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Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests

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1.1 INTRODUCTION

The history of megathermal (currently "tropical") rainforests over the last 30 kyr is now becoming relatively well-understood, as demonstrated by the many contributions in this volume. However, our perception of their longer-term history remains highly fragmentary. There is a real need for a better understanding of rainforest history on an *evolutionary* timescale, not only to have a better idea of the biological, geological, and climatic factors which have led to the development of the most diverse ecosystem ever to have developed on planet Earth, but also since the implications of rainforest history on an evolutionary timescale are inextricably linked to a plethora of other issues currently receiving wide attention. Determining the place and time of origin and/or radiation of angiosperms (which overwhelmingly dominate present day megathermal rainforests), establishing patterns of global climate change, clarifying the nature of global temperature gradients through time, understanding the successive switching from greenhouse to icehouse climates, global warming, patterns of dispersal of megathermal plants and animals, higher rank (ordinal) taxonomy and the nature of controls on global diversity gradients are but some issues which are being clarified with the better understanding of the long-term history of megathermal rainforests.

This chapter attempts to examine climatic controls on megathermal rainforests since their first appearance in the Cretaceous Period up until the end Pliocene, a period more than 60 times longer than that considered by the other contributions in this book. The first part summarizes the pattern of initial radiation of angiosperms, and the first physiognomic evidence for closed multistratal forests during the Late Cretaceous. For the earlier Tertiary, the pattern of changing rainforest climates is viewed on a very broad scale, through the construction of rainforest maps, each representing periods of perhaps 5 Myr. These maps follow those of Morley (2000a) but have been substantially improved by integrating the comprehensive database on the global distribution of climatically sensitive lithologies (primarily evaporites, bauxites and coals) compiled by Boucot *et al.* (in press). Bauxites were given little consideration in the Morley (2000a) maps due to difficulties regarding age determination, but are critical in evaluating past megathermal climates since they are generated under hot and wet climates that are strongly seasonal. They therefore reflect the former occurrence of monsoonal climates. Boucot's comprehensive database allows bauxites to be placed within an appropriate perspective, despite difficulties of precise dating.

For the mid- and younger Tertiary, in addition to presenting generalized global maps, the approach followed allows climate change over this period to be viewed more from the perspective of the Quaternary. For the later Quaternary, radiometric dates and oxygen isotope signals provide a precise time framework within which scenarios of climate change can be established and regionally correlated. The pattern is of astronomically driven climate cycles each comprising (a) an initial period of rapid warming, followed by (b) warm, everwet climates, and (c) by a period of gradual, sometimes intermittent temperature decline with reduced moisture availability, culminating in (d) a period during which everwet tropical climates were of much more restricted distribution (Flenley, 1979; Morley, 2000a). In synchronization with climate fluctuations, global sea levels have risen and fallen following shedding from and subsequent sequestration of seawater in polar ice caps.

The precision of dating which can be applied in the younger Quaternary is rarely available for Tertiary sediments. By applying a *sequence stratigraphic* approach in the Tertiary, which is widely used in the petroleum industry, and emphasizes patterns of sediment deposition in relation to fluctuating sea levels (e.g., Wilgus *et al.*, 1988; Posamentier and Allen, 1999) by equating periods of sea level lowstand with "glacials" and highstand with "interglacials", patterns of climate change from fossil data relative to sea level change can be viewed in the same perspective as Quaternary fluctuations even where independent dating is of relatively low precision (Morley, 2000a). Such an approach is applicable for the post Middle Eocene, during which time ice accumulation has been taking place in polar areas, and most sea level changes are thought to reflect the sequestration of seawater into polar ice caps (Abreu and Anderson, 1998; Bartek *et al.*, 1991; Zachos *et al.*, 2001). Consequently, over the period from the Late Eocene to Pliocene global sea level change may be used as a proxy for global climate change. However, there remains debate about the nature of sea level fluctuations during earlier "greenhouse" phases (e.g., Hallam, 1992; Miller *et al.*, 2004).

Indications that many Tertiary sea level changes parallel periods of climate change are illustrated by palynological analyses through successive transgressive/regressive cycles, especially in areas of high rates of sedimentation, as may occur in Tertiary deltas, such as the Niger (Nigeria) or Mahakam (Indonesia). Palynological signals from such sections, albeit on a different timescale, can be compared with those seen in Late Quaternary deep-sea cores, such as the Lombok Ridge core G6-4 from Indonesia reported by van der Kaars (1991), Papalang-10 core offshore Mahakam Delta by Morley *et al.* (2004) Niger Delta core GIK 16856 by Dupont and Weinelt (1996), Amazon Fan ODP Leg 155 cores by Haberle (1997), Haberle and Malin (1998), and Hoorn (1997). The current phase of active, deep-water hydrocarbon exploration in these areas provides a rich source of (mainly unpublished) data which emphasizes periods of lowest sea levels (and coolest climate), since the main exploration targets in these settings are sands which would have been swept down the continental slope when sea levels dropped below the level of continental shelves.

1.2 DIFFERENCES BETWEEN QUATERNARY AND TERTIARY MEGATHERMAL FORESTS

Using Quaternary analogs to interpret ecological and climatic successions from the Tertiary raises two main issues; (1) was there a fundamental difference between Quaternary and Tertiary rainforests and (2) were Tertiary species compositions so different from the Quaternary as to make comparison fruitless?

With respect to the first of these issues, it is now clear that there was one major difference between Quaternary rainforests, and those from the Miocene and Early Pliocene. Over the last 2.8 Myr, equatorial climates were, at least intermittently, significantly cooler than at any time since the Oligocene, as indicated by the sudden dispersal of numerous microthermal taxa into equatorial montane forests of each rainforest block in the mid-Pliocene (Morley, 2000a, 2003; Van der Hammen and Hooghiemstra, 2000 and Figure 1.1). This also implies that pre Late Pliocene equatorial climates were a few degrees warmer than today. Quaternary rainforests in the equatorial zone are therefore likely to have exhibited greater altitudinal stratification than in the Neogene since lowland rainforests, which exhibit little internal altitudinal stratification, would have extended to higher altitudes, giving less room for montane forests. During the Early Pliocene, and most of the Miocene, microthermal taxa were essentially missing at equatorial latitudes, or so poorly represented as to go virtually unrecorded in palynological analyses. During the Oligocene, cooler climates resulted in the intermittent expansion of frost-tolerant vegetation into the equatorial zone in a manner not even seen in the Quaternary, clearly shown for the Southeast Asian region (Morley *et al.*, 2003).

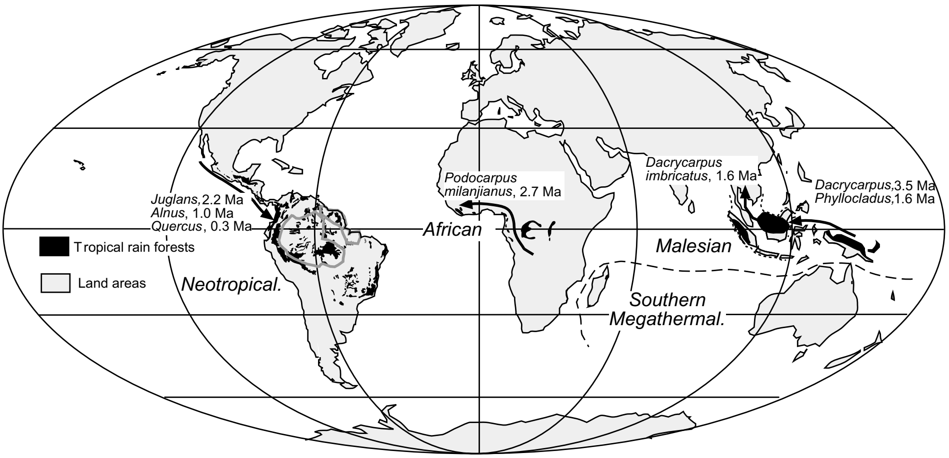

Figure 1.1. Ice-age distributions of closed canopy megathermal rainforests has been a subject of debate. The refugial hypothesis depicted substantial replacement of forest by savanna during ice ages (e.g., Whitmore and Prance, 1987) (*shaded areas*) and for Amazonia (Van der Hammen and Hooghiemstra, 2000) (*circled by gray line*; figure after Morley, 2000a). While historically important, this view of forest fragmentation has now been replaced by paleoecologically-based reconstructions that show much less change in forest cover. Also shown are noteworthy instances of Pliocene and Pleistocene dispersal directions of microthermal taxa into low latitudes.

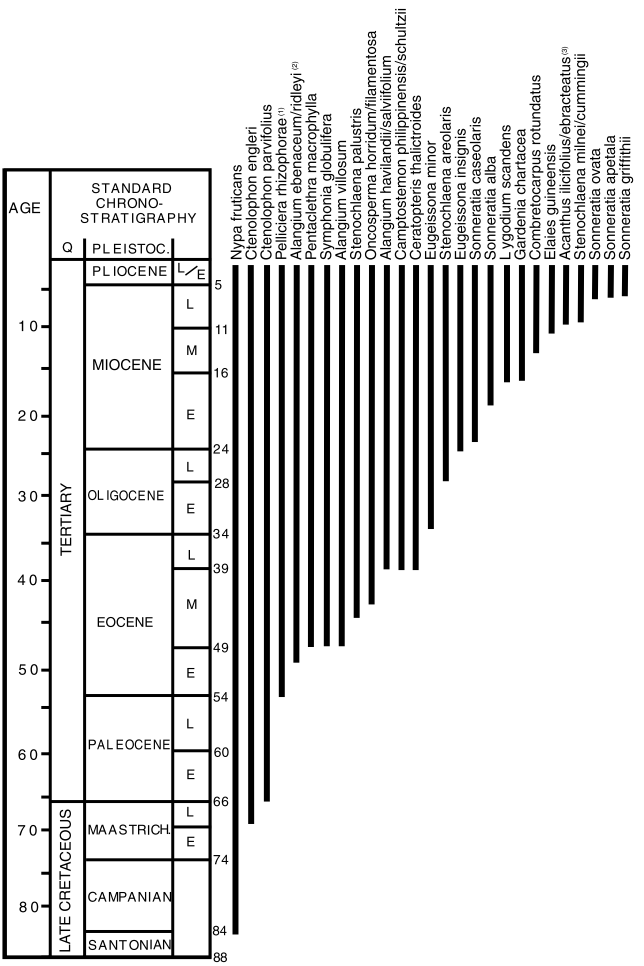

Figure 1.2. Stratigraphic range of angiosperm and pteridophyte megathermal species, or species pairs, which can be identified on the basis of pollen and spores, and have a well-defined Tertiary fossil record: (1) from Rull (1999); (2) Morley (unpublished); (3) Morley (1991); others from Morley (2000a). Age shown in Myr.

The second issue, regarding species composition, can be approached from two angles: rates of speciation, and comparison of Quaternary and Tertiary ecological successions. During the heyday of the "glacial refuge" hypothesis, the suggestion was frequently made that most of the diversity of present day rainforests was essentially a Quaternary phenomenon, with new species being generated by successive isolation and subsequent expansion of populations (Haffer, 1969; Prance, 1982). This scenario always seemed at odds with the pollen record of those megathermal *species* that can be differentiated on the basis of pollen (Figure 1.2), most of which show very long histories. It is thus comforting that this theory is now discredited on paleoecological grounds (Colinvaux *et al.*, 2000; Bennett, 2004); also, current molecular studies of rainforest trees demonstrate species longevity of the same order as the pollen record (e.g., Dick *et al.*, 2003), emphasizing that rainforests contain many species of great antiquity; Kutschera and Niklas (2004) estimate that shrubs and hardwoods have mean species durations of 27–34 Myr. With respect to comparing Quaternary and Tertiary ecological successions, the classic study of a Middle Miocene coal from Brunei (Anderson and Muller, 1975), that showed a peat swamp succession with phasic communities with close similarities to those seen in present day peat swamps (Morley, in press), demonstrates close ecological parallels between Neogene and Quaternary vegetation. There is therefore a just case for using Quaternary analogs to interpret Tertiary vegetational scenarios, particularly back as far as the Oligocene.

1.3 LATE CRETACEOUS EXPANSION OF MEGATHERMAL FORESTS

Angiosperms, which dominate megathermal rainforests today, first radiated during the Early Cretaceous from mid- to low latitudes (Crane *et al.*, 1995; Hickey and Doyle, 1977) in response to climatic stress (Stebbins, 1974; Doyle and Donaghue, 1987). They are unlikely to have become initially established in a closed, rainforest setting as previously inferred by Takhtajan (1969) and Thorne (1976) on the assumption that "primitive" angiosperms such as members of Winteraceae, *Trochodendron* and *Tetracentron* (with vesseless wood which require a mesic climate) evolved in such areas. The vesseless habit in these angiosperms is now considered a derived character (Doyle and Endress, 1997). They came to dominate over other plant groups in the Albian and Cenomanian (Crane, 1987). The equatorial zone at this time was likely to have been hot (Barron and Washington, 1985; Pearson *et al.*, 2001) and strongly monsoonal (Parrish *et al.*, 1982; Morley, 2000a), but not necessarily "semi-arid" as suggested by Herngreen and Duenas-Jimenez (1990) and Herngreen *et al.* (1996). The equatorial zone was therefore an unlikely zone for the establishment of the first megathermal, mesic forests. The paucity of mesic low-latitude settings in the Turonian is emphasized by the particularly low diversity of fern spores from the equatorial regions at this time, but their diverse representation in mid-latitudes continued (Crane and Lidgard, 1990).

It was in mid-Cretaceous mid-latitudes, which were in part characterized by perhumid, frost-free climates, that mesic forests first became an important setting for angiosperms in both hemispheres, and by the Cenomanian most of the physiognomic leaf types characteristic of megathermal forests—including simple entire leaves with drip tips, compound and palmate leaves—were already in place (Upchurch and Wolfe, 1987). From the Turonian to the Maastrichtian, many groups that we consider as strictly "tropical" have their first records from these areas, with families such as Bombacaceae, Clusiaceae, Cunoniaceae, Icacinaceae, Menispermaceae, Rutaceae, Sabiaceae, Saurauiaceae, Theaceae, and Zingiberaceae (Mai, 1991; Morley, 2000a; Davis *et al.*, 2005) first appearing within northern hemisphere mid-latitudes, whereas southern hemisphere mid-latitudes saw the appearance of Aquifoliaceae and Proteaceae, and became a harbour for Winteraceae and Chloranthaceae (Dettmann, 1994).

Within the equatorial zone, mesic angiosperm-dominated forests did not appear until some time after their appearance in mid-latitudes (Morley, 2000a). The first evidence for the development of everwet equatorial climates is probably from Nigeria, where coal deposits are represented from the Campanian to Maastrichtian (Reyment, 1965; Salami, 1991; Mebradu *et al.*, 1986), suggesting an everwet climate. Groups that show their initial radiation in the Cretaceous of the equatorial zone are Annonaceae, Arecaceae, Ctenolophonaceae, Gunneraceae, Fabaceae, Myrtaceae, Restionaceae, and Sapindaceae (Morley, 2000a).

Molecular studies sometimes help to determine which taxonomic groups originated as Northern Megathermal (or Boreotropical) elements, and which have always been equatorial lineages; thus, Davis *et al.* (2002) indicate that Malphigiaceae are likely to be Boreotropical. Doyle and Le Thomas (1997) show that Anonaceae are an equatorial group, as did Givnish *et al.* (2000) for Rapataceae. However, care needs to be exercised in assessing the often geographically biased and scattered fossil record of groups being assessed by molecular analyses since the macrofossil record is strongly biased to Europe and North America where most collecting has been done (Morley and Dick, 2003).

The biogeographical histories of the major groups of megathermal angiosperms for the remainder of the Cretaceous and Tertiary periods can be divided into two main phases. During the first phase, from the latest Cretaceous to Middle Eocene, the Earth was characterized by greenhouse climates, and predominantly by plate tectonic disassembly (Morley, 2000a, 2003). This was a period of widespread range expansion and diversification of megathermal plants. The post-Middle Eocene, on the other hand, was a period essentially of global cooling and the successive expansion of icehouse climates, coupled with plate tectonic collision, and was mainly a period of range retraction of megathermal taxa.

The time from which mesic megathermal forests can be visualized as closed, multistoreyed forests, and thus resemble modern rainforests in terms of physiognomy, is debatable. Upchurch and Wolfe (1987) suggested that leaf morphologies from the Cenomanian Dakota Formation reflect such a setting, but at this time angiosperm wood fossils are generally small-dimensioned, and seed sizes small (Wing and Tiffney, 1987), militating against the presence of modern aspect rainforests at this time. A re-examination of leaf assemblages from the same Dakota Formation locality by Johnson (2003, and pers. commun.) show that this locality was dominated by large, lobed angiosperm leaves, not reminiscent of rainforest physiognomy. However, Davis *et al.* (2005) have used molecular evidence to show that the clade Malpighiales, which constitute a large percentage of species in the shaded, shrub and small-tree layer in tropical rainforests worldwide, radiated rapidly in the Albian–Cenomanian, and suggest that this radiation was a response to adaptations to survive and reproduce under a closed forest canopy.

The first evidence for typical closed, multi-stratal forest synusiae based on fossils comes from the latest Cretaceous of Senegal and Nigeria in West Africa. Evidence includes the presence of casts of large seeds from the Campanian of Senegal (Monteillet and Lappartient, 1981), a large supply of endosperm in an enlarged seed allowing successful germination under a forest canopy (Grime, 1979). A molecular link between life form and seed size has recently been established (Moles *et al.*, 2005) with large seeds being linked with tropical trees. The presence of seeds or fruit attributable to climbers from Nigeria (Chesters, 1955) and the presence of large-girth angiosperm wood (Duperon-Ladouneix, 1991) also suggests the presence of tall canopy trees. The oldest locality for multi-storeyed forests is therefore likely to have been in the

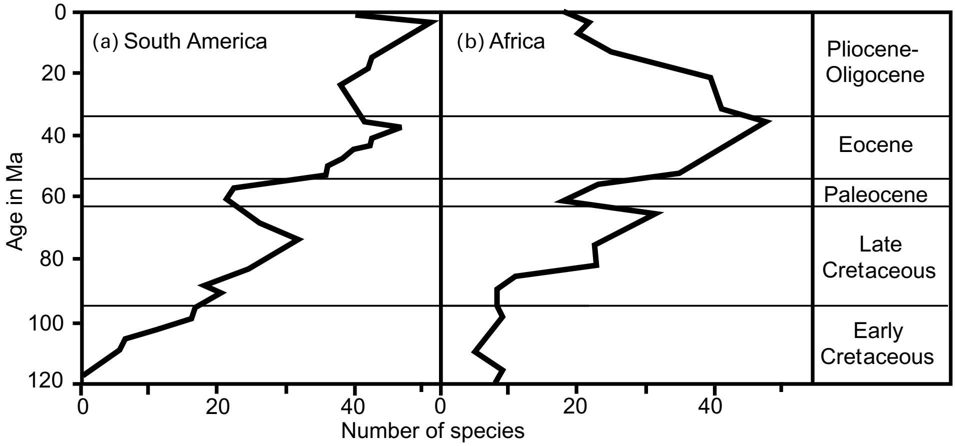

Figure 1.3. Numbers of stratigraphically useful angiosperm pollen types per epoch, for: (a) South America (data from Muller *et al.*, 1987) and (b) West Africa (data from Salard-Chebaldaeff, 1990), providing a rough proxy for angiosperm diversity through time (from Morley, 2000a).

equatorial zone. Subsequently, large-dimensioned seeds are widespread from the Paleocene onward in North America (Wing and Tiffney, 1987) suggesting that following the demise of the dinosaurs, closed multi-storeyed forests became widespread, perhaps coinciding with the radiation of frugiverous mammals. The appearance of evidence for multi-storeyed forests in West Africa coincides with a distinct diversity increase of fossil angiosperm pollen (Figure 1.3, from Morley, 2000a), which was thought to reflect evolutionary adaptations associated with the development of the forest canopy by Niklas *et al.* (1980).

Kubitski (2005) considers the development of the rainforest canopy in the Late Cretaceous of Africa and South America to be one of the major stages in the development of all land plants. The presence of the rainforest canopy not only facilitated the diversification of most angiosperm families in a manner not seen previously, but also provided a setting for the renewed diversification of pteridophytes, under its shadow, as suggested both from molecular data (Schneider *et al.*, 2004), and also from changes in pteridophyte spore assemblages in the low-latitude palynological record from the latest Cretaceous onward, with the increased representation and diversification of monolete, as opposed to trilete spores from this time.

The K-T meteorite impact probably had a major effect on rainforests globally (Figure 1.3) but did not substantially affect the main angiosperm *lineages* that characterized each area. Gymnosperms, however, fared particularly poorly in the low latitudes following the K-T event. In the earliest Tertiary gymnosperms were virtually absent from each of the equatorial rainforest blocks. Recovery of rainforest diversity after the K-T event is generally acknowledged to have taken some 10 Myr (Fredriksen, 1994), but a recently discovered leaf fossil flora from the Paleocene of Colorado (Johnson and Ellis, 2002) suggests much more rapid recovery, perhaps within 1.4 Myr, suggesting that much more work needs to be done to determine just how long it takes for rainforests to re-establish their diversity after a cataclysmic event.

1.4 MEGATHERMAL RAINFORESTS DURING THE EARLY TERTIARY PERIOD OF GREENHOUSE CLIMATE

At the beginning of the Tertiary, megathermal rainforests were thus established in three parallel latitudinal zones (Figure 1.4). In the northern hemisphere, Northern Megathermal (termed "Boreotropical" in Morley, 2000a) mesic and monsoonal forests extended from North America and Europe, to East Asia, Southern Megathermal forests were present in mid-latitude South America, Australasia and southern Africa, and equatorial forests of the Palmae province were well-developed in northern South America, Africa, India and probably Southeast Asia (Morley, 2000a). The Paleocene saw global temperatures rise dramatically (Figure 1.5), due to increased atmospheric CO_2 (Pearson and Palmer, 2000). At the Paleocene–Eocene boundary, megathermal forests were thus at their most extensive (Figure 1.6), more or less reaching the polar regions, as far as 60°N in Alaska (Wolfe, 1985), and with *Nypa* swamps at 57°S in Tasmania (Pole and McPhail, 1996). At this time, intermittent land connections from North America to Europe via Greenland, from South America to Australasia via Antarctica and with a filter dispersal route between the Americas (Hallam, 1994; Morley, 2003) megathermal plants were able to disperse globally in a manner seen at

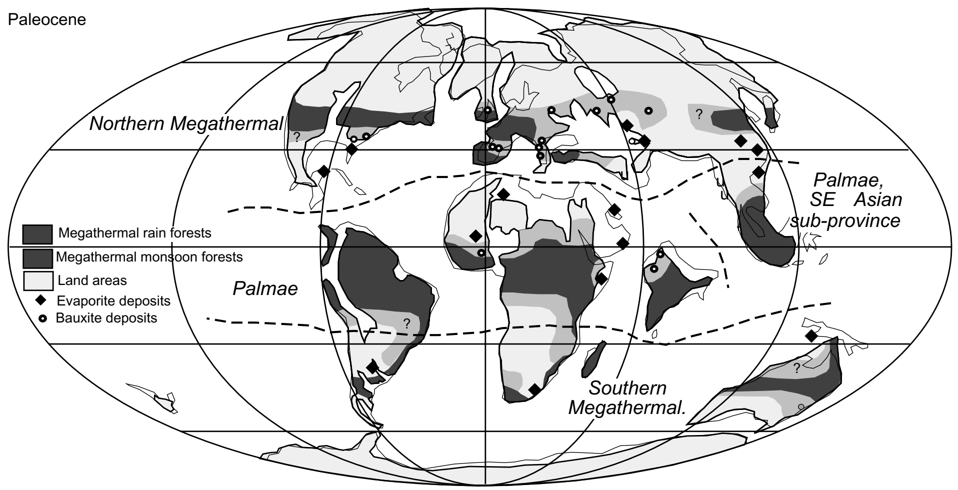

Figure 1.4. Closed canopy megathermal rainforests first became widespread during the Paleocene (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

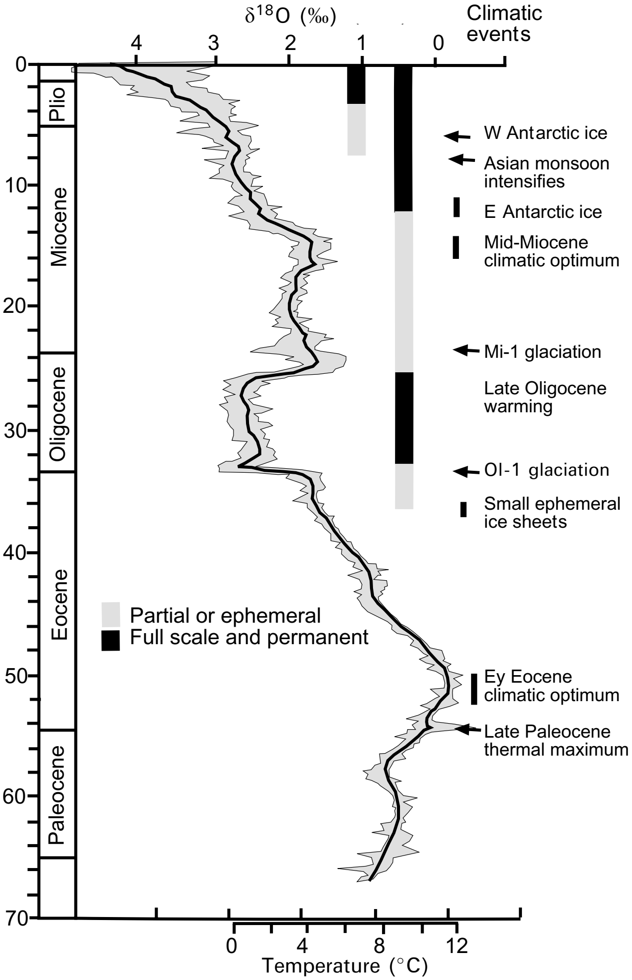

Figure 1.5. Generalised oxygen isotope curve for benthonic (bottom dwelling) foraminifera through the Cenozoic (from Zachos *et al.*, 2001). The ratio of ^{16}O to ^{18}O for benthonic foraminifera provides a proxy for high-latitude surface marine temperatures (Hudson and Anderson, 1989), and therefore is a guide to global temperature trends: Oi = glacial interval at beginning of Oligocene; Mi = glacial at beginning of Miocene. The temperature scale was computed for an ice-free ocean, and thus applies only to the pre-Oligocene period of greenhouse climates.

no other time—with, for instance, members of the family Bombacaceae spreading from North America to Europe, on the one hand, and via South America and presumably Antarctica to Australia and New Zealand, on the other (Morley, 2000a; 2003). In the Middle and Late Eocene, subsequent to the thermal maximum, climate oscillations resulted in the successive expansion and contraction of megathermal forests in mid-latitudes, as recorded for North America by Wolfe (1977).

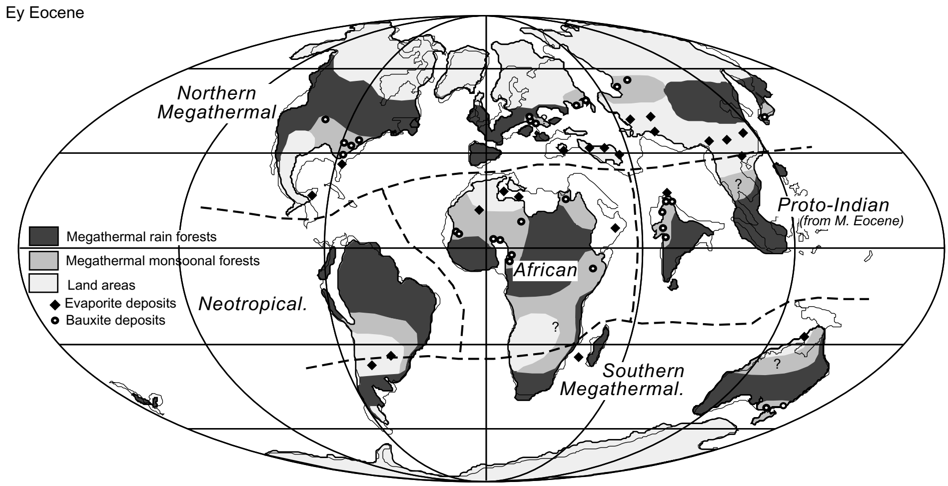

Figure 1.6. Distribution of closed canopy megathermal rainforests during the Late Paleocene/Early Eocene thermal maximum (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

The nature of the vegetation that characterized mid-latitudes at the time of the thermal maximum has been widely studied, with classic fossil localities in Europe, such as the London Clay (e.g., Reid and Chandler, 1933; Chandler, 1964; Collinson, 1983) and Messel in Germany (Collinson, 1988), North America (Wolfe, 1977; Manchester, 1994, 1999), South America (Wilf *et al.*, 2003) and Australia (Christophel, 1994; Greenwood, 1994), but the character of equatorial vegetation at the time of the thermal maximum remains unclear. There has been some discussion as to whether mid-latitude areas experienced a "tropical" climate at this time (Daley, 1972; Martin, 1992). Most authors logically conclude that climates at this time were different from any present day climates. The critical factors were lack of frosts and absence of a water deficit. Summer-wet climates in Indochina and Mexico are probably the closest modern analogs, not surprisingly, in areas where many Boreotropical elements are relict (Morley, 2000a, Figure 11.9).

Very few studies demonstrating ecological succession from low latitudes from this critical period of the Paleocene–Eocene thermal maximum have been published. Reference has been made to "reduced global climate gradients" based on oxygen isotope analysis of calcareous foraminiferal tests (e.g., Shackleton and Boersma, 1983), but current evidence shows that low-temperature estimates from the equatorial zone are erroneous and due to diagenetic effects. Recent sea surface estimates based on very well-preserved microfossils from the equatorial zone suggest Eocene sea surface temperatures were at least 28–32°C (Pearson *et al.*, 2001; Zachos *et al.*, 2003). Evidence from paleofloras suggests that there was a marked vegetational zonation from the equator to mid-latitudes (Morley, 2000a)—for instance, equatorial and South Africa were characterized by very different floras at this time, indicating a climatic zonation from mid- to low latitudes and current Eocene sea surface estimates are in line with those expected by modelling climates from vegetational data.

A study of the palynological succession through the Venezuelan Guasare, Mirador and Misoa formations by Rull (1999) provides a glimpse of the evolutionary and ecological changes that characterized the Late Paleocene to Early Eocene thermal maximum onset in northern South America. A conspicuous ecological change took place at the Paleocene–Eocene boundary. The Late Paleocene flora is similar to other low-latitude pollen floras of similar age, such as that from Pakistan (Frederiksen, 1994), emphasizing its pantropical character, whereas the Early Eocene palynoflora is geographically more differentiated, owing to a high proportion of restricted elements caused by the extinction of Paleocene taxa and the incoming of new components. The incoming of new Eocene taxa was gradual (or possibly stepped), and diversities increase in a manner that parallels global temperature estimates. At a detailed level several palynocycles could be defined, both in terms of assemblage and diversity changes, suggesting cyclic forcing mechanisms controlling vegetation changes. This study clearly suggests that vegetation change at low latitudes at the beginning of the thermal maximum was as pronounced as at mid-latitudes. A substantial temperature increase most likely accounted for the vegetation change recorded.

Some recent studies suggest that Early and Middle Eocene low-latitude climates were moisture-deficient or strongly seasonal in some areas. A well-dated Middle Eocene leaf flora from Tanzania, about 15°S paleolatitude, suggests the presence of wooded, rather than forest vegetation with near-modern precipitation estimates for this area (Jacobs and Heerenden, 2004). The plant community was dominated by caesalpinoid legumes and was physiognomically comparable to miombo woodland. Data from a very thick Early and Middle Eocene succession from southwest Sulawesi in Indonesia indicates alternating phases of dry climate (possibly reflecting periods of low sea level), in which Restionaceae were prominent members, and wetter climate, dominated by palms (Morley, unpublished).

1.5 MIDDLE EOCENE TO OLIGOCENE CLIMATES

1.5.1 General trends

From the Middle Eocene through to Late Eocene global climates show an overall cooling, with a further rapid temperature decline at the end of the Eocene (Miller *et al.*, 1987; Zachos *et al.*, 2001) following which mid-latitude northern hemisphere climates mostly became too cold to support megathermal vegetation. The decline in global temperatures is associated with a major build-up of polar ice, initially over Antarctica; and consequently sea levels fell globally, especially during the Oligocene.

With cooler temperatures in mid-latitudes, megathermal rainforests underwent a major retraction to low latitudes (Figure 1.7). This retraction was particularly pronounced in the northern hemisphere, with megathermal forests virtually disappearing from most of the North American continent (Wolfe, 1985) and becoming much more restricted in Europe, some elements possibly being maintained along the Atlantic

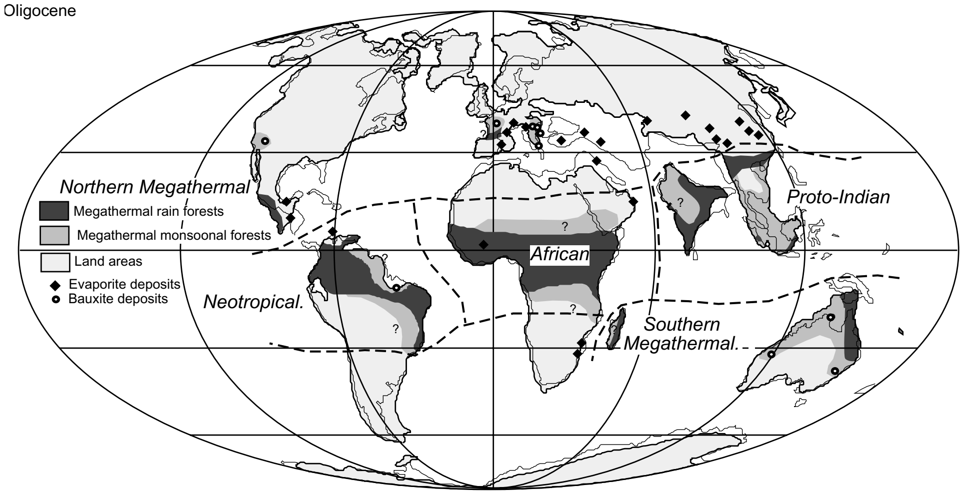

Figure 1.7. Distribution of closed canopy megathermal rainforests during the Oligocene, following the terminal Eocene cooling event (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

coast as a result of warm currents. Northern hemisphere megathermal forest species had to disperse equatorward or face extinction. Their success at southward dispersal was related to the different tectonic setting in each of the three main areas. Because there was a continuous land connection from East Asia to the equatorial zone, many Boreotropical elements were able to find refuge in the forests of Southeast Asia. The Boreotropical relicts included many so-called primitive angiosperms, and as a result there is a concentration of such taxa in that area, especially in the rainforest refugia of southern China and Vietnam (e.g., Magnoliaceae, *Trochodendron*). This area has also provided a refuge for many Boreotropical gymnosperms, such as *Cunninghamia*, *Glyptostrobus*, and *Metasequoia*.

With respect to North America, Northern Megathermal elements may have been able to find refuge along the southern margin of the North American Plate, but could not disperse to the equatorial zone until the formation of the Isthmus of Panama in the Pliocene (Burnham and Graham, 1999). As a result, many more Northern Megathermal elements are likely to have become extinct in the Americas than in Southeast Asia. Many of those that did survive, and have parallel occurrences in Southeast Asian forests, are now extant as the amphi-Pacific element of van Steenis (1962).

For Europe, the east–west barriers of Tethys, the Alps, and the Sahara combined to limit equatorward dispersal to Africa to just a few taxa; hence, there are barely any true Northern Megathermal elements in present day African rainforests (Tiffney, 1985; Morley, 2001).

In the southern hemisphere, the end Eocene cooling event had a negative impact on the Southern Megathermal forests of South Africa and southern South America. However, the northward drift of the Australian Plate at the time of the period of major mid-Tertiary climate decline, allowed most Australian Southern Megathermal elements to survive this event. Today, the concentration of primitive angiosperm elements in the rainforests of northeast Australia is testament to reduced Australasian climate stress during the period of mid-Tertiary global cooling. The isolation of Australia and associated continental fragments has resulted in opportunities for many primitive elements to survive in this area compared with elsewhere. The concentration of primitive angiosperms in the area from "Assam to Fiji", which Takhtajan (1969) termed his "cradle of the angiosperms", has nothing to do with angiosperm origins, but is the response of these groups to finding refugia in a tectonically active global plate-tectonic setting during the period of mid- to Late Tertiary climate decline.

1.5.2 Climate change in low latitudes

Coinciding with the end Eocene cooling event, low-latitude climates also changed substantially, becoming significantly cooler and drier. This was particularly the case in Southeast Asia, where both palynological and lithological evidence suggests that everwet climates became of very limited extent, except, perhaps in the areas of Assam and Myanmar, where Oligocene coals yield rainforest leaf floras (Awasthi and Mehrota, 1995). There may also have been small refugia in other areas, such as the southeast margin of Sundaland (Morley, unpublished). The terminal Eocene event resulted in numerous extinctions across the tropics—for example, of *Nypa* from Africa and South America (Germeraad *et al.*, 1968). However, the impact of this event was probably felt less in South America than other areas, since several taxa persisted there into the Neogene, such as mauritioid and other palm lineages. In general, equatorial floras began to take on an increasingly modern aspect during the course of the Oligocene.

A detailed pattern of climate change for the Oligocene is forthcoming from the Indonesian West Natuna Basin, which contains thick deposits of latest Eocene to Oligocene freshwater lacustrine and brackish lagoonal, followed by Neogene paralic, deposits that yield a rich palynomorph succession (Morley *et al.*, 2003). Sediments were sourced primarily from the paleo Chao Phraya/Pahang catchments (Figure 1.8) and pollen data probably reflect vegetation change on a catchment rather than local scale. The latest Eocene and earlier Oligocene are characterized by pollen assemblages rich in Gramineae and with the very limited representation of "wet climate" elements, such as pollen of peat swamp trees, suggesting a warm, but seasonally dry climate (Figure 1.9). However, the mid- and Late Oligocene contains four maxima of temperate gymnosperms, which include *Abies*, *Picea*, and *Tsuga*, associated with *Alnus*, and also with *Pinus* and Poaceae (seasonal climate elements) and some pollen of rainforest taxa, followed by acmes with rainforest elements correlating with periods of higher relative sea level. These assemblages suggest alternating cool, seasonal, followed by warm, seasonal climates. The maxima of temperate gymnosperms suggest that cool climate oscillations brought freezing temperatures to tropical mountains, and consequently relatively cool lowland climates must also have been present.

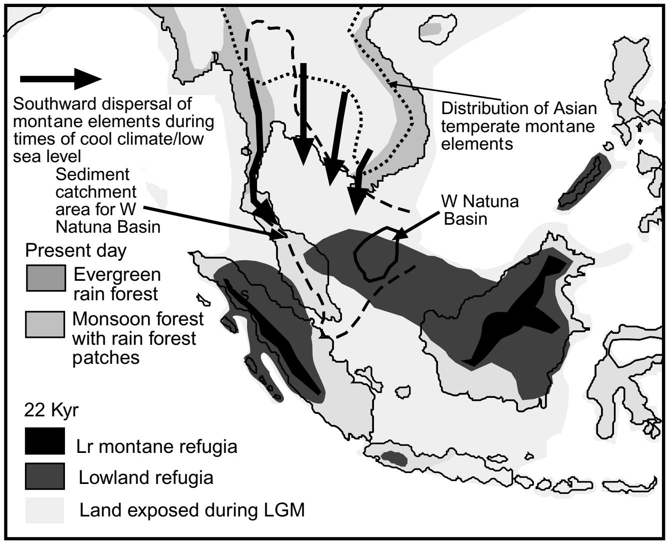

Figure 1.8. Present day distribution of megathermal (and tropical) rainforests in Southeast Asia, and probable distribution at c. 22 cal. yr BP showing positions of rainforest refugia. The shoreline at c. 22 cal. yr BP is also shown, together with the position of the catchment that fed the Malay/West Natuna Basins, and Natuna Basin, modified from Morley (2000a) using current palynological data (especially Morley *et al.*, 2004), and taking account of the mammalian data of Meijaard (2003) and Bornean generic diversity data of Slik *et al.* (2003).

Previously, the high representation of montane gymnosperms in the Southeast Asian area has been interpreted as reflecting a source from high mountains (Muller, 1966, 1972), but geological data suggest an inverse relationship between phases of mountain building and the general abundance of temperate elements (Morley, 2000b), emphasizing that most abundance variation within montane gymnosperms is climatic. The four cool climate intervals in Natuna coincide roughly, but not precisely, with the Oligocene cooler climate episode indicated from benthic isotope data (Miller *et al.*, 1987; Zachos *et al.*, 2001), and can be approximately tied to positive oxygen isotope excursions in the high-resolution oxygen isotope curve of Abreu and Anderson (1998).

Grass pollen also shows a series of maxima through the Oligocene of West Africa (Morley, 2000a, p. 140), reflecting similar drier and wetter periods, but without evidence for temperature change.

1.6 EARLY AND EARLIEST MIDDLE MIOCENE, RETURN OF GREENHOUSE CLIMATES

1.6.1 General trends

The latest Oligocene/earliest Miocene was characterized by globally warmer climates but with some cooler episodes (Zachos *et al.*, 2001). The highest global temperatures

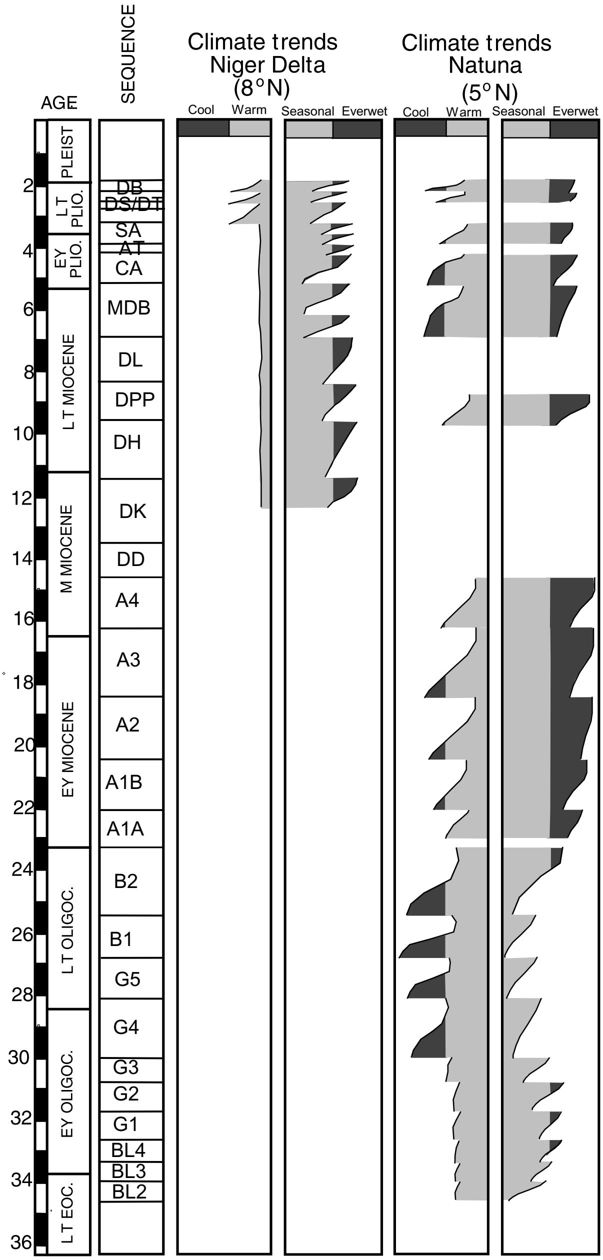

Figure 1.9. Summary of Oligocene to Pliocene climatic change in relation to sea level change, suggested from Natuna Basin palynological studies, together with Middle Miocene to Pliocene climate cycles for the Niger Delta. Sequence nomenclature follows Morley *et al.* (2003) for Oligocene to Early Miocene and Morley (2000a, Figure 7.13) for Middle Miocene to Pliocene. Timescale used is that of Berggren *et al.* (1995).

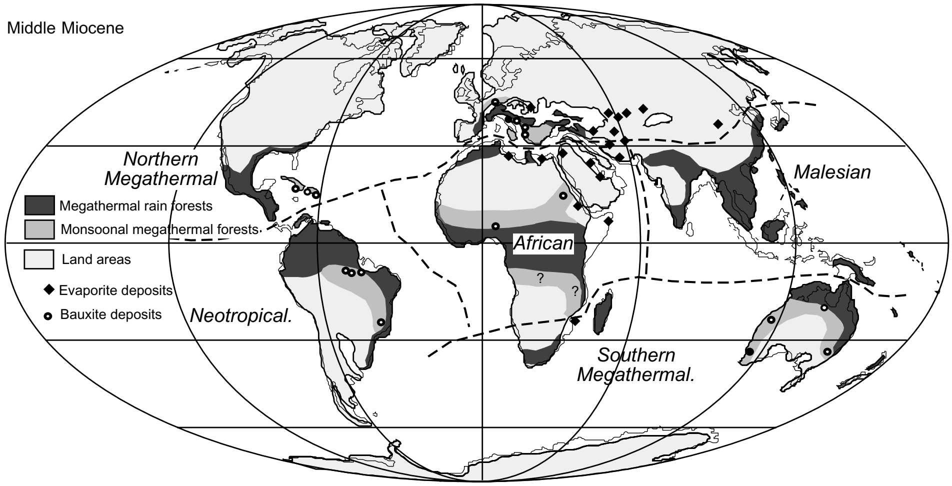

Figure 1.10. Distribution of closed canopy megathermal rainforests during the Middle Miocene, coinciding with the Miocene thermal maximum (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

were at the beginning of the Middle Miocene (mid-Miocene climatic optimum), although CO_2 levels remained stable over this period (Pearson and Palmer, 2000).

The renewed warming in the Early and earliest Middle Miocene once again resulted in the expansion of moist megathermal forests poleward of subtropical high-pressure zones, although this time for only a short period (Figure 1.10). In the northern hemisphere, mangrove swamps with *Rhizophora* and rainforests with *Dacrydium* extended northward to Japan (Yamanoi, 1974; Yamanoi *et al.*, 1980), *Symplocos* and *Mastixia* diversified in southern and central Europe (Mai, 1970), and megathermal elements extended along the eastern seaboard of North America (Wolfe, 1985). In South Africa, palm-dominated vegetation became widespread at two successive time intervals (Coetzee, 1978), and in southeast Australia the combination of warmer climates and northward drift once again resulted in the development of megathermal forests as far south as the Murray Basin (McPhail *et al.*, 1994). Climates in India again became moist, and as a result many elements of the Malesian flora spread to the Indian Plate, with well-preserved macrofossils in the Siwaliks (Awasthi, 1992).

1.6.2 Climate change in low latitudes

The most pronounced climate change in low latitudes occurred in the Southeast Asian region, where climates change from seasonally dry (monsoonal) to everwet at about the Oligo-Miocene boundary, 23.6 Myr (Morley *et al.*, 2003; previously estimated at about 20 Myr in Morley 1998, 2000a). This dramatic change is reflected both by pollen floras (disappearance of Gramineae pollen, dramatic increase in pollen from peat swamps) and the sudden appearance of coals in the lithological record. It is from the Oligo-Miocene boundary that the Southeast Asian region has an essentially ''modern'' flora (''Malesian'' flora in Morley, 2000a), with only minor subsequent modifications.

This change coincides almost precisely with the time of collision of the Australian Plate with the Philippine and Asian Plates (Hall, 1996, 2002), and I suggest that the dramatic climate change may relate to this collision, which is likely to have caused major disruption to Indonesian throughflow (Morley, 2003), with the result that warm moist air from the Pacific Warm Pool probably shed its moisture content in Sundaland, rather than farther to the west, from this time onward. This suggestion has significant implications. First, it is likely that a single climatic scenario, with mainly warm, wet phases followed by cooler, locally drier phases, for the major part of the Sunda region had been in place for the subsequent 23 Myr. Second, it is likely that the El Niño oscillation, which provides the main trigger for Sundanian rainforest regeneration (Ashton *et al.*, 1988; Curran *et al.*, 2004) by cueing all trees to fruit at the same time (mast-fruiting), thus reducing total seed predation (Janzen, 1974, 1976), may also have been in place since this time. This may explain why so many Southeast Asian rainforest taxa depend on El Niño for their reproductive success. In this respect, it is noteworthy that Dipterocarpaceae pollen (together with Poaceae) was very common over a wide area of the Southeast Asian region just prior to the change to wetter climates, with dipterocarps presumably being seasonal forest elements (Morley, 1991, 2000a, 2003). This raises the possibility that dipterocarps were able to take advantage of the new everwet climate scenario that came about following the disruption of Indonesian throughflow by establishing a rhythmic flowering pattern along with El Niño, and become dominant elements in Southeast Asian rainforests.

Detailed trends of climate change from the Natuna Basin (Morley *et al.*, 2003) indicate that over this period climates oscillated from cool and wet, during periods of low sea level, to warm and wet following sea level rise. Low sea level ''glacial'' settings were often characterized by thick coal deposits, often containing common *Casuarina* and *Dacrydium* pollen, suggesting Kerapah peats (Morley, 2000a, 2004) rather than basinal peats of the type which are currently characteristic of the coastal areas of Borneo and Sumatra today. Low sea level intervals are also characterized by common temperate elements—such as *Abies*, *Alnus*, *Picea*, and *Tsuga*—but in lower abundance than in the Oligocene. High sea level periods, on the other hand, were characterized by the expansion of basinal peats and mangroves, and the disappearance of temperate elements (Figure 1.9).

In equatorial Africa and South America, there is less evidence for a sudden change of climate at the beginning of the Miocene. African forests are thought to have gone through a period of decline at this time in a manner not seen in either Southeast Asia or South America, for many extinctions are recorded in the pollen record (Legoux, 1978; Morley, 2000a). Also, grasslands increased in representation, especially during periods of low sea level, from about 21 Myr onward, and the first evidence for burning of grasslands, from the occurrence of charred grass cuticle, is from about 15 Myr (Morley and Richards, 1993).

1.7 LATER MIDDLE MIOCENE TO PLIOCENE, GLOBAL COOLING AND RETRACTION OF MEGATHERMAL RAINFORESTS TO THE TROPICS

The phase of global cooling—starting at about 15 Myr in the Middle Miocene, and subsequently from about 2.8 Myr in the mid-Pliocene—resulted in the restriction of moist megathermal vegetation to the tropical zone, and coincided with the expansion of grasslands and deserts across much of the lower to mid-latitudes.

Megathermal elements disappeared from the mid-latitudes, with the exception of the Australasian region; here the drift of the Australian Plate into the southern hemisphere mid-latitude high pressure zone accentuated the effect of late Neogene desiccation in Australia, and rainforests became restricted to tiny pockets along the east coast, but its northerly drift maintained frost-free climates allowing mesic megathermal elements to survive in areas of everwet climate. This was not the case for New Zealand, being positioned a little farther to the south, which lost its megathermal elements in the Pliocene. The northern drift of the Australian Plate, coupled with global climate deterioration, resulted in the expansion of high pressure over northern Australia and this was primarily responsible for Pliocene development of the Javanese monsoon and the establishment of seasonal climates across Nusa Tenggara (Pribatini and Morley, 1999). With the drift of India into the northern hemisphere high-pressure zone, it also lost most of its moist vegetation.

The effect of global climate change on equatorial floras is illustrated by comparing histories over the last 15 Myr from Africa, where climatic perturbations have had a particularly deleterious effect, and Southeast Asia, where everwet climates have been much more the rule.

The record from the late Neogene of the Natuna Basin (5°N) is intermittent compared with that for the Oligocene and Early Miocene (Figure 1.9). However, some critical trends are clear. Climates have been predominantly moist for most of the late Neogene even during periods of low sea level; however, seasonal climate elements, such as Gramineae pollen, are much more persistently present than in the Early Miocene. It is likely that the Natuna area was characterized by wet climates, but seasonal, open vegetation may have been well-developed to the north in the mid- and upper region of the catchment that fed the basin.

For Africa, pollen data are available from the Niger Delta (Morley, 2000a) with macrofossil records from Tanzania (Jacobs, 2002). In the Niger Delta the pattern is of much drier "glacial" intervals throughout the late Neogene during low sea level periods with relatively little evidence for temperature change until about 2.7 Myr, corresponding closely to the time of cooler climates in Borneo (Figure 1.8). The Late Quaternary pollen diagram from offshore the Niger Delta by Dupont and Wienelt (1996), which spans the last interglacial/glacial cycle, shows that rainforests covered the delta during the Holocene and last interglacial, and savanna during the last glacial, and provides an excellent analog for climate changes in the delta region over the remainder of the Quaternary as well as the late Neogene back to at least 13 Myr. Over the late Neogene many oscillations of grass and rainforest pollen can be seen in sections studied from Niger Delta well sections (e.g., Morley, 2000a, Figures 7.11, 7.13); during periods of low sea level, climates were substantially drier, with widespread grasslands, whereas rainforest elements expanded during high sea level periods. Grasslands were associated with burning, for charred Gramineae cuticular debris, suggesting widespread savanna fires, is a persistent feature of low sea level periods at least since the beginning of the Late Miocene (Morley and Richards, 1993). Both grass pollen and charred cuticle become more common after about 7 Myr, suggesting that grasslands and burning were more widespread after that time, a date that fits well with the retraction of forest and expansion of C4 grasses in other areas (e.g., in Pakistan, Quade *et al.*, 1989; and Siwaliks, Nepal, Hoorne, 2000). Grasslands were probably less extensive during the Early Pliocene, but expanded further after about 3.0 Myr and into the Quaternary.

Leaf floras recently reported from the Late Miocene of Tanzania indicate different degrees of drying (Jacobs, 1999, 2002). One leaf flora (Waril), dated at 9–10 Myr, suggests an open vegetation and a climate with a pronounced dry season, whereas a leaf flora dated 6.6 Myr (Kapturo) suggests a woodland or dry forest setting. Jacobs suggests from these data that there was not a unidirectional change from forested to open environments in the Kenya rift valley during the Miocene (which is often proposed to explain the evolution of hominids in Africa). As with the Niger Delta area, it is more likely that a succession of alternately wetter and drier phases occurred, but with an overall trend toward cooler and drier climates, in line with global models. The Neogene vegetational history of Amazonia has recently been reviewed by Hooghiemstra and Van der Hammen (1998), and Van der Hammen and Hooghiemstra (2000). They emphasize that temperature oscillations took place over the entire Neogene, with cooler phases interrupting a climate that was mostly warmer than today. During the Pliocene the climate seems to have been generally cooler than during the Miocene, and between 3.0 and 2.5 Myr a strong cooling produced the first glacial period, closely paralleling the pattern seen in Southeast Asia and West Africa.

The likelihood that grass pollen maxima indicate the successive expansion of savanna has been downplayed by Hoorn (1994), Hooghiemstra and Van der Hammen (1998) and Bush (2002), who emphasize that grass pollen may be sourced from a variety of vegetation types, including swamp forest (where grasses are often found as a component of floating vegetation communities). However, in cases where grass pollen acmes occur in association with charred grass cuticle the likelihood of a derivation from more seasonal climate sources is much greater (Morley and Richards, 1993). For Amazonia such assemblages are probably derived from "cerrado" (wooded grassland) or semi-deciduous woodland. Maxima of charred grass cuticle associated with Gramineae pollen maxima have been recorded from the Late Pliocene of the Amazon Fan (Richards, 2000; Richards and Lowe, 2003), suggesting that during Late Pliocene times, Amazon climates were substantially drier than either the Miocene/Early Pliocene or the Pleistocene. This has implications regarding the long-term history of Amazonian vegetation and the "refuge" theory. Whereas the Amazon may have existed under continuous forest cover during the Pleistocene (Colinvaux *et al.*, 2000), this may not have been the case during the Late Pliocene, during which time fragmentation of Amazonian rainforests may have been a real possibility.

The climate oscillations discussed here from West Africa and Southeast Asia based on petroleum exploration data must be considered generalized compared with the high-resolution patterns seen in the later Quaternary. A study of a deep marine Pliocene profile from ODP 658, offshore northwest Africa by Leroy and Dupont (1994) shows high-resolution oscillations of grassland and desert elements and emphasizes that Milankovich scale climate changes, driven by astronomical cycles, were the rule just as in the Quaternary. The Pliocene section of the Sabana de Bogotá core from Colombia shows similar scale oscillations (Hooghiemstra, 1984; Hooghiemstra and Ran, 1994). It is therefore not unrealistic to suggest that astronomical cycles were also the driving force behind cyclical climate change throughout the Miocene and Oligocene.

1.8 TRENDS IN RAINFOREST DIVERSITY BASED ON THE PALYNOLOGICAL RECORD

Obtaining meaningful data regarding palynomorph diversity, which can be interpreted in terms of species diversity of vegetation, is fraught with difficulties, and so is rarely attempted (Birks and Line, 1990). Differences in depositional environment, as well as taphonomic factors, have a significant effect on such estimates, making "number of pollen types", or pollen diversity indices difficult to interpret. Also, individual analysts may have different concepts of what constitutes a "pollen type" (and how to deal with "undetermined" pollen) with the result that data from different analysts sometimes cannot be directly compared.

Trends in taxon richness from the Paleocene into the Eocene have been demonstrated by Rull (1999) in Venezuela and by Jaramillo and Dilcher (2000) in Colombia. Rull (1999) calculated diversity indices (Shannon–Weaver index) and pollen richness (number of palynomorph taxa per sample analyzed), and showed that there is a clear trend to increasing species richness into the Paleocene–Eocene thermal maximum from about 15 pollen types per sample in the Paleocene to about 20 in the Middle Eocene (in a count of 200 grains). Jaramillo and Dilcher (2000) compared diversities in the Late Paleocene and Middle Eocene principally using rarefaction (Raup, 1975) and the "range through" method of Boltovskoy (1988) to estimate standing diversity, with both methods indicating an increase in diversity from the Late Paleocene into the Middle Eocene. Late Paleocene samples yielded an average of 28 types and Middle Eocene samples averaged 54 pollen types, while estimates of standing diversity averaged 38 for the Late Paleocene and 73 for the Middle Eocene. Eocene taxon richness in both Venezuela and Colombia is low compared with palynomorph richness in modern low-latitude assemblages, where 60–70 pollen types in a count of 250 are more the rule.

Palynomorph assemblages from the Middle Eocene from the southern margin of Sundaland (Java) also show higher diversities than those from South America with typically 70–80 types in counts of 250 (Lelono, 2000), and standing diversities of 115–140 depending on the calculation method (Morley, unpublished). The diversity of the

Southeast Asian flora increased following collision of the Indian and Asian Plates and the mixing of Indian and Southeast Asian elements, resulting in the formation of the Proto-Indian Flora (Morley, 2000a, b). A parallel diversity increase within the palynoflora of the Malay Basin (Malesian Flora) is noted in the Middle Miocene (Jaizan Md Jais, 1997; Morley and Jaizan Md Jais, new data) following collision of the Australian and Asian Plates. This raises the possibility that floristic interchange following plate collision may be a general feature in promoting high levels of species diversity in tropical floras.

The trend of gradually increasing floristic diversity through the Paleocene and Eocene in South America and Africa (Figure 1.3) has previously been brought to attention by Morley (2000a). This trend comes to an abrupt halt at the end of the Eocene. Following the end Eocene cooling event, low-latitude floras show a sudden reduction in diversity in South America and Africa and also Southeast Asia (Morley, unpublished), coinciding with cooler and drier low-latitude climates.

A large Mio-Pliocene database is currently being generated from the Makassar Straits, east of Borneo, by analysis of boreholes on the continental slope and basin floor offshore the Mahakam Delta, all in very uniform, deep marine (1,000 m+) depositional settings. The Mahakam River catchment occupies a rainforest refuge area (Morley *et al.*, 2004). Preliminary results show very uniform numbers of pollen types per sample from the Middle Miocene (typically 60 types in a count of 300) up to the mid-Pliocene (typically 70–80 types per sample), with the possibility of a minor reduction in numbers per sample in the Late Pliocene. Pollen floras yield about 170–200 determinable types per stratigraphic section of 60–100 samples (Morley, new data). Trends closely parallel those seen in Miocene Mahakam Delta plain sediments (Morley, 2000a, Figure 7.13). The conclusion from these studies is that Bornean rainforests slowly increase in diversity over time from the Early Miocene to mid-Pliocene; data are currently insufficient to confidently demonstrate any real diversity reduction after 2.8 Myr.

For Amazonia, however, Van der Hammen and Hooghiemstra (2000) note that Hoorn (1994) found 280 pollen types in the Rio Caquetá area in Miocene river valley sediments, but note that Holocene river sediments from the same area yield only 140 pollen types, despite the present day vegetation in the area being very diverse, with 140 species per 0.1 ha (Ureggo, 1997). On the basis of these data they suggest that present day Amazonian vegetation is less diverse than that of the Miocene, a proposition also discussed by Flenley (2005) on the basis of the same data. Many questions need to be answered before reaching such conclusions: (1) Were the depositional settings directly comparable, and the same facies/subfacies represented? (2) Could taphonomic factors be in play to account for these differences? (3) Did the Miocene and Holocene river systems have the same vegetation types growing in the upper catchment? (4) How did the Holocene sediments recruit pollen from the surrounding vegetation, and were the same taxonomic concepts applied to both Miocene and Holocene sediments? Experience from working in fluvial sediments in Southeast Asia suggests that the number of pollen types preserved may vary considerably from one depositional locality to another, and that a large database from different depositional facies is needed to assess the richness of the pollen flora on a regional basis.

Palynomorph richness data from the Niger Delta (Morley, 2000a, Figure 7.13) based on analyses of petroleum exploration boreholes suggests that floristic diversity underwent several sudden reductions following phases of sea level fall and expansion of seasonal climate vegetation, especially at the beginning of the Late Miocene (about 11.7 Myr using the timescale of Berggren *et al.*, 1995), at about 7.0 Myr and following 2.8 Myr. There were also numerous extinctions during the Early Miocene as noted above. I suggest that the present day low diversity of African rainforest flora is a result of the successive expansion of seasonally dry climates in a manner not seen in either Southeast Asia or South America. These dry climate episodes occurred from the Early Miocene onward and were not just a Quaternary phenomenon. Successive dry climate episodes go some way to help explain why present day African equatorial flora is more species-poor than elsewhere.

1.9 SCENARIO FOR RAINFOREST EVOLUTION AND DIVERSIFICATION

The evolution and diversification of megathermal rainforests has been dependent on, and proceeded parallel with, a succession of geological and climatic and dispersal events, controlled largely by plate-tectonic and astronomical processes, in parallel with evolutionary pressures for plants to reproduce and colonize all available land space. These events have occurred in a unique time sequence. The result is that today each geographically separated rainforest area contains its own association of species, largely descended from ancestors that were established perhaps over 70 Myr ago, and subsequently became modified, and diversified, so as to occupy the available niches within each region.

From the perspective of Quaternary studies in relation to the explanation of rainforest diversity, processes of evolution of rainforest taxa have mostly focused on the "refuge hypothesis", which maintains that the successive isolation of populations in relation to the expansion and contraction of forested areas following Quaternary Milankovich cycle driven climate changes acted as a "species pump", triggering speciation. Such an approach has paid little attention to the antiquity of rainforest species as suggested from the Tertiary fossil pollen record, and now being substantiated by molecular studies, or to the high Tertiary floristic diversities suggested by pollen diversity data. For instance, a molecular analysis of one of the fastest-evolving rainforest taxa, the species-rich Neotropical genus *Inga* (Fabaceae), shows that its radiation is thought to have been promoted by the later phases of Andean orogeny and the bridging of the Panama Isthmus, perhaps coupled with climatic fluctuations, (Richardson *et al.*, 2001), but as noted by Bermingham and Dick (2001) provides little support for the idea that Pleistocene ice ages played a grandiose part in generating tropical species diversity.

This chapter attempts to show that—to understand the diversity of tropical rainforests—their development must be viewed on a much longer timescale. The climate changes which characterize the Quaternary were also taking place over much of the Tertiary period, the only difference between Quaternary and later Tertiary climate changes being one of degree of change, since "glacial" climates from the equatorial zone were clearly cooler from 2.8 Myr onward, and the vertical vegetational migration on tropical mountains over this period was likely to be more pronounced from this time onward.

From the Early Miocene to the mid-Pliocene, rainforest diversity in Southeast Asia (based on pollen-type richness) has gradually increased. A slight reduction in pollen-type richness after 2.8 Myr is not reliable in reflecting a diversity reduction in rainforest flora. Data from the Niger Delta regarding pollen-type richness suggests that West African flora has reduced significantly in diversity over the same period, with taxon losses throughout the Miocene, and with significant reductions at 11.7 and 7.0 Myr, and a particularly sharp reduction at about 2.8 Myr in the mid-Pliocene.

Palynological data from the Southeast Asian Neogene also demonstrates that the diversity of Southeast Asian flora may well have become accentuated as a result of the successive reformation of lowland vegetation on the continental shelves following periods of sea level fall over a period of at least 20 Myr (Morley, 2000a). Over this period major areas of the region have experienced everwet climates during both high and low sea level periods, with wet/dry oscillations being restricted to the Oligocene, and to some degree the Late Miocene.

In West Africa the pattern was of the alternating expansion and contraction of rainforests in relation to more open vegetation with grasslands over a period of some 30 Myr, with dry episodes—which included burning of savanna—becoming more pronounced, particularly after 7 Myr, and then again in the Late Pliocene. The depauperate nature of African rainforest flora compared with other areas is thought to be due to the decimating effect of these dry climate events, not on a Quaternary timescale, but over some 20 Myr, as emphasized by the higher number of extinctions seen in the West African Miocene pollen record than in other areas.

The scene for evolution of rainforest species is thus of gradual differentiation over a long time period with different forcing mechanisms inhibiting dispersal and isolating populations. The high diversities seen in rainforest refugia—or hot spots—are likely to relate to areas of long-term continuity of moist climates within those areas rather than to allopatric speciation driven by habitat fragmentation. The highest diversities, however, are seen where climatic stability coincides with areas which have experienced phases of orogeny and especially of plate collision, as seen from pollen data for Java following the Middle/Early Eocene collision of the Indian and Asian Plates, and for the Middle Miocene of the Sunda region following the collision of the Australian and Asian Plates. From the neotropics, molecular and biogeographical data suggest that high diversities may relate to the uplift of the Andes in the Miocene and the formation of the Panamanian Isthmus in the Pliocene.

Low equatorial floristic diversities may follow periods of cool, and particularly dry climates, as was the case following the end Eocene cooling event, when in Southeast Asia cool climate oscillations brought freezing temperatures to tropical mountains with corresponding seasonally dry lowland climates. Similarly, for equatorial Africa increased seasonality of climate from the Early Miocene onward accounts for the current depauperate nature of African rainforest flora.

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