overall CCN levels are at low values more typical of oceans rather than continents, leading to the moniker 'Green Ocean' being applied to Amazonian forests (Roberts *et al.* 2001). Perhaps rather counter-intuitively, low CCN concentration encourages the formation of a few large droplets and rapid formation of raindrops in shallow, low reflectivity clouds. Conversely, the conversion of the South American atmosphere to a 'continental' atmosphere ('turning the green ocean into a brown dustbowl') leads to multiple small droplets rather than large rain droplets, deeper, fewer but more highly reflective rain clouds, enhanced convection and lightning, and uncertain changes in rainfall patterns (Roberts *et al.* 2003; Feingold *et al.* 2005). Clear changes in cloud occurrence and properties in recent decades have already been observed (Chagnon *et al.* 2004; Koren *et al.* 2004).

Finally, the South American MTMFs hold about 12 per cent of global C reserves (and 25 per cent of global vegetation biomass). The complete removal of these forests into grasslands or agriculture would cause global CO₂ concentrations to rise by about 16–36 ppm, and global mean surface temperatures by 0.1–0.3°C (House *et al.* 2002; Malhi *et al.* 2002a). The wetland areas of Amazonia produce 22 Tg/year of methane (Melack *et al.* 2004), a major greenhouse gas with an Amazon-wide global warming potential equivalent to 0.5 Pg C/year, and a sink for hydroxyl radicals that are the principle 'cleansing agents' of the atmosphere. The extent and productivity of South American MTMFs means that there are probably additional major impacts of global biogeochemistry that are as yet poorly understood or quantified (e.g. production of other volatile organics, fixation and transport of nitrogen).

Hence the South American rainforests have been one of the oldest and most influential of the present-day units of the global biosphere–atmosphere system. Yet they face the threat of almost complete disappearance within a century, with immense loss of biodiversity and poorly determined global consequences. The threat is two-fold: clearance and degradation through direct human consequences, and poorly understood threats associated with a global atmosphere and climate that is being pushed into a regime with probably no comparable past ana-

logue, with the possible exception of the Paleocene–Eocene Thermal Maximum at 55 Ma (Bowen *et al.* 2004) (see Figure 10).

The direct threat is very visible: approximate 16 per cent of Amazon forest area has been lost in the twentieth century, primarily as clearance for pasture and, more recently, soya-bean agriculture. The recent rate of deforestation of the humid South American tropics is 2500±1400 km²/year (Achard *et al.* 2002), approximately 0.38 per cent of existing forest area per year. Model simulations suggest that a proposed intensive road expansion programme in the Brazilian Amazon could stimulate 120 000–270 000 km² of additional deforestation (i.e. above the recent rate) in the next few decades (Nepstad *et al.* 2001). Away from the regions of direct deforestation there is a much wider area of degradation, such as the 'cryptic deforestation' associated with both legal and illegal logging which impoverishes 10 000–15 000 km² of forest each year (Nepstad *et al.* 1999), and declining mammal and bird populations (with associated impacts on seed dispersal) because of intensified hunting and bushmeat extraction (Robinson and Bennett 2000). It is unrealistic to oppose any form of human and economic development of the Amazon region: the challenge is to find approaches that have long-term viability and that can maintain regional biodiversity and the biogeochemical and hydrological functioning of the region that is a legacy of its long history, rather than short-term 'mining' and overexploitation that threatens to leave an environmental wasteland within the space of a century.

The indirect threat of atmospheric change is more difficult to quantify, but potentially just as grave. The most serious threat comes from possible *regional reductions in precipitation*, but these are notoriously difficult to quantify in climate change simulations. One of the admittedly more pessimistic scenarios comes from one of the more advanced ocean–atmosphere–biosphere models, the UK Hadley Centre Model, which suggests that much of eastern Amazonia is under threat of slipping into a permanent 'El Nino-like state', leading to the large-scale replacement of rainforest by savannas (Cox *et al.* 2004). A recent reanalysis by Betts *et al.* (2004) shows that 25 per cent of the simulated reduction in rainfall is caused by positive feedbacks, with dieback of forests modifying the local climate and inducing further dieback. *Changes in temperature* are more consistently predicted (Cramer *et al.* 2004) and suggest a tropical land temperature increase

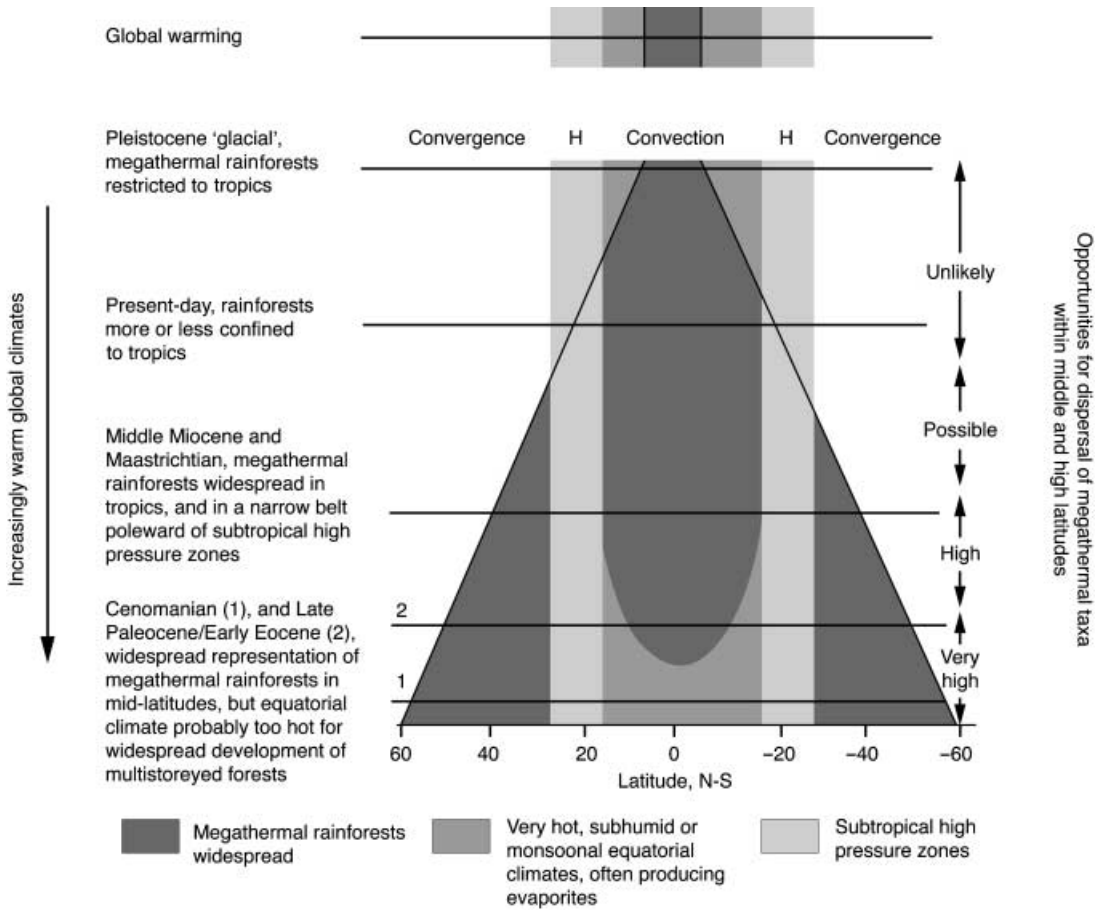


Figure 10 Summary of the changing distribution of megathermal moist forests over the last 100 Ma (adapted from Morley 2000). Top bar provides the suggested distribution of the non-analogue global warming future based on the work of Cox *et al.* (2000) and Cowling *et al.* (2004)

of between 2 and 8°C (typically 5°C), but their impacts on vegetation are less clear (Lewis *et al.* 2004). Higher temperatures may accelerate nutrient recycling and accelerate growth, but also enhance evapotranspiration and respiration. Cowling *et al.* (2004) suggest that equatorial rainforests may not be far short of an upper temperature limit, when productivity and viability will begin to decline with increasing temperature. *Changes in sunshine* associated with cloudiness or aerosol haze may also have important consequences, but it is as yet unclear whether this is increasing or decreasing over Amazonian forests (Nemani *et al.* 2003; Lewis *et al.* 2004).

Increases in atmospheric CO₂ are indisputable, and there is a general expectation that they will acceler-

ate growth, possibly increase forest biomass, and competitively favour C₃ forests over C₄ savanna grasslands. The magnitude of any such carbon fertilization effect is still disputed, however (Lloyd 1999; Lewis *et al.* 2004; Chambers and Silver 2004; Korner 2004). In-field evidence from long-term monitoring of permanent sample plots (Malhi *et al.* 2002b 2002c) suggests that Amazonian forests are accelerating substantially in both growth and mortality (thus reducing mean tree lifetime) (Phillips *et al.* 2004; Lewis *et al.* 2004), and increasing in biomass (Baker *et al.* 2004). However, any shift in the forest carbon cycle is likely to have consequences in forest ecology, and recent field studies have suggested a large increase in the abundance and

productivity of lianas (Phillips *et al.* 2002; Wright *et al.* 2004) and fast-growing canopy trees over slow-growing understorey trees (Laurance *et al.* 2004). There are suggestions that such ecological feedbacks (such as proliferation of lianas) may be more important than ecophysiological feedbacks (such as temperature effects on respiration). They are, however, even more difficult to quantify, and not included in any global change models.

In summary, the South American rainforests are today facing a suite of combined threats unprecedented in their long, long history.

Conclusions

Palaeo-climate and -ecological records suggest that the Amazon rainforest originated in the late Cretaceous and has been a permanent feature of South America for at least the last 55 million years. The geological record is a testament to the longevity and resilience of the Amazon rainforest. However, there is extreme concern about the future of the Amazon rainforest, both from the threat of deforestation and from climatic and atmospheric change (e.g. Cramer *et al.* 2004; Laurance 2004; Lewis *et al.* 2004). For example, the most extreme climate/vegetation models suggest the possible loss of half the Amazon rainforest in the next 50 years (Cox *et al.* 2000; Betts *et al.* 2000 2004; Cowling *et al.* 2004). We are entering a non-analogue future. Figure 10 shows the compression of the megathermal moist forests in response to global cooling. However, the future will clearly not simply involve a transition to warmer Miocene-type climates. This is because there are significant differences to past climates:

- 1 Despite the predicted global warming, the Pole–Equator temperature gradients are still large, and will remain relatively large this century, preventing a large shift of the frost-free zones to higher latitudes.
- 2 The speed of global warming would not allow for the large-scale movement of rainforests across the arid subtropical latitudes.
- 3 Even if migration of rainforest to the convergence rainfall zone were possible, the mid-latitudes are already dominated by human activities such as farming.
- 4 CO₂ may rise rapidly in the next 100 years to levels (>700 ppmV) without precedent during at least the last 25 and possibly 65 million years.

A better analogue for our future climate may be the Late Eocene (number 2 on Figure 10), with the possibility of widespread aridity in the tropics, but without the mitigating presence of megathermal moist forests in the high latitudes. Understanding these earlier periods of tropical aridity is essential to our understanding of future climate change. At the moment it appears that the Amazon rainforest, which has survived for 55 million years in the face of enormous global climate changes, may now risk destruction within as short a space as a century.

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