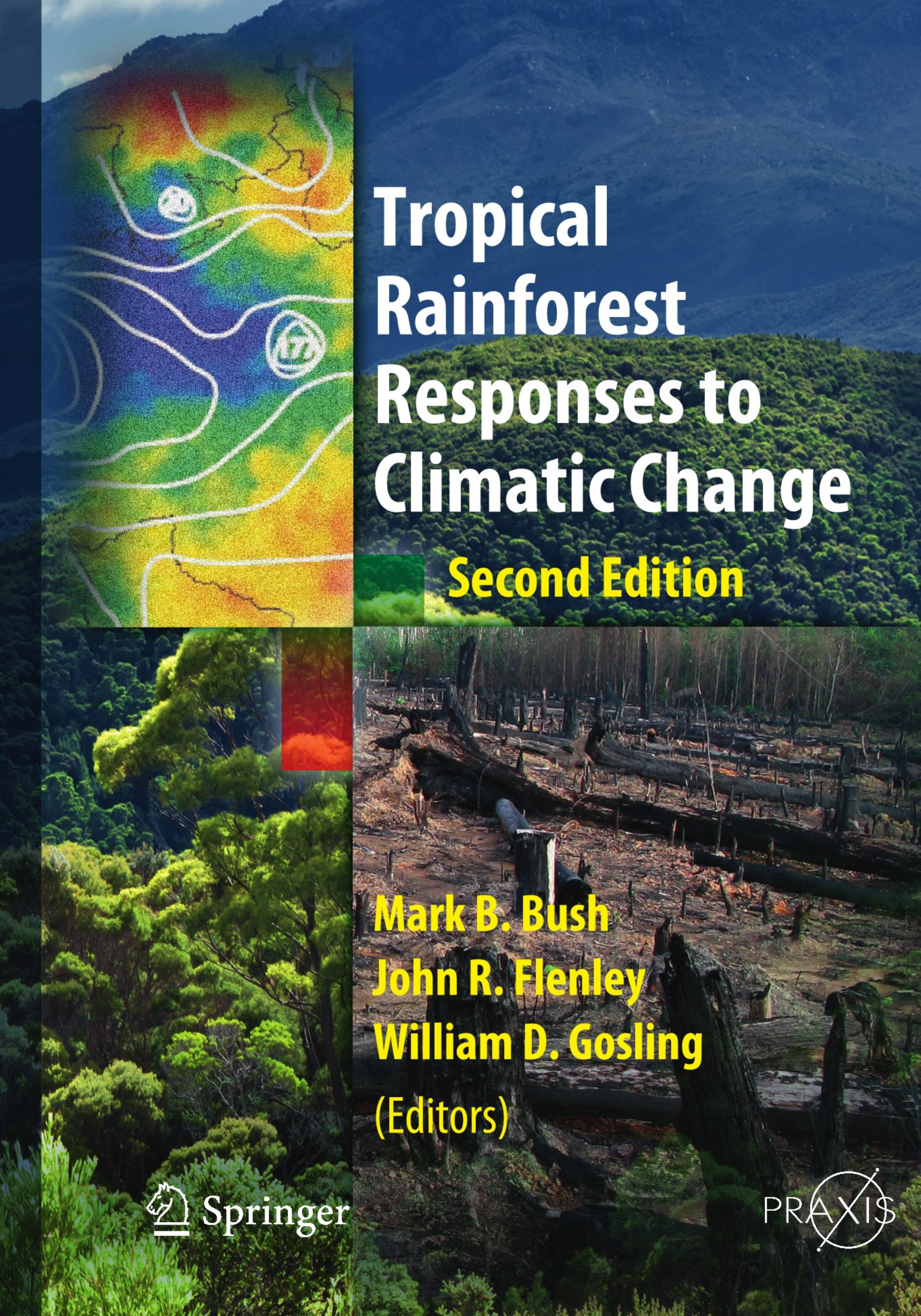

Tropical Rainforest Responses to Climatic Change

Second Edition

Mark B. Bush
John R. Flenley
William D. Gosling
(Editors)

Springer

PRAXIS

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Contents

Preface to the Second Edition

The First Edition of this book was well received and when a new print run was proposed we took the opportunity to revise, update, and expand the book. Our goal in the revision was to incorporate the most significant recent studies, yet retain the framework of the First Edition. Of course, the plight of tropical rainforests in response to climate change has not changed, and the political process that might have limited the effects of ongoing climate change appear to have faltered. For several decades the clarion call to save the rainforest biodiversity from the worst excesses of human exploitation has been loud. However, the threat to these systems from the synergy of climate change, logging, ranching, and other land use change appears to be cumulative. An investigation of the role that climate plays in shaping tropical rainforest biodiversity and, ultimately, how biodiversity may be lost is clearly needed. To that end we present chapters that deal with long-term climate and vegetation change, ecophysiology, and ecosystem processes in addition to considerations of how predictive models are constructed.

In this edition, we have added one entirely new chapter on fire, effectively replaced a chapter on Amazonian climate, and substantially modified most of the other chapters. We have attempted to minimize the period between author submission and printing of the book so that the most contemporary knowledge is portrayed. As part of that process of hastening the editing process we have been joined by William Gosling as an editor.

Mark Bush

Preface to the First Edition

Never before in human history has the need for an understanding of climatic change been so great. Nowhere in the world is that need so serious as in the tropics, where deforestation and extinction are at their most rapid, biodiversity greatest, and human lifestyles at their most precarious. We therefore hope and believe that this book will be timely and useful, as it attempts to describe and explain in scientific terms the past, present, and future changes in Earth's most complex terrestrial ecosystem, the Tropical Rain Forest.

The project grew from a discussion between Clive Horwood of Praxis and Mark Bush on the status of climate change research in Tropical Rain Forest settings. Mark's own involvement in attempting to apply lessons learned from the past to the formulation of conservation theory and practice led to a desire to move beyond a simple review of paleoclimatic data. The text aims to build upon and update the foundation of John Flenley's (1979) *The Equatorial Rain Forest: A Geological History* (Butterworth, London). In the intervening period our understanding of individualistic species migration, of potential interactions between climate and physical process, phylogenies, and of the looming impact of global climate change has revolutionized community ecology. In that same period the coverage of tropical paleoecological data has exploded—for example, there was not a single datum from Amazonia when John wrote his book.

John Flenley was called in to help when the sheer enormity of the task became evident to Mark. John had recently moved onto part time so was able to bring his experience of tropical regions fully into play, especially in the area of vegetational history.

We hope that the book will be used by scholars and senior students throughout the world, but especially in the developing countries of the Tropics, where climatic change may spell ecological and economic disaster very soon indeed. Perhaps it is not too much to hope that our book may contribute to influencing world policies in relation to technology and economics, before the climatic changes become irreversible.

We are deeply indebted to all our contributors, a varied selection of excellent researchers, who have given their time and effort unstintingly to make this book possible. We are also grateful to those who have helped with the editing, especially Olive Harris. John Flenley wishes particularly to thank his wife, Helen, for her understanding and support. Our publishers, especially Clive Horwood, deserve exceptional thanks for their patience, tolerance and skill. Any remaining errors are of course our responsibility.

Mark Bush *John Flenley*

To

VHB, HCF, and CHG

Figures

Tables

Abbreviations and acronyms

AP	Arboreal Pollen
AGCM	Atmospheric General Circulation Model
ALLJ	American Low-Level Jet
AMIP	Atmospheric Model Inter-comparison Program
AMS	Accelerator Mass Spectrometry
ANN	Artificial Neural Network
ATDN	Amazon Tree Diversity Network
BIOCLIM	BIOlogical CLIMate model
BIOME-3	BIOsphere Model
CBD	Convention on Biological Diversity
CDI	Climate Decomposition Index
CMIP	Coupled Model Intercomparison Project
DBH	Diameter at Breast Height
DCA	Detrended Correspondence Analysis
DGVM	Dynamic Global Vegetation Model
DIF	Differentials
DO2	Dansgaard–Oeschger event 2
ELA	Equilibrium Line Altitude
ENSO	El Niño–Southern Oscillation
EVI	Enhanced Vegetation Index
FATE	Functional Attributes in Terrestrial Ecosystems
FORCLIM	FORests in a changing CLIMate
FORET	FORests of East Tennessee
GAM	Generalized Additive Modeling; Generalized Additive Model
GARP	Genetic Algorithm for Rule-set Prediction
GCM	General Circulation Model; Global Climate Model; Global Circulation Model

GHG	GreenHouse Gas
GISP	Greenland Ice Sheet Project
GLM	Generalized Linear Modeling
IBIS	Integrated BIosphere Simulator model
IPCC	Intergovernmental Panel on Climate Change
IPSL	Institute Pierre and Simon Laplace model
ITCZ	Inter Tropical Convergence Zone
kcal yr BP	Kilo calibrated years before present
LAI	Leaf Area Index
LGM	Last Glacial Maximum
LPJ	Lund–Potsdam–Jena Dynamic Global Vegetation Model
LTM	Long-Term Mean
MAT	Mean Annual Temperature
MIS	Marine Isotope Stage
MWP	Medieval Warm Period
NAP	Non-Arboreal Pollen
NPP	Net Primary Productivity
PFT	Plant-Functional Type
PVT	Potential Vegetation Model
RAINFOR	*Red Amazónica de INventarios FORestales,* *Red Amazônica de INventarios FlORestais*
RCM	Regional Climate Model
REDD	Reducing Emissions from Deforestation and forest Degradation
SALLJ	South American Low-Level Jet
SASM	South American Summer Monsoon
SDGVM	Sheffield Dynamic Global Vegetation Model
SDM	Species Distribution Model
SENAMHI	Meteorological service of Peru
SPI	Standard Precipitation Index
SST	Sea Surface Temperature
TDF	Tropical Deciduous Forest
TEF	Tropical Evergreen Forest
TRIFFID	Top-down Representation of Interactive Foliage and Flora Including Dynamics
TRMM	Tropical Rainfall Measuring Mission
TSEF	Tropical Semi-Evergreen Forest
UKMO	United Kingdom Meteorological Office
UMRF	Upper Montane RainForest
UNFCCC	United Nations Framework Convention on Climate Change
VECODE	VEgetation COntinuous DEscription Model
VPD	Vapor Pressure Deficit
WCRP	World Climate Research Program
WUE	Water-Use Efficiency

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1

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

R. J. Morley

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* time scale, 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 time scale 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 of the 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,

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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 time scale, 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; 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 additional altitudinal stratification than in the Neogene since lowland rainforests, which exhibit little internal

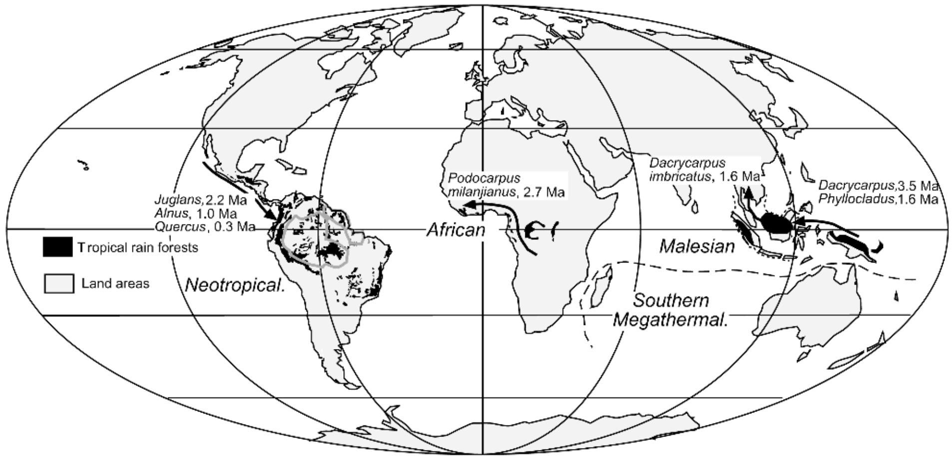

Figure 1.1. Ice age distributions of closed canopy megathermal rainforests has been a subject of debate. The refugial hypothesis depicted substantial replacement of forest by savanna during ice ages (e.g., Whitmore and Prance, 1987) (shaded areas) and for Amazonia (Van der Hammen and Hooghiemstra, 2000) (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.

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).

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,

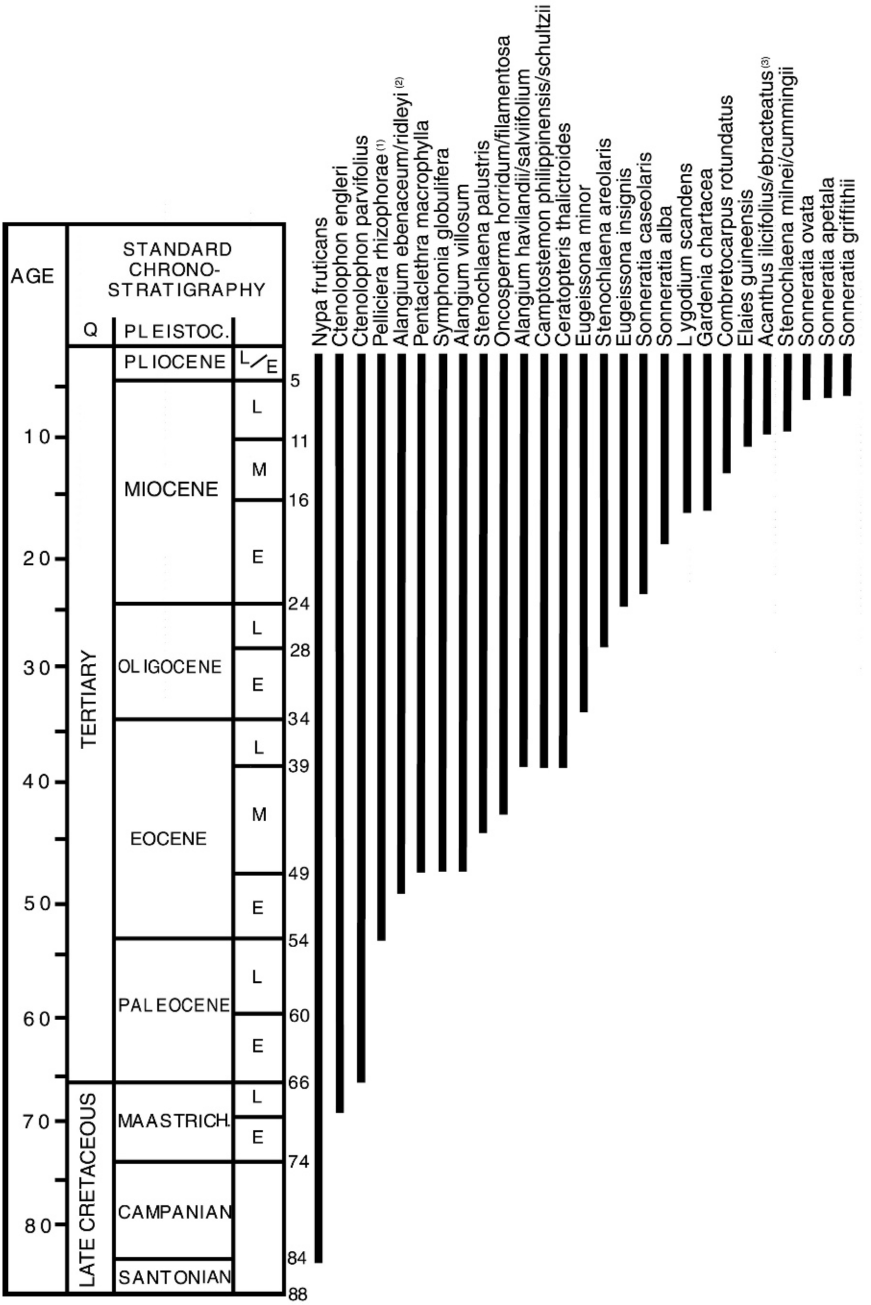

Figure 1.2. Stratigraphic range of angiosperm and pteridophyte megathermal species, or species pairs, which can be identified on the basis of pollen and spores, and have a well-defined Tertiary fossil record: (1) from Rull (1999); (2) Morley (unpublished); (3) Morley (1991); others from Morley (2000a).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

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 harbor 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 Malpighiaceae 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, multi-storeyed 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, 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 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.

With respect to the overwhelming dominance of angiosperms in megathermal forests, Bodribb and Field (2009) established that angiosperm leaf vein density increased rapidly just before their rise to dominance in the Mid Cretaceous, and suggested that this increased their photosynthetic capacity and gave angiosperms a competitive advantage over other plant groups (Figure 1.4). Boyce and Jung-Eun Lee (2010) took this further using climate modeling, and suggested that due to their high transpiration capacities, dominance of angiosperms ensured aseasonally high levels of

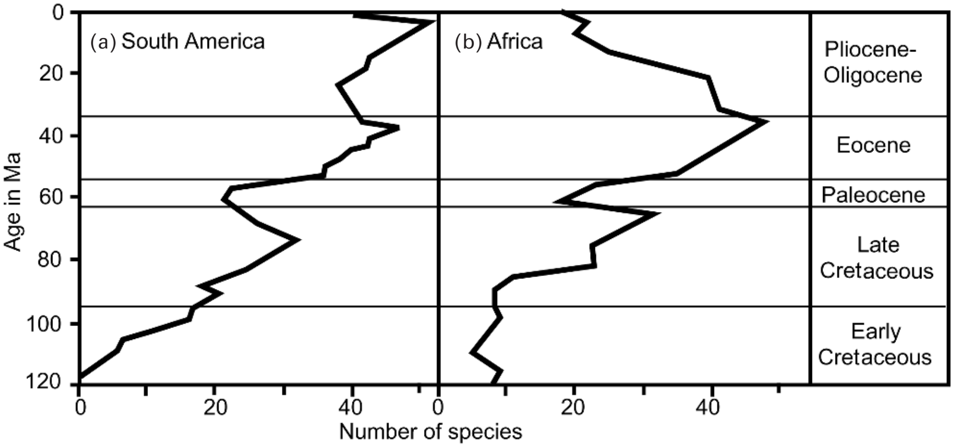

Figure 1.3. Numbers of stratigraphically useful angiosperm pollen types per epoch, for: (a) South America (data from Muller *et al*., 1987) and (b) West Africa (data from Salard-Chebaldaeff, 1990), providing a rough proxy for angiosperm diversity through time (from Morley, 2000a).

precipitation in the tropics, and, most strikingly, that replacement of non-angiosperm with angiosperm-dominated vegetation at low latitudes resulted in cooler, wetter, and more aseasonal climates. Thus, flowering plant ecological dominance has strongly altered tropical climate and the global hydrological cycle.

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 1.5). 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,

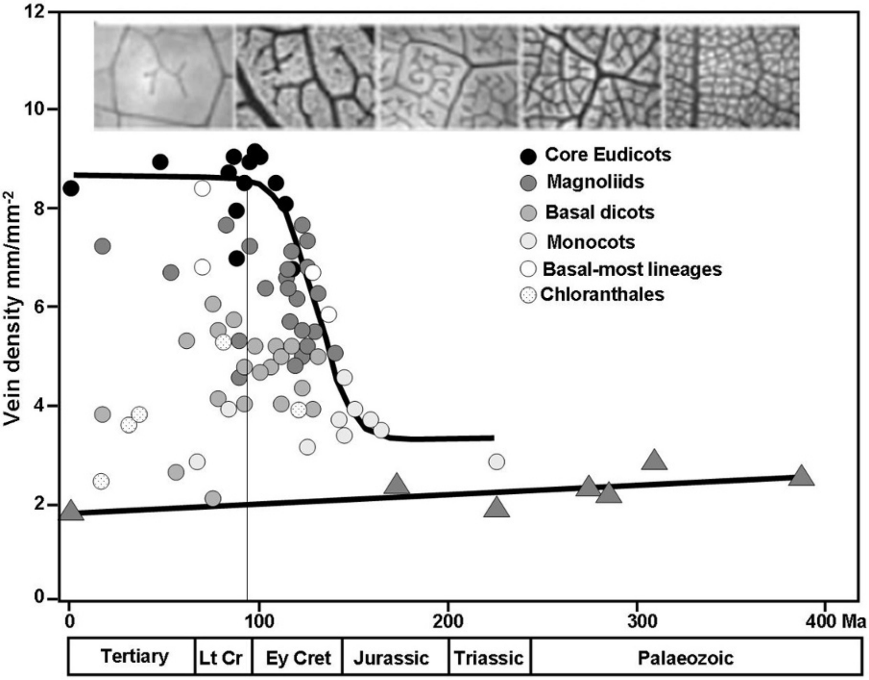

Figure 1.4. Leaf vein density reconstructed for key nodes of extant angiosperm phylogeny (circles) shows a dramatic increase during the Mid to Late Cretaceous *c.* 5 Ma before the massive rise in angiosperm diversification. No such pattern was observed for a sample of non-angiosperm fossil and living plants (triangles) which showed no significant trend in vein density over a period of 400 Ma to the present. A timeline of angiosperm evolution is denoted by a solid line regression. Angiosperm reconstructions are based on data from extant species The inset shows leaf vein densities for the most basal living angiosperm (*Amborella*, left) and an advanced Fabaceae on right (Brodribb and Field, 2009).

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 1.6), due to increased atmospheric CO_2 (Pearson and Palmer, 2000). At the Paleocene–Eocene boundary, megathermal forests were thus at their most extensive (Figure 1.7), 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 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

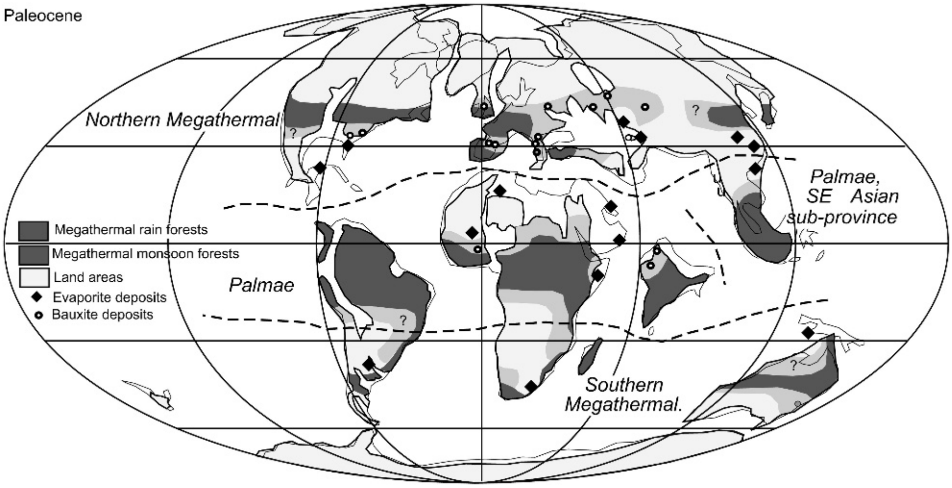

Figure 1.5. Closed canopy megathermal rainforests first became widespread during the Paleocene (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

oscillations resulted in the successive expansion and contraction of megathermal forests in mid-latitudes, as recorded for North America by Wolfe (1977).

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).

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

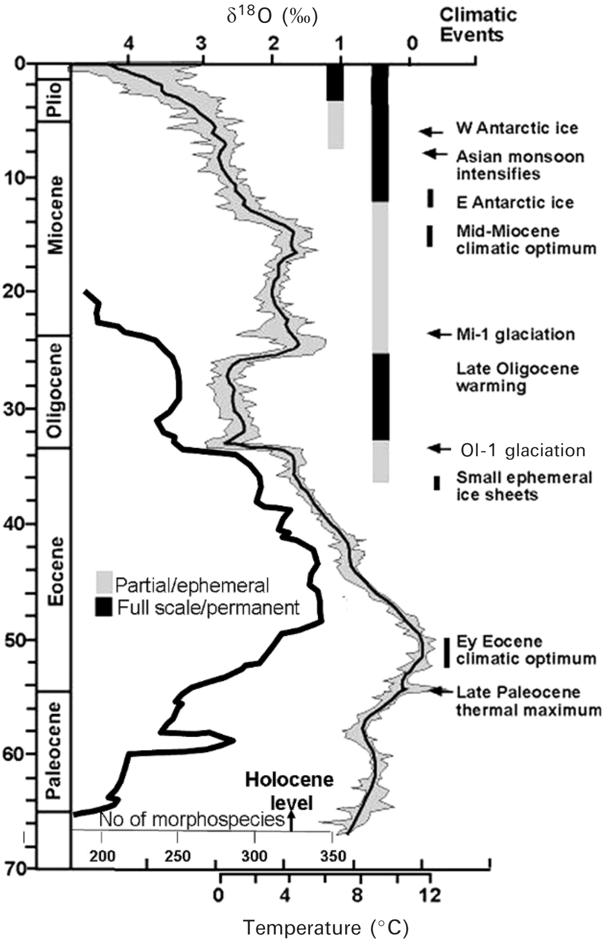

Figure 1.6. Generalized oxygen isotope curve for benthonic (bottom-dwelling) foraminifera through the Cenozoic (from Zachos *et al.*, 2001). The ratio of ^{16}O to ^{18}O for benthonic foraminifera provides a proxy for high-latitude surface marine temperatures (Hudson and Anderson, 1989), and therefore 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. Thick line shows pollen and spore standing diversity for Paleocene to Early Miocene of Colombia/Venezuela using the "Range Through" method according to Jaramillo *et al.* (2006).

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 modeling climates from vegetational data.

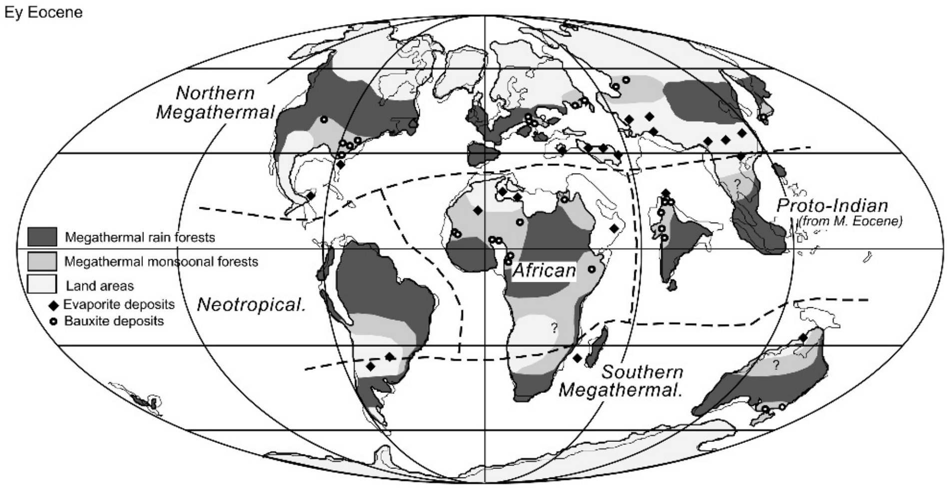

Figure 1.7. Distribution of closed canopy megathermal rainforests during the Late Paleocene/Early Eocene thermal maximum (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

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, with a particularly sharp dip at the very beginning of the Oligocene, at the beginning of the O1 glaciation (Miller *et al.*, 1998).

With cooler temperatures in mid-latitudes, megathermal rainforests underwent a major retraction to low latitudes (Figure 1.8). 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 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

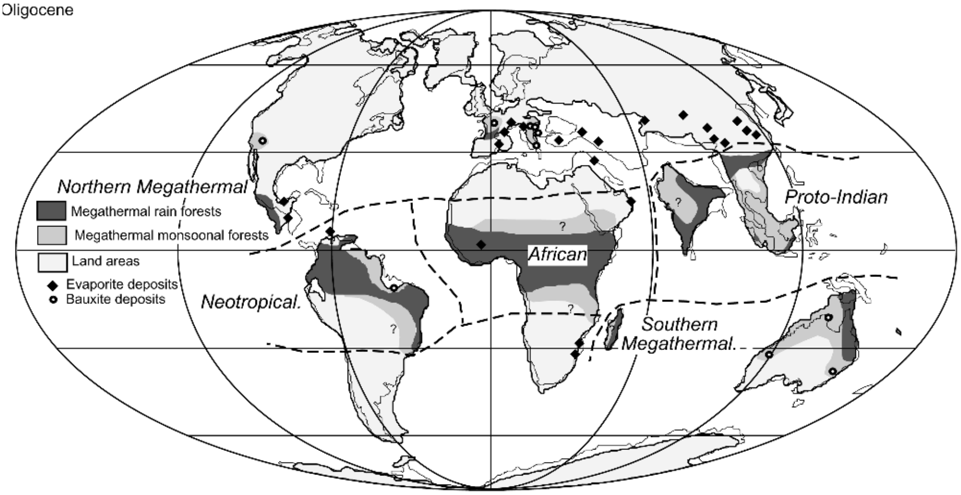

Figure 1.8. Distribution of closed canopy megathermal rainforests during the Oligocene, following the terminal Eocene cooling event (Morley, 2000a; Lelono and Morley, 2010). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

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 somewhat limited extent, except, perhaps in the areas of Assam and Myanmar, where Oligocene coals yield rainforest leaf floras (Awasthi and Mehrota, 1995), and along the southern margin of Sundaland based on palynological data (Lelono and Morley, 2010). The terminal Eocene event resulted in numerous extinctions across the tropics—for example, *Nypa* disappeared from Africa and South America (Germeraad *et al.*, 1968) probably as a result of the sea level fall at the beginning of the O1 glaciation. However, the impact of this event was

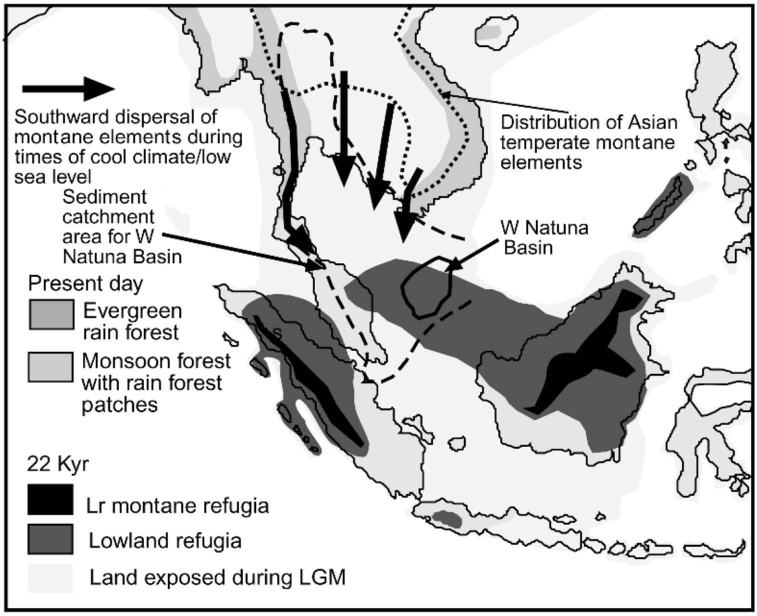

Figure 1.9. Present day distribution of megathermal (and tropical) rainforests in Southeast Asia, and probable distribution at *c.* 22 cal yr BP showing positions of rainforest refugia. The shoreline at c. 22 cal yr BP is also shown, together with the position of the catchment that fed the Malay/West 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).

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 1.9) 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 1.10). 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,

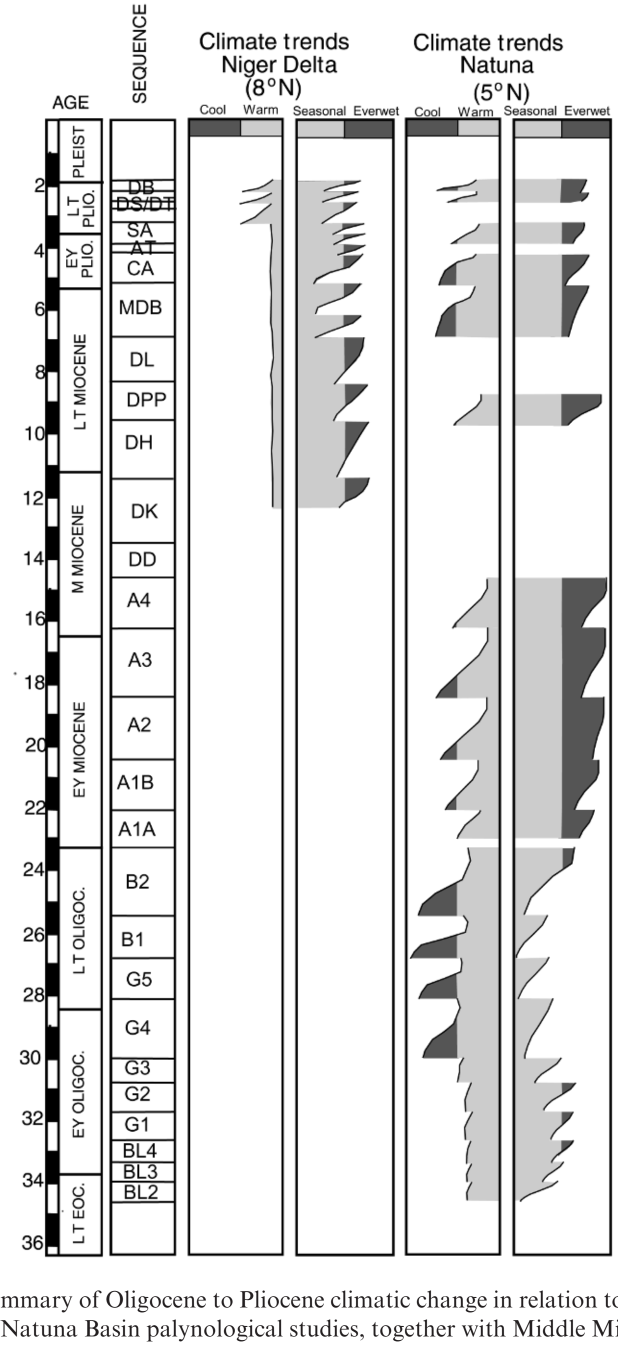

Figure 1.10. Summary of Oligocene to Pliocene climatic change in relation to sea level change, suggested from Natuna Basin palynological studies, together with Middle Miocene to Pliocene climate cycles for the Niger Delta. Sequence nomenclature follows Morley *et al*. (2003) for Oligocene to Early Miocene and Morley (2000a, figure 7.13) for Middle Miocene to Pliocene. Timescale used is that of Berggren *et al*. (1995).

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.

Previously, the high representation of montane gymnosperms in the Southeast Asian area has been interpreted as reflecting a source from former high mountains (Muller, 1966, 1972), but geological data from Borneo suggest a poor 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 are now thought to correlate to glacial episodes suggested by O^{18} data from ODP 1219 by Palike *et al.* (2006) at between 25.0 and 29.0 Myr (Morley and Morley, 2010).

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 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 1.11). 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, 23.3 Myr (Morley *et al.*, 2003; previously estimated at

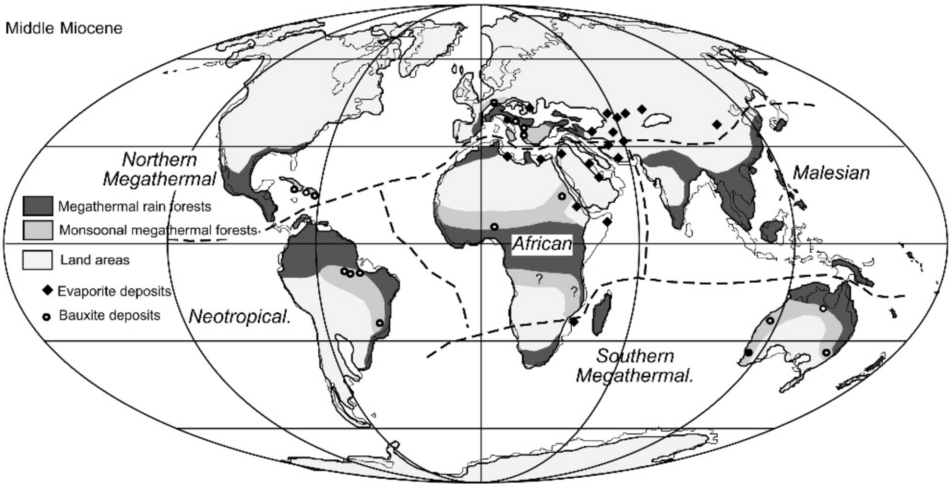

Figure 1.11. Distribution of closed canopy megathermal rainforests during the Middle Miocene, coinciding with the Miocene thermal maximum (Morley, 2000a). Paleogeography and paleocoastlines from Smith *et al.* (1994). Occurrences of evaporites and bauxites from Boucot *et al.* (in press). *Dotted lines* are floristic province boundaries.

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 1.10).

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 1.10). 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.

A detailed record from the Late Miocene to Pleistocene from close to the Mahakam Delta, East Kalimantan (Figure 1.12), shows that uniformly wet climates were the rule for equatorial Borneo back to at least 12 Myr (Morley and Morley, 2011). Over the interval 8.4–7.0 Myr, during a period of very high sedimentation rates, the palynological record suggests 100 ka climate cyclicity, with 13 eustatic fluctuations in 1.4 Myr.The persistence of everwet climates in equatorial Borneo over a very long period would have been implemental in maintaining rich and diverse rainforests which would have facilitated the diversification and maintenance of all elements of the Bornean rainforest fauna and flora which characterize the region today, possibly helping to explain why some areas of Borneo, such as the Lambir Forest Reserve in Sarawak, contain the world's most floristically diverse rainforests (Lee *et al*., 2002; Wright, 2001).

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 1.9). 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 C_4 grasses in other areas (e.g., in Pakistan, Quade *et al*., 1989;

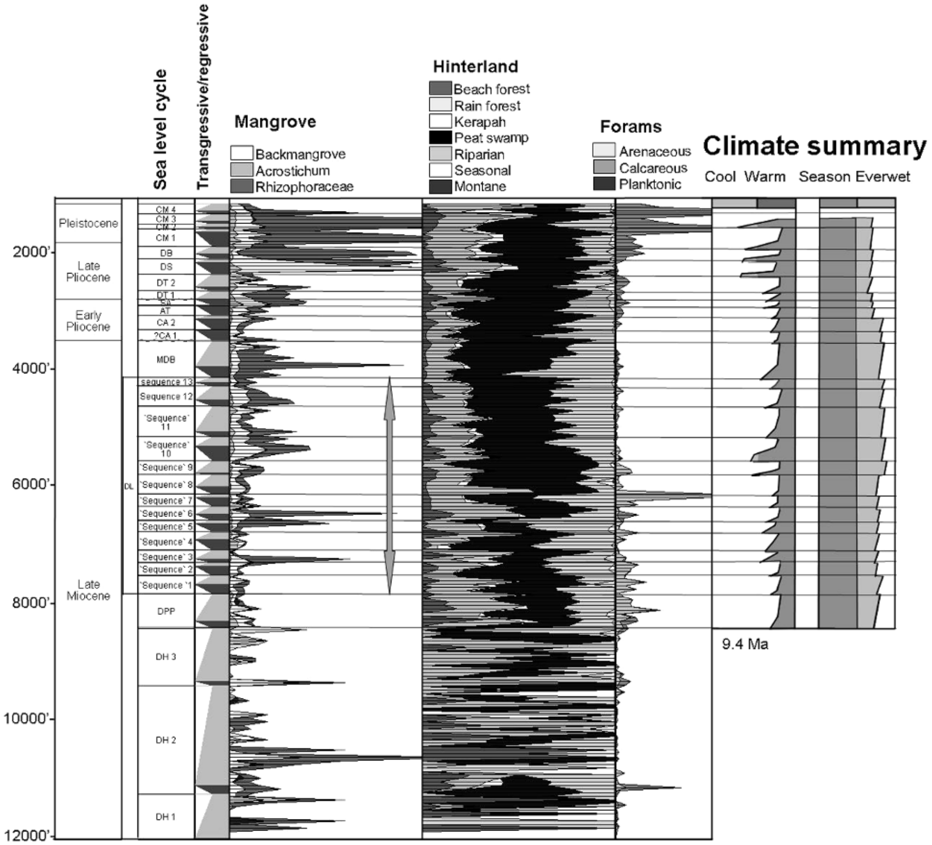

Figure 1.12. Palynological and foraminiferal record for Attaka Well B, located to the NW of Mahakam Delta, showing age, mangrove and hinterland pollen record, foraminiferal abundance and palaeoclimate trends. Interval with 100 kyr cycles (8.4–7.0 Myr) marked with grey arrow (Morley and Morley, 2011). Main components of palynomorph assemblage groupings as follows: "Backmangrove", *Sonneratia* and *Brownlowia* pollen; "Coastal", *Terminalia*, *Thespesia*, *Barringtonia* pollen; "Rain forest" pollen of Dipterocarpaceae, Burseraceae, Fabaceae, and many others; "Kerapah", *Casuarina* and *Dacrydium* pollen; "Peat swamp", *Austrobuxus*, *Blumeodendron*, *Cephalomappa*, *Calophyllum*, *Durio* and Sapotaceae pollen; "Seasonal", Poaceae and Asteraceae pollen; "Montane", *Lithocarpus* type, *Podocarpus*, *Phyllocladus* and *Alnus* pollen.

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.

Sepulchre *et al.* (2006) emphasise that the development of dry climates in equatorial East Africa relates largely to the effects of uplift, which led to a reorganisation of atmospheric circulation engendering strong aridification.

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.

The most comprehensive assessment of pollen/spore diversity is that of Jaramillo *et al.* (2006) who determine palynomorph assemblage diversity from the basal Paleocene to the Early Miocene, based on a massive database involving 1530 samples. They estimated standing diversity using the "Range Through" method of Boltovskoy (1988). They concluded that there was a clear (but not perfect) correlation to global temperature (Figure 1.6) with low-diversity assemblages in the major part of the Paleocene, with a sudden fall in diversity during the Late Paleocene coinciding with the time of coolest global temperatures. Diversity values then increased, particularly after the Paleocene/Eocene thermal maximum, but peaked just after the temperature maximum suggested by the oxygen isotope data of Zachos *et al.* (2001). Diversity then declined during the Middle and Late Eocene, with a sharp drop at the beginning of the Oligocene. Alternatively, the good correspondence may result from the control that climate exerts on the area available for megathermal plants to grow (Jaramillo *et al.*, 2006). Another factor may be introduced by the "Range Through" method, which exaggerates mid-range values, so Jaramillo *et al.* (2006) used rarefaction analysis to compare assemblage diversities with those recorded from the Holocene. They found that Oligo–Miocene and Paleocene floras were less diverse than in the Holocene, but that Eocene floras were significantly more diverse. Diversity estimates of Neotropical pollen floras have also been made by Rull (1999), Jaramillo and Dilcher (2000), and Morley (2000a).

Palynomorph assemblages from the Middle Eocene from the southern margin of Sundaland (Java) also show very high diversities 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 is also repeated in Africa (Morley, 2000a). As in the neotropics, this trend comes to an abrupt halt at the end of the Eocene in both 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). 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) 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 time scale 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 time scale. 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 time scale, 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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2

Andean montane forests and climate change

M. B. Bush, J. A. Hanselman, and H. Hooghiemstra

2.1 INTRODUCTION

The montane forest habitats of the Andes support exceptionally high biodiversity, with many species occupying narrow elevational ranges (e.g., Terborgh, 1977). These attributes, combined with the short migratory distances, often < 30 km separates the lowlands from the upper forest line, allows montane forests to be extremely sensitive monitors of climatic change.

Andean montane forests, which we define to encompass temperate and montane rainforests within the tropical zone (after Huber and Riina, 1997), range from *c.* 1,300 m up to *c.* 3,600 m elevation. The mean annual temperature at the lower limit of the montane forest is about 20°C, with minima of *c.* 7°C (Colinvaux *et al.*, 1997). Annual precipitation generally exceeds *c.* 1,000–1,200 mm, and ground level cloud is frequent. Montane forests are diverse in form, composition, and adaptations, and their response to a common forcing, such as a drought event, can vary significantly according to latitude, altitude, aspect, local precipitation, and soil type (Gentry, 1988). A further variable that must be included is that humans have occupied and modified these landscapes for millennia (Erickson, 1999; Kolata *et al.*, 2000). Consequently, uncertainty exists regarding the elevation of the natural upper forest limit in many parts of the Andes (Erickson, 1999; Wille *et al.*, 2002).

In this chapter we will address some of the larger scale issues—for example, the migration of species in response to tectonic and climatic change, the stability of systems despite instability of communities through time, the out-of-phase climatic influence on southern and northern Andean sites during the last glacial maximum (LGM), and the possibility of climate change inducing non-linear responses in ecosystems.

M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

2.2 TECTONIC CHANGES AND THE RISE OF THE ANDES

For the last 20 million years, the Andes have been rising as a result of the subduction of several oceanic plates beneath the South American Plate. The uplift transformed a rather flat continent into one with strong physical separation of lowlands and a host of new habitats ranging from humid foothills to ice covered summits. The rise of the Andes had no less radical an effect on the biogeography of the continent. Drainages of great rivers were reversed (Damuth and Kumar, 1975; Hoorn *et al*., 1995), and the related orogeny in Central America provided first stepping stones, and ultimately a landbridge connecting a Gondwanan to a Laurasian flora and fauna (Terborgh, 1992; Webb and Rancy, 1996). The great American faunal interchange (Webb, 1997), in which successive waves of taxa moved north and south and then underwent adaptive radiation, began as early as 16 million years ago. Migrations between North and South America peaked following the closure of the Isthmus of Panama, a progressive process that produced a continuous landbridge between 5 and 4 million years ago.

The arrival of eutherian mammals (e.g., monkeys, dogs, bears, sloth, elephantids, camelids, rats, and cats) left a lasting impression on South American systems. Many of these mammals entered unoccupied niches, while others may have gone into direct competition with marsupial counterparts or the indigenous array of flightless, predatory birds. The net result was rather lop-sided with relatively few genera moving into North America, though *Glyptodon*, a re-radiation of sloth species, possum, armadillos, and porcupines were clear exceptions. While, only the latter three have surviving representatives in North America, >50% of mammal genera in South America were derived from Laurasian immigrants (Terborgh, 1992).

In contrast to mammals, where an adaptive advantage lay with eutherian mammals over marsupials, the plants of North and South America shared the same basic biology. Among plants, the pattern of migration and competitive success obeyed the basic biogeographic rule that the species of larger source areas outcompeted those of smaller source areas (Rosenzweig, 1992). Consequently, lowland rainforest taxa from South America surged up into Central America, and became the dominant vegetation of the lowland tropics. Contrastingly, Laurasian elements swept south along mountain chains occupying the climatically temperate zone of Central and South American mountains (Hooghiemstra, 2006; Hooghiemstra e*t al*., 2006).

Many modern genera were extant and clearly recognizable in the pollen of Miocene sediments (23–6 Myr ago) (Jaramillo and Dilcher, 2002). During this time the Andes were rising, attaining about half their modern height, reaching *c*. 2,500–3,000 m about 10 Myr ago (Hoorn *et al*., 1995). For millions of years, the spine of the Andes comprised forested ridges that trapped clouds. Low passes—such as the Guayaquil gap and the Maracaibo area—maintained lowland connectivity from the Pacific to the interior of the continent until the Mid to Late Miocene (Hoorn *et al*., 1995). Only in later stages of uplift did large areas of the Andes rise above elevations capable of supporting diverse montane forests (i.e., above 3,300–3,600 m).

Importantly, as the Andes rose, entirely novel habitats were created for the continent. Mid- to high-elevation settings with steep slopes, varying moisture abundance, light limitation where clouds formed, increased exposure to ultraviolet radiation, and cool temperatures, offered new growing conditions. Speciation occurred among plants and animals as vacant niches were exploited. The radiation of families such as Lauraceae, Rubiaceae, and Ericaceae that filled the Andean forests was a huge biogeographic departure from patterns arising from the diversification of lowland elements. Today, the within-family diversity statistics (i.e. the ranking of families based on their species diversity) of lowland Amazonia and the Congo are much more similar to each other than either is to those of an Andean forest (Gentry, 1988).

Montane-dwelling migrants into this setting from North America had to island-hop through the Caribbean or move from hilltop to hilltop including making passage across a broad lowland plain in central Panama. This gap, without highlands over 1,000 m, was at least 130 km in length and may have acted as a severe filter to large seeded species, such as *Quercus*. Indeed, *Quercus* diversity in Panama was reduced from *c.* 13 species in the west, to one species in eastern Panama (Gentry, 1985).

The southward migrations of arboreal Laurasian taxa (e.g., Annonaceae, *Hedyosmum*, *Salix*, and *Rumex*) were inferred rather than observed, but the arrival of *Myrica*, *Alnus*, and *Quercus*, were apparent in the paleoecological records from the high plain of Bogotá (Hooghiemstra, 1984; Van der Hammen, 1985; Van der Hammen *et al.*, 1992; Van't Veer and Hooghiemstra, 2000). *Myrica* arrived in the Mid Pliocene, whereas *Alnus* first occurred in the Colombian pollen record about *c.* 1.37 million years ago. The last of these three species to arrive was *Quercus*, which first occurred about 478 kyr BP (Van't Veer and Hooghiemstra, 2000), but probably only attained its modern dominance between 1,000 m and 3,500 m elevation about 200,000 years ago (Hooghiemstra *et al.*, 2002). Since the first arrival of these species, *Alnus* spread as far south as Chile, whereas the southernmost distribution of *Quercus* coincided with the Colombian–Ecuadorian border (Gentry, 1993). *Alnus*, a pioneer species, thrived in disturbed settings, whereas *Quercus humboldtii* was a dominant of Andean forest. The arrival of *Quercus* in Colombia clearly impacted previously established taxa such as *Hedyosmum*, *Vallea*, and *Weinmannia* (Hooghiemstra, 1984); species that remained the common components of upper Andean forest from Peru to Colombia.

Progressive cooling during the Quaternary led the upper limit of diverse forest to move downslope, ranging between 3,600 m and 2,800 m during warm periods and probably reaching as low as 2,000 m during peak glacial conditions. The consequent expansion of montane grasslands, through a combination of uplift, cooling, and a reduction in atmospheric CO_2 concentrations, provided habitat for newly arriving holarctic species that enriched Puna and Paramo floras.

The new arrivals to forest and grassland settings created novel communities. Paleoecologists introduced the term no-analog communities to indicate that communities of the past differed from those of the present (e.g., Overpeck *et al.*, 1985). Ecologically, a no-analog community was most significant if it formed a novel community compared with those that preceded it, rather than compared with those of today. The sequential arrival of *Myrica*, *Alnus*, and *Quercus*, each established such novel communities. Furthermore, the faunal interchange between the Americas altered predator–prey relationships, seed-dispersal, and plant recruitment (Janzen and Martin, 1982; Wille *et al.*, 2002).

Among those seed-dispersers and predators were the megafauna. While the traditional view has been that the megafauna died out in the terminal Pleistocene (Steadman *et al.*, 2005), very real questions exist regarding the exclusion of Holocene ages from those analyses (Hubbe *et al.*, 2007). The probability that relatively low densities of people could have exterminated these large creatures quickly in the forests of the Andes and Amazon is much lower than in the open grasslands of North America or Patagonia. If the later ages for extinction are accepted, the collapse of megafauna appears to have occurred around 9–7 kcal yr BP, a time of strong climatic change and increased fire activity (Paduano *et al.*, 2003; Bush *et al.*, 2007), coupled with increased human impacts on ecosystems (Bush *et al.*, 2007).

Tapir survive in the lowlands and camelids continue to exert a significant grazing influence on montane grasslands. Such a basic observation is an important reminder that the loss of some of the other megafauna could have a substantial impact on the openness of all Neotropical settings and in the transport of large-seeded fruit (Janzen and Martin, 1982; Guimarães *et al.*, 2008). Thus, during the Quaternary, plate tectonics caused a major reorganization of plant and animal communities, featuring long-range migrations, species invasions, and adaptive radiation. In contrast, most responses to glacial–interglacial climate change appear to have been essentially local to sub-continental migrations.

2.3 SENSITIVITY AND QUANTIFYING COOLING

Modern pollen studies are the backbone of any attempt to quantify past vegetation changes. Over the past 25 years, a series of studies in Colombia (Grabandt, 1985), Ecuador (Bush, 1991; Moscol-Olivera *et al.*, 2009), and Peru (Weng *et al.*, 2004), have demonstrated a broad coherence between vegetation types and local pollen inputs. Indeed, apart from low-productivity settings (e.g., the highest grasslands), long-distance transport of pollen forms a very small proportion of the pollen rain. Weng *et al.* (2004) analyzed modern pollen data on an elevational transect in southern Peru and calculated that the accuracy of assigning an elevation to an unknown sample is about ±260 m at that location. Local moist-air adiabatic lapse rates are almost exactly 5.5°C per 1,000 m of ascent (Weng *et al.*, 2004). From this study it appeared that palynology can be used to provide a temperature estimate of *c.* ±1.5°C (Figure 2.1). It will be noted that the samples in Figure 2.1 from 3,350 m and 3,400 m do not fall close to the regression line. Both of these samples were collected from sheltered gullies that contained shrubs of *Weinmannia*, woody Asteraceae, and *Polylepis*, giving these samples a "low" signature in the analysis.

The Weng *et al.* (2004) study was in mature second growth forest, disturbed by road construction. As disturbance-tolerant species tend to produce a lot of pollen and are often generalist species, ongoing study of less disturbed transects may provide even narrower error ranges in temperature estimates.

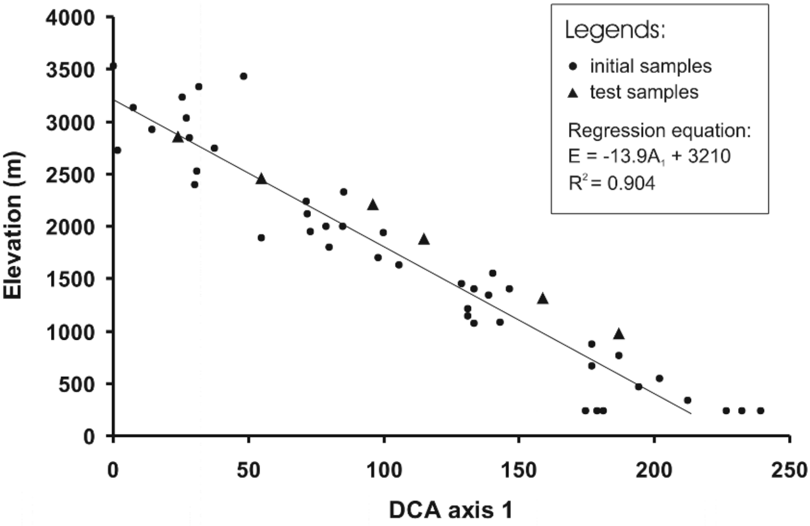

Figure 2.1. Modern pollen rain and elevation. Regression of first axis DCA scores against elevation for log-transformed modern pollen data. All data from a line transect from Amazonia into the Andes in eastern Peru (Weng *et al.* 2004). Black circles represent samples of known elevation (to the palynologist). The six triangles represent a blind study in which the analyst did not know sample elevation.

2.4 SITES IN SPACE AND TIME

Almost all Andean lakes are a product of glaciations, formed less than 20,000 years ago. The lowest of these lakes are usually moraine-dammed and may lie at the upper limit of modern Andean forest (e.g., Lakes Surucuchu (3,180 m elevation; Colinvaux *et al.*, 1997), Chochos (3,300 m; Bush *et al.*, 2005), and Refugio (3,400 m; Urrego *et al.*, 2010a)). However, such lakes that provide paleoecological records from within modern montane forest settings are thinly scattered. The cause of this paucity lies in the geography of the Andes themselves (Figure 2.2). The flanks of the Andes are so steep that the vertical elevation occupied by montane forest is often spanned by just 10–30 km laterally. In the inter-Andean plateaus montane forests are restricted to the wetter and somewhat lower sections of the northern Andes. The small area and lack of glacially-formed lakes within the elevations occupied by modern montane forest, combined with frequent rockslides and active tectonism, contribute to a landscape in which few ancient lakes formed and even fewer survive.

The obvious and important exceptions to this pattern are the great lakes of the Altiplano (e.g., the Salar de Uyuni and Lake Titicaca) and deep grabens such as Lake Junin, but these have probably never lain within forest. The High Plain of Bogotá, at *c.* 2,550 m elevation contains an extensive series of lakes and marshes that provide much of what we know about the response of montane forest to Quaternary climate change (Torres *et al.*, 2005). Newly described lakes, such as Lakes Pacucha (3,050 m; Hillyer *et al.*, 2009; Valencia *et al.*, 2010) and Consuelo (1,360 m; Bush *et al.*, 2004;

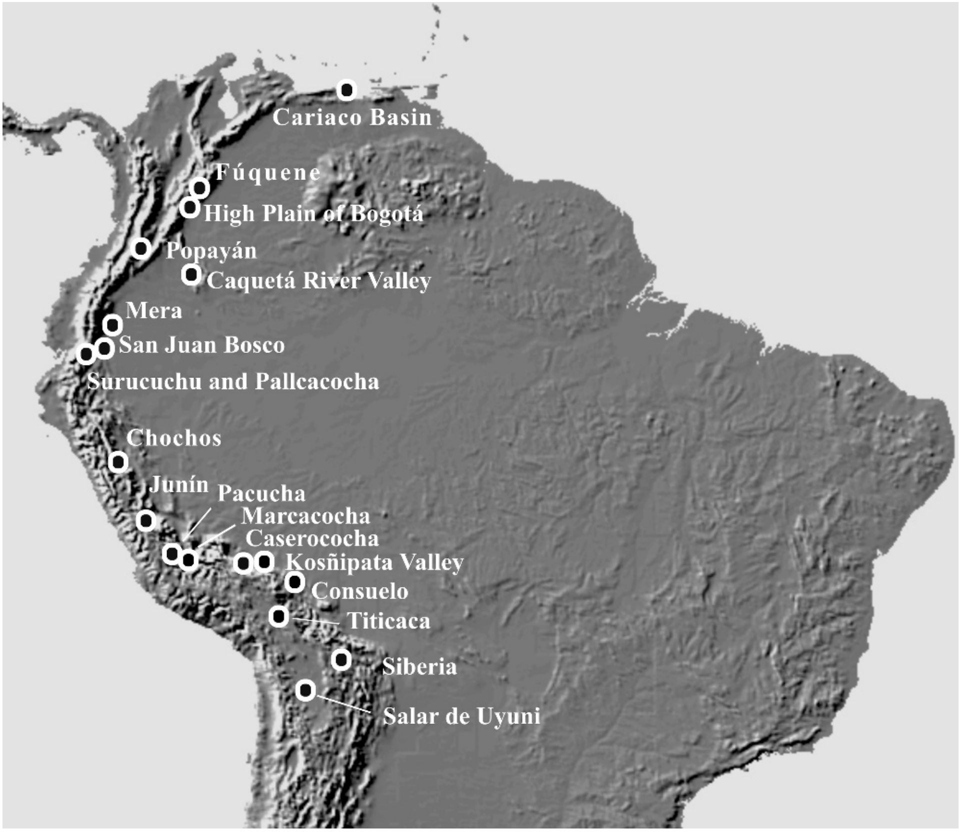

Figure 2.2. The location of sites of paleoecological importance mentioned in the text relative to topography.

Urrego *et al.*, 2010b) augment this understanding by providing additional detail of the last glacial maximum and subsequent deglaciation.

2.5 QUATERNARY GLACIAL–INTERGLACIAL CYCLES

The list of montane forest sites is expanded when we include those that have supported montane forest in the past. During the thermal optima of previous interglacials such as marine isotope stages (MIS) 5e, 7, 9, and 11, it appears that montane forest may have extended upslope by as much as 200 m from its present location (but see below for the case of Lake Titicaca). The influence on the lower limit of montane forest during these episodes is more difficult to establish. Bush (2002) hypothesized that as climates warm the elevation of cloud formation on the flank of the Andes will increase.

Under such warm conditions the change in the elevation of cloudbase may have been greater than the upslope expansion of the montane forest, creating a narrower total elevational range supporting montane forest. Contrastingly, during the glacial periods, montane forest species invaded downslope in response to cooling and the lower formation of cloud. Although the descent of montane taxa and the lowering of the upper forest line appear broadly similar (*c.* 1,500 m) along the Andes, the movement of the lower limit of the cloudbase may be more variable regionally. In the drier lowlands of Colombia this cloudbase may not have moved far downslope (Wille *et al.*, 2001; Hooghiemstra and Van der Hammen, 2004), compared with the wetter systems of Peru and Ecuador (Colinvaux *et al.*, 1996; Bush *et al.*, 2004).

Translating the migration of fossil pollen types in sedimentary records into an estimate of temperature change was pioneered in South America by van der Hammen and González (1960). They documented a periodic 1,500-m descent of vegetation types based on the replacement of forest with grasslands, and then a widening downslope distance to the estimated position of upper forest line. Since that initial study of the High Plain of Bogotá, virtually every Andean record from the last ice age has indicated at least a 1000-m descent of vegetation and often a 1500-m descent of some pollen taxa at the LGM (Figure 2.2). The moist air adiabatic lapse rate (Chapter 10) evident on the Andean flank provided a means to translate this vegetational movement into a change in temperature.

Modern lapse rates vary according to local humidity, ranging between −5.5°C and −6.2°C (Witte, 1994) in Colombia, and *c.* −5.5°C per 1,000 m of ascent in Peru and Ecuador (Colinvaux *et al.*, 1997; Bush and Silman, 2004). Accordingly, for a 1,000–1,500-m descent of vegetation the inferred change in paleotemperature is a cooling relative to the modern values of 5°C to 8.5°C.

Most Andean LGM pollen records are consistent with a cooling of *c.* 8°C in the highest elevations tapering down to a cooling of *c.* 4–5°C in the lowlands. This temperature differential suggests a steeper-than-modern temperature gradient. As there is no suggestion that the Andean slopes were ever without forest, it is improbable that the moist-air adiabatic lapse rate would change very much (Webster and Streten, 1978; Rind and Peteet, 1985). Evidence from studies of glacial moraines lead to reconstructions of the equilibrium line altitude (ELA) for glaciers. Glaciers in Peru and Ecuador are generally inferred to have ELAs about 800–1,000 m lower than modern counterparts, suggesting a cooling of 4–5°C (Rodbell, 1992; Seltzer, 1992; Smith *et al.*, 2005). Hence the inferred temperature signal from plants at high elevations may contain a more complex signal than first envisaged. Bush and Silman (2004) proposed one such effect in which black-body radiation would elevate sensible heat loss under low atmospheric CO_2 concentrations; an effect that would be more extreme at high elevations. Other additive effects probably contributed to the observed high-elevation cooling.

Within the dating resolution available to us, Neotropical interglacials appear to coincide in timing, and general character, with those documented elsewhere. The interglacials are known as MIS 5e (*c.* 130–116 kyr BP), MIS 7 (*c.* 240–200 kyr BP), MIS 9 (330–300 kyr BP), and MIS 11 (425–390 kyr BP), and generally last about 15,000–40,000 years. While a 100,000-yr cycle appears to underlie the glaciations of the last half million years, the intensity of interglacial periods appears to be related to precessional amplitude (Broecker, 2006). Three records provided insights into multiple glacial cycles in the Andes: the High Plain of Bogotá, Lake Titicaca (Hanselman *et al.*, 2005), and the Salar de Uyuni, although only the MIS 6 to MIS 1 portion of this record has been published so far (Fritz *et al.*, 2004).

Long sediment cores raised from Lake Titicaca provided a record of vegetational change spanning the last 370,000 years (Hanselman *et al.*, 2011). During interglacials, warming increased local productivity, and the upper Andean forest began to migrate closer to the lake. At the peak of MIS 5e and 9, Titicaca was reduced to a shallow lake with extensive adjacent saltmarsh, while having deeper water and somewhat more mesic vegetation, including *Polylepis* woodland, in its catchment in MIS 7 and 1.

Fire, which these data demonstrated was natural to the high Andes, became a transforming factor and limited the expansion of woody taxa during interglacials. Both the Colombian and Bolivian records indicated that the peak of MIS 5e may have been relatively dry. This drying was especially evident in Lake Titicaca, where the abundance of benthic and saline-tolerant diatoms, and peak abundances of pollen of Amaranthaceae, suggest the lowest lake levels of the last 370,000 years. Amaranthaceae pollen types are commonly derived from salt-tolerant plants, or from plants that grow in areas subject to irregular inundation (Marchant *et al.*, 2002).

At Lake Titicaca substantial differences were evident in the manifestation of the last four interglacials. Trajectories of vegetational change during MIS 1 and 5e were revealed through Detrended Correspondence Analysis (DCA) (Hill, 1979; McCune and Mefford, 1999) for fossil pollen data from Lake Titicaca (Figure 2.3). The scores for Axis 1 were plotted against time since the start of the relevant interglacial. The data were drawn from a deep-water core from Lake Titicaca LT01-2B (240-m water depth), a shallower water core (40-m water depth) from the Huinaymarca sub-basin (Core LT01-3B; Gosling *et al.*, 2008), and a piston core from 130-m water depth that provided a detailed Holocene record from the main basin (core NE98-1PC; Paduano *et al.*, 2003). Core LT01-3B had a hiatus in the middle of the interglacial, but showed a very similar pattern of community change leading into and out of the event as found in the deep-water core LT01-2B. This comparison revealed that while starting similarly, MIS 5e continued on a path to increasing aridity, while in the latter part of the Holocene conditions diverged from this path (Hanselmann *et al.*, 2011).

The evident difference between the interglacials was probably underlain by precessional forcing, however, Bush *et al.* (2010) invoked microclimatic feedbacks as amplifying mechanisms that enhanced the precessional pattern. Lake levels fluctuated on the Altiplano (below) and as deglacial highstands gave way to interglacial lowstands there was a concomitant loss of a regional lake effect.

Lake Titicaca is the world's highest "Great Lake" and it produces a halo of warm ($\sim +4^\circ$C), moist (doubling local precipitation) conditions that significantly alters local growing conditions. If, as in the time of MIS 5e, the lake area is reduced by more than 50%, some of these moderating influences would be lost, rendering the local area cooler and drier. Triggered by outside forcing such as changes in insolation and sea surface temperature (SST), local positive feedback mechanisms involving

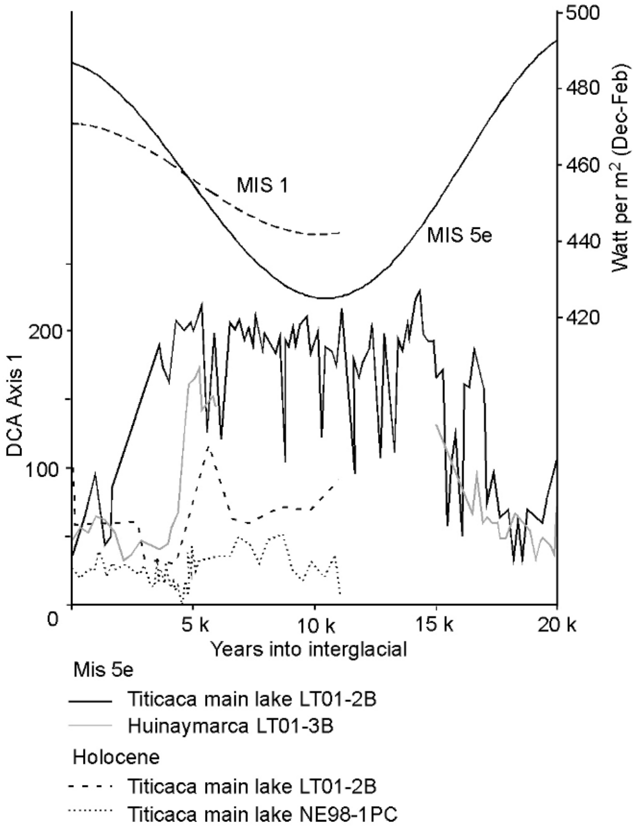

Figure 2.3. A comparison of MIS 5e and the Holocene based on insolation and changes in community composition revealed through DCA. The onset of MIS 5e is taken to be at 136 kyr BP based on the chronology used in Hanselman et al. (2005) and 11 kyr BP is taken as the start of the Holocene. Data are from Hanselman *et al.* (2005) and insolation curves from Analyseries 1.2 (Berger, 1992; Paillard *et al.*, 1996).

cloudiness, evaporation, precipitation, and temperature, may have been critical in altering local microclimates.

Bush *et al.* (2010) suggested that at least twice before, during MIS 9 and 5e, the Altiplano had warmed, and then passed a tipping point leading to falling lake levels and aridity (Figure 2.4). Upslope migration of forest stopped, even if temperatures continued to rise as the Altiplano became too dry to support montane forest. Based on the observation that dense Andean forest never reached an elevation of 3800 m, but can grow at 3,500–3,700 m elevations, it is probable that this tipping point occurred within +1–2°C of modern temperatures. This case-study provides an example of how vegetation–climate feedbacks are not always linear.

While it is our expectation that plants will migrate poleward or upslope in response to warming, the interaction of temperature with other climatic parameters,

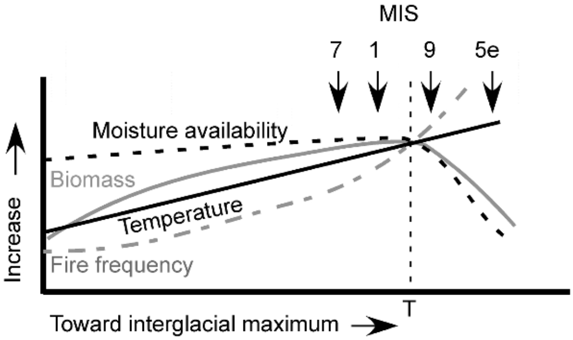

Figure 2.4. Schematic diagram of a non-linear response to warming and a turning point reached in some Andean interglacials based on paleoecological data from Lake Titicaca, Peru/Bolivia. Arrows indicate the approximate peak state of the last 4 interglacials relative to the schema.

in this case precipitation : evaporation ratios and microclimates, can induce non-linear feedbacks that change migrational patterns. Even these responses are not symmetrical as it is possible to slow or halt migration but, as it is believed that plant migrations are often dispersal-limited (McLachlan and Clark, 2005) and outstripped by the rate of climate change, it is unlikely that migration rates can be accelerated.

2.6 THE LAST GLACIAL PERIOD

In the Andes, the termination of the last interglacial was marked by a substantial and rapid cooling, perhaps 3°C, marking the onset of glacial conditions (Van't Veer and Hooghiemstra, 2000). Following this cooling, temperatures bumped up and down, tracking the Milankovitch and Dansgaard/Oeschger Cycles, but gradually declined to the coldest time at the LGM (Hooghiemstra *et al.*, 1993).

The precipitation record for this period is harder to decipher, and inferred lake depth is a major proxy for changes in annual precipitation. Precipitation patterns are often highly localized and, when one is dealing with relatively few sites it is possible that such local effects skew our view of systems. However, if we look outside the montane forest region and include data from ice cores, high Andean lakes, and from the Amazonian plain, a coherent pattern begins to emerge (Table 2.1).

In Colombia, the Funza-2 record terminates about 30 kcal yr BP when the lake dries out. The Fuquene-3 record suggests a progressive lowering of lake level beginning around 60 kyr BP and culminating in a depositional hiatus between *c.* 22 kcal yr BP and 12 kcal yr BP (Van der Hammen and Hooghiemstra H., 2003). The Altiplano of Peru and Bolivia appears to have become wetter after *c.* 60 kyr BP (Fritz *et al.*, 2004); given the uncertainties in dating, this may or may not be related to the beginning of the drier conditions in Colombia. However, the

LGM does provide support for asynchrony in wet episodes, as this is a time of flooding in the Altiplano, and low lake-level in Colombia.

At least three giant paleolakes occupied the Altiplano at various times during the Quaternary (Servant, 1977; Baker *et al.*, 1999). The timing of these events is actively discussed (Mourgiart *et al.*, 1997; Baker *et al.*, 2001; Placzek *et al.*, 2006; Gosling *et al*, 2008). Here we adopt the chronology of Baker *et al.* (2001) as it seems most consistent with other regional records (e.g., Fritz *et al.*, 2004, 2010; Ekdahl *et al.*, 2008; Hillyer *et al.*, 2009), but recognize this issue is far from settled. The most recent, paleolake Tauca, appears to have formed about 26 kcal yr BP (Baker *et al.*, 2001), coincidental with the onset of ice accumulation at Sajama (Thompson *et al.*, 1998). This wet event appears to have lasted until *c.* 16 kcal yr BP when Lake Tauca drained (Baker *et al.*, 2001). The combination of extreme cold and wet conditions during the Tauca period caused ice lobes to advance to within 100 m vertically of the modern Titicaca shoreline (a vertical descent of about 1,300 m; Seltzer *et al*, 1995, 2002). Baker *et al.* (2001) determined that lake level in the Salar de Uyuni followed the precessional cycle for the last 50,000 years. Highstands corresponded to maxima of insolation occurring during the wet season (December–February), and lowstands during the corresponding minima.

While the evidence of precessional oscillations have a long history in Colombia (Hooghiemstra *et al.*, 1993), on the Altiplano this synchrony is only evident in the last two glacial cycles. Prior to *c.* 60 kyr BP, the Salar de Uyuni was predominantly dry, with only sporadic flooding episodes (Fritz *et al.*, 2004; Chepstow-Lusty *et al.*, 2005). Two plausible scenarios have yet to be tested, one is that the climate was significantly drier prior to 60 kyr BP, and the other is that tectonic change altered the hydrology of the basin at this time, making it more probable that it would hold water (Wille *et al.*, 2001).

In Colombia, the Caquetá River valley (Van der Hammen *et al.*, 1992) documents a relatively wet time between *c.* 50 kcal yr BP and 30 kcal yr BP and a drier LGM, consistent with the records from the High Plain of Bogotá. A record from Popayán (1,700 m; Wille *et al.*, 2000) reveals the presence of either a cool open forest or closed montane forest throughout the last 30,000 years. The data from this site suggest a cooling of 5–7.5°C at the LGM. In Ecuador, the premontane sites of Mera and San Juan Bosco (1,100 m and 970 m, respectively; Bush *et al.*, 1990) match this interpretation closely, suggesting synchrony at least as far south as the equator.

Lake Consuelo, southern Peru, provides a detailed view of the lower Andes during the last glacial maximum (Urrego *et al.*, 2010b). At 1360 m elevation, the modern lake lies at exactly the elevation of cloud formation in this section of the Andes. The modern flora is dominated by lowland elements (e.g., *Alchornea*, *Brosimum*, *Euterpe*, *Ficus*, *Guatteria*, *Maquira*, *Unionopsis*, and *Wettinia*). Premontane elements such as *Dictyocaryum*, *Myrsine*, *Alsophila*, *Oreopanax*, and *Cyathea* are also present. The pollen types of the Holocene reflect this lowland mixture of species, but those of the glacial clearly indicate the presence of a montane forest. *Podocarpus*, *Alnus*, *Hedyosmum*, *Weinmannia*, *Bocconia*, *Vallea*, *Ericaceae*, and *Polylepis*/*Acaena* replaced the lowland flora. This flora was remark-

Table 2.1. Inferred LGM moisture from described sites in the northern and southern Andes. All ages in cal yr BP.

	Latitude (°S, unless otherwise stated)	*Elevation*	*LGM wet/dry*	*Onset of deglaciation*	*Timing of mid-Holocene dry event*	*Literature source*
Venezuela						
Cariaco Basin	10.5°N	—	Dry	—	—	Peterson *et al.* (2003), Lee *et al.* (2009)
Colombia						
Fúquene	5°N	2,580	Dry	—	—	van der Hammen and Hooghiemstra (2003)
High Plain of Bogotá	4–5°N	2,600	Dry	*c.* 24,000	—	Hooghiemstra (1984)
Popayán	2°N	1,750	Dry	*c.* 24,000	—	Wille *et al.* (2000)
Caquetá River Valley	1°N	c. 400	Dry	—	—	van der Hammen *et al.* (1992)
Ecuador						
Mera	0	1,100	Dry	*c.* 30,000	—	Bush *et al.* (1990)
San Juan Bosco	0	970	Dry	*c.* 30,000	—	Bush *et al.* (1990)
Pallcacocha	2	4,060	—	—	*c.* 7,500–4,000	Hansen *et al.* (2003)
Surucucho	3	3,180	Wet^a	—	—	Colinvaux *et al.* (1997)
Negra	7	3,300	—	*c.* 15,000	*c.* 9,000–3,800	Bush *et al.* (this volume)
Peru						
Chochos	7	3,285	—	*c.* 17,000	*c.* 9,500–7,300	Bush *et al.* (2005)
Baja	7	3,575	—	—	*c.* 9,000–6,000	Hansen and Rodbell (1995)
Huascaran	9	6,048	Dry^a	—	*c.* 8,400–5,200	Thompson *et al.* (1995)
Junín	11	4,100	—	—	*c.* 6,000	Hansen *et al.* (1994)
Junín	11	4,100	Wet	*c.* 22,000	—	Seltzer *et al.* (2002)
Marcacocha	13	3,355	—	—	—	Chepstow-Lusty *et al.* (2002)
Pacucha	13	3,050	Wet	*c.* 19,000	*c.* 10,000–8,700	Valencia *et al.* (2009), Hillyer *et al.* (2009)
Caserococha	13	3,900	—	*c.* 16,500	*c.* 7,900–4,250	Paduano *et al.* (2001)

	Latitude (°S, unless otherwise stated)	*Elevation*	*LGM wet/dry*	*Onset of deglaciation*	*Timing of mid-Holocene dry event*	*Literature source*
Consuelo	13	1,360	Wet	*c.* 21,000	*c.* 8,200–4,000	Bush *et al.* (2004)
Arequipa	16	2,350–2,750	Wet	—	Mid-Holocene	Holmgren *et al.* (2001)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	*c.* 21,000	*c.* 6,000–4,000	Paduano *et al.* (2003)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	*c.* 21,000	*c.* 8,000–5,500	Baker *et al.* (2001a)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	*c.* 22,000	—	Seltzer *et al.* (2002)
Titicaca (Peru/Bolivia)	16–17	3,810	Wet	—	*c.* 6,000–3,500	Tapia *et al.* (2003)
Bolivia						
Lago Taypi Chaka Kkota	16	4,300	—	—	*c.* 8,500–2,500	Abbott *et al.* (2000, 2003)
Huinaimarca	17	c. 3,800	Wet[a]	—	—	Mourguiart *et al.* (1997, 1998), Mourguiart (1999)
Siberia	17	2,920	Wet[a]	*c.* 21,000	*c.* 11,000–4,000	Mourguiart and Ledru (2003)
Sajama	18	6,452	Wet	*c.* 21,000	*c.* 9,000–3,000	Thompson *et al.* (1998)
Salar de Uyuni	20	3,653	Wet	—	—	Chepstow-Lusty (2004), Fritz *et al.* (2004)
Salar de Uyuni	20	3,653	Wet	—	—	Baker *et al.* (2001b)

All ages are cal yr BP.

[a] As interpreted by the authors of this chapter.

ably constant between *c.* 45 kcal yr BP and 24 kcal yr BP and was probably buffered from precipitation changes by the presence of persistent cloud cover (Urrego *et al.*, 2010). Similar vegetation descents of *c.* 1,300 m and persistent forest cover were recorded in the mid-elevations of the Colombian Andes at Pitalito (1300 m elevation; Will *et al.*, 2001) where upper montane forest rich in *Quercus*, *Hedyosmum*, *Myrsine*, and *Weinmannia* occupied the site during the LGM.

2.7 DEGLACIATION

The timing and rate of Andean deglaciation is somewhat contentious, as it has been suggested that the southern Andes mirrors the Vostok record from Antarctica, while the northern Andes mirrors the Greenland Ice Sheet Project (GISP) record (Seltzer *et al.*, 2002). It appears that the more southern tropical Andes entered a deglacial phase between 21 kcal yr BP and 19 kcal yr BP (within the classic LGM of the northern hemisphere), while the northern Andes may not have warmed until *c.* 16 kcal yr BP. This relatively early deglaciation is manifested in most of the Central Andean records (Figure 2.5).

A further issue that needs to be resolved is whether the warming associated with the deglacial period was protracted and steady or if it occurred rapidly. Abrupt changes in fossil pollen records are certainly apparent in almost all high Andean locations, but whether the sudden change was due to temperature or changes in precipitation and fire regime has yet to be established fully.

On present evidence, the trend out of the last ice age appears to be more gradual in the southern tropical Andes than in the northern Andes. The gradualism of the southern sites could be argued to be buffered by the maximum rate of tree migration (i.e., the forest cannot respond to maintain equilibrium with climatic change). However, abrupt changes in forest abundance are evident in many high Andean settings (e.g., Hansen *et al.*, 2003; Niemann and Behling, 2009; Valencia *et al.*, 2010), where the communities were clearly responding to rapid pulses of climate change.

Further investigation is needed into the role of microrefugia (McGlone and Clark, 2005; Rull, 2009; Mosblech *et al.*, 2011), and how these may have influenced the timing of observed migrations. For the time being, the migrational data appear to support an Antarctic-style deglaciation in the Andes south of *c.* 10°S, while further north (perhaps progressively), paleoclimate records appear to reflect the characteristic climatic oscillations of the North Atlantic and Greenland. Consequently, in Peru and Bolivia the deglaciational warming appears to have been on average <1°C per millennium, whereas in the northern Andes a relatively large jump in temperatures at the onset of the Holocene, perhaps 4°C within the space of few hundred years, is thought to have occurred. Thus, these systems have responded to warming events whose rates differed by about an order of magnitude.

The deglacial period highlights periods of rapid landscape change. The upslope expansion of forest taxa and novel climates (*sensu* Williams *et al.*, 2007) jumbled competitive relationships producing short-lived formations that are rare today, or

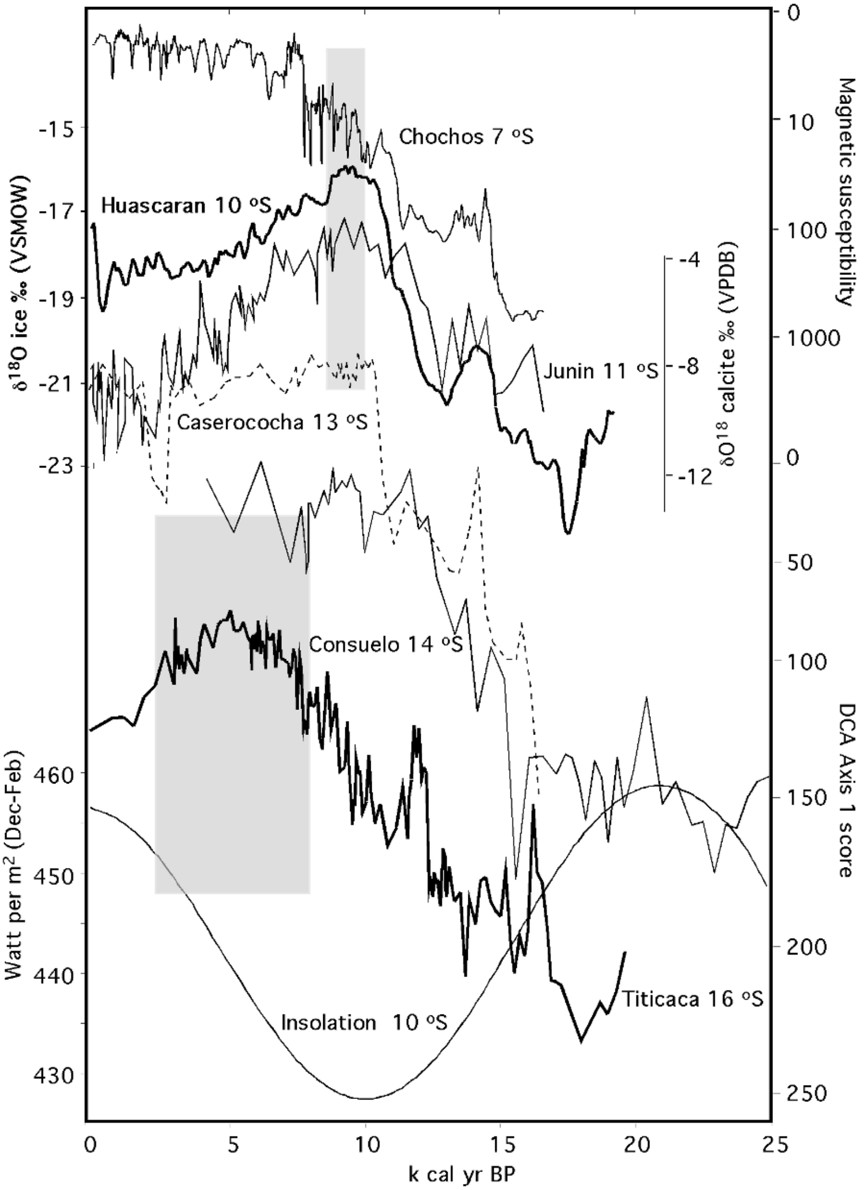

Figure 2.5. Central Andean insolation, and the extent of physical and community change during deglaciation and the Holocene. Datasets are Lake Chochos magnetic susceptibility (note inverted log scale; Bush *et al.*, 2005); Huascaran δO^{18} ice core (Thompson *et al.*, 1995); Lake Junin δO^{18} calcite (Seltzer *et al.*, 2000); Lake Caserococha fossil pollen DCA Axis 1 (Paduano, 2001); Lake Consuelo fossil pollen DCA Axis 1 (Bush *et al.*, 2004; Urrego *et al.*, 2010); Lake Titicaca fossil pollen DCA Axis 1 (Paduano *et al.*, 2003); Insolation (DJF) for 10°S from Analyseries1.2 (Berger, 1992; Paillard *et al.*, 1996). Shaded boxes represent periods of low-lake level or drought recorded at those sites.

possibly without modern analog. However, some of the rapid changes in community structure associated with deglacial settings may indicate a longer no-analog status within the forests. For example, the important tropical families of Moraceae and Urticaceae, which produce copious amounts of pollen, and are important components of every modern mesic Neotropical forest pollen record, do not appear to have been equally abundant in glacial times at any elevation (Valencia *et al.*, 2010). If further research supports this view, the glacial-age rarity of these families, especially the Moraceae, would have had profound impacts on forest ecology.

Evidence for the presence, or absence, of the Younger Dryas event in South America has engendered considerable debate (Heine, 1993; Hansen, 1995; Van der Hammen and Hooghiemstra, 1995; Rodbell and Seltzer, 2000; Van't Veer *et al.*, 2000; Bush *et al.*, 2005). In the sedimentary sequences from Guatemala (Hodell *et al.*, 2008), the Cariaco Basin (Peterson and Haug, 2006), and Colombia reveal a strong and apparently synchronous climatic event corresponding to the Younger Dryas (e.g., Van't Veer *et al.*, 2000). However, other records, such as those of Titicaca and of glacial advances in Ecuador and Peru, reveal an oscillation that predates the Younger Dryas by 500 years (Rodbell and Seltzer, 2000; Paduano *et al.*, 2003). In summary, it appears that the Younger Dryas is better represented in the northern section of the neotropics than south of the equator. In the northern tropics the Younger Dryas appears to be manifested in both temperature and precipitation signals, whereas in the southern tropics, precipitation provides the best cue for this event (Clapperton, 1993; Rodbell and Seltzer, 2000; Smith *et al.*, 2005).

2.8 THE HOLOCENE

Further south in Ecuador, the related sites of Surucuchu (3,180 m; Colinvaux *et al.*, 1997) and Pallcacocha (4,200 m; Moy *et al.*, 2002) begin their sedimentary record at *c.* 15 kcal yr BP. These two sites lie in the same drainage basin and each has a markedly laminated stratigraphy. The laminations have been suggested to reflect El-Niño-related storm intensity (Rodbell *et al.*, 1999; Moy *et al.*, 2002). While these sites cannot inform us of climate change in the Pleistocene, they do suggest an affinity with the Colombian sites rather than sites of southern Peru and Bolivia that show a very marked dry event in the Mid Holocene (Wirrmann *et al.*, 1992; Ybert, 1992; Paduano *et al.*, 2003; Rowe *et al.*, 2003). Again the southern and northern sites appear to be asynchronous in their precipitation signals, with all sites north of Junin exhibiting a dry start to the Holocene followed by rising lake levels between 10 kcal yr BP and 8 kcal yr BP. Sites in the southern tropical Andes are generally entering a dry phase at that time, and experience low lake levels until *c.* 4 kcal yr BP (Bradbury *et al.*, 2001). The only record from the southern tropical Andes that spans a portion of this event is Lake Siberia (Mourguiart and Ledru, 2003). This record terminates at *c.* 5.1 kcal yr BP, but the period from 10 kcal yr BP to 5 kcal yr BP shows the expansion of grassland, consistent with more open conditions, but the return of some forest taxa in the uppermost samples.

When records resume regionally, human impacts are evident in many sites (e.g., Marcacocha (Chepstow-Lusty *et al.*, 2002), Titicaca (Paduano *et al.*, 2003), Pacucha (Valencia *et al.*, 2010), and Junin (Hansen and Rodbell, 1995); the uplands were being transformed by burning and deforestation). The modern upper forest line may be a result of millennia of manipulation. How different a truly natural upper forest line would be from that observed in the modern Andes is a matter of ongoing debate. Ellenberg (1958) suggested that *Polylepis* could have formed extensive woodlands up to elevations of 4,000 m on the wetter slopes and 5,000 m on the drier slopes of the Andes. Though falling from favor for many years, his ideas have been resurrected (e.g., Fjeldså, 1992; Kessler, 1995). No resolution has been reached regarding either the natural elevation of upper forest lines, or the past importance of *Polylepis* in Andean floras. Gosling *et al.* (2009) suggested that *Polylepis* was most abundant as a member of transitional communities between full glacial and interglacial conditions. Other evidence of the migration of upper forest lines has been largely equivocal with modest or no migration reported in the last few thousand years in Colombia and Ecuador (Wille *et al.*, 2002; Bakker *et al.*, 2008; Di Pasquale *et al.*, 2008). Two patterns have emerged: the first is that the often stark separation of forest and grasslands is an artifact of millennia of human landuse (Young and León, 2006). The second observation is that human impacts on the Andes have been taking place for thousands of years, and that the "natural" state or ecological baseline is often unknown.

While humans altered the highland landscape, it is also probable that climate influenced human populations. The Mid Holocene drought on the Altiplano induced a period termed the "Silencio Arqueológico" in which there was widespread abandonment (Núñez *et al.*, 2002). Where did these populations go? Into the montane forest? The Lake Siberia record shows an increase in charcoal coincident with the peak of this drought (Mourguiart and Ledru, 2003). Whether these fires resulted from human occupation of a moister site than could be found in the highlands, or whether this area was merely more drought prone has yet to be resolved. Later droughts are implicated in the cultural collapse of civilizations such as the Huari, Tiwanaku, and Chiripó (Brenner *et al.*, 2001; Chepstow-Lusty *et al.*, 2002). Too few records exist to document the effect of these Late Holocene droughts on montane forests and these are data that are badly needed.

2.9 THE PAST AS A KEY TO THE FUTURE

The potential for previous interglacials to serve as a guide to the climatic future of the Holocene has attracted considerable attention (e.g., Ruddiman, 2003; Broecker, 2006). That the full biodiversity of the Andean system appears to have survived the intensity of MIS 5e offers some hope that systems will be able to adjust to the next 50–100 years of projected climate change. Most of the climate simulations project the Amazon Basin to become warmer and drier over the next century, and for a warming of tropical mountains to be about 2–3°C (IPCC, 2007). Estimates of species migrational responses to such climate change suggest that the tropical Andes will be one of the most sensitive regions to biome-level change; that is, the Andes have a high proportion of pixels representing the region that changes from one biome type to another (Malcolm *et al*., 2006).

Melting tropical icecaps (Thompson *et al*., 2002) and the upslope migration of species (Pounds *et al*., 1999) represent evidence that these changes are already taking effect. The stress of warming, may induce complex interactions (e.g., between droughts, chytrid fungae, and frogs), that may lead to extinctions (Pounds, 2001; Pounds *et al*., 2006).

The rate of response of communities to climate change has been tested in temperate northern latitudes by rapid warming events such as the termination of the Younger Dryas. That warming was similar in its rate of change to the anticipated warming of the next century. If the tropics were similarly exposed to rapid warming, and there was no corresponding wave of extinction, we might be able to predict a sturdy migrational response that would accommodate climate change. However, such a clear, sharp warming is evident in montane Colombia, but lacking in lowland Peru.

The flat spot in the ^{14}C record that provides relatively large possible calibration solutions between *c*. 10,000 and 11,000 ^{14}C years often frustrates efforts to provide a definitive chronology. From the available records, it appears that there was no rapid warming at the onset of the Holocene in much of Amazonia and the tropical Andes. Species in the biodiversity hotspots of the Peruvian Andes have not contended with change faster than *c*. 1°C of warming per millennium (Bush *et al*., 2004) and therefore while the range of temperatures projected for the next 50–100 years may be within their Quaternary experience, the rate of climate change probably is not.

2.10 CONCLUSIONS

Paleoecological research in the Andes has provided some exciting insights into the both long-term migrations of species and also responses to rapid climatic oscillations. In Europe and North America the accumulation of thousands of pollen records allowed Holocene migrations to be mapped in great detail. From those studies emerged the understanding that temperate communities are ephemeral, perhaps the most important ecological insight to arise from Quaternary paleoecology. However, simply applying the rules of temperate ecology to the tropics has been shown repeatedly to be unwise. The Andes offer a very different migratory environment to the great plains of Europe and eastern North America. The Amazonian lowlands are often separated from Andean snows by <30 km. The complex topography of Andean valleys, ridges, and streambeds offer a mass of microhabitats that can range from xeric scrub to lush forest in a few tens of meters. The consequence of this heterogeneity is that migration could have been nearly instantaneous rather than lagging by thousands of years. Under these circumstances continuity of habitat availability, rather than ability to migrate in and out of refugia, may be the key to diversity.

Paleoecological records from the Andes show a remarkable continuity of montane forest availability for species. Although the area with ground level cloud moved up and down a mountain, it appears probable that this niche has been a continuous feature of the environment since the Andean orogeny created uplands high enough to induce cloud formation. Where it can be measured, rates of community change are low for tens of millennia, though communities are changing throughout that time. Novel assemblages arose due to continental-scale, as well as local, migrations, but the overall niche of living within a montane forest may have changed less than its cloud-free counterparts up and downslope.

Regional asynchrony is a feature of the paleoeclimatic literature with Lake Junin, Peru (11°S) cited as the southernmost record that had a full glacial precipitational pattern common to sites south of Mexico (Bradbury *et al.*, 2001; further south tropical systems were somewhat out of phase with this northern group of sites). However, Seltzer *et al.*, (2000) argue that moisture change between Lake Junin and sites in the Caribbean were asymmetric in the Holocene. This latter argument is based on the apparent fit of moisture availability and regional wet season insolation. These apparently contradictory assessments can be reconciled by recognizing the temporal migration of the Inter Tropical Convergence Zone (ITCZ) (southward in stadial events and northward in the early Holocene (e.g., Haug *et al.*, 2001)), producing a climatic equator that is not geographically constant. The important points that can be derived from the paleoecological data are that precipitation and temperature patterns varied substantially with latitude along the tropical Andes, and that regions exhibiting synchronous changes in one period could be asynchronous in another.

The paleoecological record needs to be incorporated into conservation thinking to devise appropriate strategies to avert an imminent loss of biodiversity. However, for paleoecology to become genuinely integrated with conservation science we will need to provide more detailed records, especially increasing our taxonomic precision. Furthermore, new paleoecological records from the montane forest region are desperately needed to expand our spatial dataset and test the many emerging theories relating to this fascinating ecosystem.

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3

Climate and vegetation change in the lowlands of the Amazon Basin

M. B. Bush, W. D. Gosling, and P. A. Colinvaux

3.1 INTRODUCTION

Data from palynology, taxonomy, and isotopic analyses, allied to climate models, reveal the complexity of the history of Amazon ecosystems. Evidence from these records suggests that Pleistocene climatic change was neither uniform nor synchronous across the basin, but that its effects were pervasive.

A major obstacle to Amazon paleoecology is paucity of lakes containing uninterrupted sedimentary sequences spanning one or more glacial cycles. To date, the only fossil pollen records from lowland Amazon lake sediments to span the Last Glacial Maximum (LGM) are those of Carajas (Absy, 1991), Maicuru (Colinvaux, 2001), three from the Hill of Six Lakes (Colinvaux, 1996; Bush, 2004a), together with Lakes Chaplin and Bella Vista on the southwestern forest–savanna ecotone in Bolivia (Mayle, 2000; Burbridge, 2004) (Figure 3.1). All of these are relatively small, shallow bodies of water that are vulnerable to desiccation. That these lakes retained water for most of their $>50{,}000$-year histories is testament to the relative constancy of Amazonian precipitational regimes. However, none of these records presents an ideal archive, as they all contain sedimentary gaps or extremely slow rates of sediment accretion, are not necessarily located in optimal locations for studying past climate change, and only represent a small portion of the Quaternary. These lake records are supplemented by the pollen history of the Amazon lowlands from sediments of the Amazon fan (Haberle, 1997; Haberle and Maslin, 1999) and records near the upper limits of wet Amazon forest on the flanks of the Andes. These lower montane records include Lake Consuelo at 1,360-m elevation in Peru (Bush, 2004b), and Mera (1,100 m) and San Juan Bosco (970 m) in Ecuador (Liu and Colinvaux, 1985; Bush, 1990) (Figure 3.1).

A combination of new paleoecological records, improved understanding of climate systems, and the proliferation of molecular phylogenetic data advanced understanding of past climate and vegetation change within the Amazon Basin.

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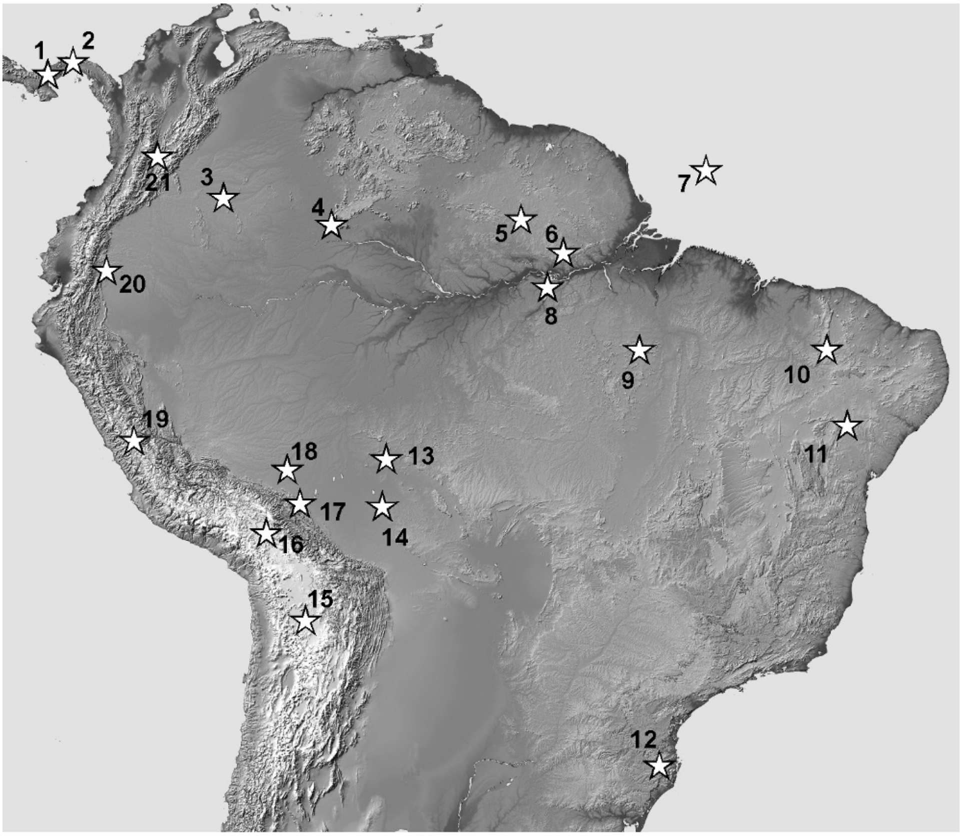

Figure 3.1. The location of paleoecological sites mentioned in the text in relation to topography. Citations are given for locations not specifically identified in text: (1) Lake Gatun (Bartlett and Barghoorn, 1973); (2) El Valle; (3) Loma Lindo (Behling and Hooghiemstra, 1999); (4) Hill of Six Lakes (Pata, Verde, and Dragao; (5) Maicuru; (6) Geral, Santa Maria, and Saracuri (De Toledo, 2004); (7) Amazon fan; (8) Tapajos; (9) Carajas; (10) sites in northeastern Brazil (Stute *et al.*, 1995); (11) Lapa dos Brejões and Toca da Barriguda caves (Wang *et al.*, 2004); (12) Botuverá cave; (13) Acre transect (Pessenda *et al.*, 1998); (14) Lakes Chaplin and Bella Vista (Mayle *et al.*, 2000); (15) Salar de Uyuni; (16) Titicaca (Paduano *et al.*, 2003); (17) Lake Consuelo; (18) Gentry, Werth, Parker, Vargas (Listopad, 2001; Bush, new data); (19) Junin; (20) Mera and San Juan Bosco; (21) High Plain of Bogotá.

The nature of Amazon climate during the last glacial period and its impact on vegetation continues to be actively debated. The focus upon glacial and interglacial climate differences was driven by a desire to determine the significance of these global cycles in the origins of the astonishing biodiversity found within Amazonia (Haffer, 1969; Colinvaux *et al.*, 2001; Haffer and Prance, 2001). As new evidence emerged a consensus developed that during the last glacial period climates were cooler and drier than today.

The transition from no empirical data of past Amazonian climates to a little, revealed that climatic changes were not uniform or synchronous across the basin. The climate changes at the LGM (*c.* 21 kcal yr BP) seem to have resulted in a constriction of the forested area at the margins of the Amazon Basin, but did not cause a basin-wide fragmentation of the forest. The degree to which glacial Amazon forests differed from those of the Holocene, however, remains ambiguous. Evidence from Holocene records suggests that a dry event (*c.* 7–5 kcal yr BP) impacted dramatically upon the vegetation in some areas but not others. The picture of heterogeneous climate and vegetation change within the Amazon Basin should not be a surprise. The vast area, diversity of ecosystems, and spatial variation in climate systems suggest that any uniform, basin-wide climate change or vegetation response is unlikely. In this chapter, we discuss the nature of the climate in the Amazon Basin during the last glacial period and the impact of Mid Holocene drying on the vegetation. Finally, we examine new phylogenetic data in the light of this paleoecological understanding to gain an insight in to the likely origins of Amazonian biodiversity.

3.2 EVIDENCE OF TEMPERATURE CHANGE

3.2.1 The last glacial period

The first evidence that Amazonia experienced substantially cooler-than-modern conditions during the last ice age came from the discovery of *Podocarpus* timbers in an exposure of silty peat near the town of Mera, Ecuador, at 1,100-m elevation (Liu and Colinvaux, 1985). *Podocarpus* spp. are generally found in cloud forests above 1,800 m, and this observation was used to draw the inference of a *c.* 800-m descent of *Podocarpus* populations at *c.* 30–36 kcal yr BP. Indeed, because *Podocarpus* is not restricted to modern montane forests, Gentry (1993) lists four species that occur above 1,800 m and one that is found in the lowlands—the use of this genus as a paleoecological indicator of cooling has been criticized (van der Hammen and Hooghiemstra, 2000). However, further work on Mera and the site of San Juan Bosco that lay about 160 km to the south of Mera (Bush *et al.*, 1990) revealed a suite of macro- and microfossils of additional taxa that were similarly most abundant in modern montane forests. *Drimys*, *Alnus*, *Weinmannia*, and *Hedyosmum*, were found to be abundantly represented in glacial age samples that also were depauperate in the taxa currently associated with this elevation—for example, *Cecropia*, Urticaceae/Moraceae, *Iriartea*. This finding reinforced the probability that these sites supported cold-adapted elements at the peak of the last ice age. Every Pleistocene-aged pollen record recovered from Amazonia provides similar evidence of cool-tolerant populations moving into the lowland forests. In each case, floral elements became abundant 800 m to 1,500 m below the modern centers of their population. Similar patterns have been found in regions adjacent to the Amazon Basin—for example, southern and central Brazil (de Oliveira, 1992; Ledru, 1993; Salgado-Labouriau, 1997), the Andes (reviewed in Chapter 2), and Central America (Bartlett and Barghoorn, 1973; Bush and Colinvaux, 1990).

Quantifying this cooling has relied on translating the altitudinal descent of species into temperature change via the moist-air adiabatic lapse rate, generally taken to be *c.* 5.5–6°C. Hence, the observed 800-m to 1,500-m descent of thermally sensitive populations translates into a 4°C to 7°C cooling. A similar estimate of cooling was developed from the isotopic analysis of groundwater in eastern Brazil. Stute (1995) found the temperature of "fossil" groundwater to be *c.* 5°C cooler than that of groundwater formed under modern conditions.

Van der Hammen and Hooghiemstra (2000) and Wille (2000) have argued for a flexible lapse rate during the ice ages that would significantly steepen the temperature gradient from the lowlands to the highlands. Their contention is that the Colombian Andes at 2,580 m cooled by *c.* 8°C while the lowlands cooled only between 2.5 and 6°C (according to the data source). If these are taken at face value, one interpretation is that the moist-air adiabatic lapse rate must have steepened. The implied lapse rate to accommodate the difference in montane versus lowland temperature increases from a modern rate of *c.* 6°C in Colombia (Wille, 2000) to unrealistically high values of between 6.7 and 8.1°C. Such high lapse rates are unlikely as they imply very dry air, and—given that no mid-elevation Andean setting with that kind of aridity has been documented so far—a flexible lapse rate is not the solution to the observed variability in data. The moist-air adiabatic lapse rate is controlled by atmospheric humidity and is not seen to vary greatly from one tropical setting to another despite differences in precipitation and seasonality—that is, it is almost always 5.8 ± 0.5°C per 1,000 m of elevation. While narrow fluctuations can be expected through time, lapse rates are unlikely to vary beyond a constrained range (Rind and Peteet, 1985).

On first principles it is difficult to envisage a very strong change in lapse rate in humid sections of the Andes, and yet the foothill regions consistently provide a slightly lower (typically 5°C change) temperature reconstruction than the highlands (typically 8°C change). Given that the LGM in Colombia was dry (Hooghiemstra and van der Hammen, 2004), while it was wet in Peru and Bolivia (Baker, 2001), we can assume that lapse rates may have risen close to *c.* 6.3°C in Colombia and been near modern (i.e., 5.5°C) in the central Andes. However, these changes are inadequate to describe the *c.* 3–6°C discrepancy between the lowlands and the uplands. We advocate taking a step back and considering other mechanisms than lapse rate change to account for the observed data.

We observe that paleovegetation response in mountains does not provide a pure temperature signal and is likely to be exacerbated by factors correlated with elevation. If not parsed out, these factors can lead to an exaggerated paleotemperature change estimate. For example, changes in black body radiation due to lowered atmospheric CO_2 content (Bush and Silman, 2004 and Chapter 10) and feedback mechanisms involving ultraviolet radiation (Chapter 8) are more extreme with increasing elevation. With a thinner atmosphere—that is, LGM conditions of 170 ppm CO_2 and 350 ppb CH_4 compared with pre-industrial Holocene concentrations of 280 ppm CO_2 and 650 ppb CH_4—more heat is lost during night-time re-radiation of stored heat than under modern conditions. This black body radiation effect would increase with elevation, be strongest under cloudless skies, and might add an apparent *c.* 2.3°C of cooling to the true change in temperature (Bush and Silman, 2004). As it is the coldest night-time temperatures that a plant must survive, the black body radiation imposes an additive thermal stress that can cause mortality as physiological thresholds are exceeded. This mechanism provides one example, more probably exist, contributing to the differential migration distances in montane and lowland settings.

Although the seminal work on the High Plains of Bogotá set a new path for Neotropical paleoecology, many other records now exist that suggest somewhat more modest temperature departures both in the lowlands and in the mountains than the reported 7–9°C. Thus, we suggest that the migration of tree line as inferred from the pollen records is accurate, but that there may be more mechanisms at work than simply temperature change contributing to those shifts. If estimates of glacial descent and Equlibrium Line Altitude (ELA) (Seltzer, 1990; Rodbell, 1992; Seltzer, 2003; Smith, 2005) are also considered, the actual LGM cooling at all elevations may have been *c.* 4–6°C, making it more consistent with data obtained from marine paleotemperature reconstructions (Ballantyne, 2005).

It is important to note that this degree of cooling was not temporally uniform throughout the last ice age and that there were other high-magnitude changes (comparable with the Pleistocene/Holocene transition) during this period. That all the lowland records contain gaps in sedimentation makes it difficult to put a firm timeline on when Amazonia was coldest. At the Hill of Six Lakes, montane taxa are clearly abundant in samples that are radiocarbon-infinite in age, and they have their peak occurrence between 21 kcal yr BP and 18 kcal yr BP (Bush, 2004a). Looking farther afield, Lake Titicaca and Lago Junin in the Peruvian Andes were probably coldest between *c.* 35 kcal yr BP and 21 kcal yr BP (Hansen 1984; Seltzer, 2000; Smith, 2005). But, at the lowest elevation of modern cloud formation, the record from Lake Consuelo (1,360-m elevation) indicates a protracted, steady cooling of about 6°C between 40 kcal yr BP and 22 cal yr BP (Urrego, 2005). In some records, particularly those in eastern Amazonia and coastal Brazil (de Oliveira, 1992; Ledru, 1993; Behling, 1996; Behling and Lichte, 1997; Haberle and Maslin, 1999; Ledru, 2001; Sifeddine, 2003), cold-tolerant taxa persist and in some cases reach their peak abundance as late as 14 kcal yr BP, when western Amazonian and selected Andean records are showing considerable, steady, warming (Paduano, 2003; Bush, 2004b). Such short-term variability has yet to be explained, but it is a marked characteristic of these records that climatic events are neither synchronous nor basin-wide.

3.2.2 The Holocene

With so many questions regarding the ice age climates of Amazonia, those of the Holocene have received less attention than they deserve. Servant (1981) wrote of a major Holocene drought and Meggers (1994) discussed the potential impact of climate change on human societies. The role of human occupation and its impact on the landscape of Amazonia and Central America is a matter of active debate (Denevan, 2003; Heckenberger, 2003; Meggers, 2003) and is addressed by Piperno (Chapter 6).

Independent of the archeological record speleothem data from Cueva del Tigre Perdido (Peruvian Amazon, 7°S) suggests that temperature has varied by *c.* 4°C during the last 10,000 years in the lowlands (van Breukelen *et al.*, 2008). Two warm peaks, at *c.* 5.5 kcal yr BP and 8.9 kcal yr BP, indicate that temperature has not been stable though the current interglacial. Unfortunately, there are no other equivalent estimates of Holocene temperature from elsewhere in the Amazon Basin. However, it seems reasonable to assume that, like the glacial–interglacial transition, variations within the Holocene were not spatially uniform in magnitude or timing.

3.3 EVIDENCE OF PRECIPITATION CHANGE

3.3.1 The last glacial period

The topic of Amazonian precipitation has been divisive, and positions for or against Amazonian aridity relatively entrenched. We have been proponents of an Amazonian system that remained relatively moist during the last ice age, a view contrasted by those who see Amazonia as having been much drier than present (e.g., Haffer, 1969). At first, it was easy to argue either position as the field of debate was uncluttered by empirical data. Now both sides are drifting toward the middle as we recognize that Amazonia did not dry out sufficiently to fragment its forests, but that relatively dry periods that lasted for perhaps as much as 11,000 years were a reality. Furthermore, some migration of the forest boundary, and its replacement by semi-deciduous dry forest or even savanna close to ecotonal boundaries is indicated both by paleoecological studies and models (Absy, 1991; Behling and Hooghiemstra, 1999; Cowling, 2004; Cowling, 2004).

The only long terrestrial sedimentary records that span a significant portion of the last glacial cycle come from a string of massifs that arc from northwestern Amazonia across eastern Amazonia down to the south. The Hill of Six Lakes (three records), Maicuru, and Carajas are the five longest Amazonian paleoecological records, and all come from lakes that sit atop edaphically dry massifs or inselbergs. All five records contain a sedimentary hiatus, but the timing of these hiatuses differs between the sites. It is thought likely that these hiatuses are the product of dry periods. At the Hill of Six Lakes the dry event is most intense between *c.* 40 kcal yr BP and 27 kcal yr BP (Bush, 2004a), at Maicuru it is most intense between 33 kcal yr BP and 19 kcal yr BP (Colinvaux, 2001), while Carajas is driest between 28 kcal yr BP and 16 kcal yr BP (Absy, 1991; Ledru, 2001). Hence, during the Late Pleistocene relatively short dry events occurred asynchronously across the basin. Of these sites, only Carajas appears to have shifted away from a forested setting at any time in the last 180 kyr.

The sensitivity of lowland Neotropical ecosystems to short-term fluctuations in moisture availability was revealed by the fossil pollen record of the marine cores obtained from the Cariaco Basin, on the northern continental shelf of Venezuela (Gonzalez *et al.*, 2008). The moisture balance in the Cariaco Basin, was linked to northern hemisphere climate events (e.g., Heinrich and Dansgaard/Oeschger events) and was sensitive to the movement of the Intertropical Convergence Zone (ITCZ) (Peterson and Haug, 2006). Interaction between these climate controls resulted in multiple millennial scale humid/dry oscillations from *c.* 68 to 27 kcal yr BP. The regional vegetation responded to the moisture availability change by switching between three modes:

1. humid (interstadial) conditions that resulted in a greater abundance of evergreen and semi-deciduous taxa,
2. drier (stadial) conditions that were characterised by mountain forest and marshland taxa, while
3. the driest conditions, coincident with Heinrich events, saw an expansion of salt marsh taxa.

We can anticipate that the Atlantic circulation also influenced Amazonia, providing a basic driver of sub-millennial-scale change.

The records of lake level suggest both a west-to-east and south-to-north variation in climate history within the basin. Comparison of isotope records obtained from speleothems across South America suggested that precipitation on the eastern and western sides of the continent was in antiphase (Cruz Jr. *et al.*, 2009). Global circulation models of Amazonian climatic responses at the LGM are similarly regionalized with opposing signatures of precipitation change evident across the basin (Hostetler and Mix, 1999; Vizy and Cook, 2007). Indeed, climatic responses to the modern El Niño–Southern Oscillation (ENSO) reiterates this regionalization with markedly different climatic responses across the basin (Bush and Silman, 2004). The over-arching conclusions are that scenarios calling for a uniform basin-wide climate change are inherently implausible, and that when dry events occurred they were relatively short-lived. Equally, it is unlikely—in view of the variation in hydrology, topography, soils, and species richness of Amazonia—that the highly diverse vegetation responded uniformly to a given forcing.

3.3.2 The Holocene

Although many Amazonian lakes were filled by the Early Holocene, sedimentary hiatuses in many records suggest a widespread Mid-Holocene dry event (Servant, 1981; Absy, 1991; Mayle, 2000; Burbridge, 2004; Bush, 2004a; Gonzalez *et al.*, 2006; Bush *et al.*, 2007). In the Andes on the south-western edge of the Amazon Basin drying between 7 kcal yr BP and 5 kcal yr BP induced the highest rates of change and caused the most significant reorganisation of the cloud forest during the last *c.* 46 kcal yr BP (Urrego *et al.*, 2010). However, the timing of this event and its severity is not uniform across the basin. In central Amazonia records from Lakes Geral (Bush, 2000) and the Tapajos (Irion, 2006) suggest a very modest drying compared with most other sites. Even in some more marginal areas there is evidence that vegetation was not impacted by Holocene drying. Isotope analysis of soils in the forests and savannas of French Guiana indicate resilience to any dry event (Freycon *et al.*, 2010). In general, this dry event reaches its peak between 7 kcal yr BP and 4 kcal yr BP, and—though no direct link has been shown—this is the period when ENSO was very weak (Sandweiss, 2001). However, as more records accumulate, it appears that this was not a single sustained drought, but a period of increased drought probability compared with the Early or Late Holocene (Bush *et al.*, 2007).

3.4 CHANGES IN ATMOSPHERIC CO_2

Continental-scale simulations of the response of ecosystems to reduced CO_2 suggested that dry forest and savannas occupied the modern ecotonal areas, particularly in the southern Amazon Basin (Mayle and Beerling, 2004; Mayle *et al.*, 2004; Beerling and Mayle, 2006). Vegetation dynamic models from the Amazon Basin confirmed that "natural" rainforest could have been resilient to Late Quaternary changes in precipitation, temperature, and CO_2 (Cowling and Shin, 2006). Lowering atmospheric concentrations of CO_2 is generally considered to induce drought stress in plants with a C_3 photosynthetic pathway, as they must have their stomates open longer than C_4 plants to assimilate enough CO_2 for growth. In very dry systems plants that have C_4 or CAM pathways, which can open and close stomata to retain water and photosynthesize more efficiently under intense light and temperatures, may displace C_3 species. However, such a change is not detected in any of the paleoecological records during the period of relatively lower atmospheric CO_2 concentrations. These observations are consistent with the lack of observed changes in $^{13}C : ^{12}C$ ratios across a transect of ecotonal sites in southern Brazil that straddle the Pleistocene–Holocene boundary (Pessenda, 1998). Cowling has suggested that lower CO_2 at the LGM induced plants to support reduced leaf area indices and forests to be structurally simpler (Cowling, 2001, 2004; Cowling, 2004). If such systems had more light and higher rates of evaporation at the soil surface the ramifications would be far-reaching for microclimates and soil carbon flux. Clearly, the role of CO_2, and the adaptations that plants show toward it, is an important area of research and provides a substantial variable that is hard to quantify.

Although there has been considerable emphasis on the potential role of CO_2 as a potent limiting factor in the Late Pleistocene, an alternative view is also worth considering. Due to the temporal asymmetry of ice ages it can be argued the rate of change in atmospheric CO_2 concentrations was much slower in the transition into cold episodes than during the warming associated with the onset of interglacials (Figure 3.2). Fast increases in CO_2 concentration may have acted as a fertilizer and influenced community structure, but the declines in CO_2 were so slow there may have been little negative effect on productivity. The Vostok ice-core data reveal rates of change seldom exceeding 0.001 ppm and averaging 0.0001 ppm when CO_2 concentrations were falling (Figure 3.2). Given that modern seasonal oscillations in CO_2 are about 5 ppm, the changes imposed on plants drifting towards an ice age were imperceptibly slow and may have been within the range accommodated by natural selection, thereby minimizing its effect.

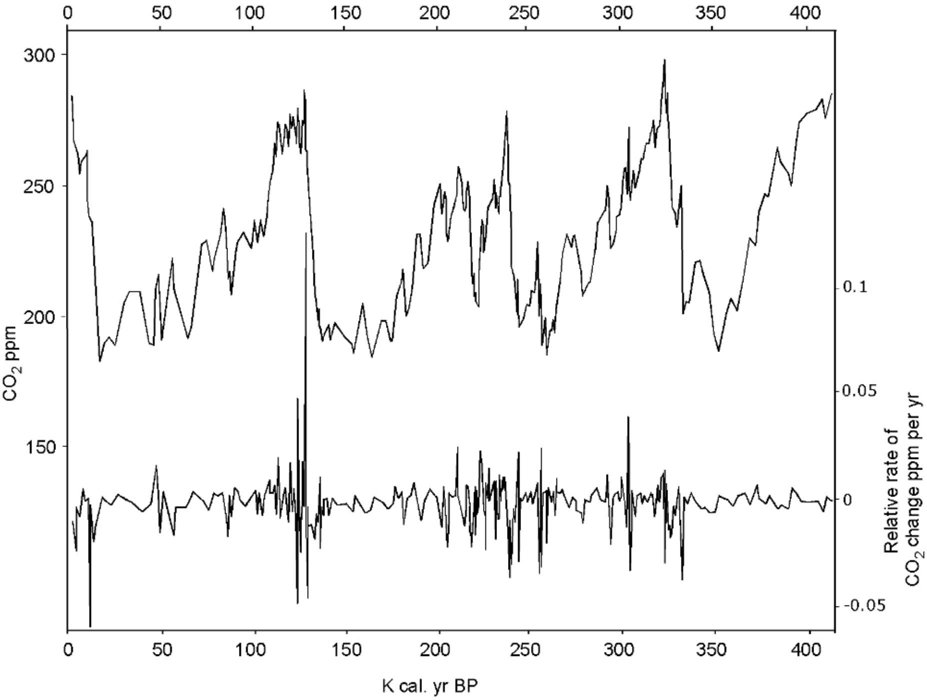

Figure 3.2. CO_2 concentrations from the Vostok core (Petit *et al.*, 1999) (*upper line*) and the relative rate of change in CO_2 concentrations between samples (*lower line*).

3.5 THE PERIODICITY OF CHANGE

For substantial periods western Amazonian and southern Andean sites do appear to have similar histories. Sedimentary records in the Colombian Andes, the Bolivian Andes, the Chilean pampas, and the Cariaco Basin all reflect precessional forcing during the last 50,000 years, and so too does the paleoecological record of Lake Pata in the Hill of Six Lakes (Bush, 2002). Records from speleothems collected in southern and northeastern Brazil also document a precessional pattern in moisture supply (Wang, 2004; Cruz, 2005).

However, upon closer inspection, some other patterns emerge. Although precessional forcing is evident in all these records, the Colombian Andes are out-of-phase with the southern Andes (Bush and Silman, 2004), which is not surprising as the wet season for each occurs 6 months apart. Consequently, precipitation in Colombia is in phase with July insolation, whereas that of Titicaca correlates with December insolation. Interestingly, the highstands and lowstands of Lake Pata (0° latitude) are in phase with those of Lake Titicaca (17°S) and so a simple geographic placement of the site is not enough to predict the orbital forcing. The clue to the connection comes from the speleothem record from Botuverá Cave near Rio de Janeiro in southeastern Brazil. This record reveals an oscillation in the strength

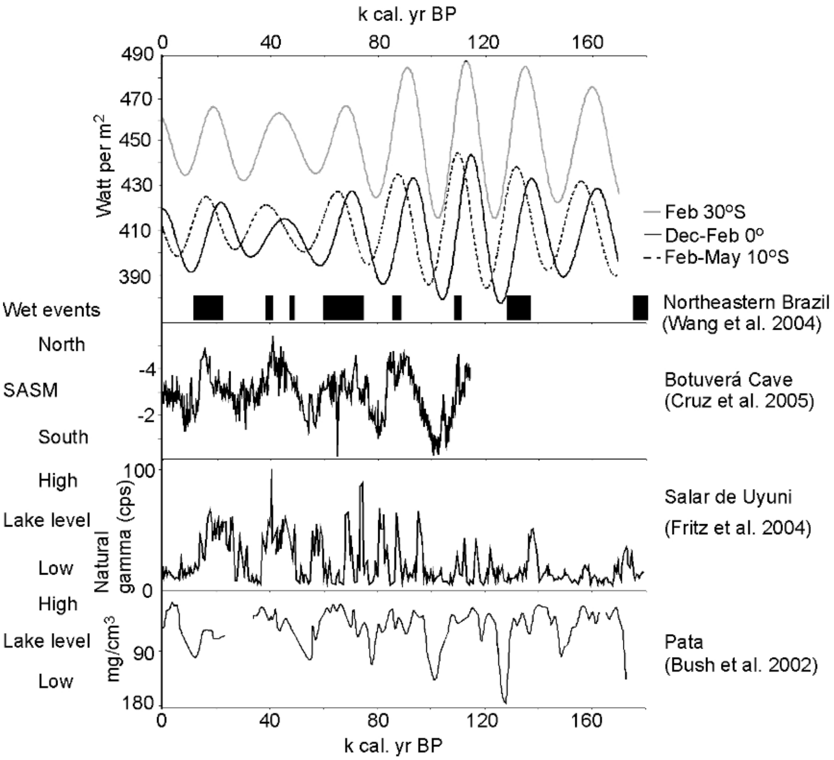

Figure 3.3. Precipitation data for Amazonia based on satellite monitoring (TRMM) showing the corridor (*dotted lines*) identified by Nepstad *et al.* (1994) where evergreen trees are dependent on deep soil moisture.

and position of the South American Summer Monsoon (SASM) resulting from changes in insolation intensity (Cruz, 2005) (Figure 3.3). SASM is driven by the convective activity over Amazonia and fed moisture via the South American Low-Level Jet (SALLJ). The SALLJ is strengthened as convection intensifies with the net result of drawing more moisture from the northern tropical Atlantic into Amazonia. As most of the basin heats most strongly in December, this sets the precessional rhythm for sites receiving moisture from the American Low-Level Jet (ALLJ) (Bush, 2005). The position of SASM is influenced by convection, so that during strong convection SASM expands farther south, bringing rain to Botuverá Cave. During weaker convection Amazonia is drier and SASM is more restricted in its southerly range. SASM expands progressively southward during the austral summer and so the best correlation with orbital forcing is obtained by tracking peaks in February (late summer) insolation (Figure 3.3). SASM also transports Amazonian moisture to the Altiplano, and hence lake levels in the Titicaca and the Salar de Uyuni records, but here it is the entire wet season that is the time of critical insolation (December–February).

Another tantalizing speleothem data set from eastern Brazil shows a precessional pattern with wet peaks aligning to austral autumn (February–May) peaks in insolation, as opposed to the December cycles of the other sites (Wang, 2004). As we gain more high-resolution paleoclimatic records it may be possible to test whether past dry events can truly be predicted based on precessional influences on the prevailing moisture source (Figure 3.3).

Interestingly, the long sedimentary record from the Salar de Uyuni reveals that precession is not strong enough to counteract some other drivers of precipitation change. For example, Fritz (2004) suggest that global ice volume is another significant variable in Pleistocene Andean precipitation and that—until ice volume reaches a critical point—precession does not emerge as a significant factor. A similar argument was made that the climate of Panama shows poor correlation with climatic events in the North Atlantic prior to *c.* 45,000 years ago, but between that time and about 14,000 years ago a closer relationship is evident (Bush, 2002). Thus, in Panama at *c.* 7°N and in the Altiplano it appears that prevailing controls on climate were modified by global ice volume. Indeed, in Colombia the record from the High Plains of Bogotá appears to reflect faithfully the three main Milankovitch Cycles (Hooghiemstra, 1993), whereas in the tropical lowlands farther south, precession is by far the most important pacemaker of climate change—an observation that corresponds well with modeled data that highlights precession as a potential driver of tropical paleoclimates (Clement, 1999, 2001).

3.6 THE TYPE OF FOREST

Almost all Amazonian pollen records that extend back into the Late Pleistocene reveal higher inputs of pollen from montane forest taxa—for example, *Podocarpus*, *Alnus*, and *Hedyosmum*. Available data suggest that these forests lack exact modern counterparts. Lowland species persisted alongside montane species during the coldest episodes, but for much of the glacial period there may have been minimal penetration of the lowlands by montane taxa. These data argue that lowland Amazon forests of the Pleistocene were mesic systems periodically stressed by strong cooling and drought.

An emerging view supports the presence of forest cover across Amazonia throughout the Quaternary, but raises the possibility that the forests were much drier than those of today and may have supported less biomass (Prado and Gibbs, 1993; Pennington, 2000, 2004; Cowling, 2004; Mayle and Beerling, 2004). A suggestion for a dry arc of vegetation connecting southern Amazonian savannas to those of Colombia (Pennington, 2000) has been revised in the light of new paleoecological data from lowland Bolivia (Mayle 2000; Burbridge 2004; Pennington, 2004). The finding that dry forest did not expand as predicted in the Bolivian ecotonal region investigated by Mayle's team was a major obstacle to the corridor concept. Similarly, misidentified stone lines within the Belterra clays that were taken as a signal of aridity, have been re-evaluated and are now seen to support continuous Pleistocene edaphic moisture (Colinvaux, 2001).

Pennington (2000) suggested that the Hill of Six Lakes data could equally represent dry forest as represent wet forest. However, this suggestion was based on the abbreviated list of species presented in the first reporting of the Lake Pata record (Colinvaux, 1996). The full species list of > 300 pollen and spore types includes many species that are strong indicators of cool mesic forest—such as *Cedrela*, *Cyathea*, *Podocarpus*, *Ilex*, *Brosimum*, and *Myrsine*. Indeed, the most plausible connection from south to north across Amazonia is via the eastern corridor of low precipitation that extends from southern Guiana to eastern Brazil (Figure 3.3). Given the large river barriers, complex orographic features of western Amazonia, and the overall climatic heterogeneity of the basin, it is more appropriate to consider Amazonia as a series of patches, and connectivity as a shuffling within the patchwork rather than migration in corridors.

Although the dry forest flora is a minority component of the lowland Neotropical system, it is worth exploring the potential for connection between isolated sites as the lessons learned are applicable to the wetter systems as well. A first observation is that many of the sand savannas peripheral to, and within, Amazonia contain endemic species and probably have not been completely connected recently, if ever (Pennington, pers. commun.). However, migration through the Amazonian landscape may not have been through white sand soils, as many of the dry forest species demand better soils (Pennington, 2004), and their migrational corridors may have been through riparian settings.

A significant problem in this arena is the iconography of biome-watching. Concepts such as "caatinga", "semi-deciduous tropical forest", or "wet forest" are at best the abstractions of mappers. These broad vegetation classifications can help us to think about a system, but we should not believe that they are sharply distinct in their ecology. Many of the same species that occur in a lowland, semi-deciduous forest are found at the edge of their ecological tolerance within mesic forest. Nuances of a month more or less of dry season may substantially alter the dominant taxa, though perhaps resulting in much less change in the long tail of rare species (*sensu* Pitman, 1999). Tuomisto (1995) recognize > 100 biotopes of tierra firme forest types in Peruvian Amazonia alone; Duivenvoorden and Lips (1994) some 20 plant communities within a small rainforest near Araracuara, Colombia; and Olson (2001) recognize 35 types of dry forest. Even within this wealth of forest types a given species may be facultatively deciduous in one setting, or in one year. The dry valleys scattered along the eastern flank of the Andes are probably the result of interactions between prevailing winds and topographic blocking (Killeen *et al.*, 2007). As such these features are probably relatively fixed and have offered the potential for "island-hopping" around western Amazonia for several million years. The most probable path for migration through Amazonia would be where vegetation is potentially susceptible to fluctuations in precipitation.

A corridor of low precipitation crosses north–south across Amazonia at *c.* 50°W (Figure 3.4). Based on the seasonality and totals of precipitation, Nepstad (1994) suggest that in this region evergreen forest trees are reliant on deep soil water when seasonal drought deficits occur in the surface soils. If this reliance on hydrology is true, any factor that lowers water tables beyond rooting depth could lead to a substantial

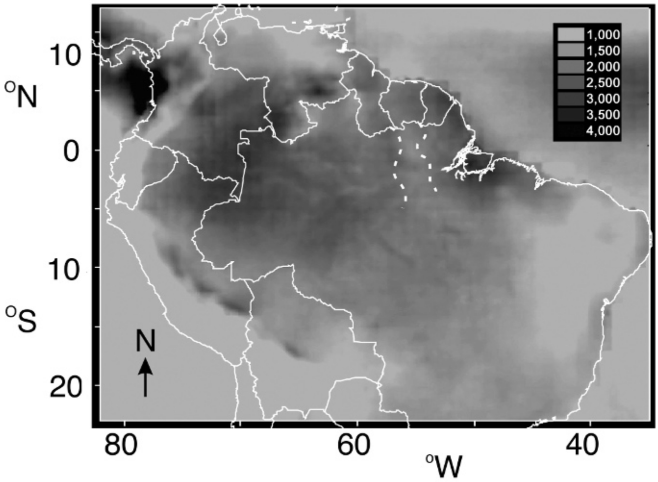

Figure 3.4. Data for δO^{18} from Brazilian speleothem records, downcore gamma radiation from Salar de Uyuni and K^+ concentration from Lake Pata, compared with mean insolation calculated in Analyseries 1.2 for 0°, 10°S, and 30°S (Berger, 1978). Periods selected are those used by authors in original descriptions relating data to insolation.

change in the flora. This same corridor was suggested by Bush (1994) to have been the section of Amazonia most sensitive to reduced precipitation. Whether this region experienced drought synchronously—or whether portions of it were wet while other portions were dry—would not inhibit the eventual migration of a species north to south through this region.

Finally, the distribution of dry forest arc species show some disjunctions across the Andes. As it is implausible that continuous habitat for these species spanned the mountains during the Quaternary, we are left with three possibilities. Congeners might have been mistaken for conspecifics. Or the species in question might be capable of dispersing across a major biogeographic barrier such as the Andes, in which case dispersal across lesser barriers within Amazonia obviates the need for any kind of habitat continuity. The third possibility is that these biogeographic patterns are relictual and derived from the pre-Andean biogeography of South America—that is, at least Mid Miocene in age (Hoorn, 1995). We consider the latter two of these options to be the most probable.

The message emerging from this analysis is that simplistic notions requiring the whole of the vast Amazon lowlands to have a single climate subject to uniform change are bound to fail. Pleistocene forests were shaped by cooling, low atmospheric CO_2 concentrations, and at differing times by lessened rainfall. There is a strong suggestion of no-analog communities based on the prevalence of montane taxa interspersed with a full suite of lowland taxa. Some species that we now consider to be dry forest species may also have been able to survive within this forest, especially if it was structurally somewhat more open than modern forests. Thus, asking if a "dry forest arc" once existed may be much less relevant as a question, than "to what extent (if any) would conditions have to change to allow species to migrate through or around Amazonia?'' The answer to this latter question may be ''surprisingly little''.

3.7 PHYLOGENIES

The empirical paleoenvironmental data discussed above have provided an improved understanding of the response of the vegetation in the Amazon Basin to known global climate change. New phylogenetic studies question some long-held assumptions about the nature and pace of Amazonian speciation and offer some critical insights into when speciation occurred.

Examples of biological insights arising from phylogenies come from a variety of organisms. *Heliconius* butterflies (Brown, 1987), frogs, and primates (Vanzolini, 1970) were all advanced as exemplars of refugial evolution, and each group has been revisited using modern molecular cladistic techniques.

Heliconius butterflies provide an excellent example of how reliance on modern biogeographic patterns can result in false assumptions about past evolution. *H. erato* and *H. melpomene* are co-mimetics, whose close co-evolution has been taken to indicate a similar biogeographic history (Brown, 1987), but a genetic analysis reveals that their patterns of divergence are markedly different (Flanagan, 2004). Sub-populations of *H. erato* show little geographic structure in rapidly evolving alleles, telling us that there is a relatively ancient divergence among a species with fairly high rates of gene flow. *H. erato* is the model, and the initial mimic, *H. melpomene*, has discrete sub-populations consistent with a history of local population isolation and expansion. These data—rather than suggesting environmental change as a cause of phenotypic variation—demonstrate the power of positive feedback in Mullerian mimicry when an abundant model (*H. erato*) is already present (Flanagan *et al.*, 2004).

Studies of the molecular clock suggest that speciation of birds and *Ateles* (spider monkeys) was more rapid in the Miocene or Pliocene than the Pleistocene, and that many of the species purported to reflect allopatry in an arid Amazon were already formed prior to the Quaternary (Zink and Slowinski, 1995; Collins and Dubach, 2000; Moritz, 2000; Zink, 2004). The important messages to emerge from these studies are that different environmental factors serve as barriers to different lifeforms, that common biogeographic patterns do not imply similar evolutionary demographies, that speciation is—and has been—a continuous feature of these systems, and lastly that the scale and ecological complexity of Amazonia can serve to induce species to specialize and perhaps even speciate without a vicariant event.

Simple assumptions about the compositions of Amazonian clades were also challenged by an analysis of small mammals that found an overlap of species—and genetic similarity—between specimens from the central Brazilian dry forests and those from adjacent rainforests (Costa, 2003). In some clades, samples collected from the dry forest were more similar to those from rainforests than other rainforest samples. This study highlighted the integrated, polyphyletic

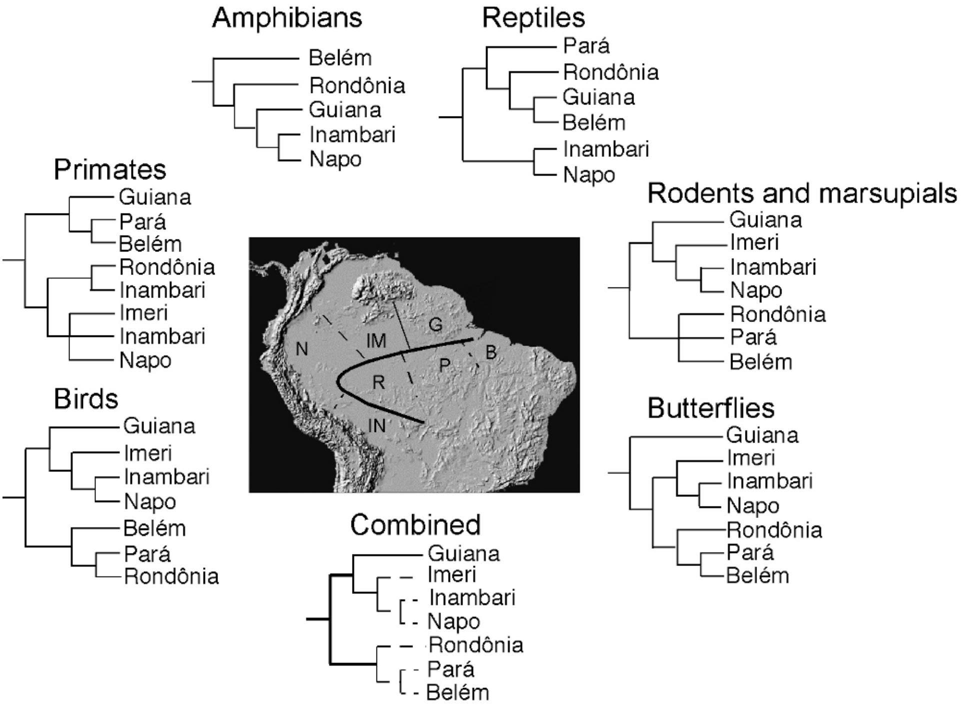

Figure 3.5. Summary phylogenies for a variety of Amazonian animal taxa (after Hall and Harvey, 2002) compared with their biogeographic relationship. The overall combined phylogeny is reproduced on the map. Levels of the phylogeny are reflected in the weight and dash patterns of lines on both the tree and the map: B = Belém; G = Guiana; Im = Imeri; In = Inambari; N = Napo; P = Para; R = Rondônia.

history of clades and that no simple model of vicariance is likely to explain their biogeography.

Phylogenetics has played an important role in demonstrating the temporal pattern of speciation and the development of biogeographic regions within Amazonia. Reviews by Moritz (2000) and Hall and Harvey (2002) reveal that the geographic divergences contain broadly similar themes between groups. Within the Amazon Basin, many clades show a basal split that separates northern and western clades from southeastern ones (Figure 3.5), but there is no fine-scale pattern indicating distinct centers of endemism (Bates, 1998; Collins and Dubach, 2000; Patton, 2000; Hall and Harvey, 2002; Symula, 2003). Ideally, the dating of the divisions between clades should be underpinned by multiple dated calibration points derived from the fossil record (Near, 2005). However, in Amazonia the fossil record for many taxa is so depauperate that many of these studies rely on previously estimated rates of molecular evolution to convert observed genetic distances to absolute age estimates. As these estimates are consistent with records derived from those in phylogenies supported by fossil data, it is probable that their age estimates are correct within a factor of 2.

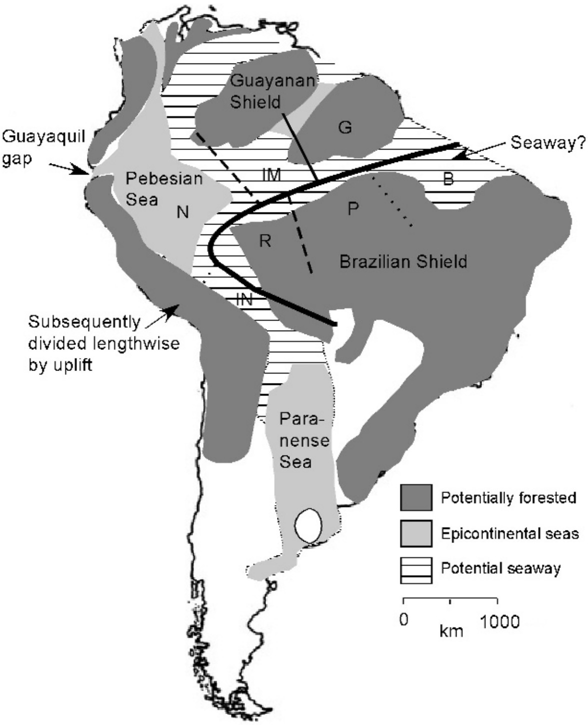

Figure 3.6. Summary diagram showing the relationship between flooding caused by a 100 m marine highstand and proposed known epicontinental seas in Amazonia, and biogeographic patterns. The darkest area is the postulated Miocene seaway (after Räsänen *et al.*, 1995). The biogeographic divisions and phylogenies are derived from Figure 3.5: B = Belém; G = Guiana; Im = Imeri; In = Inambari; N = Napo; P = Para; R = Rondônia

In general, for clades that extend into the wider lowland Neotropics (e.g., the Chocó), there is a deeper divergence consistent with division of the clade by Miocene Andean orogeny (Hoorn, 1995). However, even in Amazonian clades there is increasing evidence that the basal splits took place within the Miocene (Moritz, 2000).

Nores (1999) and Grau (2005) have suggested that high sea levels during the Pliocene or Quaternary may have fragmented bird populations and account for their patterns of vicariance. The presence of higher Miocene sea levels has been suggested to be linked to the isolation of the northern and southern massifs within the Guianan highlands and allowed divergence of geographic amphibian clades (Noonan and Gaucher, 2005). Considerable uncertainty exists regarding Miocene and Pliocene sea levels; Miller (2005) suggest that they may have been only 30–60 m higher than present, whereas other estimates place them 110–140 m higher (Räsänen, 1995; Naish, 1997).

The rise of the Andes caused forebasin subsidence in western Amazonia. Although sea-level rise was only *c.* 30–60 m higher than present, when coupled with tectonic subsidence the effect was a *c*. 100 m rise in relative sea level. Repeated highstands approached 100 m above modern levels—as suggested by Räsänen (1995) and Nores (1999)—the basal splits between northern and southeastern Amazonian clades, and the Guiana clades separating from other northern clades, are explicable (Figure 3.6). Molecular evidence for a more recent evolution contributing to the vast diversity of Amazonia is also growing. Harlequin toads (*Atelopus*) (Noonan and Gaucher, 2005) and poison frogs (*Dendrobates*) (Noonan and Gaucher, 2006; Noonan and Wray, 2006) have been suggested to diversify during the Quaternary (last 2.6 million years) (Rull, 2006). It is interesting to note that both the studies examine species from the region of the eastern Amazon. Today eastern Amazonia is one of the driest regions within the basin and consequently is likely to have been sensitive to climate drying through the Quaternary. However, the factors driving these speciation events remain ambiguous; they could reflect wet–dry climate cycles or another mechanism, such as sexual selection (Roberts *et al*., 2007). The picture emerging for the origins of Amazonian biodiversity is of a complex history of ongoing evolution influenced by many and various pressures. To obtain a clear understanding of the major processes more complete geological research and improved phylogenies are clearly needed.

3.8 CONCLUSIONS

The Quaternary history of Amazonia is only partly revealed, and each detailed record adds fresh perspective to what is emerging as a complex history. The weight of evidence suggests that the lowlands remained predominantly forested during the last ice age, and therefore, it is assumed, during preceding Quaternary glacial events. The nature of the forest, its openness, the dissimilarity from that of modern times, and the extent to which it was invasible by cool or dry forest elements are worthy subjects for future research. While advancing the case against the existence of continuous arcs of dry forest within the last ice age, we establish the more general argument that the vast Amazon Basin has a dynamic and complex environment that cannot be treated as a climatic or ecological monolith. The many and various changes in Amazon environments during the Quaternary have combined to produce the modern distribution of plants and animals. However, it seems increasingly likely that these changes were not the driving factors generating the high diversity found within this region. Biogeography has a vital role to play in helping us to ask appropriate questions and to move toward a better understanding of this system. However, to quote the paper stemming from a memorable talk recently given by Russell Coope to the Royal Society of London "reconstructing evolutionary history on the basis of present-day distribution alone is rather like trying to reconstruct the plot of a film from its last few frames". Amazonian paleoecology came of age testing biogeographic hypotheses, now the challenge will be to provide the lead so that biogeographic theory can be based on empirical data, not on assumption.

3.9 ACKNOWLEDGMENTS

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4

The Quaternary history of Far Eastern rainforests

A. P. Kershaw, S. van der Kaars, and J. R. Flenley

4.1 INTRODUCTION

4.1.1 Present setting

This region differs from those supporting tropical rainforest in other parts of the world in that it is less continental and geologically much more dynamic. It incorporates some major pieces of continental plate, but its center—the so-called "Maritime Continent" (Ramage, 1968)—is largely a complex interaction zone between the Asian and Australian Plates resulting from the continued movement of the Australian Plate into Southeast Asia (Metcalfe, 2002). The effects of tectonic and volcanic activity have resulted in mountain uplift, particularly in New Guinea, and formation of the volcanic island chain of Indonesia. Vulcanicity also occurs out into the Pacific beyond the "andesite line" where most "high" islands are volcanic and most "low" islands are coral islands developed on sunken volcanoes.

The extensive areas of continental shelf—particularly the Sunda and Sahul Shelves—but including the shelves along the east coast of northern Australia and around the South China Sea, combined with the impact of the Indonesian throughflow that restricts the movement of warm water from the Pacific to the Indian Ocean, have resulted in the highest sea surface temperatures on Earth in the form of the West Pacific Warm Pool. The enhanced convective activity associated with the warm pool results in high rainfall through much of the year in the heart of the Maritime Continent and dominance of the vegetation by evergreen rainforest. The area also provides the major source of heat release that drives the East Asian–Australasian summer monsoon system reflected in the strong summer rainfall patterns beyond the Intertropical Convergence Zone (ITCZ) in each hemisphere, and resulting in the occurrence of seasonal, raingreen or "monsoon" semi-evergreen to deciduous rainforest over much of continental Southeast Asia and the very north of Australia (Figure 4.1). Additional influences on rainforest distribution are the warm

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M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

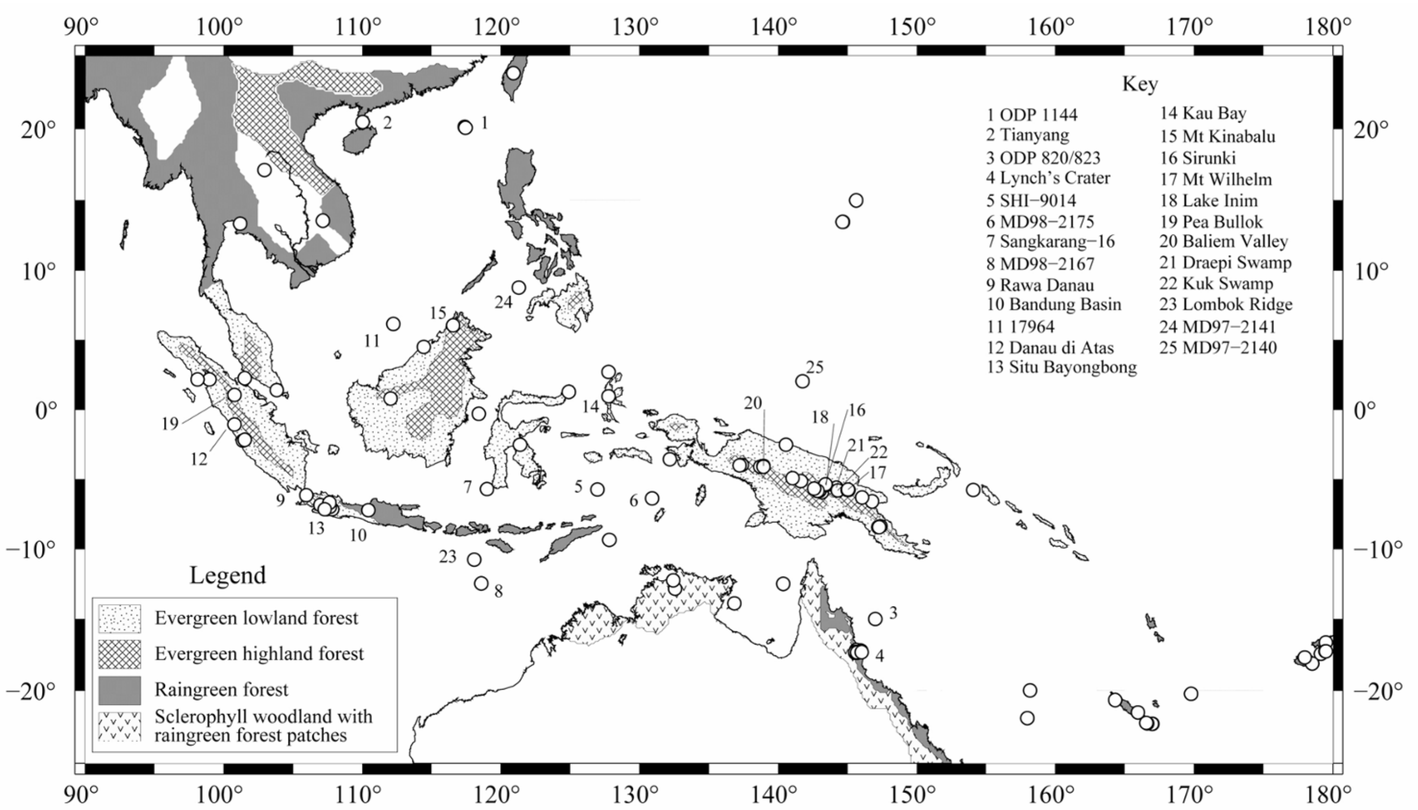

Figure 4.1. Distribution of rainforest vegetation in the Far East and pollen-analyzed sites covering at least the last 6,000 years. Rainforest types have been simplified from distributions and descriptions of communities identified by Fedorova *et al.* (1993, 1994). Those sites mentioned in the text are numbered.

northerly and southerly currents emanating from the Pacific equatorial current that, in combination with the southeast and northeast trade winds from the Pacific, result in the production of high orographic rainfall and associated rainforest along mountainous eastern coastal areas of Southeast Asia and Australia.

Most of the region is subjected to high interannual rainfall variability that is also, to a large degree, a product of its particular geography and the dynamics of oceanic and atmospheric circulation systems. The energy provided by convective activity within the Maritime Continent is the major contributor to the operation of the east–west Walker circulation that breaks down periodically, resulting in the movement of the warm water banked up against the Indonesian throughflow eastwards and resulting in a substantial reduction in precipitation from all sources over most of the region. These El Niño phases of the so-called "El Niño–Southern Oscillation" (ENSO)—that have also been linked to a weakening of the monsoon (Soman and Slingo, 1997)—can cause severe droughts and fires, even within rainforest, especially where there is disturbance from human activity.

Although tropical influences dominate the climate of the region, the Tibetan Plateau is important in creating a strong winter monsoon influence. The height and extent of this plateau results in the production of cool dry air that exacerbates seasonal contrasts in the northern part of the region and has a push effect on summer monsoon development in the southern hemisphere.

4.1.2 Nature of the evidence

Most of the evidence for past vegetation and climate from the region is derived from palynological studies. Perceived problems of pollen analysis in the lowland tropics—due to the richness of the flora, dominance of effective animal pollination, and lack of strong winds within the core area—resulted in most early research being focused on highland communities (Flenley, 1979). In these per-humid areas, a major interest has been and continues to be on altitudinal variation in the changing position and composition of montane rainforest and alpine zones in relation to global climate influences. Studies have been restricted mainly to swamps and shallow lakes covering the latter part of the last glacial period and Holocene.

Ventures into the terrestrial lowlands have generally not proved particularly successful due not only to original perceptions but also to the dearth of continuous sediment sequences in both perennially and seasonally wet environments, and lack of differentiation of peatland, riparian, and dryland forest communities in the extensive peatlands that are otherwise very suitable for pollen analysis. Notable exceptions are deep defined basins of volcanic origin that have revealed detailed records of both vegetation and climate change, sometimes covering long periods of time.

A major feature of the region—that has been exploited in recent years—is the maritime setting whereby ocean basins occur in close proximity to land areas. A number of sediment cores have provided long and fairly continuous regional records of vegetation and climate change, securely dated from associated oxygen isotope records. Nevertheless, none of these records yet covers the whole of the Quaternary and reliance is placed on geologically isolated glimpses of past environments for some indication of the nature of the early part of this period.

4.2 MODERN POLLEN SAMPLING

Some basis for interpretation of Quaternary palynological records is derived from examination of patterns and processes of modern pollen deposition recorded in pollen traps and surface sediments. Such sampling examines deposition both within the rainforest and outside the rainforest in lake, swamp, and marine environments used for reconstructions of vegetation history.

The first quantitative study of pollen deposition in rainforest was by Flenley (1973). In the lowland rainforest of Malaysia he found significant pollen influx (between 800 and 2,020 grains/cm^2/annum) and relatively high pollen diversity (60 to 62 taxa) although representation within taxa through time was very variable. Similar results were found by Kershaw and Strickland (1990) in a north Queensland rainforest. They also found, from a knowledge of the distribution of trees surrounding the traps, that two-thirds of the pollen could have been derived from within 30 m of the traps. An examination of traps situated less than 100 m outside rainforest, in a small crater lake on the Atherton Tableland in north Queensland, demonstrated an enormous reduction in pollen deposition and substantial sifting out of pollen of local producers (Kershaw and Hyland, 1975). Pollen influx values dropped to below 200 grains/cm^2/annum and spectra were dominated by a relatively small number of taxa with significant regional pollen dispersal. It was determined that there was about equal representation of pollen from above canopy and rainout components. Any trunk space component was small and the high degree of correspondence between trap assemblages and those derived from the topmost part of a sediment core from the lake (Kershaw, 1970) suggested also that there was little inwash of pollen, though this component may have been trapped by marginal swamp.

Despite the great variability of pollen deposition within rainforest, patterns of representation appear to reflect systematic vegetation variation on a regional scale. Numerical analysis of a number of surface litter samples from throughout the lowland and sub-montane forests of northeast Queensland (Kershaw, 1973; Kershaw and Bulman, 1994) revealed a similar pattern to floristic analysis of forest plots from which the samples were derived. Although there was little in common between taxon representation and abundance in the two groups, it suggested that pollen assemblages could be used to characterize the broad environmental features of the landscape, including the vegetation. A similar result was achieved with the use of percentages of only those taxa that had been identified from lake-trapping and existing fossil pollen records as regionally important. This finding indicated the potential for analysis of pollen diagrams from tropical rainforest in a similar manner to those from other vegetation types where variation in abundance of a small number of taxa provides the basis for interpretation. Bioclimatic estimates for such "common taxa" in northeastern Queensland (Moss and Kershaw, 2000) demonstrate their potential for quantitative paleoclimatic reconstruction (Figure 4.2). The presence of numerous

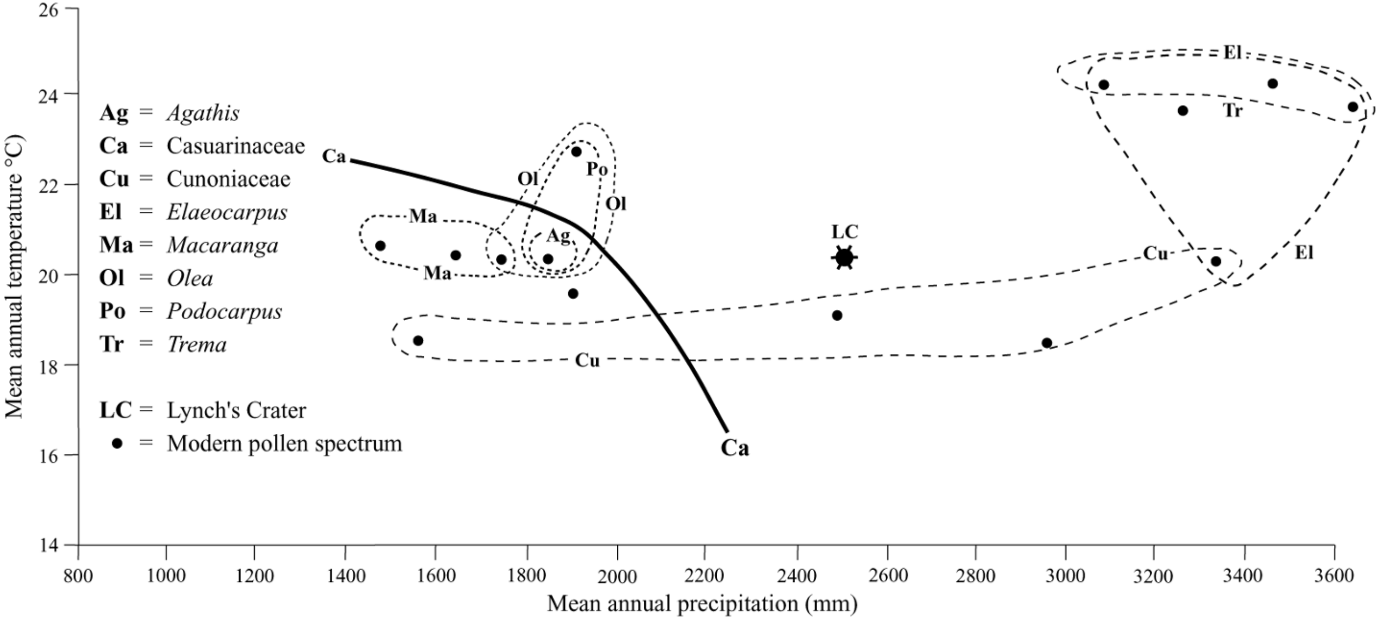

Figure 4.2. Climatic ranges for highest representation of major rainforest taxa in relation to bioclimatic estimates for modern pollen samples from northeast Queensland rainforests. The extent of penetration of high values for the sclerophyll woodland taxon Casuarinaceae is also shown (adapted from Moss and Kershaw, 2000).

other taxa can allow refinement of interpretation (Kershaw and Nix, 1989) although insufficient pollen may be present in samples to allow counts of a sufficient size to demonstrate presence or absence in potential source vegetation. Figure 4.2 also demonstrates the degree of penetration into rainforest of pollen from the dominants of surrounding sclerophyll vegetation, *Eucalyptus* and *Casuarina* or Casuarinaceae, that have generally wider pollen dispersal than rainforest taxa.

The heterogeneous nature of lowland tropical rainforest is an impediment to determination of the actual sources of "common" taxa and, therefore, their relative degree of dispersal. This complication is reduced at higher altitudes where widely dispersed taxa, many of which are clearly wind-pollinated, make up significant and identifiable components of the vegetation. The compilation of Flenley (1979) provides an excellent summary of variation in pollen representation along an altitudinal transect in New Guinea (Figure 4.3). Above the highly human-modified vegetation, clearly recognized by high values of Poaceae or *Casuarina*, the montane zones of oak and beech forest are dominated by pollen of their dominant taxa: *Lithocarpus/Castanopsis* and *Nothofagus*, respectively. Upper montane mixed forest is characterized by *Quintinia* while alpine vegetation is recognized by the only occurrences of "alpine pollen taxa". The bare ground on the mountain summit has a unique pollen signature that clearly identifies those taxa, *Nothofagus* and *Casuarina*, which have wide pollen dispersal. Flenley (1979) remarks on the tendency for pollen to be carried uphill and suggests it is due to the fact that pollen is released during the day when anabatic winds are active.

A much broader indication of pollen transport, including a potentially major water-transported component, is provided by recent analyses of suites of core-top pollen samples from the Indonesian–Australian region (van der Kaars, 2001; van der Kaars and De Deckker, 2003; van der Kaars, new data) and the South China Sea (Sun *et al*., 1999). Isopolls interpolated from samples along the steep precipitation gradient from east Indonesia to northwest Australia are shown for major pollen groupings based on a dryland pollen sum, excluding pteridophytes (Figure 4.4). This gradient is clearly reflected in the pollen with predominantly rainforest taxa including pteridophytes showing high values in the rainforested Indonesian region and then progressively declining relative to the predominantly sclerophyll taxa of Myrtaceae (attributable mainly to *Eucalyptus*) and Poaceae that dominate Australian vegetation. Compared with other pollen types, the pollen of rainforest angiosperms reflect most faithfully the distribution of rainforest. Rainforest conifers are much better represented than angiosperms considering their almost total restriction to montane forests, a feature no doubt due to obligate wind dispersal of pollen and greater opportunity for wind transport from higher altitudes. The major concentration of montane pollen types between Sulawesi and New Guinea reflects also the proximity to mountainous areas within the study area. Pteridophyte spores have a very similar distribution to the rainforest conifers and, although this pattern can be accounted for—to some degree—by the fact that they are most abundant in wet tropical and often montane forest, transport is facilitated also by water. The fact that percentages of pteridophytes are so much higher than those of pollen is probably the result of effective water transport.

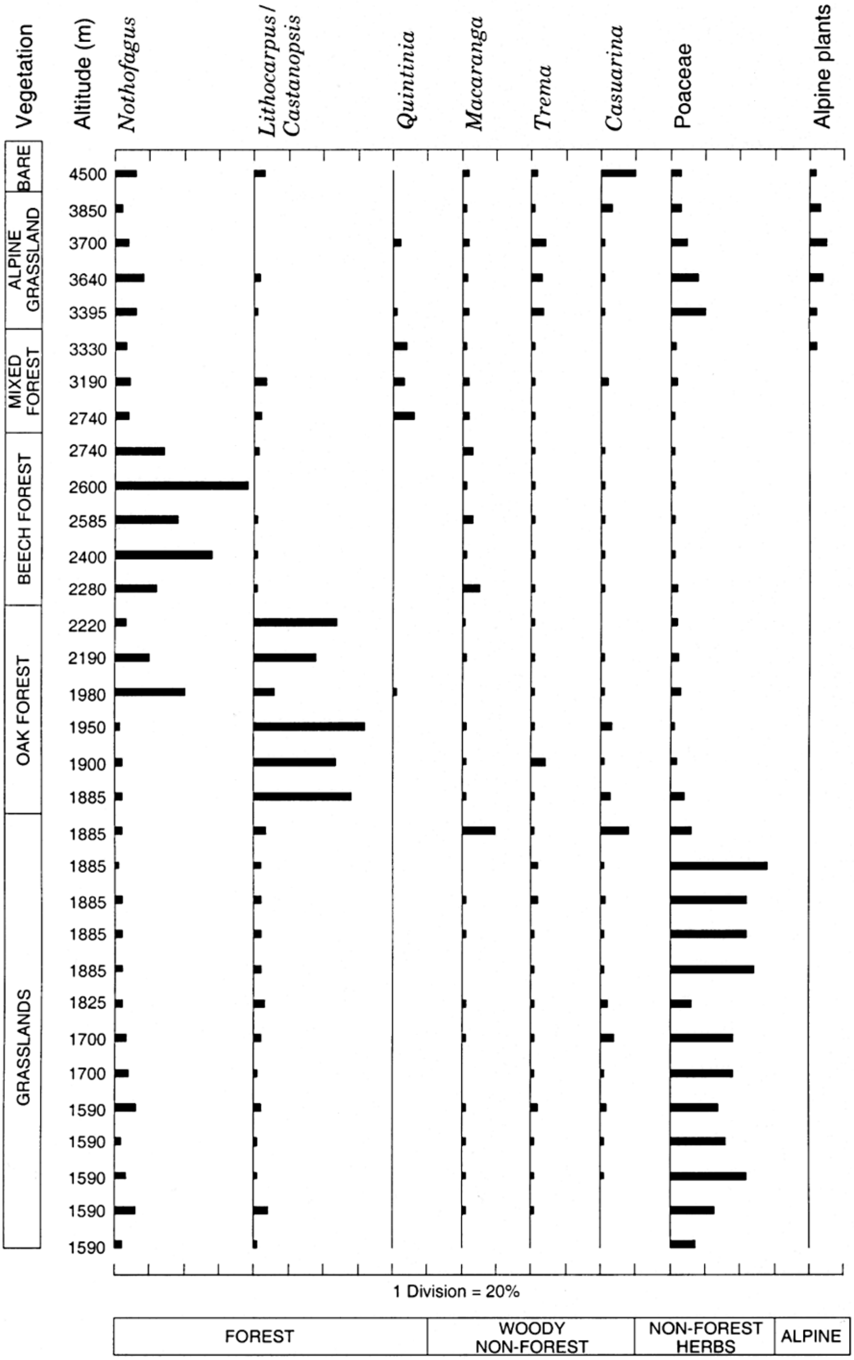

Figure 4.3. Representation of major pollen taxa in relation to vegetation along an altitudinal surface sample transect in Papua–New Guinea (modified from Flenley, 1973).

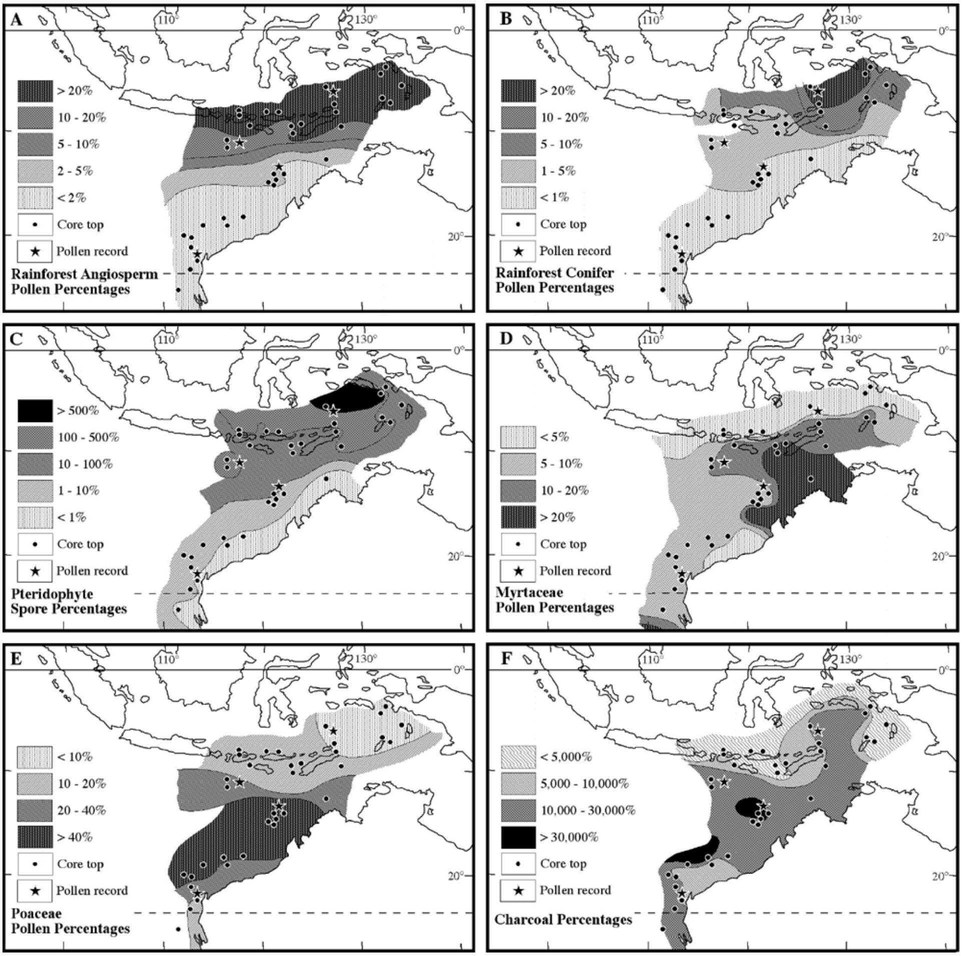

Figure 4.4. Relative abundance of major pollen groups, taxa, and charcoal derived from core-top samples in the northwestern Australian–southern Indonesian region based on a pollen sum of total dryland pollen excluding pteridophytes. Data from van der Kaars and De Deckker (2003) and van der Kaars (2001).

In contrast to pollen—that generally reflects the regional representation of vegetation—charcoal, derived from the same samples, shows a less certain pattern, at least in percentage terms. It is very unlikely that fire activity is highest in the open ocean where charcoal values are highest. This clearly indicates that charcoal particles, on average, are transported farther than pollen. However, it is clear from a general decline northwards that charcoal is, as expected, derived mainly from Australia. The reduction in charcoal percentages in the very northwest of Australia may be realistic as, within this very dry area, a lack of fuel would allow only the occasional burn.

The South China Sea shows largely an inversion of the southern hemisphere pattern (Figure 4.5). Here, tropical rainforest angiosperm pollen is derived largely from the equatorial humid region centred on Borneo and decreases northwards relative to *Pinus* which may be regarded as the equivalent of Australian sclerophyllous trees, in its dominance of drier and more seasonal open forests that cover large areas of Peninsular Southeast Asia and more subtropical forests of southern China. The much higher values of *Pinus* are considered to result from the influence of the strong northerly winter monsoons that blow while *Pinus* trees are still in cone, in addition to the high production and dispersal rates of its pollen (Sun *et al.*, 1999). The rainforest gymnosperms—represented in Figure 4.5 by their most conspicuous genus,

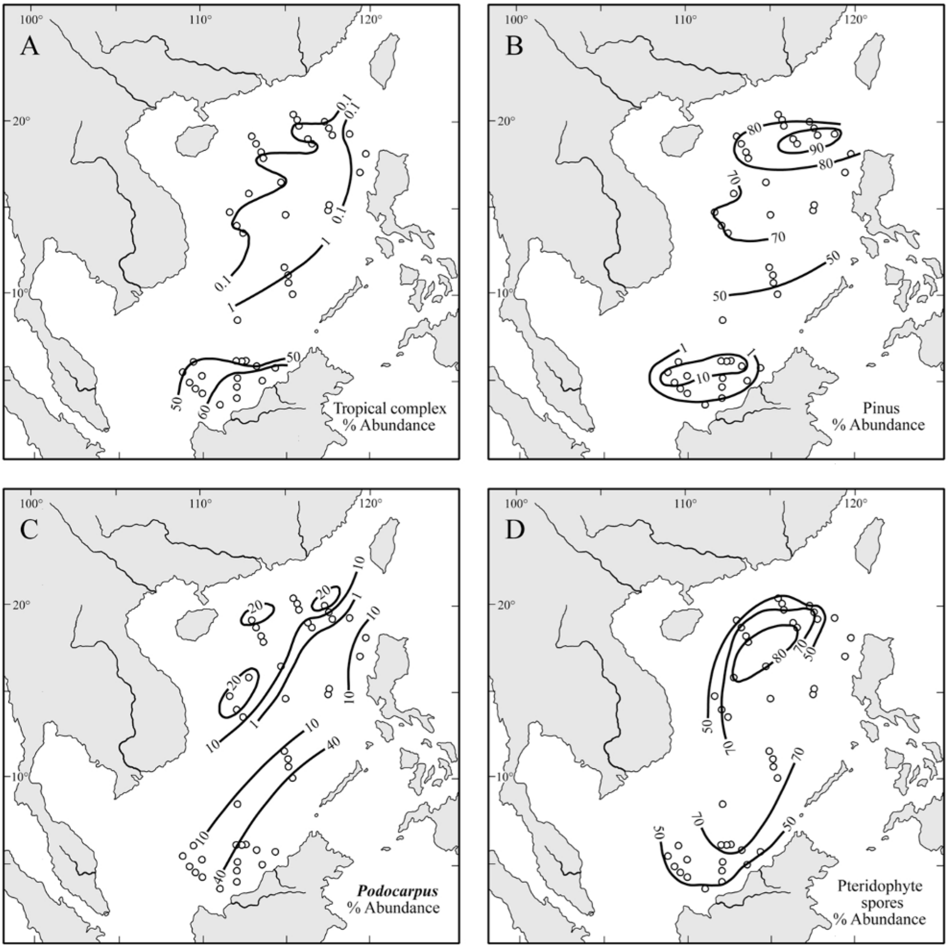

Figure 4.5. Relative abundance of major pollen groups and taxa derived from core-top samples in the South China Sea based on a pollen sum of total dryland pollen excluding pteridophyes. Adapted from Sun *et al.* (1999).

Podocarpus—clearly show much broader pollen dispersal than the angiosperms and sources in both the equatorial tropics and mountains in southern China. Pteridophyte values, when consideration is given to the different basis for calculation of the pollen sum, are similar to those in southern waters, but are demonstrably well dispersed with highest percentages towards the center of the basin. Although not illustrated, mangroves in both data sets show highest values close to coastal locations with a substantial fall away from the coast.

4.3 REGIONAL TAXON REPRESENTATION

Some indications of those taxa that contribute to a regional picture of the vegetation within the tropical rainforest-dominated regions of Southeast Asia and Australia are shown in relation to major ecological groups in Table 4.1. The distinctions between the major taxonomic groups—between essentially evergreen or raingreen and winter deciduous trees, and between rainforest and open forest trees—are fairly clear but those between altitudinally defined rainforest groups are somewhat arbitrary due to the continuous nature of floristic variation, the influences of factors other than temperature on distribution, and the variety of terminologies used for vegetation description in different areas. With the "montane" conifers, for example, Morley (2000) questions the designation of *Podocarpus* and *Dacrydium* as indicative of high-altitude rainforest as they can occur in lowlands, particularly in association with low nutrient-status soils. The inclusion of New Caledonia with its ultra-mafic soils would result in an almost total breakdown of an altitudinal classification.

Despite the long period of isolation of the Australian and Southeast Asian continental plates (Morley, 2000) and apparent limited taxon exchange—apart from New Guinea, within the period of potential contact, the Late Miocene—there are major similarities between pollen floras from the different regions, at least at identified levels. This similarity is most evident with the lowland angiosperms. This group is large, usefully reflecting the floristic diversity of these forests, though low pollen taxonomic resolution disguises much variation in regional representation. Much of this diversity can be accounted for by the lack of dominant wind-dispersed taxa. Although many of the important families and genera in the forest are recognized, there are major biases in representation. For example, the dominant family in Southeast Asian lowland forests, Dipterocarpaceae, is very much under-represented in pollen spectra while the pollen of the dominant family in Australian rainforests, Lauraceae, is hardly recorded. Secondary or successional taxa—such as many Moraceae/Urticaceae, *Macaranga*/*Mallotus*, *Trema*, and *Celtis*—are, by contrast, over-represented.

The greater differentiation in montane and lower montane elements is due to refined identification of a more limited suite of taxa, many of which contain few species, as well as distinctive northern or southern origins. There is no evidence of taxa—such as *Engelhardia*, *Myrica*, *Altingia*, *Liquidambar*, *Lithocarpus*/*Castanopsis*, or *Quercus*—reaching Australia although a number have reached New Guinea, while *Dodonaea*, *Nothofagus*, *Quintinia*, and *Araucaria* have not expanded northwards into,

Table 4.1. Common pollen taxa of major ecological groups in the Far East.

Major ecological groups	*Common pollen taxa*	*China Sea region*	*Southern Indonesia*	*New Guinea*	*Northeast Queensland*
Montane conifers	*Dacrycarpus*	×	×	×	
	Dacrydium	×	×	×	
	Podocarpus	×	×	×	×
	Phyllocladus	×	×	×	
Montane angiosperms	*Coprosma*			×	
	Dodonaea		×		(×)
	Drimys	×		×	×
	Engelhardia	×	×		
	Epacridaceae	×			×
	Ericaceae	×	×	×	
	Leptospermum	×			×
	Myrica	×			
	Myrsinaceae	×		×	×
	Nothofagus			×	
	Quintinia			×	×
Lower montane conifers	*Agathis* (Araucariaceae)			×	×
	Araucaria (Araucariaceae)				×
Lower montane angiosperms	*Altingia*	×			
	Cunoniaceae			×	×
	Hammamelidaceae	×			
	Liquidamber	×			
	Lithocarpus/*Castanopsis*	×	×		
	Quercus	×	×		
Lowland angiosperms	*Acalypha*	×		Insuf. data	×
	Anacardiaceae	×	×		×
	Barringtonia		×		
	Bischoffia		×		×
	Calamus		×		×
	Celastraceae	×			×
	Celtis	×	×		×
	Calophyllum		×		×
	Dipterocarpaceae		×		
	Elaeocarpaceae	×	×		×
	Euphorbiaceae	×	×		×
	Ilex	×	×		×
	Macaranga/*Mallotus*	×	×		×
	Melasomataceae	×			×
	Meliaceae	×	×		×

(*continued*)

Table 4.1 (*cont.*)

Major ecological groups	*Common pollen taxa*	*China Sea region*	*Southern Indonesia*	*New Guinea*	*Northeast Queensland*
Lowland angiosperms	Moraceae/Urticaceae	×	×		×
	Myrtaceae	×	×		×
	Nauclea		×		
	Oleaceae	×	×		×
	Palmae (Arecaceae)	×	×		×
	Proteaceae		×		×
	Rubiaceae	×	×		×
	Rutaceae	×	×		×
	Sapindaceae	×	×		×
	Sapotaceae	×	×		×
	Sterculiaceae				×
	Trema	×	×		×
Open forest (savanna)	*Casuarina*		×	×	×
	Eucalyptus		×	×	×
	Melaleuca		×	×	×
	Pinus	×			
Herbs	*Artemisia*	×			
	Cyperaceae	×	×	×	×
	Poaceae	×	×	×	×
Alpine herbs and shrubs	*Astelia*			×	
Pteridophytes		×	×	×	×
Winter deciduous forest		×			

or through the whole of, the Southeast Asian region. It is interesting that the southern podocarps have their lowest diversity in northeast Queensland despite the fact that they probably dispersed from the Australian region. *Dacrycarpus* and *Phyllocladus* did not arrive in Southeast Asia until the Plio-Pleistocene, but *Dacrydium* and *Podocarpus* have had a much longer residence (Morley, 2002). *Phyllocladus* has extended no further north than Borneo, so its pollen representation in the South China Sea region must derive from this source. *Nothofagus brassospora* has failed to cross into montane Southeast Asia and has also been lost from Australia. Indeed, percentages of *Nothofagus* pollen fall off rapidly with distance from New Guinea. The poor representation of *Nothofagus* pollen in marine sediments is perhaps unexpected considering its proposed high dispersal capacity (Flenley, 1979). Pollen of the open forest regional dominants of the northern and southern subtropics—*Pinus* and

Eucalyptus/Casuarinaceae, respectively—hardly extend into the other hemisphere despite proposed continuity of monsoon influences across the equator. This pattern is probably explained by limited direct wind connections and the efficiency of pollen removal from the atmosphere within the everwet equatorial zone. Patterns for Casuarinaceae and *Eucalyptus* are regionally complicated: the former by the existence of several component species within rainforest in Southeast Asia and New Guinea, and the latter by problems in consistent separation from rainforest Myrtaceae and, less importantly, from the other major, myrtaceous, sclerophyll genus, *Melaleuca*.

There are no identifiable extratropical elements in pollen assemblages from the Australasian region. Both subtropical and warm temperate rainforest floras are essentially depauperate tropical floras, while sclerophyll elements have a recognizable pollen flora similar to that in the tropics. In contrast, assemblages from the South China Sea contain notable percentages of deciduous temperate taxa—as well as the temperate steppe taxon, *Artemisia*—and no doubt a temperate *Pinus* component transported, at the present day, by the winter monsoon.

Herbs other than *Artemisia* would have been derived mainly from the tropical savannas. However, some component would have been derived from anthropogenic grasslands and perhaps also—in the case of the Cyperaceae, in particular—from coastal rivers and swamps, although under natural conditions peat swamp forests and mangroves would have dominated many coastal communities. Rhizophoraceae is the most conspicuous mangrove taxon, and especially so in pollen assemblages. The percentages of pollen from mangroves fall off rapidly from the coast in marine assemblages.

No differentiation is made within the pteridophyte category that is composed largely of fern spores. It is clear from the surface samples that fern spores have highest values in wetter forests. They are derived mainly from tree ferns and epiphytes, with ground ferns becoming common in higher altitude forests and in some mangroves.

4.4 LONG-TERM PATTERNS OF CHANGE

The general composition and distribution of tropical rainforest was established well before the onset of the Quaternary period (Morley, 2000), with the only recognized major dispersal since this time being the expansion of *Phyllocladus*, probably from the New Guinea highlands into the highlands of the southern part of Southeast Asia.

There are only two records that cover much of the Quaternary period—one from the northern part of the South China Sea, and the other from the Coral Sea off northeastern Australia—and these necessarily provide the framework for establishment of temporal patterns of change during much of this period.

4.4.1 The South China Sea region

Sun *et al.* (2003) provide a near-continuous, high-resolution (i.e., 820-year average time interval between samples) record from ODP Site 1144 (20°3″N, 117°25″E) taken from a water depth of 2,037 m equidistant from southern China, Taiwan, and the

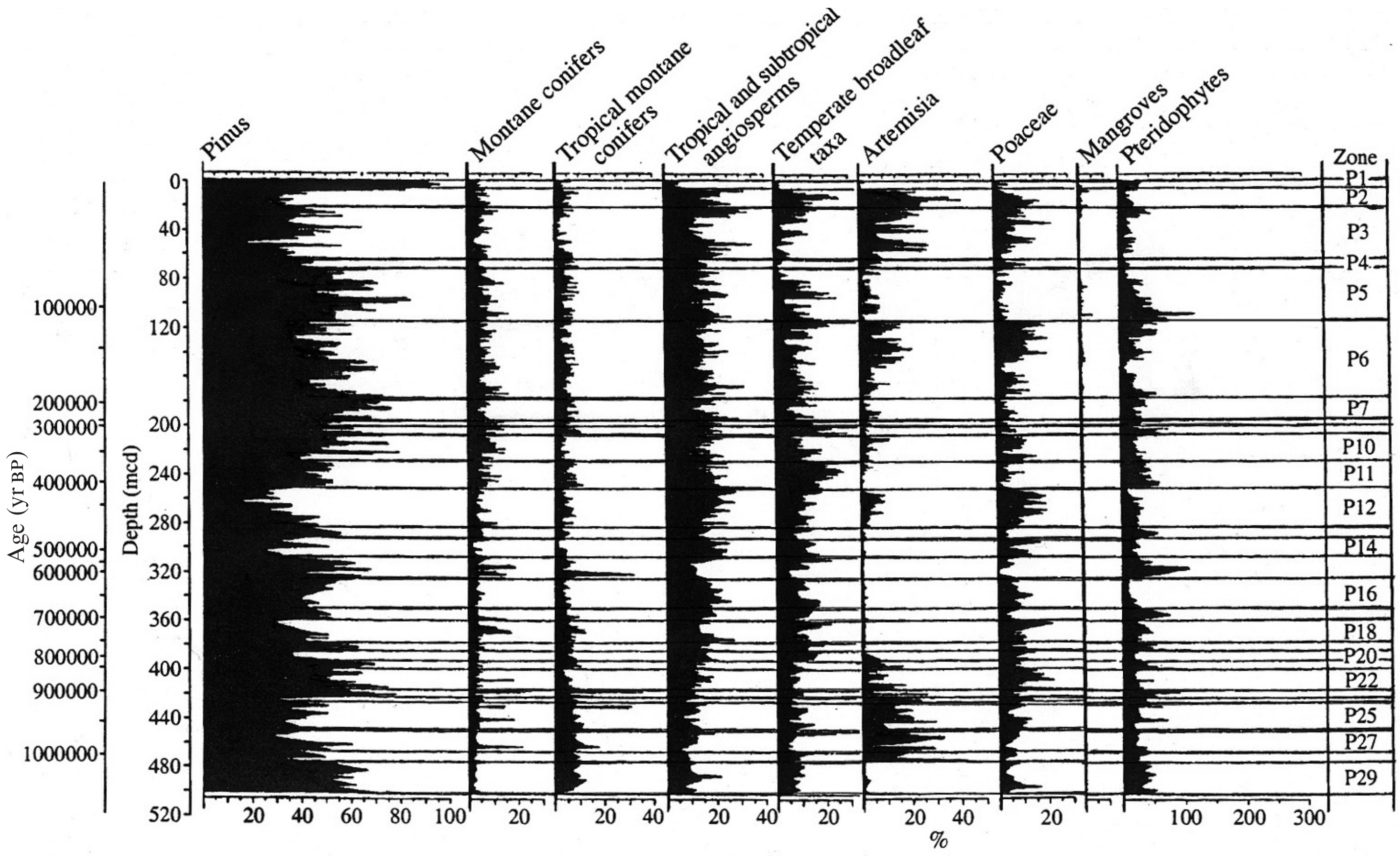

Figure 4.6. Relative abundance of major taxa and taxon groups in the pollen record from ODP Site 1144, South China Sea (after Sun *et al.*, 2003). All taxa are expressed as percentages of the dryland pollen sum, that excludes Pteridophyta and mangroves.

Philippines (Figures 4.1 and 4.6). The record covers marine isotope stages (MIS) 29 to 1 or the last 1.03 Myr. In terms of major ecological groups represented, there is little consistent change in representation and variability is generally lowest in the rainforest groups, tropical and lower montane (subtropical) taxa, montane conifers, and, to some degree, pteridophytes. There is some indication that lower altitude rainforest has generally expanded from about 600 kyr, after the Early–Mid-Pleistocene Transition, while there has been an overall reduction since this time in montane conifers. Throughout the record, the greatest variation is in the dominant groups: the herbs and *Pinus*, with the former showing highest values during the glacial periods and the latter during interglacials. It is proposed that some of this variation is a result of glacials being drier than interglacials, an interpretation supported by generally higher values of pteridophytes during interglacials. It is suggested by Sun *et al*. (2003), however, that it was not a simple replacement of herb vegetation by *Pinus*, but that herbs were largely derived from the exposed continental shelf and *Pinus* from more distant mountain areas. The substantial component of *Artemisia* at times within the herb component might suggest also that temperatures during glacial periods were much reduced, even at sea level. However, the very high values for *Artemisia* steppe vegetation during the Last Glacial Maximum (LGM) are interpreted not in terms of climate but considered the result of a tectonically-induced broader continental shelf relating to an uplift of the Tibetan Plateau around 150 kyr. This interpretation seems inconsistent, though, with the presence of equally high values of *Artemisia* through much of the period from 1,000 to 900 kyr, where no expansion of the continental shelf area is inferred.

This overview of major pollen components in the ODP Site 1144 record masks some important changes that have taken place in the representation of tropical rainforest taxa over the last million years. From a separate portrayal of relative taxon abundance in relation to a lowland and montane tropical rainforest sum, Sun *et al*. (2003) identify three major periods. The earliest, before 900 kyr, is characterized by relatively high values for tropical montane taxa and *Altingia*, suggesting cool conditions, consistent with a climatic interpretation for the high *Artemisia* values. The period corresponds with minimum variation in the marine isotope record. Increased temperature is inferred for the subsequent period, 900 kyr to 355 kyr, where lowland taxa including Dipterocarpaceae, Celastraceae, *Macaranga*/*Mallotus*, and *Trema* were more conspicuous. This interpretation appears counter to that from the accompanying isotope record where generally lower temperatures may be inferred. From about 355 kyr, the submontane taxa *Quercus* and *Castanopsis* markedly increase their dominance. The abundance of these taxa in seasonal forests in southern China suggests that the climate was more seasonal as well as cooler. The period also marks the entry into, and consistent representation of, Moraceae, Oleaceae, and *Symplocos* in the pollen record as well as marked increases in Apocynaceae, Rubiaceae, Sapindaceae, and Sapotaceae, indicating a substantial change in the composition of lower altitude rainforest. The restriction of mangrove pollen to this period may seem surprising but could relate to the achievement of higher temperatures periodically with more pronounced glacial–interglacial cyclicity or to changes in coastal configuration. However, the marine isotope record indicates that the amplitude of glacial oscillations increased about 600 kyr, much before the onset of this period.

A pollen record from the lowland Tianyang volcanic basin of the Leizhou Peninsula on the northern coast of the South China Sea, and at a similar latitude to ODP Site 1144 (Zheng and Lei, 1999), provides a useful terrestrial comparison of vegetation changes for the region to the marine core for the Late Quaternary period. Optically-Stimulated Luminescence (OSL) and radiocarbon dating combined with paleomagnetic analyses have allowed tentative correlation of the record with the marine isotope record over the last 400 kyr. In contrast to the marine record, the dominant pollen types are the evergreen oaks (*Quercus* and *Castanopsis*) that derive from the mountains surrounding the site. The fact that there is only low representation of lowland rainforest taxa, despite the fact that tropical, semi-evergreen rainforest surrounds the site, supports the evidence for relatively low pollen production and dispersal from this vegetation formation within modern pollen studies. However, the much lower values for *Pinus* and pteridophytes—together with the fact that they tend to peak in glacial rather than interglacial periods—brings into question the regional climatic significance of these taxa in the marine record. It is inferred by Zheng and Lei (1999) that glacial periods generally remained wet, although the last glacial period was an exception, with abnormally high values for Poaceae and the only significant values for *Artemisia* interpreted as indicating much drier conditions than present. Temperatures are estimated, from an inferred lowering of montane forest by at least 600 m, to have been some 4°C lower than today during earlier glacial periods, and even lower during the last glacial period. However, there is little variation in lowland forest elements through the record.

4.4.2 The Coral Sea region

Marine records from the Coral Sea adjacent to the humid tropics region of north-eastern Australia provide a coarse resolution coverage of much of the last 10 Myr (Kershaw *et al*., 1993, 2005; Martin and McMinn, 1993) (Figures 4.1 and 4.7). Throughout almost all of the period, the dry land pollen assemblages are dominated by the rainforest taxa Araucariaceae (predominantly *Araucaria*) and *Podocarpus* that, in this region, may have been abundantly represented in lowland as well as higher altitude communities, and the predominantly sclerophyll taxon Casuarinaceae. Late Miocene to Early Pliocene assemblages also contain notable percentages of other montane rainforest taxa—especially *Dacrydium guillauminii* type, *Dacrycarpus*, *Phyllocladus*, and *Nothofagus*—while rainforest angiosperms (including lowland taxa, herbs, and mangroves) are poorly represented. The climate was wet and probably substantially cooler than today. There is a gap in the record from the Early Pliocene to the very early Quaternary, but dominance of a Late Pliocene terrestrial sequence on the Atherton Tableland by *Podocarpus*, *Nothofagus*, and Casuarinaceae, with the full complement of southern conifers, suggests a continuation of wet and cool conditions until at least close to Pleistocene times (Kershaw and Sluiter, 1982). The reduced representation of *Araucaria* at this site can be explained by the per-humid conditions as araucarian forest is generally confined to drier rainforest margins. Conversely, *Nothofagus* would have thrived under the high rainfall as well as the higher altitude of the Tableland.

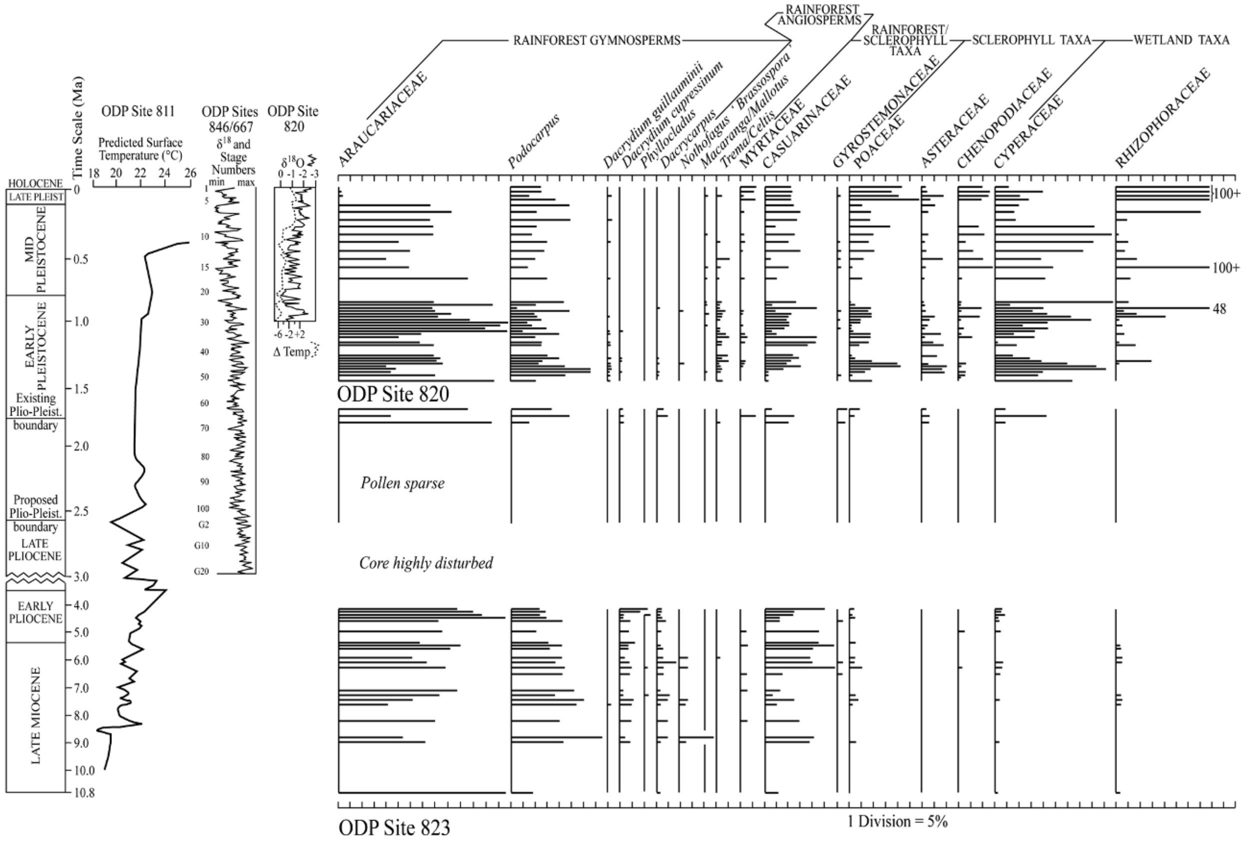

Figure 4.7. Representation of major and indicator taxa in pollen records from ODP Site 823 (Martin and McMinn, 1993) and ODP Site 820 (Kershaw *et al.*, 1993) in relation to the Coral Sea marine isotope record from ODP Site 820 (Peerdeman, 1993) and inferred sea surface temperature records from ODP Sites 820 and 811, and the combined "global" isotope record of Sites 846 and 667 (Shackleton *et al.*, 1995). All terrestrial pollen, excluding mangroves and pteridophyte spores, make up the pollen sum on which all percentages are based.

At the time of recommencement of pollen preservation in the marine record about 1.6 Myr, values for Casuarinaceae, Araucariaceae, and *Podocarpus* are maintained, but other southern conifers have much reduced percentages, with *Phyllocladus* having disappeared from the record. *Nothofagus* also was probably regionally extinct with occasional grains most likely derived by long-distance transport from New Guinea There are marked increases from 1.4 Myr in Poaceae, Asteraceae, Chenopodiaceae, rainforest angiosperms, and mangroves, but—as the record changes at this point from a deep-sea (ODP Site 823) to a continental slope (ODP Site 820) core—these changes may reflect differential pollen transport as much as source vegetation. However, differences between late Tertiary and Early Pleistocene assemblages do indicate that rainfall had declined and temperatures had possibly increased. The trend in the marine isotope record from the Coral Sea towards less negative values, interpreted as an increase in sea surface temperatures, provides support for a regional temperature increase (Isern *et al.*, 1996).

Most of the Quaternary period is characterized by very variable representation of taxa. Although sample resolution is too coarse to address the cause of this variation, a detailed record from at least 1 Myr to about 950 kyr (Kershaw *et al.*, 2005) demonstrates a relationship with oscillations in the isotope record of Peerdeman (1993) that extends back to within this phase. Rainforest conifers, Casuarinaceae, and Poaceae achieve greater relative importance than rainforest angiosperms during glacial periods, indicating they were both cooler and drier than interglacials. However, the sequence remains fairly stationary until late in the record, with the only substantial change being the loss, probably within the Mid-Pleistocene Transition, of *Dacrycarpus*.

The most dramatic modification of the vegetation cover of the humid tropics of Australia within the Quaternary and, in fact, during the whole of the last 10 million years, is recorded within the last 200 kyr. This modification follows a sharp decline between 350 kyr and 250 kyr in δ^{18}O values of planktonic foraminifera within ODP Site 820 (Peerdeman 1993) that correlated with a major phase of development of the present Great Barrier Reef system (Davies, 1992). It has been proposed that the isotopic change was a result of increased sea surface temperatures within the Coral Sea (Peerdeman *et al.*, 1993; Isern *et al.*, 1996), but this hypothesis is not supported by alkenone paleothermometry that suggests temperatures have not varied by more than 1.5°C over the last 800,000 years and that diagenesis within foraminifera is a more likely explanation for the isotope trend. A detailed record through the last 250 kyr from ODP Site 820 (Moss and Kershaw, 2007) illustrates the complex nature of the vegetation changes (Figure 4.8). Dates are derived from the accompanying isotope record (Peerdeman, 1993), but—due to potential hiatuses and changes in sediment accumulation rates—are not very precise. Higher values for rainforest angiosperms in this detailed record are probably due to a reduction in sieve size during preparation, allowing the collection of small grains such as *Elaeocarpus* and Cunoniaceae. Glacial–interglacial cyclicity is most evident in the rainforest angiosperm and mangrove components that are highest during interglacial periods and during interglacial transgressions, respectively, but is over-ridden by stepwise changes in other major components. There is a substantial and sustained increase in Poaceae around 180 kyr

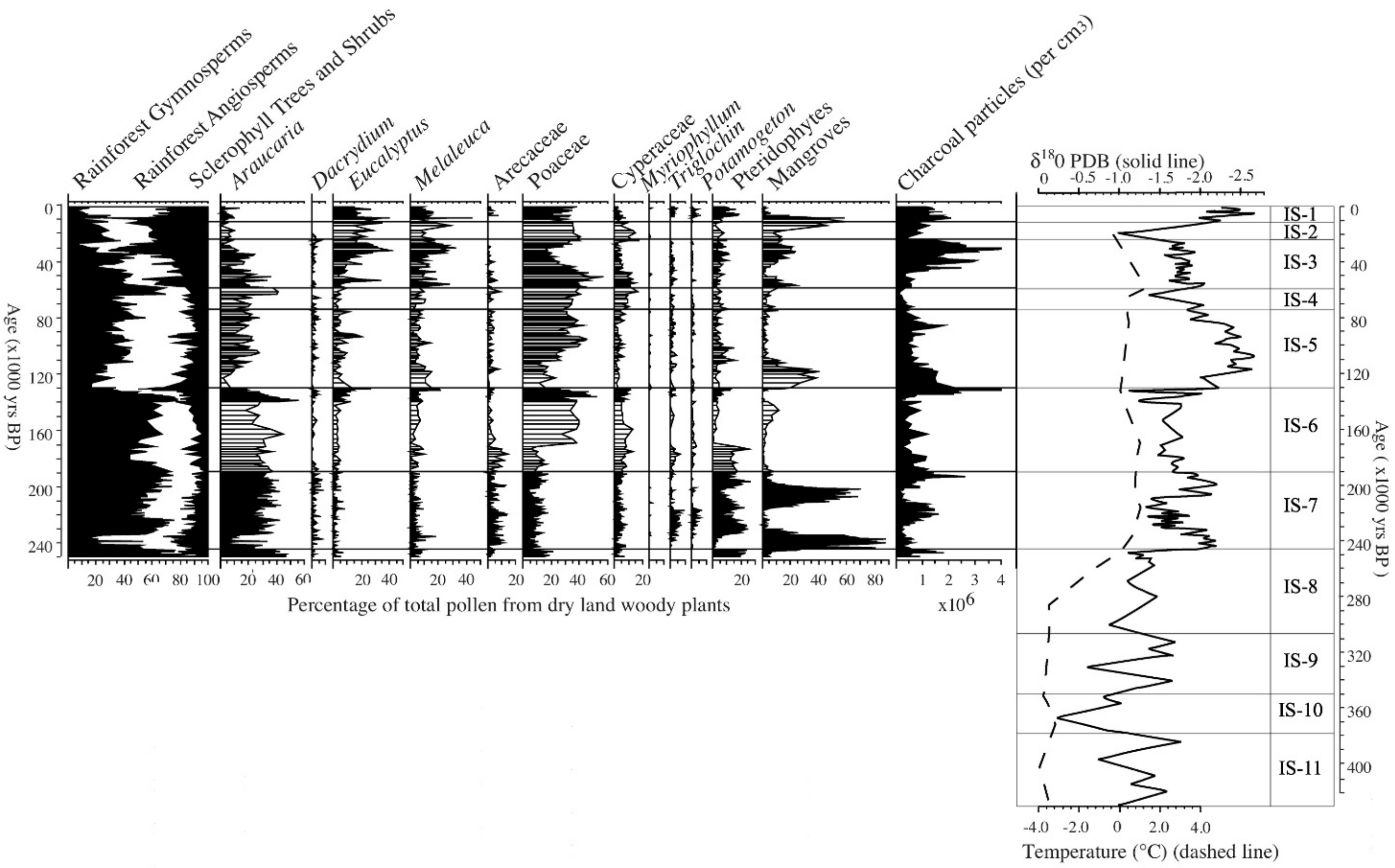

Figure 4.8. Selective features of the detailed Late Quaternary record from ODP Site 820 (Moss and Kershaw, 2007) in relation to the marine isotope record of Peerdeman *et al.* (1993). All taxon abundances are expressed as percentages of the dry land arboreal pollen sum (excluding aquatics, mangroves, and pteridophytes).

with apparent compensatory decreases in pteridophyes and Arecaceae. Southern conifers decrease through the record with the last major representation of *Podocarpus* and *Dacrydium* about 190 kyr: the latter disappearing from the record around 25 kyr, and sustained decreases in Araucariaceae about 140 kyr and 30 kyr. By contrast, *Eucalyptus* increases from very low values around 130 kyr and increases again around 40–30 kyr, with rises corresponding to highest charcoal peaks in this record. There is little sustained change in representation of rainforest angiosperms, although the trend towards higher values for Cunoniaceae—resulting in a greater contribution of sub-montane pollen—certainly does not support a general temperature increase. Many of these changes are identified within the later part of the record by those in the adjacent terrestrial record of Lynch's Crater: notably, the initiation of burning around the site, dated to about 45 kyr (Turney *et al.*, 2001), with a sustained increase in *Eucalyptus* and decline in *Araucaria* a few thousand years later, and a similar age for the disappearance of *Dacrydium*. However, there is no evidence for sustained changes before this time, back to the initiation of the record about 230 kyr (Kershaw *et al.*, 2007; Rieser and Wüst, 2010).

4.5 THE LATER PLEISTOCENE

A more spatially representative picture of changes in the distribution and composition of rainforest can be constructed for the later part of the Pleistocene from a greater number of sites that, in addition to those from ODP Sites 1144 and 820, provide continuous or near-continuous palynological records through at least the last glacial cycle (Figure 4.1). The record from core SHI-9014 in the Banda Sea (van der Kaars *et al.*, 2000) provides the most substantial evidence of vegetation change in the rainforest core of Southeast Asia and a framework for examination of variation within the broader area (Figure 4.9). The regional significance of the Banda Sea record is demonstrated by its remarkable similarity to a recent record from core MD98-2175 in the adjacent Aru Sea (Kershaw *et al.*, 2006; van der Kaars, unpublished data). Rainforest is a prominent component of the pollen spectra throughout, although the substantial sclerophyll component—largely *Eucalyptus*, that would have been derived mainly from the Australian mainland—demonstrates a very broad pollen catchment area. Highest rainforest and pteridophyte values occur during interglacials, indicating that they were much wetter than glacial periods. However, expansion of the Sahul continental shelf during times of low sea level, much of which appears to have been covered largely by grassland (Chivas *et al.*, 2001), would have resulted in excessive Poaceae representation and probable exaggeration of moisture variation through the recorded period. Wet conditions and the maintenance of near-continuous rainforest are certainly evident in some areas—such as highland New Guinea (Walker and Flenley, 1979) and much of the island of Borneo (Anshari *et al.*, 2004; Morley *et al.*, 2004) during the last glacial period, including the LGM. However, grassland may have disrupted forest growth in more peripheral rainforest (see Section 4.6). The Banda Sea record displays higher values for upper montane taxa during interglacial than glacial periods, and this is surprising considering the

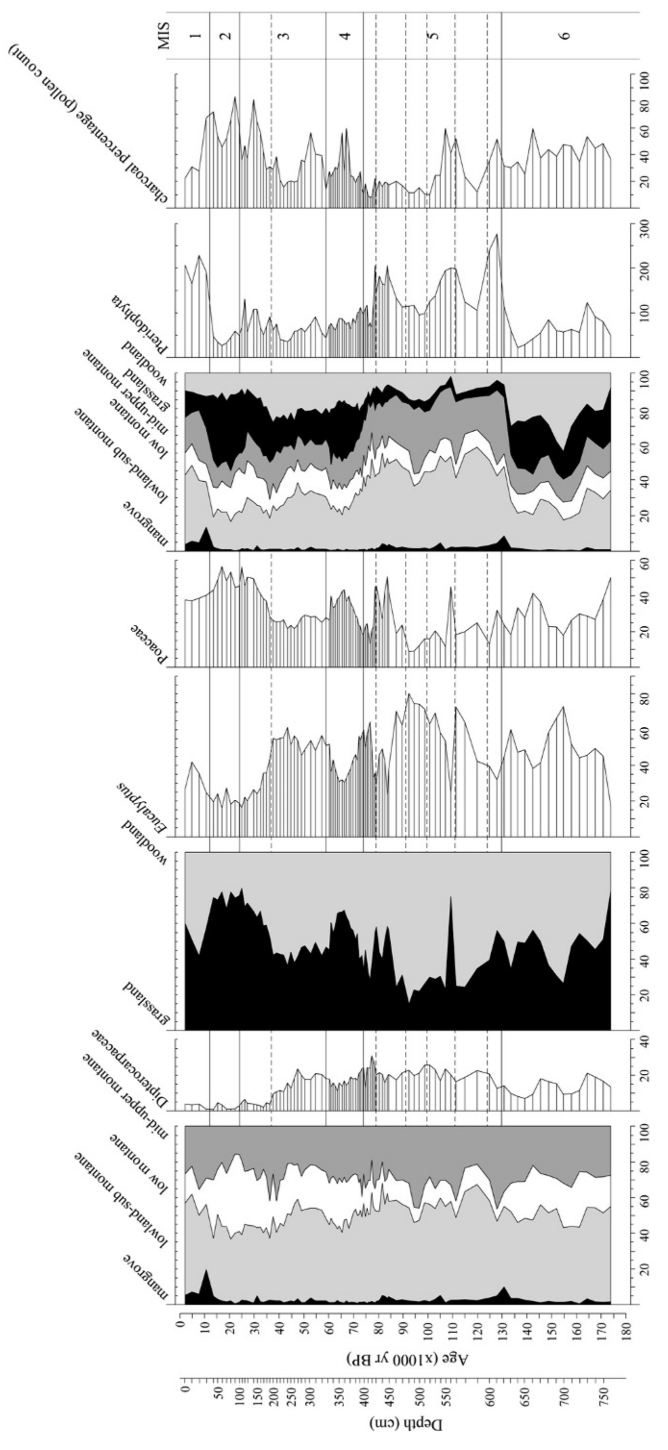

Figure 4.9. Selected features of the pollen and charcoal record from Banda Sea core SHI-9014 in relation to the marine isotope record (adapted from van der Kaars *et al.*, 2000). All taxa are expressed as percentages of the rainforest pollen sum.

abundant evidence from sites in highland parts of the region for much expanded montane vegetation with substantial temperature lowering (see Section 4.6 for discussion of this). This Banda Sea pattern may be a result of an overall reduction in lowland rainforest that is demonstrated to have covered at least parts of the Sunda continental shelf within core rainforest areas during the last glacial period (Morley *et al.*, 2004). It may also be the case that the present day terrestrial area of lowland rainforest was little reduced during glacial periods if there was a smaller degree of temperature lowering at low altitudes. One feature of the Banda Sea record that is shared with those from the Aru Sea and Sangkarang-16, offshore Sulawesi, is a dramatic and sustained reduction in pollen of the dominant lowland rainforest family Dipterocarpaceae about 37 kyr. It is possible that the present pattern of representation of the family—that is lower in abundance and diversity in the eastern than western part of the region—is as much the result of this Late Pleistocene event as it is of the historical barrier of Wallace's Line to migration of the Indo-Malaysian flora westwards as generally assumed (Whiffin, 2002). As this Dipterocarpaceae is associated with an increase in charcoal, burning is regarded as the primary cause, and the impact of early people—rather than climate—has been postulated as its major factor (van der Kaars *et al.*, 2000). Similar sustained increases in charcoal recorded in long marine cores from the Sulu Sea (Beaufort *et al.* 2003) and to the north of New Guinea (Thevenon *et al.*, 2004)—but from a different time, about 52 kyr—have been considered as providing support for the human burning hypothesis.

A rare insight into the history of rainforest on the dry margin of rainforest distribution is provided by marine core MD98-2167 in the North Australian Basin, off the coast of the Kimberley Ranges of northwestern Australia (Figure 4.10). Here, deciduous vine thickets exist in small pockets surrounded by eucalypt-dominated savanna woodland. The major representative of these vine thickets—that have generally poor pollen dispersal—is considered to be *Olea* type. It has low but relatively consistent representation through the record—showing little response to inferred changes in rainfall as indicated by broad glacial–interglacial changes in relative abundance of tree and shrub pollen, that derive largely from the Kimberley region—and particularly the pteridophyte spores that must have been derived from the core rainforest area of Indonesia. Burning appears to have increased around 130 kyr, without any notable change to the vegetation structure, apart from some evidence for increased variability in tree and shrub to herb representation. However, major changes occurred around 46 kyr that included the total disappearance of *Olea* type from the record. This decline in *Olea* may have been associated with a general further increase in burning that has continued to the present.

4.6 THE LAST GLACIAL MAXIMUM TO HOLOCENE

A much greater spread of site records as well as more detailed analysis of sites during this period is available than for previous ones (Figure 4.1), allowing more refined investigation of temporal and spatial patterns both within rainforest and between

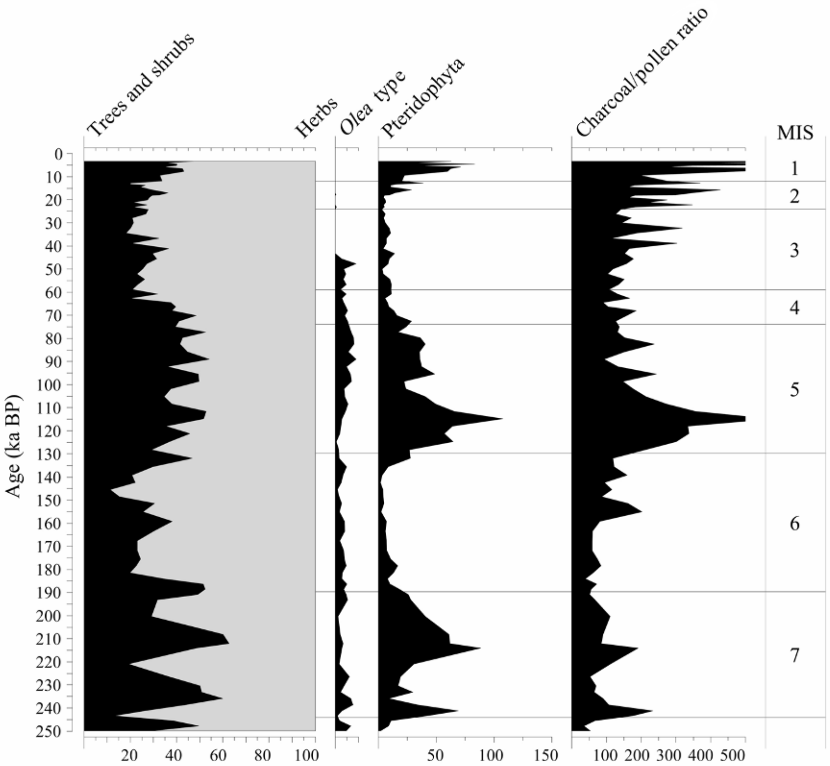

Figure 4.10. Selected features of the pollen and charcoal record from the North Australian Basin core MD98-2167 (Kershaw *et al.*, 2006; van der Kaars, unpublished data) in relation to the marine isotope record of Brad Opdyke (unpublished data). All taxa are expressed as percentages of the total dryland pollen sum.

rainforest and more open vegetation communities. Of particular interest are the extent of rainforest and altitudinal shifts in rainforest communities during the LGM that inform debates on contemporary precipitation and temperature levels.

4.6.1 Last Glacial Maximum

The idea that lowland rainforests might have been replaced by grassy savannas at the LGM is clearly not substantiated from the evidence from longer records, but there is some evidence of savanna expansion. The actual degree and areal expression of this expansion is hotly debated. In some more marginal rainforest areas, savanna vegetation did replace rainforest in part—as around Rawa Danau (van der Kaars *et al.*, 2001) and the Bandung Basin (van der Kaars and Dam, 1995)—or totally—as on the Atherton Tableland in northeastern Australia (Kershaw, 1986)—but increased representation of grasses in coastal sites may have been reflecting more open vegetation on exposed continental shelves or an increased aquatic component. Greatest debate has been over the potential existence of a north–south dry corridor extending through

Malaysia and between Sumatra and Borneo during the LGM. At one extreme is the view of Morley (2000, 2002) who considered that rainforest massifs, or refugia, were essentially restricted to southwestern Borneo and the adjacent Sunda Shelf, the western part of Sumatra, and very western tip of Java (see Chapter 1). Major migration of rainforest is implied between glacials and interglacials unless high diversity was conserved in river gallery forests, a situation proposed for northeastern Australia during the last glacial period (Hopkins *et al*., 1993). Kershaw *et al*. (2001), on the other hand, see little evidence for such a dry corridor, at least during the last glacial period. Evidence is sparse and their interpretation is based largely on the almost complete dominance of rainforest pollen in submerged peat cores from the Sunda Shelf off southeastern Sumatra (van der Kaars, unpublished data). Although undated, the peat almost certainly derives from the last glacial period rather than any earlier period as it is unlikely to have survived subsequent low sea level stands.

There is general consensus, however, that—in accordance with the reconstruction of Morley (2000)—much of Borneo retained rainforest and that this forest extended over the continental shelf within the South China Sea region. Confirmation of the maintenance of a rainforest cover within inland West Kalimantan is provided by Anshari *et al*. (2001, 2004), although drier conditions during the later part of the last glacial period are evident, while a marine pollen record from core 17964 in the southern part of the South China Sea (Sun *et al*., 1999) further substantiates the dominance of a rainforest cover.

In comparison with lowland sites, those from the highlands show the clear maintenance of rainforest through the LGM. Here attention has focused on altitudinal changes in representation of rainforest components. There is good pollen evidence from several sites showing movement of montane tree taxa to lower altitudes. An excellent example of this migration is seen in the pollen diagram from the swamp at the edge of Lake di-Atas in Sumatra (Newsome and Flenley, 1988). The site is at 1,535 m a.s.l., and—where the forest around the lake survives—it is dominated by a variety of tropical oak taxa: *Lithocarpus*, *Castanopsis*, and *Quercus*. It is believed that formerly the tree *Altingia excelsa* (Hamamelidaceae) was abundant also (van Steenis, 1972), but it has been selectively logged. Above 1,800 m the forest changes sharply and becomes dominated by gymnosperms: *Dacrycarpus imbricatus*, *Podocarpus neriifolius*, and (in swamps) *Dacrydium* cf. *elatum*. Even *Pinus merkusii* is present, its only natural occurrence in the southern hemisphere. There are also angiosperm trees, the most conspicuous being *Symingtonia populnea*. The diagram (Figure 4.11) shows that in a phase dated to between *c*. 18 kyr and *c*. 12 kyr BP (*c*. 22–14 kcal yr BP) all those gymnosperms are prominent in the record, only to disappear in the Holocene and be replaced by the distinctive pollen of *Altingia* (previously rare) and peaks of *Quercus* and *Lithocarpus*/*Castanopsis*. This replacement strongly suggests a climate cooler at the LGM, perhaps by 2°C or more. Interestingly, there is an inversion of radiocarbon dates around 18–23 ^{14}C kyr BP, which could be explained by lower water tables, permitting erosion of swamp sediments and their redeposition within the core. This depositional event would correlate with the drier lowland Pleistocene climates already mentioned.

Confirmation of these results comes from a site in Java at *c*. 1,300 m—Situ

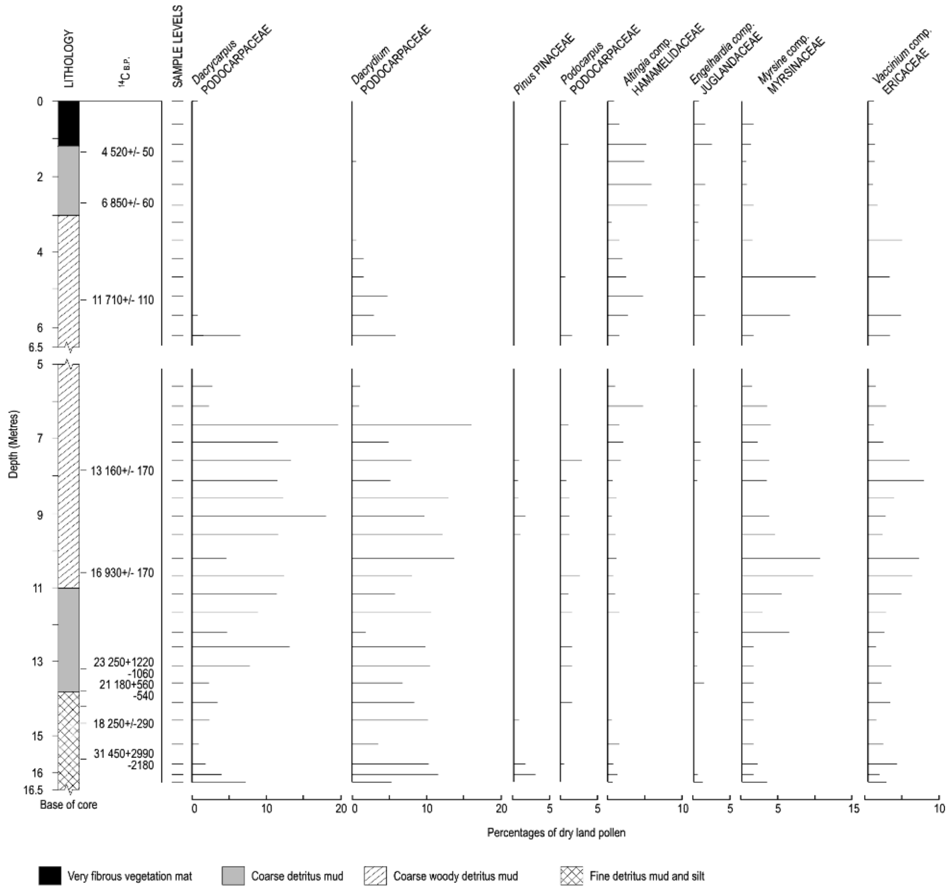

Figure 4.11. Pollen diagram from Danau di Atas Swamp, West Sumatra, altitude 1,535 m. Values are given as percentages of total dry land pollen. Only selected taxa are shown. After Newsome and Flenley (1988) and Stuijts *et al.* (1988).

Bayongbong (Stuijts, 1984)—that is close to the Bandung basin site. Lower altitude sites in Sumatra (Maloney, 1981, 1985, 1998; Morley, 1982; Maloney and McCormac, 1995) also are supportive. These data bring the records of montane gymnosperms down to 1,100 m at *c.* 22 kcal yr BP and do not conflict with the Bandung occurrence of *Dacrycarpus* pollen at 650 m, and at Rawa Danau at only *c.* 100 m (van der Kaars *et al.*, 2001). Collectively, therefore, these results support the Bandung estimate (van der Kaars, 1998) of a climate cooler at the LGM by as much as 4°C or 5°C.

The incursion of montane elements into lowland areas could have been even more marked. The site at Kau Bay in Halmahera (Barmawidjaya *et al.*, 1989) is at present-day sea level. This flooded volcanic crater was a freshwater lake when sea level was lower by >100 m at the LGM. Palynology of this site showed occurrences of *Castanopsis*/*Lithocarpus* and *Quercus* at the LGM. While it is not suggested that these taxa necessarily grew at present sea level, they apparently grew close enough for small amounts of their pollen to enter the record. This record would be consistent with a temperature lowering of *c.* 6°C at the LGM, even in the lowlands. Similar results have been obtained from lowland sites in West Kalimantan (Anshari *et al.*, 2001, 2004).

There is also evidence from the highest mountains of Indonesia for Pleistocene cooling of as much as 6°C. Leaving aside the evidence from New Guinea, we have evidence of Pleistocene glaciation on Mt. Kinabalu in northern Borneo (Koopmans and Stauffer, 1968) and of deglaciation at *c.* 10 kcal yr BP at 4,000 m a.s.l. (Flenley and Morley, 1978). Similar evidence (for solifluction at least) is claimed for the slightly lower peak of Gunong Leuser (3,381 m) in northern Sumatra (Beek, 1982).

In New Guinea the best evidence of environmental change comes from upland regions. The site at Sirunki (Walker and Flenley, 1979) appears to cover the last *c.* 40 kcal yr BP, at an altitude of 2,500 m a.s.l. The site currently lies in *Nothofagus* forest (much disturbed), and is some 1,300 m below the altitudinal forest limit at *c.* 3,800 m a.s.l. Nevertheless the pollen record clearly shows the presence of tropic-alpine herbs (*Astelia*, *Gentiana*, *Drapetes*, etc.) in the Late Pleistocene, when forest pollen values declined to a level consistent with unforested conditions. Similar results were obtained from Lake Inim at 2,550 m by Flenley (1972) (Figure 4.12).

There is, of course, geomorphological evidence of lowered snow lines (U-shaped valleys, moraines, etc.) in the New Guinea mountains. On Mt. Wilhelm, a lowering in the Late Pleistocene of *c.* 1,000 m is indicated (Löffler, 1972), and there are similar findings from Irian Jaya (Hope and Peterson, 1975). One thousand metres translates into perhaps 6°C cooling, using a modern lapse rate.

At the LGM, climates cooler than now by as much as 7–11°C can be suggested from the pollen results, but only *c.* 6°C from the geomorphology. How can this be? Possibly, snow lines were kept artificially high by the reduced precipitation that probably occurred at the LGM. This suggestion has been advanced by Walker and Flenley (1979). But, the precipitation in the mountains cannot have been too reduced, or rainforests would have disappeared there. Late Quaternary vegetational changes are summarized in Figure 4.13.

This whole question has been reviewed by Pickett *et al.* (2004) in a reconstruction of Quaternary biomes for the Southeast Asian region, Australia, and the Pacific. They conclude that the evidence from the Southeast Asian tropics indicates an LGM cooling of 1–2°C at sea level and 6–9°C at high elevation sites. This discrepancy was first noted by Walker and Flenley (1979), who attributed it to a steeper lapse rate, which was itself related to the generally drier conditions at the LGM, leading to a lapse rate closer to the dry adiabatic lapse rate. Such a steeper lapse rate was however criticized as impossible in an environment where the pollen evidence clearly showed the persistence of rainforests (Webster and Streten, 1972; Kutzbach and Guetter, 1986).

The idea has however been revived by Farrera *et al.* (1999) who give a range of plausible mechanisms by which a steeper lapse rate can occur on tropical mountains. One among these was the observation that the moist adiabatic lapse rate steepens anyway as temperature is lowered (Hartmann, 1994). Another relevant point is the possible impact of reduced concentrations of carbon dioxide at the LGM (Street-Perrott, 1994), which would favour C_4 plants (grasses) at the expense of trees.

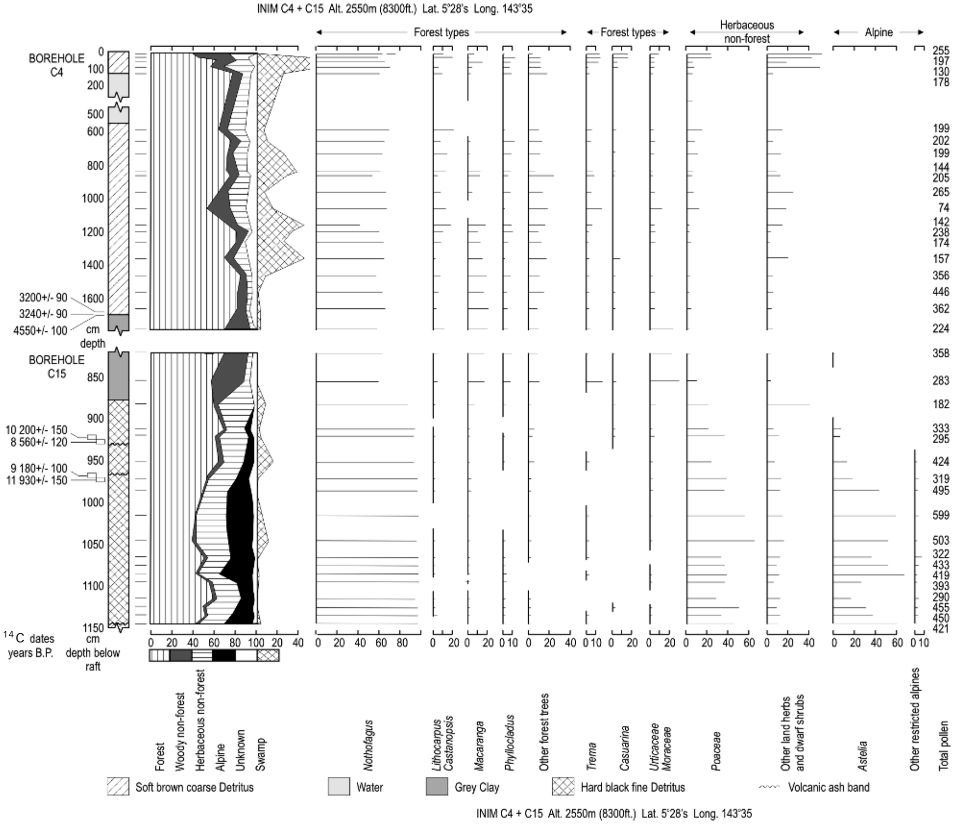

Figure 4.12. Pollen diagram from Lake Inim, boreholes C4 and C15, plotted on the same scales. The results are expressed as percentages of pollen of forest types, except in the summary diagram where the total of dry land pollen and spores forms the pollen sum. Only selected taxa shown. After Flenley (1972).

A steeper lapse rate alone is however unable to explain all aspects of observed vegetation changes. Hope (1976) demonstrated—regarding Mt. Wilhelm—the curious fact that the Upper Montane Rain Forest (UMRF) (cloud forest) did not simply migrate downhill at the LGM: it virtually disappeared. This is not a Late Pleistocene anomaly, for Upper Montane taxa were greatly reduced in each glacial period in the Banda Sea record (see Section 4.5). To understand this phenomenon we must consider the physiognomy and environment of the UMRF at the present time (Flenley, 1992, 1993). The trees are stunted, with short internodes and small thick leaves which possess a hypodermis (an extra layer of cells below the epidermis). Often extra pigments are present as well as chlorophyll: usually flavonoids and/or anthocyanins. These attributes are typical of plants experiencing stress of various kinds, including high ultraviolet-B and temperature extremes. The soils are unusual in the thickness of their litter layer. The temperature environment shows extreme variations on a diurnal basis: from very cold nights and early mornings, to sunny mornings and

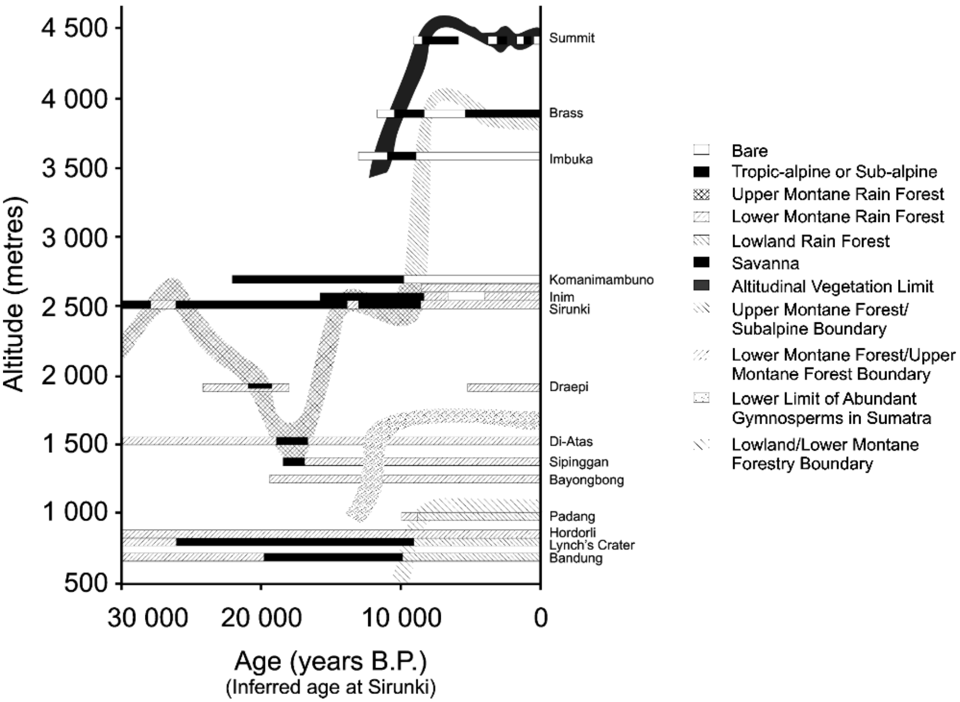

Figure 4.13. Selected vegetation records derived from pollen diagrams from tropical Southeast Asia and the West Pacific. Only the last 30,000 years are shown. Human impact is omitted. References to individual sites are as follows: Summit, Brass, Imbuka, Komanimambuno (Hope, 1976), Inim (Flenley, 1972; Walker and Flenley, 1979), Sirunki (Walker and Flenley, 1979), Draepi (Powell *et al.*, 1975), Di-Atas (Newsome and Flenley, 1988), Sipinggan (Maloney, 1981), Bayongbong (Stuijts, 1984; Stuijts *et al.*, 1988). For other sites see Flenley (1998). After Flenley (1998).

misty afternoons with 100% humidity. The morning insolation is high in ultraviolet-B because of the altitude. It is known that high UV-B can produce experimentally in crop plants exactly the same physiognomic peculiarities as the UMRF (Teramura, 1983), and can also inhibit insect activity, leading to thick litter layers in soils (Day, 2001). It therefore seems possible that UV-B is involved in the ecology of these forests. It may well be that the extreme diurnal variation of the temperature regime is also involved.

How does all this help to explain the decline of the UMRF in cold phases of the Pleistocene? Presumably, when cooler temperatures forced taxa downhill, they found themselves in an environment where the diurnal extremes of temperature and UV-B no longer existed to the same extent. The tropical lowlands are in fact usually lacking in such extremes. Assuming the UMRF taxa are genetically adapted to their present environment, the disappearance or great restriction of that environment at the LGM would have led to their reduction in the pollen record (Flenley, 1996, 1998). This argument will be elaborated in Chapter 8.

4.6.2 The Pleistocene–Holocene transition

Marine records generally show abrupt pollen shifts from glacial to interglacial conditions, suggesting strong Milankovitch forcing of climate and rapid response of the vegetation. However, altered boundary conditions, including those related to coastal landscapes and oceanic and atmospheric circulation, may have played a part in producing this degree of synchroneity. A major exception related to the Coral Sea record of ODP 820 where an increase in rainforest lags the marine isotope change from MIS 2 to 1 by several thousand years. As this lag is also evident in the Lynch's Crater record (Kershaw, 1986), it cannot easily be attributed to global climate forcing. Possible explanations are: the time taken for rainforest patches to expand from glacial "refugia" (unlikely considering the regional extent of rainforest during the last glacial period); the influence of southern hemisphere insolation forcing including ENSO on the record; and the continuing impact of Aboriginal burning; all of which slowed the rainforest advance. More detailed analysis of the earlier part of the ODP 820 record may help resolve this question.

Many terrestrial records are too coarse or insufficiently well-dated to detail local patterns of change during the last termination. However, at an altitude of 3,630 m in Irian Jaya, there is supporting evidence for a rapid replacement of grasslands and scattered shrubs by rainforest at the Pleistocene–Holocene boundary. Similar changes are evident at Lake Inim (Flenley, 1972) and in the elegant suite of sites on Mt. Wilhelm, the highest mountain in Papua New Guinea (Hope, 1976). With four sites at elevations from 2,750 m to 3,910 m, Hope was able to trace the deglaciation of the mountain and the rapid climb of the altitudinal forest limit to about 4,000 m in the early Holocene.

Walker and Flenley (1979) found a hint of a Late Pleistocene oscillation at Sirunki, though its age of *c.* 17 kcal yr BP does not correlate well with the Younger Dryas and is more consistent with the Antarctic Reversal. Support for such an oscillation has recently been demonstrated from a detailed analysis of the last termination at Rawa Danau in Java (Turney *et al.*, 2006). Towards the end of the LGM (Turney *et al.*, in press), high values for grass pollen—combined with the presence of the montane trees *Dacrycarpus*, *Podocarpus*, and *Quercus*—indicate much drier and cooler conditions than today. Initial increases in temperature and rainfall are recorded as early as 17 kcal yr BP with increased representation of lowland rainforest taxa and reduction in Poaceae. There is then a reversal of this trend between 15.4 kcal yr BP and 14.6 kcal yr BP, prior to both the Antarctic Reversal and Younger Dryas, suggesting a regional tropical rather than hemispheric control over climate variation. Although rainforest became dominant at 14.6 kcal yr BP, increased catchment erosion suggests rainfall further increased around 12.9 kcal yr BP and that the summer monsoon may not have become fully established until the early Holocene.

4.6.3 The Holocene

Rainforest achieved its maximum areal extent in the early–middle Holocene under high levels of precipitation and temperature before it opened up again mainly within the last 5,000 years. Reasons for this rainforest reduction include climate factors, although these varied regionally. Hope (1976) attributes a reduction in the altitudinal treeline of about 200 m to a reduction in temperature in New Guinea, while seasonality or increased ENSO influence is considered to have been the major influence on both a change in the composition of rainforest and slight sclerophyll woodland expansion in northeast Queensland (Kershaw and Nix, 1989; McGlone *et al.*, 1992; Haberle, 2005). However, the major impact on Holocene rainforest has been that of people.

Although people have been in the region for around 1.8 million years (Swisher *et al.*, 1994; Huffman, 2001) and have had the ability to manage vegetation through the use of fire within the last 100 kyr, the ability of people to physically clear rainforest for agriculture is essentially a Holocene phenomenon within the region. There are indications of agriculture (for rice-growing) as early as 16 kcal yr BP in the Yangtze Valley, China (Yasuda, 2002)—an area recognized as one of the cradles of crop domestication (Vavilov, 1951; Diamond, 1998)—and its spread into Southeast Asia, including those parts of the Sunda Platform which were then joined to the Asian Mainland. Several upland sites in Sumatra suggest that swiddening (slash-and-burn) was occurring for cultivation of dry (non-irrigated) rice or root crops as early as *c.* 10.3 kcal yr BP at Danau-di-Atas (Newsome and Flenley, 1988), *c.* 10 kcal yr BP at Pea Bullok (Maloney and McCormac, 1995), and *c.* 9 kcal yr BP at Rawang Sikijang (Flenley and Butler, 2001). The general pattern of evidence for the region was reviewed by Maloney (1998) and Flenley (2000).

A separate center for the origin of agriculture is found in New Guinea, based on rootcrops—such as *Colocasia* (taro)—and palynological evidence of forest destruction presumably for agriculture dates back to *c.* 9 kcal yr BP in the Baliem Valley (Haberle *et al.*, 1991), to *c.* 6 kcal yr BP or earlier at Draepi Swamp (Powell *et al.*, 1975), and to 5 kcal yr BP at Sirunki Swamp (Walker and Flenley, 1979). Early human activity in the New Guinea Highlands was confirmed by archeological finds at Kuk Swamp (Golson and Hughes, 1976; Golson, 1977; Denham *et al.*, 2003). These included evidence of swamp drainage, presumably for the growing of taro, back to at least 6.8 kcal yr BP and possibly *c.* 10 kcal yr BP. The destruction of swamp forest on Lynch's Crater about 5 kcal yr BP suggests that some form of cultivation may have spread into the rainforest areas of northeastern Australia at this time.

The progressive impact of these activities has led to the creation of permanent grasslands in many areas. These include the *cogonales* of the Philippines, the *kunai* of New Guinea, and smaller areas in Sumatra and elsewhere. In general, these areas have been maintained by frequent burning, and they tend to occur in regions where there is a more lengthy dry season (Thomas *et al.*, 1956). Recently, agriculture and logging has of course still further diminished the area of surviving forest, but consideration of that is beyond the scope of this chapter.

4.7 VEGETATION RESPONSES TO CYCLICAL FORCING

Spectral analysis is a powerful tool for examination of cyclical variation within components of well-dated, largely marine, records and has been applied to a number of sequences within the Far Eastern rainforest region in order to assess responses of various proxies to potential forcing mechanisms on orbital time scales.

Analysis of ODP Site 1144 in the South China Sea was restricted to pine and herb pollen, essentially winter monsoon indicators, and demonstrated clear Milankovitch forcing with prominent 100 kyr (eccentricity), 40 kyr (obliquity), and 20 kyr (precession) periodicities, in phase with northern hemisphere insolation and ice volume and indicating a clear link with monsoon activity (Sun *et al.*, 2003). It is interesting that the herbs demonstrate a closer correspondence with the ice volume signature than pine, reinforcing the suggested higher latitude source of its pollen. Pine displays a higher precessional than obliquity peak, indicating some tropical influence. It also shows a strong semi-precessional frequency that may be the result of an additional southern hemisphere tropical precessional signal resulting from changing mean position of the ITCZ through time. Unfortunately, as spectral analysis was performed on the whole million-year record, there is no way of determining changes in forcing through time—that may be expected with a change in the global signal—from dominant obliquity to eccentricity forcing around the Brunhes–Matuyama boundary.

A greater range of proxies has been examined from the southern hemisphere sites of Banda Sea, Lombok Ridge, ODP 820 (Kershaw *et al.*, 2003), and the North Australian Basin (Kershaw *et al.*, 2006; van der Kaars, unpublished data). In general terms, mangroves show similar frequencies to those from associated oxygen isotope records, and indicate strong northern hemisphere forcing. With mangroves, this pattern is not surprising as they are constrained by sea level changes that relate directly to ice volume. Their closer relationship with variation in sea level rather than that of climate has been explained by Grindrod *et al.* (1999, 2002). It is the broad exposure of the continental shelf during marine transgressions that facilitates mangrove colonization and peak mangrove pollen representation.

The major indicators of core rainforest—pteridophytes and rainforest angiosperms—surprisingly exhibit rather different spectral signatures. Pteridophytes exhibit strong glacial–interglacial cyclicity with a prominent obliquity signal that is not evident in the rainforest angiosperms that display a dominant precessional signal, except in the Banda Sea record. The most parsimonious explanation is that the core rainforest area is greatly influenced by the Asian monsoon and this influence extends to other marine sites in the pteridophytes due to the wide dispersal of their spores. The implication that more marginal areas are displaying a more localized tropical precessional influence is well-demonstrated in the eucalypt component of the North Australian Basin, whose variation can be clearly correlated with that of southern hemisphere precession. Although the area expresses a marked monsoon climate, the source of monsoon rainfall is most probably the southern Indian Ocean that is largely divorced from the Asian system.

Rainforest angiosperms also display significant variation in the 30-kyr frequency band, and this frequency is even more clearly expressed in rainforest gymnosperms and some charcoal records. It has been proposed by Kershaw *et al.* (2003) that this non-Milankovitch cycle is related to ENSO, due to the correspondence of peaks in burning and associated declines in fire-sensitive araucarian forests in the ODP record with peaks in ENSO frequency derived from the modeling of Clement *et al.* (1999).

From similar spectral signatures in the records of charcoal from cores MD97-2141 and MD97-2140 in similar West Pacific settings, Beaufort *et al*. (2003) and Thevenon *et al*. (2004) propose that the 30-kyr frequency can be attributed to the competing influences of long-term ENSO-like forcing and the glacial–interglacial cycle on the East Asian Summer Monsoon.

4.8 GENERAL DISCUSSION AND CONCLUSIONS

Perhaps the major feature of the Quaternary history of Far Eastern rainforest is that there has been little overall change in gross distribution over most of the area and through most of the period. Rainforest has shown tremendous resilience in the face of increasingly variable climatic conditions that have seen its partial replacement by more open vegetation types during drier and cooler glacial phases. The major spatial exception to this pattern is in tropical Australia, where the extensive occurrence of small patches of drier rainforest demonstrates survival from a much broader past distribution. This must pay testament to the aggressive nature of fire-promoting eucalypts, as it appears that grasslands alone have had much less of a long-term impact on similar vegetation in the Southeast Asian region, although poor soils and extreme climatic variability over much of tropical Australia may have contributed to this pattern. This patchy distribution is evident through the last 500 kyr in northern Australia, and it can only be surmised that this is a product of the Quaternary rather than a geologically earlier period.

In northeastern Australia, however, the impact of the Quaternary is clear with widespread reduction in drier araucarian forest within the late Quaternary. There has been speculation into the cause of this decline, elaborated by Kershaw *et al*. (2006). One explanation is human impact. However, without any evidence of the presence of people on the continent before about 50–60 kyr ago, this line of speculation is not particularly constructive, although there seems little doubt that, with the arrival of people, the trend towards more open vegetation was accelerated. A more robust hypothesis is that there has been a long-term trend towards aridity or variability in, at least, the northern part of Australia, and such a pattern is evident in physical as well as biological proxy data. The proposed changes in marine isotope signatures in the Coral Sea may be indicative of the development of the West Pacific Warm Pool, perhaps a threshold response to the movement of Australia into the Southeast Asian region and constriction of the Indonesian Gateway between the Pacific and Indian Oceans. Although an increase rather than decrease in precipitation might be expected by the rise in sea surface temperatures, any accompanying development in the ENSO system would have increased climatic variability and resulted in the frequent drought conditions required for effective biomass burning. A more direct influence of higher sea surface temperatures could be the expansion of mangrove vegetation that seems to have been a general regional feature of the Late Quaternary.

Although there are no dramatic changes in overall rainforest distribution within the South China Sea region, the suggestion by Sun *et al*. (2003) that the climate may have become more seasonal within the last 350 kyr could be significant, if the variability was interannual instead of, or in addition to, being seasonal. This would be consistent with a broad regional ENSO signal.

One important feature of the history of most, if not all, of the region is that conditions during the latter part of the last glacial period to the present day were distinctive, and are limited in the degree they can be applied to an understanding of extreme glacial and interglacial conditions or the nature of abrupt climate changes, in general. Assessment of the extent of savanna expansion during glacial periods is particularly problematic and critical to the understanding of mammal, including hominid, migrations into and establishments within the region. The separation of climatic and human influences is clearly important for patterns of change that relate to moisture variables, but the suggestion that the cooler-adapted communities were extensive during the last glacial period suggests that temperature variation also needs to be taken into consideration when comparison is made of glacial–interglacial cycles.

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5

Rainforest responses to past climatic changes in tropical Africa

R. Bonnefille

5.1 INTRODUCTION

In Africa the lowland rainforest occurs under significantly drier conditions than in other continents, within an average precipitation of 1,600 to 2,000 mm yr^{-1}, although higher rainfall is observed around the Atlantic coast of Cameroon, Gabon, and in the Central Zaire Basin. Seasonal distribution of precipitation is far from being uniform (White, 1983). Variations in the duration of the dry season follow the distance from the equator in both hemispheres and also along a west-to-east gradient. The Biafran Gulf is the only region where the minimum monthly precipitation value always exceeds the 50-mm threshold for the driest month, therefore experiencing no dry season. However, great annual rainfall variability is registered at most of the meteorological stations across tropical Africa while mean monthly temperatures usually remain constant. Inside the area occupied by the African rainforest topography is not uniform. Low elevation areas, those below 400 m a.s.l. (above sea level), are found in the coastal Atlantic plain and in the Zaire Basin. There are two main upland regions in tropical Africa: (i) the undulating plateaus of Gabon and Cameroon which are generally between 600 and 800 m a.s.l., but can reach up to 1,500 m a.s.l., and (ii) the eastern part of the Zaire Basin which joins the slopes of high mountains above 2,000 m a.s.l. bordering the Rift in the Kivu region. In addition, the active volcano Mount Cameroon stands apart from these upland regions and exceeds 4,000 m a.s.l. in elevation. The geographical distribution of tropical plant species is complex (Richards, 1981). Relationships between geographical plant distribution and ecological variables, (such as rainfall, available moisture, and seasonality) within the Guineo-Congolian domain are far from being well-established, although it is known that there are significant variations of these factors inside the areas occupied by rainforest. The only comprehensive review of African vegetation distribution relies on the continental-wide mapping and classification (White, 1983 and subsequent variants). However, classification provides challenges partly because

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M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

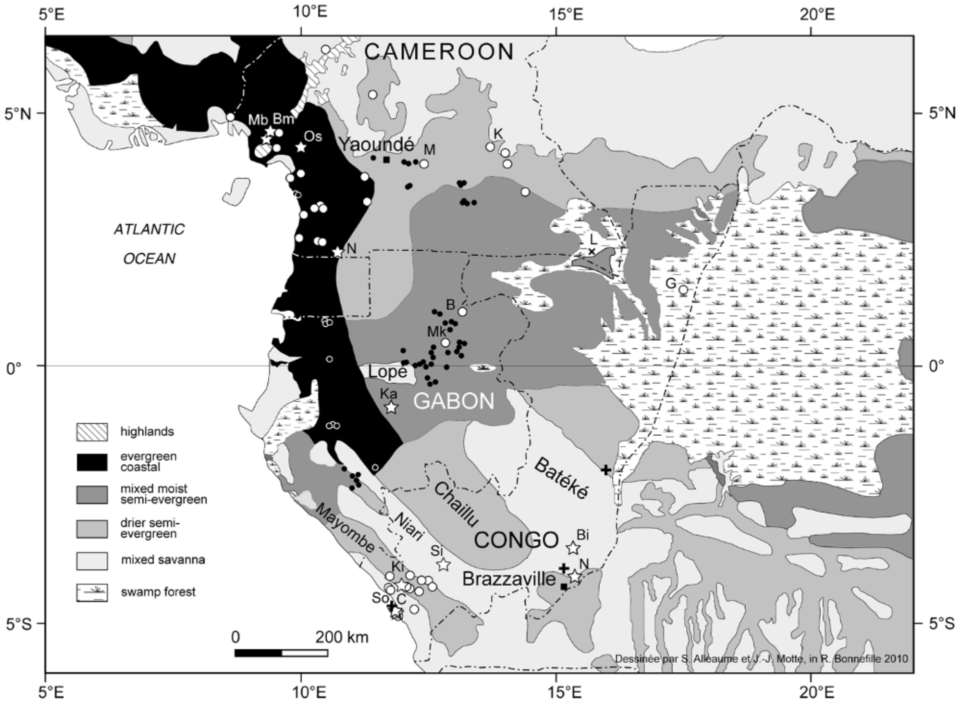


Figure 5.1. Distribution of different vegetation units within the Guineo-Congolian rainforest 6°S and 6°N) (after White 1983; Letouzey, 1965, 1985). Location of sites for modern pollen data are indicated by white and black dots, K: Kandara; L: Lobéké; B: Belinga; Mk: Makokou; G: Guibourtia for fossil pollen sequences (*) Bm: Barombi Mbo; Mb: Mboandong; Os: Ossa; M: Mengang; Ka: Kamalete; Bi: Bilanko; N: Nyabessan Ng: Ngamakala; Si: Sinnda; Ki: Kitina; C: Coraf; So: Songolo. Localities for wood sites discussed in the text (+).

variation in floristic composition, physiognomy, and phenology is largely gradual and continuous (Aubreville, 1951). This chapter focuses upon the oriental part of the Guineo-Congolian domain, where the degree of endemism is high, representing 80% of the total 8,000 species and 25% of the genera found in tropical Africa; with the greatest number of endemic genera being found among the Caesalpiniaceae. We present modern and fossil pollen data relating pollen and plant distribution within the present day and the Latest Quaternary (Figure 5.1).

5.2 VEGETATION UNITS WITHIN THE GUINEO-CONGOLIAN RAINFOREST

5.2.1 Hygrophilous coastal evergreen forest

Syn.: forêt biafréenne à Caesalpiniacées (Letouzey, 1968), forêt dense humide sempervirente à Légumineuses (Aubreville, 1957–58), wet evergreen forest (Hall and Swaine, 1981).

The evergreen Guineo-Congolian wet forest is located between 2°S and 6°N in areas that receive 2,000 to 3,000 mm yr^{-1} rainfall and may, or may not, have a dry season. The atmospheric humidity is very high throughout the year. Most individuals of most tree species are evergreen and shed their leaves intermittently. *Lophira alata* (Ochnaceae) is one of the most abundant of the widespread taller trees, although it is not confined to this vegetation unit. *Lophira alata* is light-demanding with drought-sensitive seedlings, with the potential to be a large tree that can live for several centuries. Historical remains (slave rings, pottery, charcoal, etc.) observed in excavations after deforestation for *Hevea* (rubber) plantations and road cuttings indicate that *Lophira alata* forest now occurs in areas that were cultivated perhaps a few centuries ago (Letouzey, 1968). A typical example of hygrophilous coastal evergreen forest would contain an abundance of Caesalpinioideae, including species of various genera such as *Anthonotha*, *Brachystegia*, *Julbernardia*, *Berlinia*, *Monopetalanthus*, associated with *Cynometra hankie* (Caesalpiniaceae) and *Coula edulis* (Ochnaceae).

5.2.2 Mixed moist semi-evergreen forest

Syn.: forêt congolaise (Letouzey, 1968, 1985), forêt dense humide sempervirente á Légumineuses (Aubreville, 1957–1958), forêts semi-caducifoliées sub equatoriales et guinéeennes (Lebrun and Gilbert, 1954).

Most Guineo-Congolian rainforest can be classified as mixed moist semi-evergreen forest occuring on well-drained soils and covering most of an area at low elevations (600–700 m a.s.l.). Today this forest type covers all but the wettest and driest extremes of northeast Gabon, northern Congo, southeast Cameroon, and the Zaire Basin. Mean annual rainfall is typically between 1,600 and 2,000 mm and precipitation is evenly distributed throughout the year. The forests are rich floristically and, although some species are evergreen, many are briefly deciduous. No detailed description of the floristic composition of this type of forest exists across its full geographic extent. Characteristic abundant emergent species found in mixed moist semi-evergreen forest include *Canarium schweinfurthii* (Burseraceae), *Piptadeniastrum africanum* (Mimosoideae), *Ricinodendron heudelotii* (Euphorbiaceae), and *Terminalia superba* (Combretaceae) but these species can also be found in secondary forests of the dry, peripheral semi-evergreen type. However, characteristic regional floristic associations include: (i) *Oxystigma oxyphyllum* (Caesalpiniaceae) and *Scorodophloeus zenkeri* (Caesalpiniodeae) in the Zaire Basin (Lebrun and Gilbert, 1954), and (ii) few species of Caesalpiniaceae (except *Gilbertiodendron dewevrei* which can form pure stands) with large and tall *Baillonella toxisperma* (Sapotaceae) in Cameroon (Letouzey, 1968).

5.2.3 Single-dominant moist evergreen and semi-evergreen forest

Several authors have described single-dominant forests which form isolated stands of a few hectares inside the mixed moist semi-evergreen forest or islands which occur in a broad aureole surrounding the Zaire Basin (White, 1983). In single dominant forests the upper canopy is typically formed by tall trees, usually 35–45 m high, that belong to a few or a single species (Evrard, 1968). Among the dominant species, *Gilbertiodendron dewevrei* (Caesalpiniaceae) from southeast Cameroon is normally completely evergreen, whereas the more widespread *Cynometra alexandrii* (Caesalpiniaceae) is irregularly deciduous. Simultaneous shedding of leaves within single dominant stands has been noted in Uganda for *Cynometra* trees, which are particularly abundant above 700–800 m a.s.l., and in the Zaire Basin for *Julbernardia* (Caesalpiniaceae). In the single-dominant moist evergreen forest, heliophitic trees are rare. Lianas and giant monocotyledonous herbs are also poorly represented.

5.2.4 Drier peripheral semi-evergreen forest

Syn.: forêt dense humide semi-décidues de moyenne altitude (Letouzey, 1968), forêts semi-caducifoliées, forêts semi-décidues à Malvales et Ulmacées (Aubreville, 1957–1958).

Drier peripheral semi-evergreen forest extends geographically between the moist evergreen forests and the limit of areas occupied by savanna, forming two bands running transversely across Africa to the north and south of the moister forests (described in Sections 5.2.1–5.2.3). The drier forests have been termed "peripheral" (White, 1983) because of their marginal position and occur in patches within the Lake Victoria basin. Rainfall is between 1,200 and 1,600 mm yr^{-1}, with a bimodal distribution. The dry season lasts 1 or 2 months during which relative humidity remains high. Mean annual temperatures range from 23.5 to 25°C. Most individuals of more common, larger tree species are deciduous and lose their leaves for a few weeks during the dry season. The drier peripheral semi-evergreen forest has a distinct floristic composition and includes species virtually absent from the wetter types of forest; such as *Afzelia africana* (Caesalpiniaceae), *Aningeria altissima* (Sapotaceae), and *Cola gigantea* (Sterculiaceae). Some other species that are important components of the dry peripheral semi-evergreen forest also occur in mixed moist semi-evergreen forests; these include *Celtis mildbraedi* and *C. zenkeri* (Ulmaceae), *Holoptolea grandis* (Ulmaceae), and *Sterculia oblonga* (Sterculiaceae). In Cameroon the "drier peripheral semi-evergreen forest" or forêt dense semi-decidue de moyenne altitude (Letouzey, 1968) is characterized by the dominance of *Cola*, *Sterculia*, *Celtis*, and *Holoptolea grandis*, together with *Piptadeniastrum africanum* (Mimosaceae), *Funtunia* (Apocynaceae), and *Polyalthia* (Annonaceae). While *Terminalia superba* (Combretaceae) and *Triplochiton scleroxylon* (Sterculiaceae) are two rapidly growing, light-demanding, valuable timbers that can regenerate on abandoned farmland within this region.

Besides the main four types of rainforest described above, there are different vegetation types that have also been mapped as separate units. Secondary forests, swamp forests, and a mosaic of forests and grasslands can be found in any of the four main types of forest described earlier (White, 1983).

5.2.5 Secondary rainforest

Outside the forest reserves, much of the remaining forest occurs on land that has been formerly cultivated and is therefore considered secondary. This regrowth contains abundant heliophytes and pioneers that grow quickly and have a short life;

Tetrorchidium (Euphorbiaceae) and *Trema* (Ulmaceae) are characteristic, while *Musanga cecropioides* (Moraceae) is strictly Guineo-Congolian in distribution.

5.2.6 Swamp forest

Swamp forests, including riparian forests, occur throughout the Guineo-Congolian region wherever the conditions are suitable. These forests are floristically distinct, but have a similar appearance to rainforest with the tallest trees reaching 45 m in height. The main canopy, however, is irregular and open. Inside the clearings, climbing palms *Eremospatha* and *Calamus*, shrubs, and lianas fill the gaps. Forest types with Marantaceae and *Gilbertiodendron* are located between the western side of the inundated wet evergreen forests and the mixed moist semi-evergreen forest (forêt congolaise).

5.2.7 Edaphic and secondary grasslands

On hydromorphic soils, edaphic grasslands surrounded by forest represent the transition from aquatic vegetation to forest. The origin of such grassland patches is still controversial. They may be maintained by frequent fires, but they also occupy superficial soils on rocks that are periodically inundated (Koechlin, 1961). At its northern and southern limits, the Guineo-Congolian rainforest is burned at least once a year. Where burning occurs a mosaic of patches of secondary grassland, scattered fire-resistant trees, and secondary forest clumps locally replace the rainforest. In this situation, the mosaic can regenerate into forest if fire is absent for a sufficient period. There are also patches of secondary grassland inside the Guineo-Congolian rainforest region (Descoings, 1976). However, most of these are distributed at the transition with the Sudanian zone in the north and with the Zambezian zone in the south, and show considerable local variation in floristic composition.

5.2.8 Transitional and Afromontane evergreen forests

In Cameroon, close to the border with Nigeria, Afromontane forests show a great resemblance to the montaine forests of East Africa. Two distinct altitudinal zones are evident. The lower, from 800 to 1,800 m a.s.l., is characterised by *Podocarpus latifolius* (Podocarpaceae) (syn. *P. milanjianus*) associated with *Olea capensis* (Oleaceae) (syn. *O. africana*). The upper, from 1,800 to 2,800 m a.s.l., contains *P. latifolius* together with *Prunus africana* (Rosaceae), *Myrsine melanophloeos* (Myrsinaceae), and *Nuxia congesta* (syn. *Lachnopylis*, Loganiaceae). In eastern Zaire a transitional montane forest is found between 1,100 and 1,750 m a.s.l. which includes tree species of the Afromontane forest, including *Aningeria* (Sapotaceae), *Entandophragma* (Meliaceae), *Mitragyna* (Rubiaceae), and *Ocotea* (Lauraceae), along with components of the lowland forest, such as *Cynometra alexandrii* (Caesalpiniaceae), *Pycnanthus angolensis* (Myristicaceae), plus some endemics, specific to the transitional forest. Species specific to the transitional forest between lowland and Afromontane forests include *Strombosia grandiflora*

(Olacaceae), *Symphonia globulifera* (Olacaceae), *Uapaca guineense* (Euphorbiaceae), and *Parinari* sp. (Chrysobalanaceae) (White, 1983).

5.3 MODERN POLLEN RAIN STUDIES

No systematic study of modern pollen rain within the African rainforest has addressed the relationship between the distribution of vegetation types and climatic variables. The lack of ecological work and the long-standing belief of "equatorial climatic stability" might have discouraged such studies. However, new modern pollen rain data from tropical evergreen and deciduous forests of southwest India (Barboni, 2003) and the Amazon Basin (Gosling *et al.*, 2009) should encourage further studies in tropical Africa. In India, the western coast supports many different types of forests under a single monsoonal regime, with a south-to-north increased gradient of rainfall, a west-to-east increase in dry season length (seasonality), and a temperature decrease along highland slopes reaching up to 2,500 m a.s.l. in elevation. Ecological studies showed that these factors indeed influenced the distribution of species and that of vegetation types, following the different bioclimatic regions (Pascal, 1984). Modern pollen assemblages from this region in India reproduce the pattern of bioclimatic regions and associated vegetation-mapped units. The results enable a clear distinction between the different types of forests and their associated pollen markers (Bonnefille, 1999; Barboni and Bonnefille, 2001; Anupama, 2000). In Africa, modern pollen rain studies provide a first understanding of pollen production and markers of the different forest types within the Guineo-Congolian rainforest. The main types of vegetation (Figure 5.1) have now been sampled for modern pollen, although the mixed moist semi-evergreen forest of the Zaire Basin remains poorly documented. Comparisons with floristic "relevés" have been made in the evergreen rainforest of Cameroon and the semi-evergreen forest of southern Congo. However, because of differences in sampling procedures, variable plot sizes, and access to data (inclusion within the "African Pollen Data Base"), it is not currently possible to provide a single synthetic diagram for modern pollen distribution within the rainforests of tropical Africa. In this section the published results of modern pollen studies are organized and discussed according to geographical regions and vegetation-mapping units following White (1983).

5.3.1 Tropical and equatorial forests north of the equator

The three main phytogeographical units mapped within the inter-tropical region, all of which are present in Cameroon, are: (i) the evergreen and coastal hygrophilous forests (biafréenne à Caesalpiniacées), (ii) the drier peripheral semi-evergreen (forêt caducifoliée), and (iii) the mixed moist semi-evergreen (forêt congolaise) *sensu* (Letouzey, 1968) (Figure 5.1). Recent studies document the modern pollen rain of the first two units, with the third unit documented to a lesser extent, using different sampling methods. In the first study, trees and pollen abundance are calculated within plots selected as representative of the main vegetation types (Renaud-Farrera, 1995).

In a more recent study, surface soil samples were collected randomly at localities chosen to represent "mature" forest types (Lebamba *et al.*, 2009). The sub-random sampling provides results directly comparable with modern pollen data obtained from other tropical forests in Africa (Bonnefille *et al.*, 1993; Vincens *et al.*, 1997), and therefore it is more appropriate to apply the biomization procedure at the continental scale in Africa.

5.3.1.1 Modern pollen rain–vegetation comparison

The fidelity of representation of tree species within the pollen rain of tropical African forests has been questioned in the past because some abundant tree or climber species do not produce/disperse pollen in large quantities; such as Annonaceae, Apocynaceae, Violaceae (except *Rinorea*), most Myristicaceae (except *Pycnanthus*), Chrysobalanaceae, Olacaceae (except *Strombosia*), and Clusiaceae (except *Symphonia*). To explore the representivity of arboreal pollen within tropical forests modern pollen–vegetation studies in Cameroon have focused upon the evergreen and coastal hygrophilous forests ("biafréenne à Caesalpiniacées"), with a few studies working within the mixed moist semi-evergreen "forêt congolaise" and the drier peripheral semi-evergreen "forêt semi-caducifoliée" (Letouzey, 1968).

Modern pollen samples and counts of tree species over 5 cm in diameter were obtained from within twenty 20 × 20 m plots across Cameroon (Reynaud-Farrera, 1995). The pollen counts of several plots were averaged to allow comparison between plant (Figure 5.2a) and pollen frequencies of different taxa (Figure 5.2b). An interesting finding of the study conducted by Reynaud-Farrera (1995) is that in all the samples collected inside forest plots, the ratio of arboreal pollen (AP) (including all trees and shrubs) calculated versus total pollen counts (excluding the spores) always exceeds 75% (Figure 5.2a). The samples showing the lowest AP values were collected in open vegetation areas such as at Kandara near the limit between the peripheral semi-evergreen and the forest/grassland mosaic. A good correspondence between the total AP and the tree coverage of the wet evergreen and semi-evergreen forests in Cameroon supports similar findings from other tropical regions in Africa (Bonnefille, 1993). Therefore, the distinction between AP and non-arboreal pollen (NAP), classically used in the interpretation of pollen analysis from the temperate region, remains valid for palynology in the equatorial rainforest regions.

In the modern pollen–vegetation study from Cameroon, the high number (279) of pollen taxa identified within the soil samples reflects the great floristic diversity of evergreen forests. Because of the strong heterogeneity in the spatial distribution of the tree species, the occurrence of many intermediate forest types, and the unavoidable bias between over- and under-representation of the pollen of many tropical families, a greater number of pollen samples, more evenly distributed within the different vegetation types, would have been advantageous. Nevertheless, despite evident discrepancies between vegetation cover and pollen representation, there is a certain degree of agreement between the listed plants within ecological plots and the pollen types found in the surface soil samples (Figure 5.2c). The pollen assemblages from the different forest types appear clearly distinct from each other, enabling one to

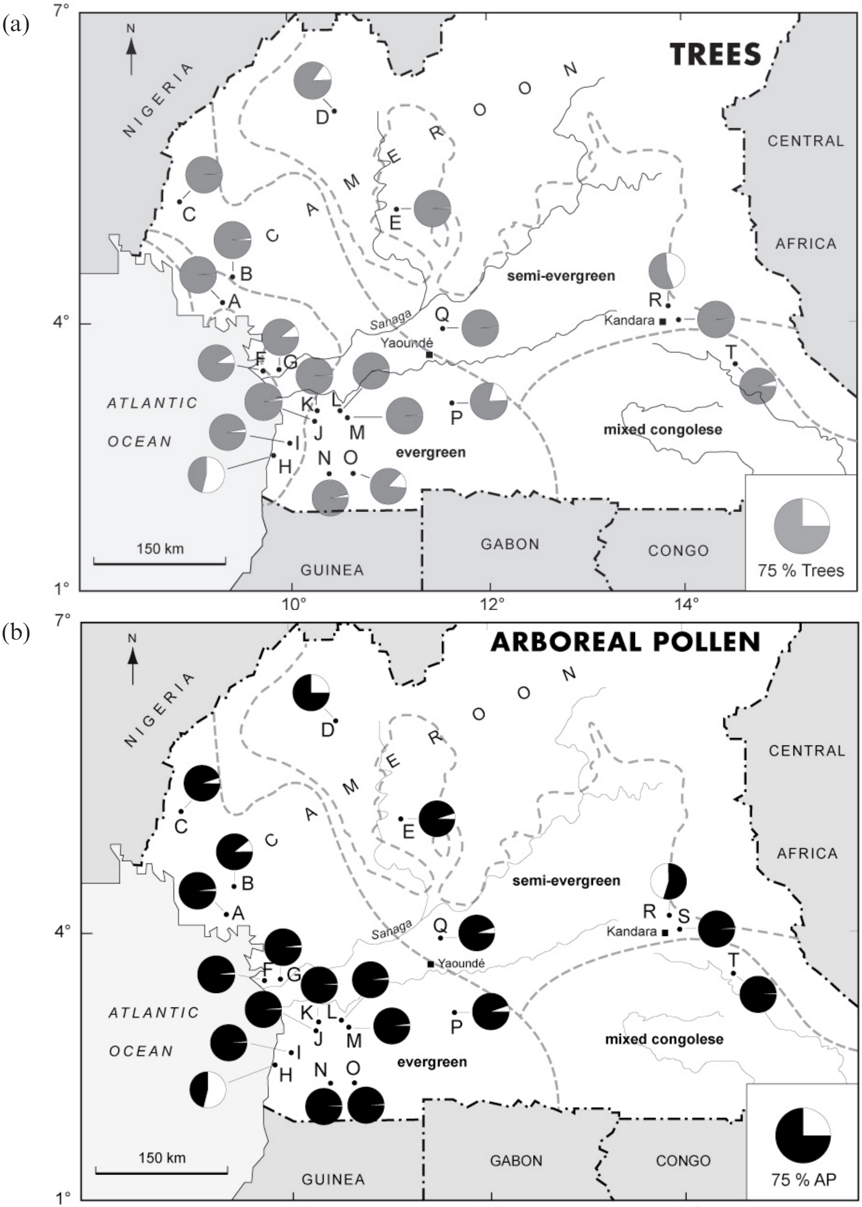
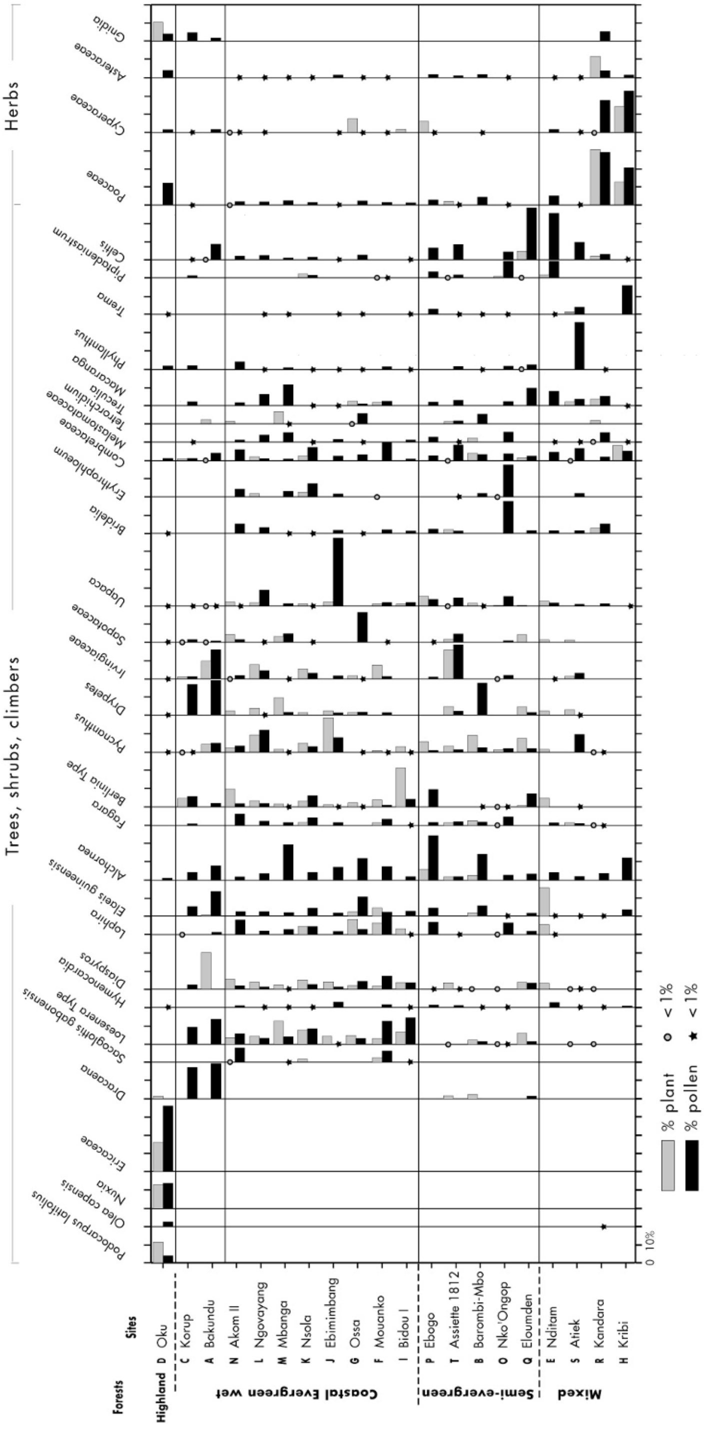


Figure 5.2. Modern pollen rain from coastal evergreen forests, mixed moist semi-evergreen, and drier semi-evergreen forests from Cameroon: (a) % of trees and shrubs among plants in the plots; (b) % of arboreal pollen in soil samples from the same plots; (c, facing page) distribution of relative frequencies of plant and pollen for the main taxa at pollen sampling sites as in (a) and (b) (after Reynaud-Farrera, 1995). Some trees, identified in floristic counts, but not found as pollen are not illustrated here such as the Maranthaceae among the herbs, fern spores are not represented (% calculated versus pollen sum after excluding spores and Cyperaceae).

(c)


Herbs
Trees, shrubs, climbers
Gnidia
Asteraceae
Cyperaceae
Poaceae
Celtis
Piptadeniastrum
Trema
Phyllanthus
Macaranga
Treculia
Tetrorchidium
Melastomataceae
Combretaceae
Erythrophleum
Bridelia
Uapaca
Sapotaceae
Irvingiaceae
Drypetes
Pycnanthus
Berlinia Type
Fagara
Alchornea
Elaeis guineensis
Lophira
Diospyros
Hymenocardia
Loesenera Type
Sacoglottis gabonensis
Dracaena
Ericaceae
Nuxia
Olea capensis
Podocarpus latifolius
0 10%
% plant
% pollen
< 1%
< 1%
Forests
Sites
Highland
D Oku
C Korup
A Bakundu
N Akom II
L Ngovayang
M Mbanga
K Nsola
J Ebimimbang
G Ossa
F Mouanko
I Bidou I
Coastal Evergreen wet
P Ebogo
T Assiette 1812
B Barombi-Mbo
O Nko'Ongop
Q Eloumden
Semi-evergreen
E Nditam
S Atiek
R Kandara
H Kribi
Mixed

recognize the different forest types. Joint occurrences of *Saccoglottis* and *Lophira*, together with "*Berlinia*-type" pollen including many Caesalpiniaceae, are good markers of the coastal Biafran forest, in agreement with the dominant trees. Pollen of *Irvingia* (Irvingiaceae), *Lophira*, *Diospyros* (Ebenaceae), and Sapotaceae (which might include *Baillonella toxisperma*, the pollen of which cannot be identified at the generic level), show highest representation in the mixed semi-evergreen "Congolese" forest. The *Pycnanthus* (Myristicaceae) and *Piptadeniastrum* (Mimosoideae) pollen association characterizes the dry evergreen (semi-deciduous) forest, although *Pycnanthus* alone can be abundant within the coastal Biafran forests. *Macaranga*, *Alchornea*, *Celtis*, and sometimes *Uapaca* tend to be over-represented in the pollen rain. The two pollen assemblages corresponding to the mountain forest are well-characterized by the association of *Podocarpus*, *Olea*, *Nuxia*, and Ericaceae pollen (Figure 5.2c).

5.3.1.2 Modern pollen rain, random sampling strategy

Results from 84 additional samples recently collected in Cameroon and Gabon (Lebamba *et al*., 2009) confirm that the modern pollen rain assemblages of the three types of forests (coastal, mixed moist semi-evergreen, and drier semi-evergreen) all contain predominant total AP percentages (80 to 90%). The high abundance of tree taxa is in good agreement with the study by Reynaud-Farrera (Figures 5.2a and b). It is worth noting that despite high diversity, varied floristic compositions and low pollen production (insect pollination) of many tropical tree species, the modern pollen counts reflect the abundance of local tree cover density for these tropical forests.

The compositional variation in the modern pollen assemblages reflects the different vegetation types in Gabon and Cameroon from which they were sampled (Lebamba *et al*., 2009). Correspondance analysis of 80 modern pollen assemblages is interpreted as reflecting a decreasing humidity gradient within forests (Figure 5.3, axis 3), that is, a trend from humid mixed moist semi-evergreen forest of Gabon (low scores axis 3) towards the drier semi-evergreen of Cameroon (higher scores axis 3). In addition, coastal forests appear well distinguished from other types of forest (highest scores axis 3) and characterized by the association of *Lophira alata*, *Coula edulis*, *Ceiba pentandra* together with abundant Caesalpiniaceae and Mimosaceae, in agreement with previous work in Cameroon (Reynaud-Farrera, 1995).

5.3.2 Mixed moist semi-evergreen forest

The mixed moist semi-evergreen forest exists in Cameroon, Gabon, and Congo, but it has been sampled only in Gabon so far, and following two distinct strategies for collecting modern soil samples.

5.3.2.1 Modern pollen rain–vegetation comparison

Mixed moist semi-evergreen forest was sampled in Central Gabon during a preliminary palynological investigation in the forest reserves at Makokou

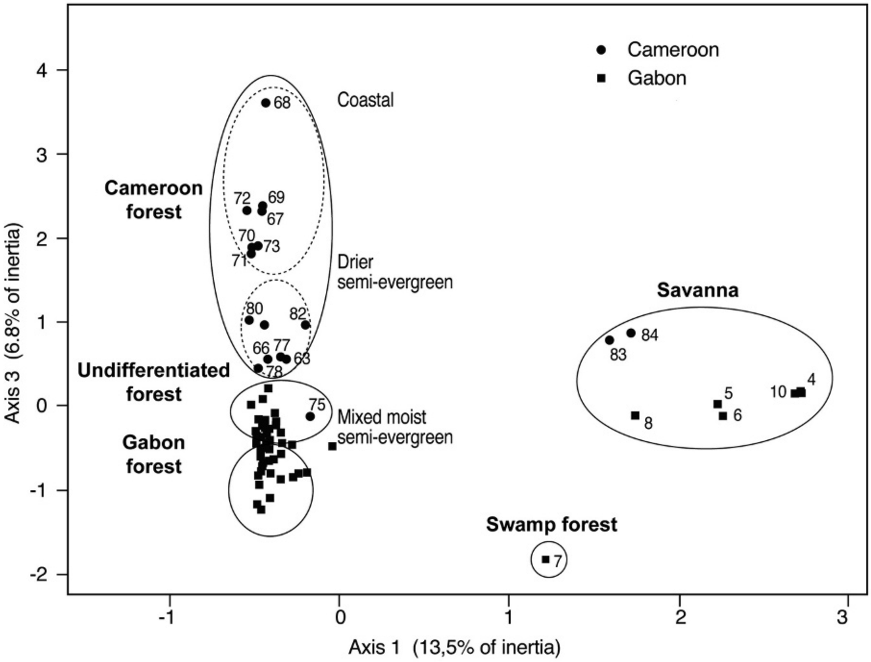


Figure 5.3. Results of correspondence analysis (Benzécri method) performed on pollen percentages of 80 modern pollen samples from the different forest types mapped in the equatorial region of Cameroon and Gabon (after Lebamba *et al*., 2009).

(0°30″N, 12°50″E) and Belinga (1°06″N, 13°10″E) (Figure 5.1; Jolly, 1996). Located at 470 m a.s.l., near the Irvindo River, the Makokou forest is dominated by *Scorodophloeus zenkeri*, *Baphia*, *Dialium*, *Pancovia*, *Dichostemma glaucescens* among the Papilionaceae, and *Polyalthia* among the Annonaceae (Caballe, 1986; Aubreville, 1967). Precipitation amounts to 1,500 to 1,700 mm yr^{-1}, and mean annual temperature is over 24°C. At Makokou, various sampling strategies (line, diagonals, random, etc.) were tested to collect surface soil samples within 120 × 40 m forestry plots along a 1 km transect. No significant differences were shown between the pollen assemblages obtained with the different collecting methods. It was concluded that a random procedure represents the most parsimonious and the least time-consuming method. Random collection should certainly be made in regions where there is an urgent need to obtain modern pollen data within forests under threat of total disappearance. The counts of 16 pollen assemblages, corresponding to the mixed moist semi-evergreen forest, include 82 pollen taxa (Jolly, 1996). The highest pollen frequencies were found in the Moraceae and Euphorbiaceae (mainly *Alchornea*), *Celtis*, Combretaceae, *Pausinystalia* (Rubiaceae), *Hymenostegia* (Caesalpiniaceae)—together with *Dacryodes* (Burseraceae) and *Pycnanthus* (Myristicaceae), which were not particularly well-represented in the vegetation. Pollen attributed to Papilionaceae has been counted but in much lower abundance than the corresponding trees in the forest. High proportions of Urticaceae and *Macaranga* characterize a plot located near to the river, and were attributed to local disturbance. The pollen spectra from the mixed semi-evergreen forest at Makokou (Gabon) has some common taxa (*Celtis*, *Macaranga*, *Alchornea*, and *Combretaceae*), with samples from Cameroon located in a forest intermediate between the evergreen Biafran and the semi-evergreen "Congolese". Interestingly, the Belinga pollen sample, located at higher elevation (950 m a.s.l.), contains significant percentages of *Syzygium* pollen, a fact also noticed in modern pollen data from highland forests in Ethiopia (Bonnefille, 1993) and South India (Bonnefille, 1999).

5.3.2.2 Modern pollen rain, random sampling strategy

The pollen results of the 33 new samples collected from the lowland mixed moist semi-evergreen equatorial forest in Gabon (Lebamba *et al.*, 2009) have been reproduced here (Figure 5.4). Associated predominance of Mimosaceae, Caesalpiniaceae, and Sapindaceae pollen characterize all the samples of the moist semi-evergreen equatorial forest. Present in lesser proportions, pollen of *Dacryodes*, Ebenaceae (*Diospyros*), *Pycnanthus*, *Zanthoxylum*, *Aucoumea*, and *Bridelia* occur regularly in most samples whereas more sporadic occurrences of Burseraceae, *Canarium*, Meliaceae, Sapotaceae, Flacourtiaceae, Moraceae, and *Martretia* account for floristic diversity of the forest communities at different localities. Herbaceous cover is poorly represented, with a few grains of Asteraceae (Compositae), Acanthaceae, and Amaranthaceae and very little representation of grass (Poaceae) which was probably introduced by human disturbance along paths.

5.3.3 Drier peripheral semi-evergreen forest north of the equator

Modern pollen data from the drier peripheral semi-evergreen forest (forêt semi-caducifoliées), which extends around the 4°N latitude between the mixed moist semi-evergreen and northern savanna, has been provided at two distinct sites: Mengang (east of Yaounde) and Kandara in Cameroon (Figure 5.1).

The Mengang forest station was located in an area receiving 1,600 mm yr^{-1} precipitation interrupted by two dry months (<50 mm)—December and January—and a minimum in July. Atmospheric pollen rain trapped monthly between April and October 1987 (Fredoux and Maley, 2000) showed that the majority of pollen was derived from forest trees (*c.* 90% of total counts and greatest monthly influx averaging 1,000 grains m^{-3}). Altogether, 118 tree taxa were identified distributed among 58 families. The Euphorbiaceae showed the greatest diversity (21 taxa) and totalled 27% of the pollen counts dominated by Ulmaceae (33%), Moraceae (26%), Urticaceae (3%)—with Papilionaceae, Caesalpiniaceae, Mimosaceae, Anacardiaceae, Sterculiaceae, Rubiaceae, and Sapindaceae being rare at $<1\%$. The greatest pollen producers indicated by influx calculations are *Macaranga* (1 to 1,000 grains m^{-3} maximum in May), *Celtis* (1 to 500 grains m^{-3} in April), and *Musanga* (or *Myrianthus*) and Combretaceae (10 to 100 grains m^{-3}). The amounts of *Pycnanthus*, *Trema*, Urticaceae, and Poaceae pollen are

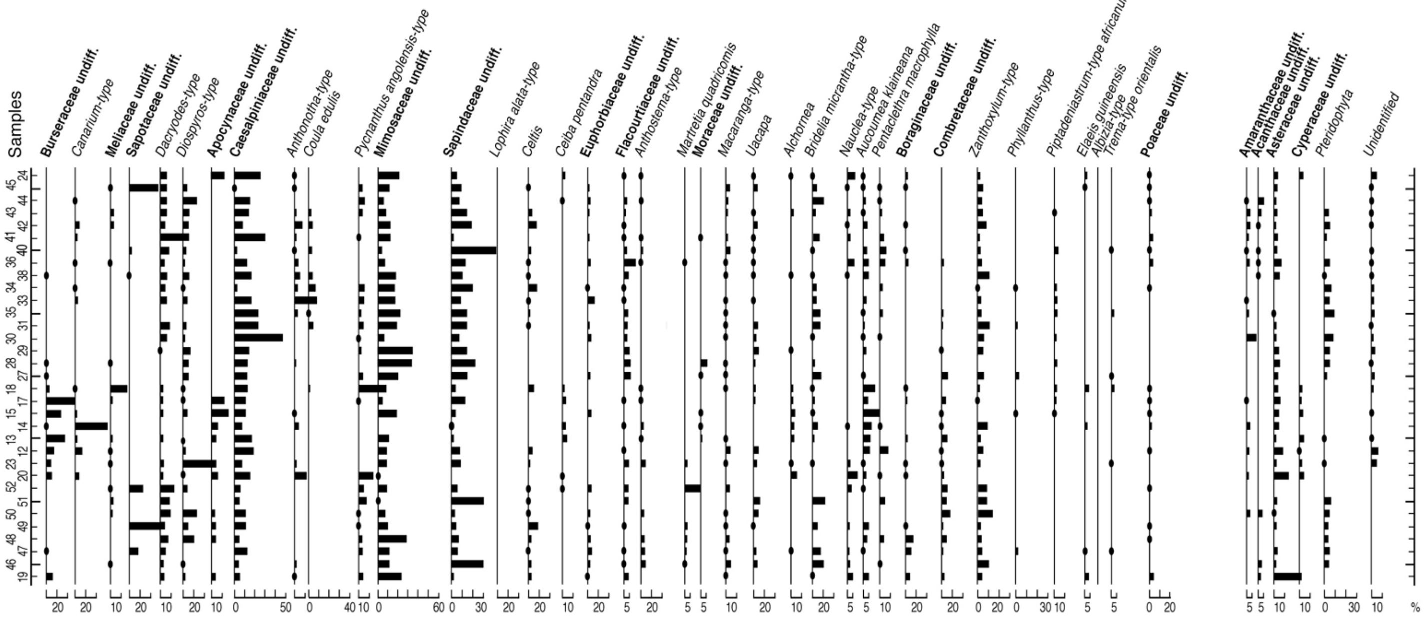


Figure 5.4. Pollen diagram of modern surface soil samples from mature forest types of the mixed moist semi-evergreen mapping unit collected at different localities in Gabon (black dots, Figure 5.1). Samples numbers refer to Figure 2 (Lebamba *et al.*, 2009).

produced in much lower proportion (<1 to 10 grains m^{-3}). The month-to-month variation in the pollen rain reflects seasonality and suggests that caution should be taken when interpreting the fossil record. It would have been most interesting to compare this distribution with parallel analysis of surface soil samples within the forest that provide an average of modern pollen rain over several years, minimizing monthly variations.

In southeastern Cameroon—east of Mengang (Figure 5.1), near the Kandara village (4°20″N, 13°43″E, 640 m a.s.l.)—the dry semi-evergreen forest encloses an area of a few square kilometers of shrub tall-grass savanna. The wet tropical climate is characterized by the same precipitation (1,600 mm yr^{-1}) and dry season, with mean annual temperature averaging 24°C. In this area the forest had expanded at a rate of 1 m yr^{-1} between 1951 and 1993 (Youta Happi, 1998; Achoundong 2000), in agreement with observations made using aerial photographs in Cameroon (Letouzey, 1968). The forest succession begins with *Raphia monbuttorum* (Palmae) swamp along the Soukato River, followed by a semi-evergreen *Rinorea* (Violaceae) forest, a young *Albizia* forest, and a savanna-forest transition (ecotone) surrounding the savanna dominated by Panicoideae grasses with some *Albizia* clusters (Figure 5.3a). Associated with *Rinorea dentata* and *Rinorea batesii* (Achoundong *et al.*, 1996), the most abundant trees of the mature forest are *Triplochiton scleroxylon* (Sterculiaceae) and *Piptadeniastrum africanum* (Mimosaceae), good indicators of dry peripheral semi-evergreen forest (Letouzey, 1968). The young *Albizia* forest includes *Albizia adiantifolia* (Mimosaceae), *Funtumia elastica* (Apocynaceae), *Canthium* (Rubiaceae), *Tabernaemontana crassa* (Apocynaceae), *Sterculia rhinopetala* (Sterculiaceae), and *Myrianthus arboreus* (Moraceae). At Kandara, 26 surface soil samples collected in contiguous 20 × 30 m plots, along a 750 m transect across the succession (Figure 5.5a), provided modern pollen rain data. Each pollen sample consisted of about 20 sub-samples randomly distributed (Vincens, 2000). The relative frequencies of the most abundant among the 101 pollen taxa identified are illustrated here (Figure 5.5c). All samples from the dry semi-evergreen forests register percentages of AP ranging from 60 to 80, in good correspondence with the canopy coverage estimated by field measurements of the leaf area index (LAI) (Cournac, 2002) and abundance of tree phytoliths counted in the same samples (Bremond, 2005). The total AP drops abruptly to less than 10% in the nearby savanna, at less than 100 m from the forest limit, indicating very little transport from the forest into the savanna (Figure 5.5b).

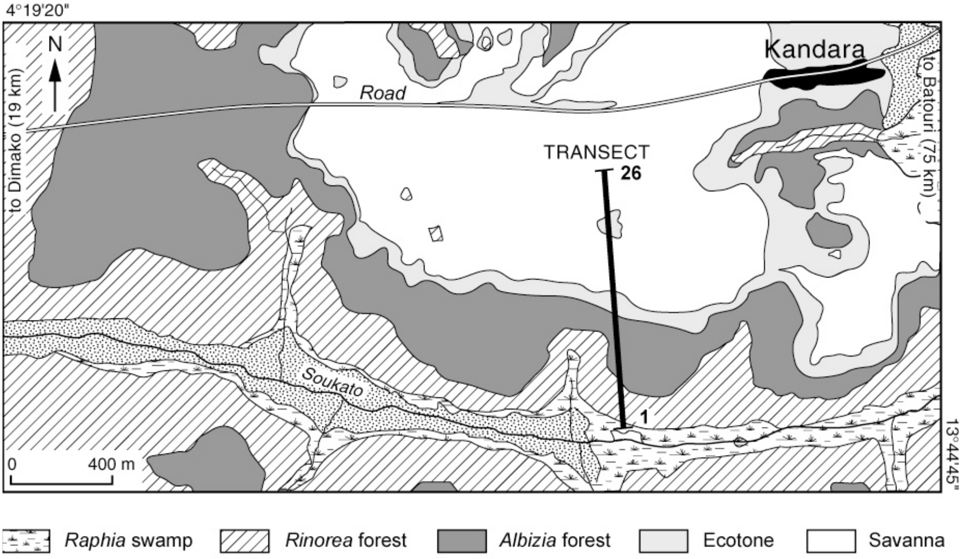
The pollen assemblages from the Kandara transect contain trees that are characteristic of the dry peripheral semi-evergreen forest, including: *Celtis*, *Chaetachme*, *Holoptolea* among the Ulmaceae, *Triplochiton* (Sterculiaceae) associated with *Piptadeniastrum* (Mimosaceae), *Margaritaria discoidea* (Apocynaceae), and Combretaceae. These taxa can be considered as good indicators of semi-evergreen forest under a seasonal climate, with a short dry season. However, as anticipated from our understanding of differential pollen production and dispersal, the pollen abundances do not exactly correspond to plant abundances in the vegetation cover. For example, the soil samples from the "*Albizia* forest" contain only a few grains of *Albizia* pollen and the pollen assemblage is dominated by *Myrianthus arboreus* (Moraceae)

(50–70%; Figure 5.5c). Typical components of the semi-evergreen forest pollen rain are *Ficus*, *Trilepisium* (both Moraceae), *Tetrorchidium* (Euphorbiaceae), *Antidesma* (Phyllanthaceae), Rubiaceae, and Sapindaceae. Towards the ecotone of the "*Albizia* forest", and the savanna, *Chaetachme* aristata (Ulmaceae) is better represented in the pollen rain (20%) than *Albizia* (5 to 10%) despite the latter being more abundant in the vegetation cover. In the other direction, at contact with the "*Rinorea* forest", *Piptadeniastrum* pollen was relatively abundant whereas none of the different species of *Rinorea* were recorded as pollen. *Raphia* pollen dominates near swamps, which is also marked by an abundance of fern spores (*Pteridophytes monoletes*). At the northern end of the Kandara transect, close to the savanna, the abundance of *Pteridium aquilinum* spores indicates frequent burning. The pollen diagram illustrates the spatial colonization of a burnt savanna by a dry semi-evergreen forest. The succession starts with Moraceae, followed by *Celtis*, and then by Sterculiaceae/*Raphia*/Pteridophyta, following dry to wetter local conditions under climatic conditions favourable to the establishment of dry semi-evergreen forest. Further studies are now required to test the regional, and extra-regional, applicability of pollen–vegetation relationships established for the northern semi-evergreen forest region at Kandara.

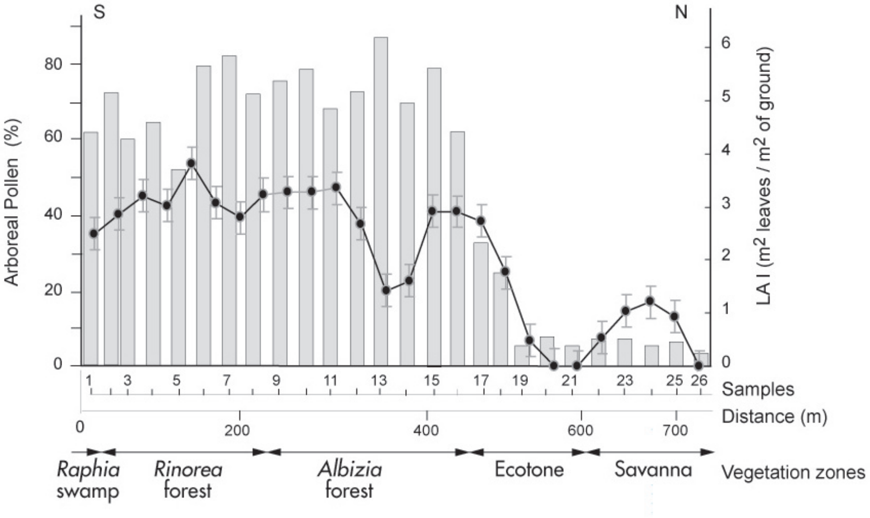
The origin of savanna "islands" in the semi-evergreen forest of southeast Cameroon still remains controversial. Analyses of opal phytolith assemblages from topsoil samples of the forests and savanna patches at Lobeke—2°17″N, 15°42″E, 300 to 700 m a.s.l., south of Kandara (Figure 5.1) in a region receiving 1,600–1,700 mm yr^{-1} precipitation—suggest stable conditions with no evidence of recent disturbances, such as fire or logging (Runge and Fimbel, 1999). Elsewhere, evidence for a recent invasion of forest into the savanna is provided from soil organic carbon isotopic studies (Guillet, 2001) while δ^{13}C values of organic matter in soil profiles indicate that forest development previously occurred in areas now occupied by savanna (Schwartz, 1996). Constant re-organization of the distribution of forest and savanna patches at the limit of the drier semi-evergreen forest may be forced by the seasonal distribution of the rain through the year and variability in dry season length. But, recent human deforestation has modified the pattern. Sorting out the respective effect of climate from that of human impact on modern vegetation deserves further thorough investigation.

5.3.4 Drier peripheral semi-evergreen forest south of the equator

The coastal semi-evergreen forest does not extend to southern Congo beyond 4°S latitude (White, 1983). Instead, a mosaic of forest–grassland occupies the Atlantic coast, receiving less than 1,100 mm yr^{-1} of rainfall and with temperatures averaging 18°C during the dry season. Several types of semi-evergreen forests are present further inland, in the Mayombe massif, which reaches 730 m a.s.l. maximum elevation and receives 1,400 to 1,600 mm yr^{-1} of precipitation. Modern vegetation and pollen data were obtained from twelve sites in the west of Congo (4°05″ to 4°50″S latitude and 11°45″ to 12°35″E longitude); among the investigated sites, 8 are distributed in Mayombe woodland and 4 correspond to the coastal plain (including the



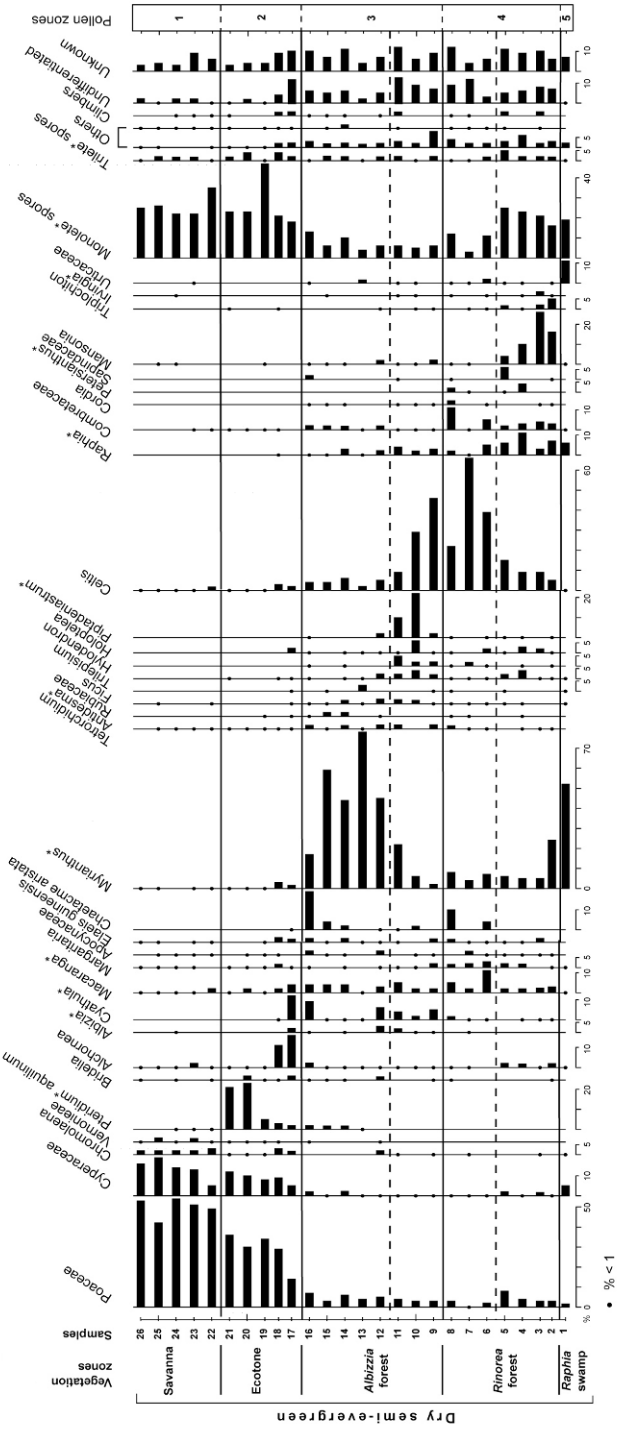
(a)



(b)

Figure 5.5. Modern pollen rain from the drier semi-evergreen forest in Cameroon, Kandara site: (a) location map of the studied transect (samples 1 to 26); (b) comparison between arboreal pollen and leaf area index (Cournac *et al.*, 2002); (c, facing page) simplified pollen diagram (after Vincens *et al.*, 2000) (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores). (*) Pollen types <1%.

(c)


Pollen zones
1
2
3
4
5
Unknown
Undifferentiated
Climbers
Others
Trilete* spores
Monolete* spores
Urticaceae
Irvingia*
Triplochiton
Mansonia
Sapindaceae
Petersianthus*
Cordia
Combretaceae
Raphia*
Celtis
Piptadeniastrum*
Holoptelea
Hylodendron
Trilepisium
Ficus
Rubiaceae
Antidesma*
Tetrorchidium
Myrianthus*
Chaetacme aristata
Elaeis guineensis
Apocynaceae
Margaritaria
Macaranga*
Cyathula*
Albizia*
Alchornea
Bridelia
Pteridium* aquilinum
Vernonieae
Chromolaena
Cyperaceae
Poaceae
Samples
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
Vegetation zones
Savanna
Ecotone
Albizzia forest
Rinorea forest
Raphia swamp
Dry semi-evergreen
% 0 50
10
5
20
10
5
10
10
10
5
5
10
0 70
5
5
5
5
20
60
10
10
5
5
20
5
10
10 40
5
5
10
10
• % < 1

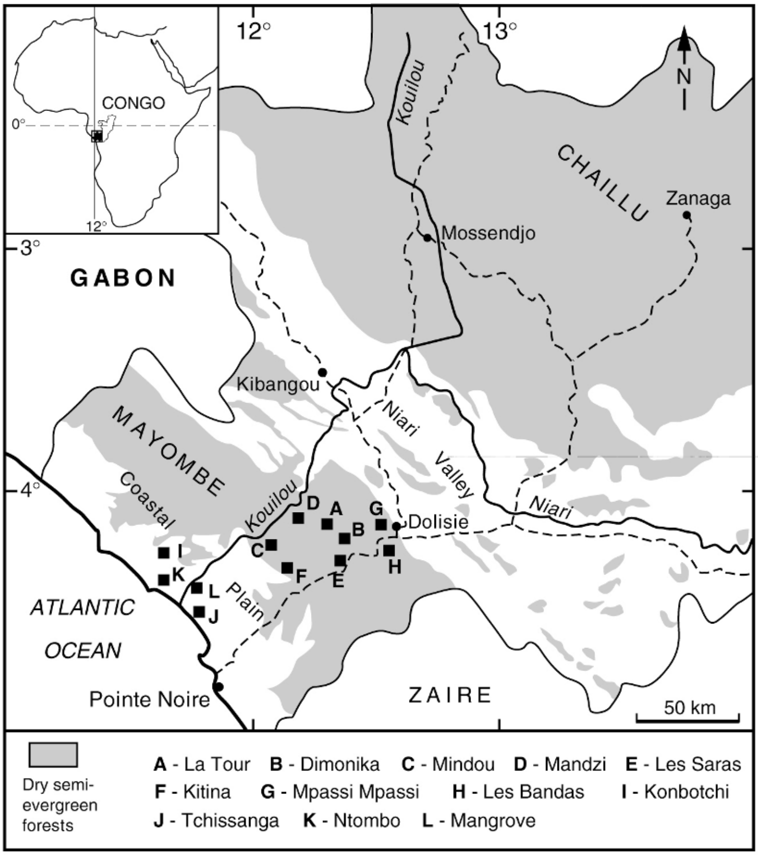


Figure 5.6. Location map of sites for floristic inventories and modern pollen surface soil samples collected within the semi-evergreen forests from Congo (after Elenga *et al.*, 2000a).

mangrove) (marked A–L on Figure 5.6). Floristic data at each site (trees with a diameter at breast height >5 cm) were collected from 20×100 m plots (Elenga, 2000a). Out of a total of 620 individual trees examined, 352 species were identified from 47 families, illustrating the high diversity and heterogeneity of the coastal semi-evergreen forest. The highest diversity of species were found within the Annonaceae (15 species), Euphorbiaceae (8 species), Caesalpiniaceae (7 species), and Rubiaceae (6 species), followed by the Burseraceae, Olacaceae, Sapotaceae, and Moraceae. Within the studied plots, 110 tree species comprise $>1\%$ of the vegetation, but only 41 species were present in two, or more, sites. The average density of trees across the plots reached 120 individuals per 100 m^2 (Elenga, 2000a). The forests of the Mayombe are remarkable for high floristic diversity and little overlap between tree composition at different localities. Palynological studies explore how such floristic diversity is reproduced in pollen assemblages extracted from 50 surface soil samples collected at the 12 sites where tree counts had been made (Figure 5.7).

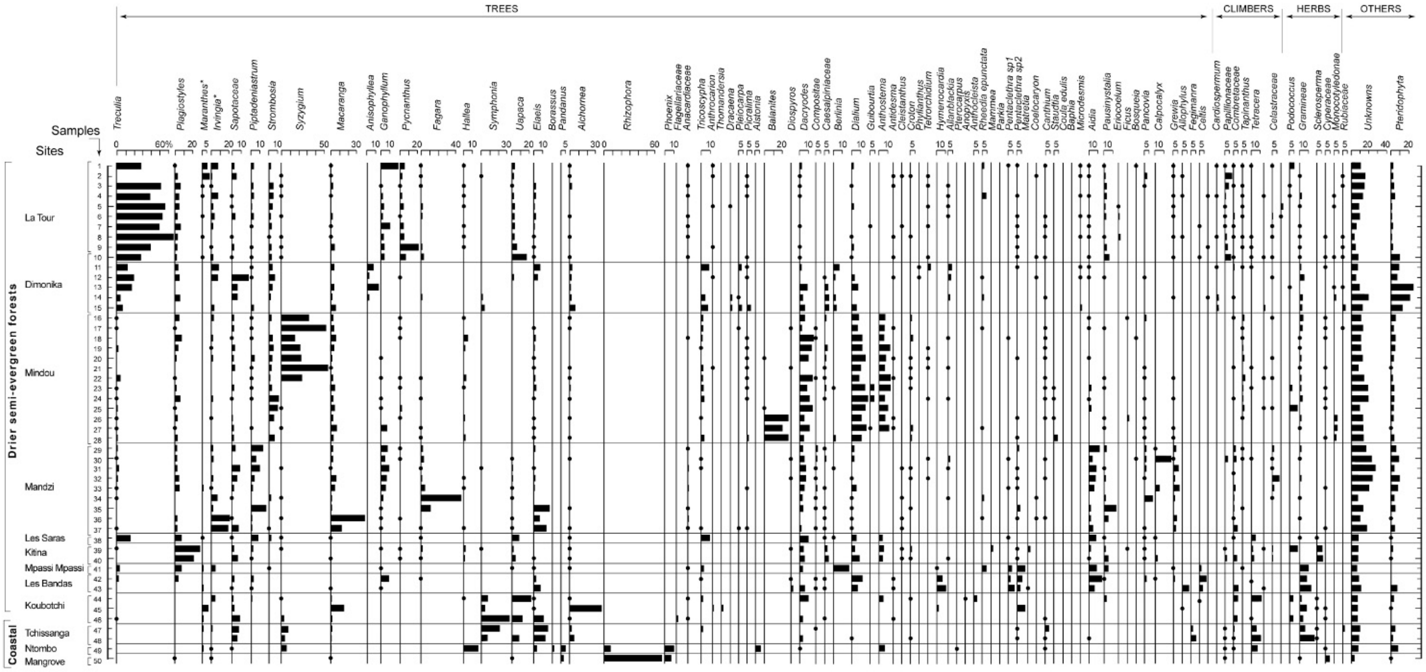


Figure 5.7. Frequencies of the main pollen taxa identified within modern soil surface samples from Southern Congo (after Elenga *et al.*, 2000a) (% calculated versus pollen sum including all identified taxa; Cyperaceae and Pteridophyta spores being unimportant, except at site B).

5.3.4.1 Mayombe forests

The vegetation data from the semi-evergreen forests of the Mayombe massif show that *c.* 19 to 23 species make up 75% of the total tree counts; however, the dominant tree species varies greatly between the 8 study plots. The modern pollen data from the same plots indicate that the variability in the vegetation is not necessarily reflected in the pollen rain:

- At La Tour (site A) *Treculia obovoidea* (Moraceae) represents 8.5% of the trees, but its pollen frequencies reach much higher percentages (30 to 60%) in all of the 10 pollen assemblages (Figure 5.7). Some trees have similar abundances in their flora (Elenga, 2000a, table 2) and the pollen rain (Figure 5.7); these include *Plagiostyles africana* (Euphorbiaceae), *Maranthes* (Chrysobalanaceae), *Irvingia*, and *Uapaca* (Euphorbiaceae). While other trees are under-represented in the pollen relative to abundance in the vegetation (e.g., *Strombosia* (Olacaceae)), or completely absent (Annonaceae and Myristicaceae) despite individuals being present within the plot.
- At Dimonika (site B) 11 of the 22 most abundant trees have been recognized as pollen taxa. Among them, *Treculia obovoidea* (Moraceae), *Anisophyllea myriostricta* (Anisophyllaceae), *Trichoscypha* (Anacardiaceae), *Dacryodes* (Burseraceae), Caesalpiniaceae, and *Allanblachia* (Clusiaceae) have significant percentages, both as plant and pollen. However, other genera among Burseraceae, Apocynaceae, Clusiaceae, and Annonaceae were under-represented or not represented at all in the pollen rain.
- At Mindou (site C) the most abundant trees—*Anthostema* (Euphorbiaceae, 13%), *Dialium* and *Guibourtia* (all Caesalpiniaceae totaling 22% trees)—are represented by significant pollen percentage values. The most abundant pollen type was *Syzygium* (20 to 50%), which was not listed as present within the trees > 5 cm in the plot (Figure 5.7). The Mindou site, is located on the humid, western slopes of Mayombe close to the coastal forest. It seems likely that long distance transport of pollen from *Syzygium* clumps in local swamps explains the high pollen percentages.
- At Mandzi (site D) the three most abundant genera in the vegetation, are *Microdesmis* sp. (Pandanaceae, 10%), *Grewia* (Tiliaceae, 8%), and Tessmania sp. (Caesalpiniaceae, 6%); of these only *Grewia* is recorded by its pollen (2 to 5%). Other tree taxa have similar abundances in the vegetation and pollen; including *Irvingia*, *Pancovia* (Sapindaceae), and *Aidia micrantha* (Rubiaceae). However, associated pollen from *Piptadeniastrum*, *Calpocalyx* (Mimosaceae), *Dacryodes*/*Santiria*, *Ganophyllum* (Sapindaceae), *Fagara* (Rutaceae), *Macaranga*, and *Elaeis* do not correspond to plot inventory (Elenga, 2000a, table 5.2), a discrepancy possibly explained by the fact that pollen origin may be found outside the sampled plots used for tree counts.
- At les Saras (site E) *Treculia*—an abundant tree (12.6%)—is represented by similar pollen frequencies, whereas three genera of Annonaceae (13.5% distributed between *Anonidium*, *Polyalthia*, and *Enantia*) are totally absent from the pollen rain.

- At Kitina (site F) the abundant (12.4%) *Anthostema* trees (Euphorbiaceae) are recorded by pollen, but at much lower percentages (< 5%). Other abundant trees—such as *Scytopetalum klaineanum* (8%, Scytopetalaceae), *Ctenolophon englerianus* (6%, Ctenolophonaceae), and *Spathandra blackeoides* (6%, Melastomataceae)—were not identified during pollen analysis. The absence of these taxa might correspond to unidentified pollen taxa, their pollen morphology not currently well-known (Figure 5.7). *Dialium* has about the same abundance (5%) both as plant and pollen.
- At Mpassi Mpassi (site G) the two most abundant trees—*Hua gabonensis* (16%, Huaceae) and *Pancovia* (7%, Sapindaceae)—were not identified in the pollen rain. *Pentaclethra* (Mimosoideae, 2 species, 5% trees) had the same representation as plant and as pollen, whereas the abundance of *Berlinia* pollen (20%) may correspond to another unknown Caesalpiniaceae pollen, since *Berlinia* was not in the list of counted trees.
- At les Bandas (site H) the dominant tree (56%) *Parkia* (Mimosaceae) was not found as pollen, whereas the diagram includes *Pentachlethra* pollen (10%), which is clearly distinguishable from the polyad of *Parkia*. Except for *Dacryodes* and *Aidia* (Rubiaceae), both present in the plant record and in the pollen, there is not much overlapping of other common trees. Joint occurrences of pollen from *Allophyllus*, *Celtis*, *Hymenocardia*, and Combretaceae, together with more Poaceae, indicate much drier climatic conditions for sites located close to the drier Niari valley in the rain shadow slope of the Mayombe massif.

5.3.4.2 Coastal forests

- At Koubotchi (site I) the dominant (30% trees) forest component *Celocaryon preussii* (Myristicaceae) was not found as pollen, nor were *Xylopia aethiopica* (Annonaceae), *Carapa* (Meliaceae), *Staudia* (Myristicaceae), and *Vitex* sp. (Verbenaceae). But the pollen representation of *Symphonia*, *Uapaca*, *Maranthes* (Chrysobalanaceae), *Pycnanthus* (Myristicaceae), and Sapotaceae corresponds fairly well to the number of trees counted in the plot. Remarkably, *Macaranga* and *Alchornea* (< 1.4% in the tree counts) are over-represented by significant pollen percentages (> 20%), and *Tetracera* (Dilleniaceae) is also over-represented by its pollen (> 10% pollen).
- At Tchissanga (site J) two pollen samples (47, 48) indicate significant pollen values for *Symphonia* and Sapotaceae, *Fegimanra* (Anacardiaceae), and *Syzygium* (Myrtaceae), that are also characteristic trees of the *Symphonia globulifera* forest in valleys of the coastal plain (Elenga, 2000b). However, they lack the record of *Memecylon* (Melastomataceae) which accounted for 34% of the total number of trees in the same plot.
- At Ntombo (site K) *Anthostema* pollen (Euphorbiaceae) was found to be less abundant (5%) than in the tree cover dominated by *Anthostema aubryanum* (51%). However, there is good correspondence between the plant and pollen representation of *Syzygium guineensis*, *Hallea ciliata* (Rubiaceae), *Elaeis*

guineensis (Palmae), and *Alstonia congensis* (Apocynaceae). *Tetracera pollen* (5%) was found, whilst this climber represents less than 1% in botanical inventories. This may indicate an over-representation of pollen from climbers, or an under-estimation of plant specimens, those with diameter lower than 5 cm not being counted.
- The mangrove (site L) is dominated by the abundance of *Rhizophora*, associated with *Phoenix* and *Pandanus*, also abundant plants in the plant cover.

Although very informative, the comparison between vegetation and modern pollen rain in this section illustrates discrepancies that may result from the plot size used in vegetation sampling being smaller than the source area of the pollen assemblages. To highlight the distribution of plants and pollen versus environmental factors, correspondence analysis on all the samples compared the composition of the floristic inventories from lowland coastal forests with those of Mayombe mid-elevation forests. Indeed, there is a west/east increasing rainfall gradient from 1,100 to 1,600 mm yr^{-1} and an increased elevation between the coastal plain (sea level) and the Mayombe (700 m a.s.l.). However, the authors favored an explanation involving different soil composition. They distinguished the pollen association of *Syzygium*, *Symphonia globulifera*, *Phoenix*, *Tetracera*, and *Sclerosperma* (Arecaceae) as characterizing swamp forests (Elenga, 2000b). However, differences in elevation and also strong variations in precipitation could partly explain the differences in the floristic and pollen composition of coastal and Mayombe forests. Variations in the amount of rainfall are not negligible. Moreover, during the dry season, the effect of clouds on evapo-transpiration (Maley and Elenga, 1993), and that of the Benguela Current, induce cooler temperatures in southern Congo (Maley, 1997).

In conclusion, the study of modern pollen rain from Congo shows that arboreal pollen percentages from 70 to 90% characterize samples collected under closed forest, lower values being found within disturbed forest. These high values were obtained despite the fact that important families—such as Annonaceae (all species), most Myristicaceae (except *Pycnanthus*), Chrysobalanaceae, Olacaceae (except *Strombosia*), Clusiaceae (except *Symphonia*), Apocynaceae, Meliaceae, Melastomataceae, etc.—were poorly documented in modern pollen rain. Well-diversified pollen assemblages from southern Congo document the floristic diversity of semi-evergreen forests south of the equator. Although there is no direct overlap between pollen and tree composition, pollen assemblages clearly distinguish the different types of forests that have produced them. Associated *Symphonia globulifera*, *Uapaca*, *Hallea*, *Dacryodes*, *Anthostema*, *Dialium*, *Plagiostyles*, and Sapotaceae, characterize the dry semi-evergreen forest of Mayombe both in vegetation and corresponding modern pollen rain. Accordingly, the semi-evergreen forests south of the equator appear palynologically distinct from the same vegetation unit mapped north of the equator in Cameroon (sites Q and E, Figure 5.2), including Kandara. Possible explanations for such differences may be found in the long-term geological history and (or) in the differential ecological requirements and threshold climatic limits of the various forest trees. More investigation of this disparity is needed.

5.3.5 Swamp forest

Preliminary information about modern pollen rain from the inundated evergreen swamp forests of Central Congo was provided by three samples collected within the *Guibourtia demeusii* (Caesalpiniaceae) dominated association. Located in the central Congo Basin below 400 m a.s.l. in elevation (1°34″N, 17°30″E), the area receives more than 1,600 mm yr^{-1} of precipitation with a very short dry season. The results show that AP again ranges from 75 to 90%. Pollen assemblages are dominated by *Lophira* (up to 60% in one sample), followed by *Guibourtia*, *Alchornea*, *Macaranga*, *Uapaca*, Combretaceae, and *Myrianthus*, in addition to a few pteridophyte spores. These pollen assemblages are different from those collected from the hygrophilous evergreen forest of Cameroon and from any types of the semi-evergreen drier peripheral forest (Elenga, 1992).

5.3.6 Summary: Modern pollen rain

The pioneering studies summarized in this chapter represent significant progress in understanding modern pollen rain in tropical Africa and its relationship with the vegetation. First, a clear positive relationship between abundance of tree cover and tree pollen has been established for tropical forests. Second, major (evergreen, semi-evergreen and mixed) and secondary vegetation units have been found to be reflected in the pollen rain produced. Third, taxa can be over-, under-, or equally-represented in the pollen rain relative to abundance in the vegetation. In conclusion, differences in pollen (taxa composition and abundance) can be used to recognize the vegetation units and sub-units within the Guineo-Congolian rainforest, despite the lack of pollen representation of some dominant trees. Although not covering continuous climatic gradients, the results discussed bear critical information for interpreting fossil pollen data from the region. Extracting individual or associated pollen markers for all the vegetation units within the rainforest, however, requires additional and more homogenously distributed samples before being statistically valid. A complete inventory of forest types is essential because of the high diversity of rainforests. Collecting along two distinct transects—one from south to north crossing the equator to address the climatic influence of the Intertropical Convergence Zone (ITCZ) (Haug, 2001), the other from west to east, to address inland monsoon penetration—would be most valuable. This section has shown that modern pollen from the rainforest can be studied in the same way as pollen from other forests in the world.

5.4 QUATERNARY HISTORY

Despite recent progress and new fossil pollen sequences obtained by coring swamps and lakes in Africa, paleoenvironmental reconstructions for all of the vegetation units described in Section 5.2 has not yet been achieved. The key fossil pollen records published to date are reviewed here in chronological order, starting with the last glacial period, and then discussing the last *c.* 10,000 years (Holocene). The list of sites

Table 5.1. List of fossil pollen sites located within the African lowland rainforest.

Sites	*Coordinates*	*Elevation* (m)	*Rainfall* (mm yr^{-1})	*Authors*
Barombi Mbo	4°67′N, 09°40′E	300	2,400	Maley and Brenac (1998),
Mboandong	4°30′N, 09°20′E	120	2,400	Richards (1986)
Ossa (OW4)	3°40′N, 10°05′E	8	2,950	Reynaud-Farrera *et al.* (1996)
Kamalete	0°43′S, 11°46′E	350	1,500	Ngomanda *et al.* (2005)
Bilanko	3°31′S, 15°21′E	600	1,500	Elenga *et al.* (1991)
Sinnda	3°50′S, 12°48′E	130	1,100	Vincens *et al.* (1994, 1998)
Coraf	4°00′S, 11°00′E	0	1,260	Elenga *et al.* (1992)
Kitina	4°15′S, 11°59′E	150	1,500	Elenga *et al.* (1996)
Ngamakala	4°04′S, 15°23′E	400	1,300	Elenga *et al.* (1994)
Songolo	4°46′S, 11°52′E	5	1,260	Elenga *et al.* (2001)

where fossil pollen records are available is given in Table 5.1 and Figure 5.1. Evidence for climate changes based upon other sources of information—such as lake sediments, paleosols, stable isotopes, phytoliths, and diatoms—has been summarized in Battarbee (2004).

5.4.1 Ice age record

Marine sediments have provided pollen data related to vegetation change on the African continent. The ocean sediment sequences have the great advantage of providing land–sea linkage on a straightforward isotopic chronology (Bengo and Maley, 1991; Dupont and Wienelt, 1996; Dupont and Behling, 2006). Indeed, marine records are the only source of information for older geological time periods (see Chapter 1). However, interpretation of terrestrial vegetation change from pollen assemblages obtained from ocean sediments is often challenging because: (i) material is collected from a wide source area that usually encompasses multiple terrestrial vegetation types, and (ii) ocean currents, and other transport mechanisms, create biases in the type of pollen deposited (i.e. wind dispersed taxa are often over-represented). Therefore, to gain the best possible insight into terrestrial vegetation change, a more detailed picture can be obtained by examining lake sediments. Here, we will discuss the oldest continental evidence provided by lacustrine pollen sequences. Lake records span the last 30,000 years including part of the last glacial period (ice age) and its maximum in the Last Glacial Maximum (LGM).

The ice age record for African tropical lowland forests is known from two sites: Barombi Mbo within a forested region of Cameroon (Maley and Brenac, 1998) and Ngamakala within secondary grassland nearby the Congo River (Elenga, 1994). A third record, from Lake Bosumtwi, West Africa, remains poorly documented through a preliminary pollen diagram (Maley, 1991). Except for *Celtis* and *Olea* the published Bosumtwi pollen record does not contain any detail about the forest composition. Although the Bosumtwi record is informative about the lowland rainforest along the

Guinean gulf, this review does not include it. A long core spanning the last 1.1 Myr was raised from Bosumtwi in 2004 (Koerbel *et al*., 2007). Key findings from physical and geochemical proxies already analyzed from Bosumtwi are that: (i) laminations within the sediments were deposited in response to seasonal cycles for at least the upper portion of the core (Shanahan *et al*., 2008), and (ii) there was a pronounced arid event between 135,000 and 75,000 years ago (Scholtz *et al*., 2007). Finer-scale fluctuations were thought to reflect global climate change such as Heinrich events during the last glacial period (Peck *et al*., 2004), and variation in the West African monsoon during the Late Holocene (Shanahan *et al*., 2009). Initial pollen analysis from the new Bosumtwi cores indicates the last glacial period was dominated by savanna ecosystems and that during the Holocene highly diverse, and dynamic, woodlands dominated the regional landscape (W.D. Gosling pers. commun.). It is anticipated that the first fossil pollen record from the new Bosumtwi cores will be published early in 2011 which will provide new insight into the responsiveness of West African vegetation to past climate change.

5.4.1.1 Barombi Mbo, evergreen and semi-evergreen forests (Cameroon)

North of the equator, the small crater lake Barombi Mbo ("Mbo" meaning lake in the local language) (4°40″N, 9°24″E) is located 15 km north of Mount Cameroon and 50 km inland of the Atlantic coast. Core BM-6 recovered from the deepest part of the lake (Maley, 1990) yields a remarkably complete record for the last 32,000 years (27 ^{14}C kyr BP), including the LGM. The lake is situated at low elevation (300 m a.s.l.) and is presently surrounded by forest. The crater lies within the wide belt of lowland evergreen Biafran forest dominated by Caesalpiniaceae bordered by two large bands of semi-evergreen forest. Patches of semi-evergreen forest occupy areas under the rain shadow of Mount Cameroon, which causes a decrease in precipitation and a reduction in the length of the rainy season. Lying within Mount Cameroon's rain shadow, Barombi Mbo receives 2,350 mm yr^{-1} with a 3-month dry season from December to February. This relatively low rainfall contrasts with 9,000 mm yr^{-1} of windward (coastal) precipitation on the other side of Mount Cameroon. Twelve accelerator mass spectroscopy (AMS) radiocarbon dates reveal that the laminated sediments of the 23.5 m BM-6 core were deposited at a steady rate with no obvious hiatus (Giresse, 1991, 1994); an exceptional situation for an African lake. In the pollen diagram each sample corresponds to a 1 cm thickness of sediment averaging *c.* 10 to 15 years of deposition. Pollen analyses were made at *c.* 200 year intervals in the Holocene, and *c.* 300 year intervals in the glacial period (Maley and Brenac, 1998; Elenga, 2004). All the results discussed here follow the ^{14}C chronology provided by the authors.

At Barombi Mbo, the curve of total arboreal pollen (Figure 5.8) is interpreted as a good estimate of the forest cover surrounding the lake; although material incorporated into the sediments is likely to integrate a much larger area. The Barombi Mbo pollen record clearly shows that, during the last glacial period—from 27 to 10 ^{14}C kyr BP (*c.* 32–11.5 kcal yr BP)—the area around the lake remained forested. However, between 20 to 10 ^{14}C kyr BP (*c.* 24–11.5 kcal yr BP) the tree cover was

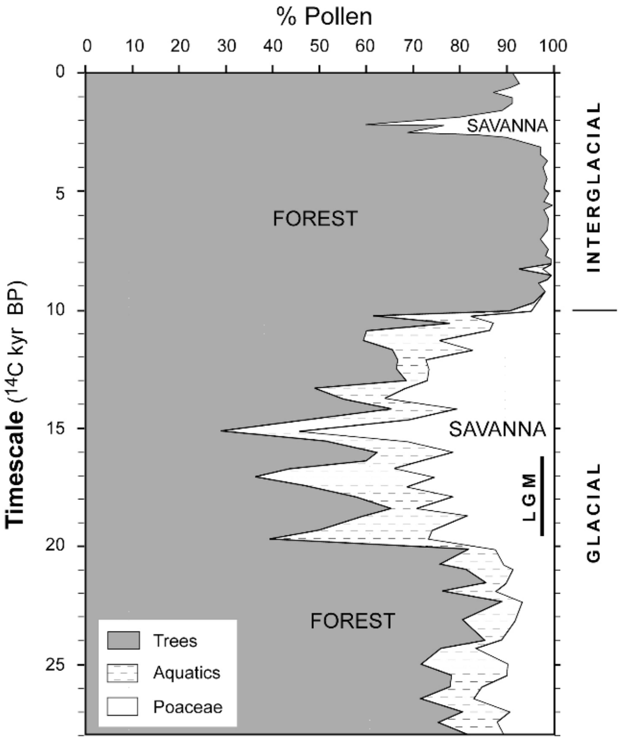


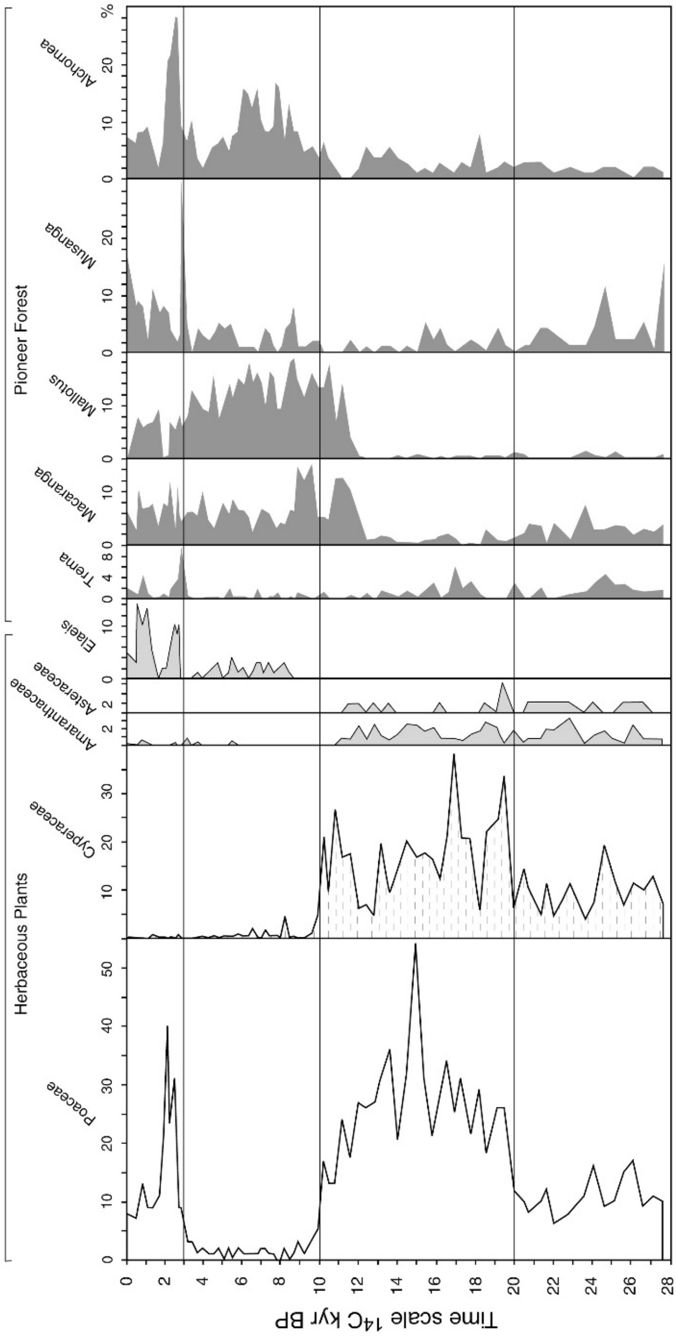
Figure 5.8. Synthetic pollen diagram from core BM-6, Lake Barombi Mbo, Cameroon, presented according to interpolated ^{14}C ages (after Maley and Brenac, 1998) (% calculated versus pollen sum including all identified taxa, excluding spores).

significantly reduced. Some fluctuations are depicted by the curve of total arboreal pollen, which would have been less marked if aquatics (sedges) had been eliminated from the pollen sum on which relative frequencies are calculated. High abundances of sedges (aquatics illustrated in Figure 5.8) coincide with the LGM. Such peaks attest to enlarged herbaceous wetlands (including grass) that occupied emerged land on the shoreline. A probable explanation for wetland expansion is falling lake levels in response to drier climatic conditions.

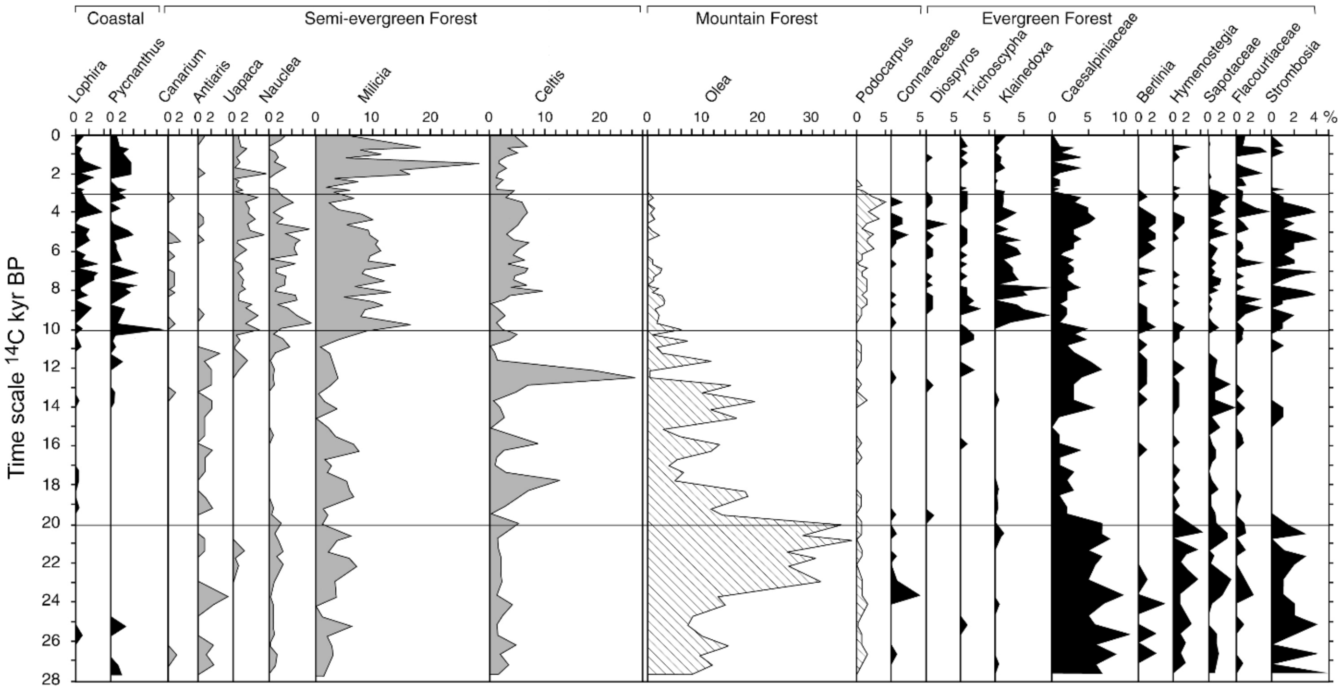
Glacial period and refuge hypothesis

Regarding the detailed pollen composition of the tree component, the last glacial period can be subdivided into two distinct phases (Figure 5.9). During the first phase from *c.* 32–24 kcal yr BP, the total AP (*c.* 80%) indicates a dense canopy cover (Figure 5.8) which remained fairly stable throughout and included the highest frequencies (7 to 10%) of the Caesalpiniaceae evergreen component. Out of the 150 identified pollen taxa, 20 different genera are included in the Caesalpiniaceae curve (Maley and Brenac, 1998). Caesalpiniaceae species have been shown to be under-represented in modern pollen rain (Reynaud-Farrera, 1995; Section 5.3), suggesting that between 32–24 kcal yr BP they may have been a very important and diverse component within the forest. Components of mature semi-evergreen forest such as Sapotaceae (1 to 3%) (Elenga, 2004), were also present. Among markers of the mountain forest, *Podocarpus* pollen was found at such low frequencies (< 1.5%) that it is unlikely that the trees occurred close to the lake. Today, *Podocarpus* is present on Mount Koupe (2,050 m a.s.l.) and its fossil occurrence could well be attributed to long-distance transport from this mountain. In marine cores, *Podocarpus* pollen is quite abundant in sediment dating from the glacial period (Marret, 1999). In contrast, the high abundance of *Olea* (> 10%) probably indicates the presence of trees near the lake.

The *Olea* pollen curve shows a remarkable pattern through time. Firstly, *Olea* increases from *c.* 24 ^{14}C kyr BP (28 kcal yr BP), reaching a maximum (30%) at 20 ^{14}C kyr BP (24 kcal yr BP), and then decreasing again to 5% at 17 ^{14}C kyr BP (*c.* 20 kcal yr BP). From 24 kcal yr BP to 20 kcal yr BP, the decreasing abundance of *Olea* pollen is in good correspondence with the 4,000 yr duration of the LGM chronozone placed between 23 kcal yr BP and 19 kcal yr BP in marine records (Mix, 2001). Today, *Olea capensis* grows on Mount Cameroon at an elevation of 1,600 m and much higher, such as in cloud forest. The abundance of *Olea* in the fossil pollen record has been explained by the impact of stratiform clouds and associated fogs produced by sea surface temperature cooling of the Atlantic (Maley, 1989; Maley and Elenga, 1993). That such processes may have played a role cannot be ruled out. Interestingly, the maximum of *Olea* percentages occurred slightly before the LGM and corresponds to the timing of the Dansgaard–Oeschger event 2 (DO2) and the last δ^{18}O maximum of the Antartica Byrd ice core (Mix, 2001). The pollen/climate transfer function in East Africa indicates a glacial continental cooling of 3 ± 2°C in the tropical region (Bonnefille, 1990, 1992; Vincens, 1993)—a maximum value—since the effect of lower carbon dioxide content of the atmosphere could not be taken into account. Using the present day lapse rate, such an estimate corresponds to a 600 m shift in elevation, much less than the 1,300 m necessary lowering for *Olea* to reach the Barombi Mbo lowlands. Originally, tropical cooling was inferred from a significant shift in altitudinal distribution of vegetation zones on East African mountains (Flenley, 1979). The descent of vegetation on tropical mountains results from the associated effects of both decreasing temperature and rainfall. The Barombi Mbo record clearly demonstrates an individualistic movement of *Olea* into the lowland vegetation during glacial time. The descent of *Olea* cannot be attributed to lower carbon dioxide concentration because, as a C_3 plant, it should remain relatively unaffected. A 3°C cooling at the Barombi Mbo suggests a mean annual temperature of *c.* 21°C ($24 - 3 = 21$°C); a value above the 18°C threshold for tropical highland forests in India (Bonnefille, 1999; Barboni and Bonnefille, 2001), and above the 15°C threshold used to define the tropical biome (Prentice, 1992). Under such conditions, *Olea* could reach the lowland rainforest where other tropical trees remained. The pattern shown by the *Olea* curve in the Barombi Mbo fossil record provides a good example of how plants individualistically responded to climatic changes. Significant rainfall decrease, during glacial time at the equatorial latitude, was estimated around


Pioneer Forest
Herbaceous Plants
Alchornea
Musanga
Mallotus
Macaranga
Trema
Elaeis
Asteraceae
Amaranthaceae
Cyperaceae
Poaceae
%
0
10
20
0
4
8
2
30
40
50
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28
Time scale 14C kyr BP

(a)



(b)

Figure 5.9. Detailed pollen diagram from core BM-6, Lake Barombi Mbo, Cameroon, presented according to interpolated ^{14}C ages: (a) trees and shrubs; (b) herbs (after Maley and Brenac, 1998) (% calculated versus pollen sum including all identified taxa, excluding spores).

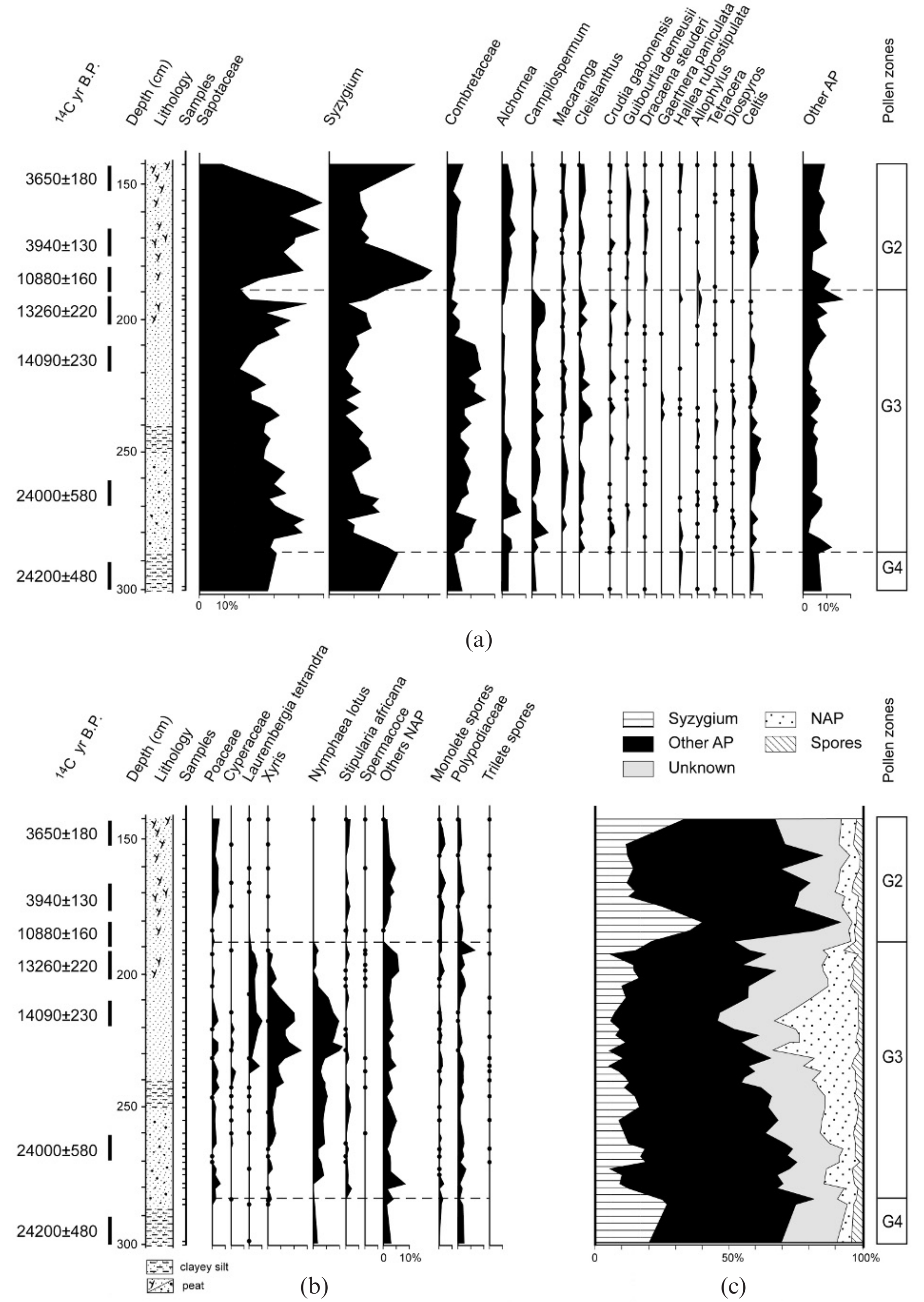
20 to 30% of the present value (Bonnefille, 1990; Bonnefille and Chalie, 2000). Applying this estimate at Barombi Mbo leaves enough precipitation (1,500 mm yr^{-1}) to maintain a forest cover, during the glacial period, prior to the LGM.

During the second phase of the glacial period (24–11.5 kcal yr BP), total AP dropped with decreasing abundance of typical Biafran evergreen forest taxa, whereas semi-evergreen components—such as *Celtis* and *Antiaris* (Moraceae)—become more abundant, although their pollen frequencies show large fluctuations. Lowland species of *Strombosia*, Flacourtiaceae, Sapotaceae, *Antiaris*, *Hymenostegia* (Caesalpiniaceae), *Berlinia*, and other Caesalpiniaceae are still present, but decreased significantly (Maley and Brenac, 1998). Isotopic studies from the same core point to an increased proportion of C_4 grasses, likely favored by low CO_2 concentration of the global atmosphere at that time (Giresse, 1994). The increase in grass pollen does not overlap the *Olea* phase (29–22 kcal yr BP), but follows it, becoming more abundant between 24 kcal yr BP and 11.5 kcal yr BP, synchronously with the increase in Cyperaceae (Figure 5.9). The different patterns of the Poaceae and the Cyperaceae curves may indicate that the peak of Poaceae is not related to subaquatic grasses, but rather come from open grassland inside the forest. Pollen/biome reconstruction at 22 kcal yr BP emphasized the replacement of rainforest by a tropical seasonal forest (Elenga, 2000c). However, during the minimum extent of forest which lasted 5,000 years (24–19 kcal yr BP), two sharp increases in tree cover are observed. They attest that forests expanded significantly during glacial time, although fluctuations in tree pollen percentages would have been minimized by excluding Cyperaceae from the pollen sum in the calculation of relative percentages. The maximum of grass pollen associated with the greatest opening of the forest is dated at 18 kcal yr BP, a radiocarbon date that fits Heinrich Event H1 (Mix, 2001), and therefore occurred a long time after the LGM. If the peak of *Olea* registers the maximum cooling and the peak of grasses the maximum aridity, these were delayed by at least 5,000 years. Aridity and cooling were decoupled and a complex pattern of forest dynamics is evidenced during the glacial period when the climatic impact of the two Heinrich Events, H1 and H2, affected the lowland rainforest at Barombi Mbo. Nevertheless, rainforest appears very sensitive to global climatic changes. While considering the high topography of Mount Cameroon and the high precipitation gradient, a great variety of climatic conditions must have prevailed in the region in the past, just as it does today. During glacial time, enough precipitation could have existed on the western slopes, allowing the persistence of evergreen forests there at the same time as semi-evergreen forests at Barombi Mbo, at the eastern base of Mount Cameroon. During glacial time, the coastal area expanded as sea level fell and offered new opportunities for new land occupation. Various forest refuges could have existed during glacial time and could be located on direct evidence by means of new palynological studies, rather than postulated on various hypotheses (Maley, 1996).

5.4.1.2 Ngamakala, savanna and semi-evergreen rainforest (Congo)

On the right bank of the Congo River, the small Ngamakala Lake (4°04″S, 15°23″E, 400 m a.s.l.) is located at the southern end of the Bateke Plateau (Figure 5.1) where mesophilous, hygrophytic forests are related to humid edaphic conditions (Descoing, 1960). The lake—1 km wide—is now covered by *Sphagnum* (Sphagnaceae) and clumps of trees of *Alstonia boonei* (Apocynaceae). It is surrounded by a wooded *Loudetia demeusei* (Poaceae) savanna, with *Pentaclethra* (Mimosoideae) new growth (Makany, 1976). The results of pollen analysis of a 160 cm core show that, from *c.* 30–17 kcal BP, the fossil pollen sequence was dominated by Sapotaceae and *Syzygium* (Figure 5.10). With Fabaceae (Leguminosae) and *Canthium*, later identified among the unknown (Elenga, 2004), percentages of tree pollen exceed 80%. This record clearly indicates a forested environment during the glacial period. This forest was developed on a swamp attested by the occurrence of aquatic plants—such as *Xyris*, *Laurembergia*, and the floating *Nymphea*. The forest existing there during the last glacial period included significant Fabaceae with Combretaceae, *Alchornea*, *Campylospermum* (Ochnaceae), *Cleistanthus* (Euphorbiaceae), *Canthium*, and *Celtis*. Rare pollen of other trees—such as *Crudia gabonensis* (Caesalpinioideae), *Guibourtia*, and *Tetracera* (Dilleniaceae)—provide a link with modern surface samples of the central Congo Basin (Elenga, 1994). But, except for *Celtis* and Sapotaceae, the glacial forest in southern Congo had no floristic resemblance to that found at Barombi Mbo in Cameroon at the same time. More specifically, the Ngamakala record does not show any of the highland taxa pointing to cooler temperatures, as observed in the Cameroon record. The swamp environment may not have been favorable to the growth of *Olea*, but the lack of *Podocarpus* is more surprising. If *Podocarpus* had been present at mid-elevation on the Bateke Plateau, its abundant pollen would have been blown away, and at least a few grains found in the Ngamakala sediment. However, no valid conclusion can be drawn until another glacial sequence from southern Congo confirms it. As in the Cameroon record, variations within the relative abundance of the different trees are observed during the glacial period, although masked by abundant *Syzygium* and Sapotaceae. The Ngamakala core had a very low sedimentation rate with only an 80 cm thickness of sediment deposited during the glacial interval (from 29 to 17 kcal BP), and conventional dating is not accurate. The time resolution interval between adjacent samples (350 years) is greater than that of Barombi Mbo and insufficient to address short-term climatic variability during the glacial period. At Ngamakala, no significant change at 24 kcal BP is clearly identified in the pollen diagram, although postulated within a change of sediment. The minimum forest cover (60% AP) occurred at *c.* 17 kcal BP when Sapotaceae and *Syzygium* decreased and Combretaceae reached their maximum relative abundance. Although the conventional dates of the Ngamakala core have a great experimental error, the minimum tree cover at Ngamakala appears synchronous with grass maximum frequencies at Barombi Mbo from which maximum aridity has been inferred. Simultaneous abundance of aquatic herbs, among which *Xyris* and *Nymphaea* dominate, may be explained by a water depth lower than 1 m. The Ngamakala record lacks evidence for cooler indicators, and therefore the decoupled effect of coolness and aridity during glacial time is not yet established for the southern tropics until further high-resolution pollen sequences are provided.

Past vegetation history of the rainforest during glacial time is only documented at two sites so far. It clearly indicates the persistence of two, well-diversified rainforests of different composition on both sides of the equator.



(a)

(b)

(c)

Figure 5.10. Simplified pollen diagram from Ngamakala, presented according to depth (Congo, after Elenga *et al*., 1994): (a) arboreal and climber taxa; (b) herbaceous taxa; (c) synthetic diagram (% calculated versus pollen sum including all identified taxa, aquatics, and spores).

5.4.1.3 Bateke Plateau, savanna (Congo)

Bilanko

Located within the Bateke Plateau (600–800 m), the Bilanko site (3°31″S, 15°21″E, 700 m a.s.l.) is a 10 km closed depression occupied by floating sedges and grass mats with abundant *Syzygium* (Figure 5.1). Shrub savanna vegetation occupies sandy soil in this region, characterized by 1,600 mm yr^{-1} rainfall, 4 month dry season and 4 to 6°C seasonal temperature range. The 60 cm short core, recovered from the 4 m thick peat deposit inside the depression, contained a wood fragment at the bottom that was dated at 10,850 ^{14}C yr BP, the top part of the core not being dated. Although the fossil pollen composition was fairly diverse (103 pollen taxa), frequencies of *Syzygium* pollen account for 90% of the total count, associated with a few trees of semi-deciduous forest. This indicated the development of a *Syzygium* swamp at Bilanko. The sediment of the core—yielding dated fossil wood—contained up to 30% *Podocarpus* pollen (Elenga, 1991). *Podocarpus milanjianus* does not occur in the Congo Basin today, but it has been collected as isolated trees in the Chaillu Mountains, in Gabon, at the same elevation as Bilanko. Although its pollen can be transported over long distances, such high *Podocarpus* percentages imply the proximity of abundant trees nearby Bilanko, suggesting cooler temperatures during a time period corresponding to the Younger Dryas. Development of stratified low clouds has been proposed to explain occurrences of mountain plants in the lowlands (Maley and Elenga, 1993).

Bateke Plateau

Macrobotanical remains have been identified from two glacial-aged sites on the Bateke Plateau (Figure 1; Dechamps, 1988a). At Gaganlingolo, 17 km north of Brazzaville (3°55″S, 15°10″E) root specimens older than 30 ^{14}C kyr BP were tentatively attributed to several species of *Monopetalanthus* (Caesalpiniaceae), with *Grewia* (Tiliaceae) and *Pterocarpus* (Fabaceae). So many species of *Monopetalanthus* within a small area is surprising and brings into question the validity of taxonomic identifications. Nevertheless, the fossil woods occurrence documents the presence of a forest in the Congo Basin during the last glacial period on the right bank of the Congo River, in a region now occupied by savanna. At Gambona (2°S, 16°E), a few hundred kilometers north, closer to the Congo Basin, wood remains of the same age yielded a more mixed assemblage including components of open woodland—such as *Nauclea latifolia* (Rubiaceae)—and evergreen forest components—such as *Detarium senegalense* (Caesalpiniaceae), *Connarus griffonianus* (Connaraceae), and *Brachystegia*.

The recovery of fossil wood at sites many kilometers apart attests to a certain geographical extension of the rainforest on land along the Congo River during the LGM. Fossil wood of *Podocarpus* was not found in these terrestrial deposits dated prior to the LGM, although its pollen was abundant in marine cores off the Congo coast (Jahns, 1996). Transported pollen from rainforest was indeed less important during the LGM than during stages 3 and 4 of the glacial period, but they showed their minimum percentages during stages 5b (90 kyr BP) and 5d (110 kyr BP) of the last interglacial, which cannot possibly be attributed to a lower CO_2 content of the atmosphere.

5.4.2 Holocene record

In west Central Africa, the past history of lowland forests for the last 10,000 years is recorded in a total of 10 fossil pollen sequences located between 5°N and 5°S latitude: Barombi Mbo, Mboandong, Ossa, Kamalete, Ngamaka, Sinnda, Bilanko, Kitina, Coraf, and Songolo (Figure 5.1). However, except for Barombi Mbo, most pollen records remain incomplete, discontinuous, and poorly dated. The persistence of rich, diversified forests until the last few thousand years, evidence for several drastic forest declines, use of oil palm accompanying (or not accompanying) Iron Age civilizations, and the Bantu expansion in Africa will be discussed in this section.

5.4.2.1 Sites located north of the equator

Barombi Mbo evergreen and semi-evergreen forests (Cameroon)

The pollen sequence from the Barombi Mbo core, yielding a record for the last glacial period discussed above, also contains one of the most complete records for the last 10,000 years (Figure 5.9). In this sequence the maximum of tree pollen abundance started around 11.5 kcal yr BP and remained constant until 2.5 kcal yr BP, with more than 90% AP indicating a dense tree canopy cover. *Olea* frequencies lower than 2% indicate that the tree had progressively disappeared from the surroundings of the lake since the beginning of the Holocene. Dominated by pioneer trees (*Mallotus*, *Macaranga*, *Musanga*, and *Alchornea*), and decreasing occurrences of *Antiaris*, the Holocene forest contained more Euphorbiaceae and fewer Caesalpiniaceae than the forest existing during the glacial period. The three types of forests occurring in the area today were already in place. The Biafran wet evergreen forest is evident from the presence of *Klainedoxa*, *Trichoscypha*, and Connaraceae, the coastal forest by *Lophira/Saccoglottis* and *Pycnanthus*, the dry evergreen/semi-evergreen forest by *Milicia*, *Celtis*, *Nauclea*, and *Uapaca*. The Biafran evergreen forest elements already existed during the glacial period but appear more diversified during the Holocene with greater abundance of *Klainedoxa* (Irvingiaceae), *Trichoscypha* (Anacardiaceae), *Diospyros*, and Connaraceae. However, there were fewer Caesalpiniaceae during the Holocene than between 31 and 24 kcal yr BP. The forest succession started at 14.7 kcal yr BP with abrupt increases of *Macaranga*, then *Mallotus*, followed by that of *Milicia* (Moraceae) which culminate around 11.5 kcal yr BP. *Alchornea* reached its first peak at *c.* 9 kcal yr BP. Such a progressive trend of forest took more than 2.5 kcal yr BP to be fully established. Although forest increase may have been triggered by increasing monsoon rains, it cannot be qualified as an abrupt onset. Higher resolution pollen analysis for this interesting transition period would have allowed a valuable comparison with the fine-resolution isotopic record obtained from the same core (Giresse, 1994). During the Holocene, several fluctuations in the pollen percentages of various components are evident (Figure 5.9)—such as decreasing trends of *Klainedoxa* and *Mallotus*, and an increasing trend for *Musanga*. But, the *c.* 200 yr sampling interval of the pollen record remains too large to interpret these variations in terms of the vegetation dynamic under climatic variability attested by global changes. The strongest change depicted by the available data occurred around 3 kcal yr BP when most components of the Biafran evergreen decreased or totally disappeared, while pioneers—such as *Musanga*—increased significantly. The sharp 40% peak of Poaceae attests to a short phase of open savanna around 2.5 kcal yr BP. At that time, the increase in grass pollen was not accompanied by that of Cyperaceae, having almost disappeared during the Holocene when the lake was high and its shore immediately surrounded by forest. This is an indication that grasses may have developed inside forest openings rather than along the shoreline itself. To what extent this savanna phase is the result of human deforestation or of significant climatic aridity will be discussed later.

Ossa, hygrophilous evergreen forest (Cameroon)

The shallow Lake Ossa (7 m depth during wet season) is located a few kilometers to the west of the Sanaga River within the *Lophira*/*Saccoglottis* hygrophilous evergreen forest (Figure 5.1). *Elaeis guineense* and *Hevea brasiliensis* plantations have been recently established on the western shoreline of the lake. The region is characterized by high rainfall—*c.* 3,000 mm yr^{-1}—with a long rainy season from March to November followed by a short dry season from December to February (Nguestop, 2004). Of the three cores recovered from Lake Ossa, one with a basal age of *c.* 10 kcal yr BP shows reversed dates that indicate perturbed deposition, although the pollen indicates the presence of a well-diversified Caesalpiniaceae forest well-established around the lake since that date (Reynaud-Farrera, 1995). Another 5 m core OW 4 (3°48″N, 10°01″E, at 8 m a.s.l.), collected from the western side, provided an accurately dated pollen sequence for the last 5.5 kcal yr BP. The pollen data include high percentages of sedges (Cyperaceae) reaching up to 50% of the total count, these perhaps due to the proximity of the river drainage, the shallowness of the lake, and associated land partially emerged during the dry season. The exclusion of Cyperaceae, as well as that of fern spores, from the total pollen sum for calculating percentages of other forest components is justified by the local context (Renaud-Farrera, 1996). The Poaceae were kept in the pollen sum, although some may belong to local edaphic wetlands. Poaceae reached 15% at most and, except around 2.8 kcal yr BP, their stable percentages would not have strongly influenced variations in other elements (Figure 5.11).

The Ossa pollen diagram clearly indicates the persistence of an evergreen forest (AP percentages >75%) in the region throughout the last 5.5 kcal yr BP. Forest composition around Lake Ossa differs significantly from that around Barombi during the same period (Renaud-Farrera, 1996). Two distinct periods of forest development could be individualized, separated by an abrupt change at *c.* 2.85 kcal yr BP, in surprisingly good correspondence with the limit between sub-boreal and sub-Atlantic palynological subdivisions in Europe (Van Geel *et al.*, 1998). From 5.5 to 2.8 kcal yr BP, forest composition is marked by the predominance of Caesalpiniaceae, Sapotaceae, and *Martretia* (Euphorbiaceae), associated with few *Lophira* and *Saccoglottis*—good markers of wet evergreen forest. Pollen input from

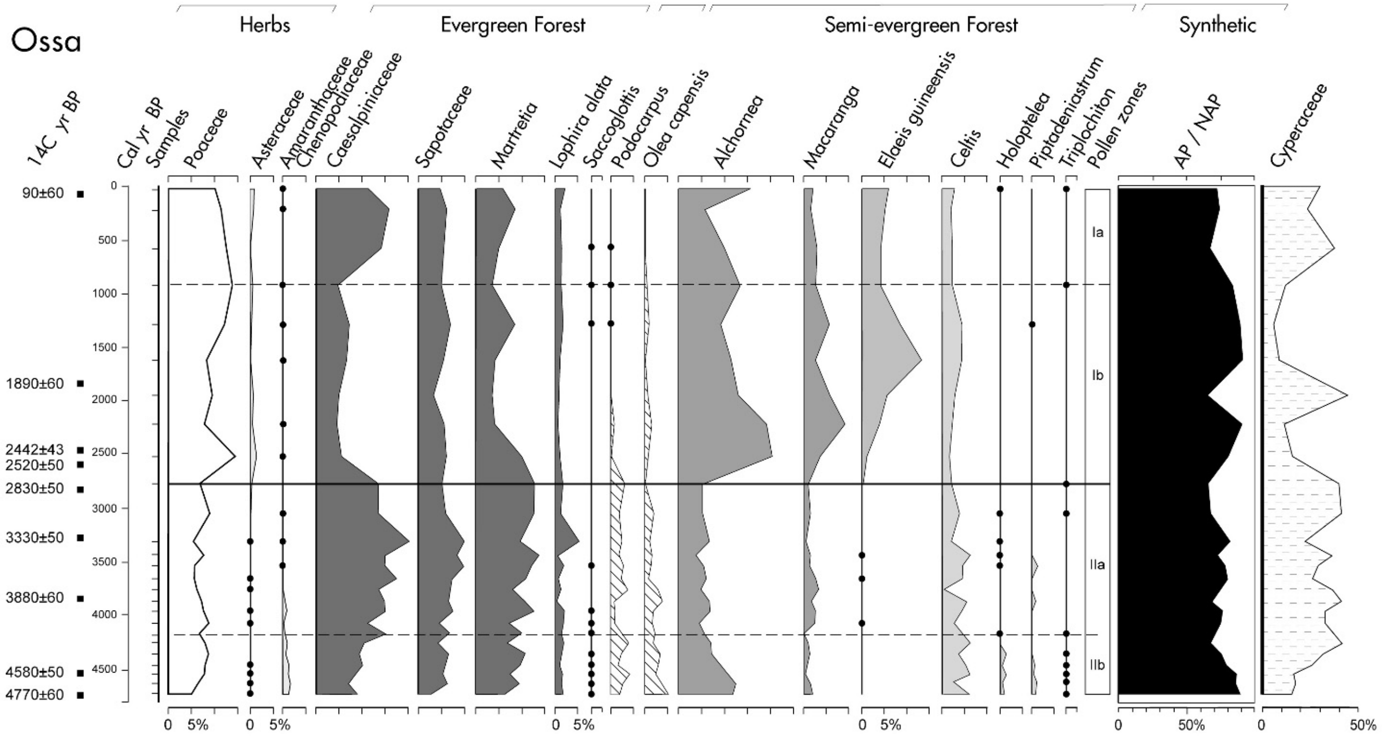


Figure 5.11. Simplified pollen diagram from Lake Ossa, Cameroon, presented according to calendar time scale (after Renaud-Farrera *et al.*, 1996) (% calculated versus pollen sum including all the identified taxa, but excluding Cyperaceae plotted at the right-hand side of the diagram).

highland forest is evident from low percentages of *Podocarpus* and *Olea* ($<5\%$), whereas the deciduous *Celtis*, *Holoptolea*, and *Piptadeniastrum* indicate a mixed semi-evergreen influence. From 2.8 kcal yr BP to the last century, *Alchornea*, *Macaranga*, and then *Elaeis* increased significantly, while the evergreen components decreased. Although these taxa have been considered as pioneer heliophytics, it is unlikely that such strong changes in tree composition can be attributed to human impact. Earlier settlements in the Lake Ossa catchment have been dated at a much younger period, between 0.7 and 0.5 kcal yr BP (Wirrmann and Elouga, 1998). From 5.5 to 2.8 kcal yr BP, vegetation changes reflect climatic changes that may be looked for within the distribution pattern of the rainfall, rather than within its total amount. Vegetation change appears in fairly good agreement with interpretation of the mineral composition of the sediment. High influxes of orthoclase feldspar have been interpreted as an indication of higher precipitation than today (Wirmann, 2001). However, a contradictory interpretation of less rainfall, but high water level—indicating an excess of precipitation versus evapo-transpiration—was supported by a hydrological model based upon diatom studies (Nguestop, 2004). Interesting variability, documented by the 50 yr resolution of diatom analysis, is not depicted in the pollen diagram provided at *c.* 200 yr resolution only. Unfortunately the different sampling resolution prevents further comparison between the diatoms and pollen. Between 2.2 and 2 kcal yr BP, complementary pollen counts (not illustrated here) showed another Poaceae increase synchronous with a significant input of Sahara dust that also contained allochthonous diatoms, attesting the stronger influence of the north trade winds and subsequent drier conditions (Nguestop, 2004). Although the wet evergreen forest was maintained, its pollen composition changed significantly throughout the last 5,000 years. To what extent such changes could be attributed to variability in the precipitation regime can be solved by performing finer resolution pollen analyses. The Caesalpiniaceae evergreen forest around Lake Ossa appears to have been re-established in its present composition *c.* 1,000 years ago. This interesting, well-dated Lake Ossa sequence with its high deposition rate deserves further analysis.

Mboandong, evergreen wet and semi-evergreen (Cameroon)

From Lake Mboandong, (4°30″N, 9°20″E, 120 m a.s.l.) located close to Barombi Mbo (Figure 5.1), a 13 m long sediment core was recovered and provides a basal age of 6.8 kcal yr BP (Richards, 1986). Although preliminary, the pollen diagram shows interesting, highly diversified forest taxa throughout this period until the present day. Many tree pollen taxa have been identified, compared with just a few from herbaceous plants. The majority of pollen comes from components of the evergreen forest. High pollen percentages were from *Alchornea cordifolia*, an understorey tree, not specific to evergreen forest. Although there are indisputable variations in relative percentages from the Caesalpiniaceae, Euphorbiaceae, *Macaranga*, *Uapaca*, *Pycnanthus*, Moraceae, *Celtis*, *Lophira*, and *Uncaria* during the past 5,000 years, the author did not attribute them to ecological or climatic changes. The event recorded at *c.* 2.5 kcal yr BP —interpreted as an indication of human impact—is discussed in Section 5.4.4 concerning the oil palm.

5.4.2.2 *Sites located south of the equator*

Coastal Congo, evergreen forest

The sandy coastal plain, north of Pointe Noire, is now occupied by a *Loudetia* (grass) savanna with *Manilkara lacera* (Sapotaceae). *In situ* fossil wood trunks with roots have been discovered included in a humic podzol bed (4°00″S, 11°45″E, Figure 5.1) that spans 7.4 to 4 kcal yr BP (Schwartz, 1990). The fossil wood specimens themselves have provided dates within the same time interval. Among the 117 collected specimens, a total of 20 species have been identified. These include *Saccoglottis gabonenesis*, *Agelaea* sp. (Connaraceae) and *Jundea* cf. *pinnata* (Connaraceae), *Uvariopsis angolana* (Annonaceae), *Cassipourea barteri*, *C.* sp. (Rhizophoraceae), *Dicranolepis* sp. (Thymeleaceae), *Dictyandra arborescens* (Rubiaceae), *Grewia* sp., *Neuropeltis acuminata* (Convolvulaceae), *Rinorea* cf. *gracilipes* (Violaceae), *Combretum* sp. (Combretaceae), *Rheedia* (Clusiaceae), and an unknown legume (possibly *Anthanotha* according to Dechamps, 1988b). Many species of *Monopetalanthus* (*M. microphyllus*, *M. pellegrinii*, *M. letestui*, and *M. durandii*), among the Caesalpiniaceae, indicate that a moist evergreen Caesalpiniaceae forest existed along the coastal plain for 3,000 years *c.* 6.8 to 3 kcal yr BP. The forest was diverse and, according to the authors, resembles the evergreen forest described in Mount Cristal in Gabon. Fossil wood remains indicate that the moist evergreen coastal forest, now observed in Gabon, occurred 500 km south of its present southern limit between 7.4 and 3 kcal yr BP, and therefore had a greater southern extension. The taphonomic conditions of preserved fossil wood—such as standing trunks in the living position—tend to indicate that the Caesalpiniaceae forest had disappeared suddenly from the coastal region of Congo and that such a disappearance was not due to human deforestation. The coastal Congo region receives 1,200 mm yr^{-1} of rainfall and experiences a 5 month dry season. There is a great contrast in seasonal temperature due to the proximity of cold oceanic upwelling offshore. The existence of a moist evergreen forest implies a greater rainfall (at least 2,000 mm yr^{-1}) or a shorter dry season. Its disappearance post-4 kcal yr BP suggests strong changes in climatic or edaphic coastline conditions (Schwartz, 1992).

Two pollen sequences extracted from nearby depressions complete the Holocene vegetation history of southern Congo. The Coraf pollen sequence (4°15″S, 11°59″E, 150 m a.s.l.) located nearby the fossil wood site (Figure 5.1) was extracted from peat deposited inside a white sandhorizon, and dated from 3 to 0.95 kcal yr BP. It documents a swamp forest progressively decreasing toward a modern savanna. The forest decrease was interrupted by a minor *Syzygium*/Combretaceae/*Tetracera* forest phase, dated around 1.4 kcal yr BP. No sign of an abrupt forest decline around 2.5 kcal yr BP was observed at Coraf, such as that in Cameroon, but the core was poorly sampled within that interval (Elenga,1992).

On the Atlantic coast, north of Pointe Noire, the Songolo pollen sequence S2 (4°45″S, 11°51″E, 5 m a.s.l., 1,260 mm yr^{-1} rainfall)—dated to 7.5 kcal yr BP at its base—indicates a well-developed *Rhizophora* mangrove, following the marine transgression at 10 kcal yr BP. The mangrove was associated with a swamp forest dominated by *Symphonia globulifera*, *Hallea*, and *Uapaca*. Humid conditions required for the development of swamp forest are confirmed by δ^{13}C values on total organic matter. There are significant and well-dated changes depicted in the mineralogical analysis of this core. These have no equivalent in the pollen data illustrating the coastal swamp forest, but the resolution of the pollen study is too low. The swamp forest persisted until *c.* 3.6 kcal yr BP, when sedges, palms, and ferns became dominant (Elenga, 2001).

In summary, during the Holocene, the coastal plain of southern Congo was occupied by two different types of forests: a highly diversified Caesalpiniaceae forest documented by fossil woods, and more localized swamp forests and mangrove since at least *c.* 7 kcal yr BP. The forests persisted until 3 kcal yr BP, clearly indicating higher humidity or precipitation than present between 7 and 3 kcal yr BP. The pattern of forest disappearance from the area remains unsolved and variations in sea levels should be considered. But the discrepancies in dating really preclude definitive identification of a widespread event at 4 kcal yr BP as suggested by Marchant and Hooghiemstra (2004). A rather more complicated pattern seems to emerge, which needs comparison of fossil data at the same resolution interval with firmly established short-term Holocene climatic variability. Nevertheless, coastal grassland in the Congo seems to have been established only after 3 kcal yr BP, and was interrupted by a minor forest increase again at *c.* 1.4 kcal yr BP.

Mayombe, evergreen transitional forests

Evergreen transitional forests dominated by Meliaceae, Fabaceae, and Irvingiaceae with a great diversity of representatives from other families occupy the Mayombe Massif today (Descoings, 1976; Cusset, 1987). On the western slope of the Mayombe, Lake Kitina (4°15″S, 11°59″E, 150 m asl) is located in a valley which receives about 1,500 mm yr^{-1} of rainfall and experiences a 4 month dry season with heavy cloud cover. The lake is surrounded by swamp vegetation with *Cyperus papyrus*, *Anchomanes* (Araceae), ferns, and a few trees—such as *Alstonia* and *Alchornea*—followed by a swamp forest including *Uapaca* (Euphorbiaceae), *Santiria* (Burseraceae), and *Memycelon* (Melastomataceae). A transitional semi-evergreen dry forest—with *Dacryodes*, *Klainedoxa gabonensis* (Ixonanthaceae), *Piptadenia* (Fabaceae), *Plagiostyles africana* (Euphorbiaceae), *Anthostema* (Euphorbiaceae), and Sapotaceae—is developed on the slopes (Elenga, 1996). The Holocene pollen record is dated 5,460 ± 70 ^{14}C yr BP at a 620 cm depth (Figure 5.12). From 5.5 to 2.7 ^{14}C yr BP, the synthetic pollen diagram indicates two, well-developed forest associations: one from dry land (*Dacryodes* (Burseraceae), *Martretia* (Euphorbiaceae), and *Anopyxis* (Rhizophoraceae), the other from swamp (*Syzygium*, *Hallea*, and *Anthostema*). Between 2.7 and 1.3 ^{14}C yr BP, four AMS dates within a 40 cm depth interval demonstrate a very low sedimentation rate (or perhaps a discontinuity). During that interval—which lasted almost 1.4 kyr—significant changes occurred. First, a sharp and important increase in dry land forest (40%) accompanied by a significant increase in amorphous silica (Bertaux, 1996) shows that Lake Kitina partially dried out. The successive increases in pioneers (*Macaranga* and *Alchornea*), associated ferns, and Poaceae (*c.* 10%) indicate a greater extent of swampy conditions contemporaneous with the appearance of *Elaeis guineense*.

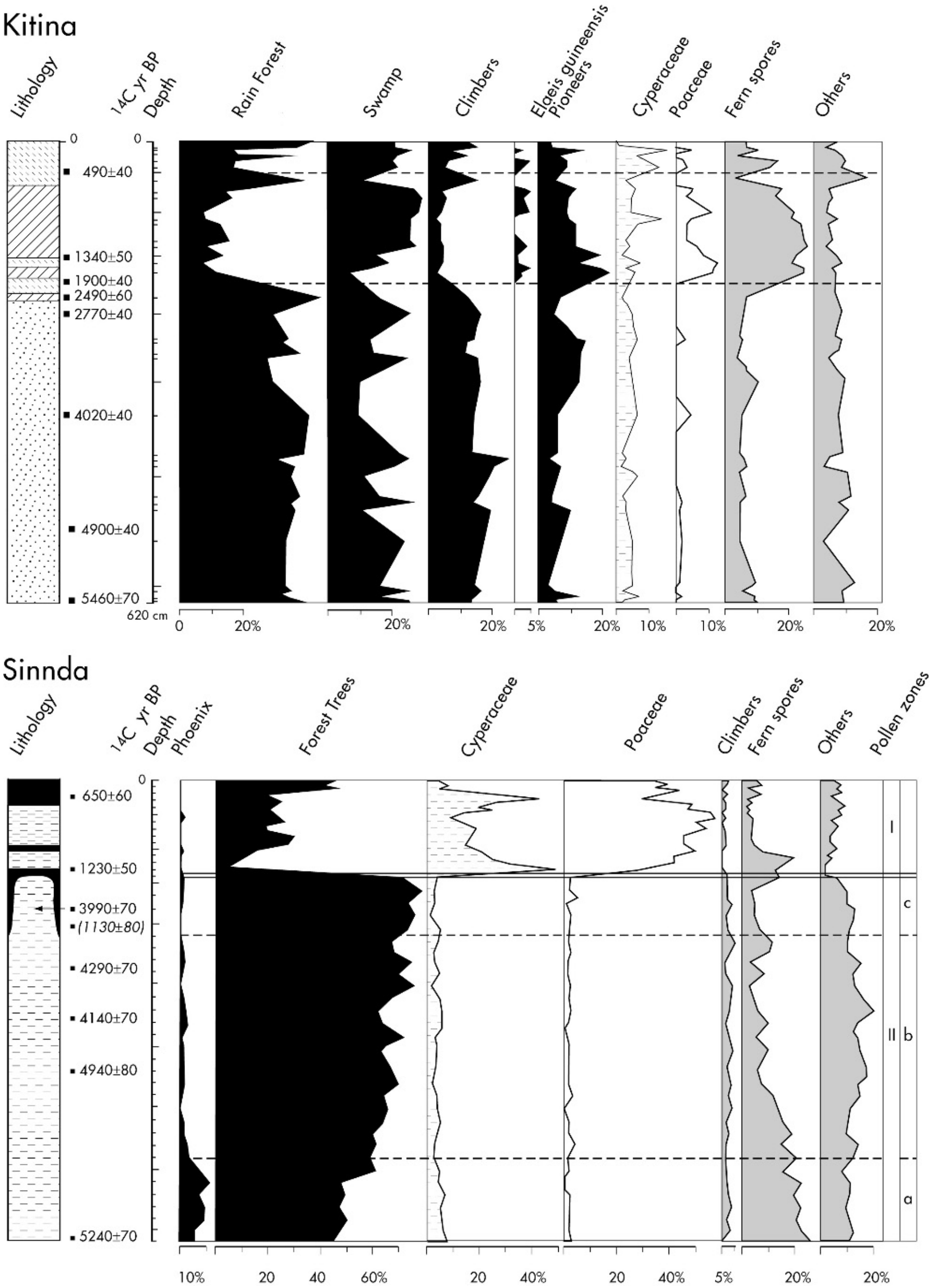


Figure 5.12. Simplified pollen diagrams from Lake Kitina (from Elenga *et al*., 1996) and Sinnda, presented according to depth (after Vincens *et al*., 1998) (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores).

Although these pollen changes appear depicted as an abrupt 2.7 ^{14}C yr BP event, several episodes of reduced lake level are shown by the lithology (Figure 5.12). No detailed modifications of pollen taxa composition have been provided for documenting the effect of aridity on the composition of the forest. There is no evidence for human impact either (Elenga, 1996). The return to humid conditions after 1.3 ^{14}C yr BP is attested by swamp forest pollen rather than a decrease in dry land forest. However, pollen from dry land forest increased again at 0.5 ^{14}C yr BP. The Kitina diagram clearly indicates that the composition of the Mayombe forest is recent—no older than 500 years at most.

Niari Valley, grasslands

The geographical location of Lake Sinnda (3°50″S, 12°48″E, 128 m a.s.l.)—inside a large band of wooded grassland separating the two massifs of Mayombe and Chaillu within the dry semi-evergreen forest to the south—is particularly interesting for addressing the origin of included grassland (Figure 5.1). Here, mean annual rainfall is about 1,100 mm yr^{-1} with a 5 month dry season from mid-May to mid-October. Two well-dated cores analyzed for both pollen (Vincens, 1994) and phytoliths (Alexandre, 1997) provide evidence for a well-diversified dense forest existing from 5,240 ± 70 to 3,990 ± 70 ^{14}C yr BP (Figure 5.12) with little impact of pollen from grasslands (Vincens, 1998; Figure 5.6). Dominated by *Chlorophora* (Moraceae), *Alchornea*, *Celtis*, *Pausinystalia* (Rubiaceae), *Macaranga*, and *Lannea* (Anacardiaceae), and a great variety of taxa, the fossil pollen indicates a semi-evergreen (semi-deciduous) forest. Noticeable changes occurred later on. *Phoenix*, *Myrianthus*, and ferns are well-represented before 5 ^{14}C yr BP whereas *Celtis*—associated with Caesalpiniaceae, Fabaceae, and many Euphorbiaceae—increased at about 4.5 ^{14}C yr BP. But, the most obvious change observed at Sinnda is situated in the interval between *c.* 4 and 1.2 ^{14}C yr BP when a strong gap is registered in the sedimentation of the core. After that gap, pollen assemblages, dominated by grasses and sedges, evidence greater development of marshes, now existing at the northeast end of the lake. The forest was considerably impoverished in taxa, although Ulmaceae (*Holoptolea*, *Trema*, and *Celtis*) and *Chlorophora* accompanied the *Alchornea*, a tree still present on the steep shores of the lake. The abrupt character of such a change may be an artefact of the 2,000-year lack of sedimentation, likely corresponding to an arid period when Lake Sinnda (4 m deep) dried out. Many forest trees disappeared during that interval. Although this is the most obvious post-4 ^{14}C kyr BP change observed in the region, the fact that the lake is shallow and located at the ecological limit for forest growth with a long dry season, would have amplified the effect of climatic change. Positive evidence for forest changes is missing. A second core in the central part of the lake contains black organic layers with abundant plant remains indicating that two subsequent drying phases occurred: one at 4.5 ^{14}C kyr BP followed by another post-1.7 ^{14}C kyr BP. An increase in tree forest taxa (AP > 40%) at the upper part of the core, dated 650 ± 60 ^{14}C yr BP, points to a recovery of the forest nearby. The pollen curve of the possibly cultivated *Elaeis guineense* became significant only during the last 600 years, probably linked to possible settlement by Bantu-speaking, proto-agricultural people (Schwartz, 1992). Charcoal dated

2,130 ± 70 ^{14}C yr BP, on the Bateke Plateau, and 1,600 ^{14}C yr BP in Mayombe clearly support the long use of fire in the region (Schwartz, 1990). A date of 1,350 ± 70 ^{14}C yr BP obtained on burned specimens of *Erythrophleum suaveloens* (Caesalpiniaceae)—an ubiquitous tree, used by local people for its toxic alkaloids and extracted from archeological sites—confirms human fire usage in Mayombe (Dechamps, 1988b). From the Sinnda record itself, it cannot be established precisely when (between 4 and 1.2 ^{14}C kyr BP) the savanna spread in the Niari Valley, but grasslands are present once fire is introduced.

Close to the Congo River, grassland/semi-evergreen forests
Near the right bank of the Congo River three cores were recovered from the Ngamakala pond (4°04″S, 15°23″E, 400 m a.s.l.) which yielded records from the glacial period (see above). None of them yielded a complete Holocene sequence. In one core, there is only 20 cm of sediment deposited between the two conventional radiocarbon dates of 10,880 ± 160 and 3,940 ± 130 ^{14}C yr BP (Elenga, 1994). Their pollen content corresponds to a *Syzygium*/Sapotaceae swamp forest, but accurate age determination is not available. Another core provided a 1 m thick accumulation of peat deposited between *c.* 3 and 1 ^{14}C kyr BP, attesting to the retreat of swamp forest at the expense of grasslands during that interval. A significant expansion of swamp *Syzygium* forest re-occupied the pond again at 930 ± 140 ^{14}C yr BP. Although far from being complete, the succession of forest associations nearby the Congo River emphasizes many successive stepped changes during the Holocene. Among those the opening of the forest at Ngamakala is sharply registered at *c.* 3.3 ^{14}C kyr BP. However, this cannot be considered synchronous with any of the previously discussed events at 4 or 2.5 ^{14}C kyr BP.

5.4.3 History of the rainforest during the last 5,000 years

During the last 5,000 years the evolution and dynamics of the rainforest forced by climatic changes appear rather complicated. Apparently, they do not depict the same pattern north and south of the equator, but the lower Holocene record is missing (or discontinuous) at all the sites except at Barombi Mbo in Cameroon. There, the depicted changes indicate significant climatic variability during the Holocene, but there is no clear identification of an "African humid period" prior to 6 kcal yr BP. At most sites, negative evidence and lack of sedimentation during the early Holocene may indicate drier climatic conditions. Hence the status of rainforest existence at that time and its composition remains unknown. The results summarized here firmly establish that evergreen and semi-evergreen rainforests persisted between 6 and *c.* 3 kcal yr BP at all of the nine investigated sites (Vincens *et al.*, 2010). Slightly before or after 3 kcal yr BP major vegetation changes are documented (Vincens, 1999). Because of discrepancies in the resolution of the analysis it is not clear, however, whether these changes reflect several short-term episodes of climatic variability at a millennial scale, concerning seasonal distribution of rainfall, or a longer single event. One major vegetation change documented in the Cameroon sites is well-bracketed between *c.* 2.8 and 2.2 kcal yr BP. Elsewhere, more attention needs to be paid to their chronological control (Russell *et al*., 2003). Discrepancies in the stratigraphy, gaps in the sedimentation, different time resolutions of pollen data, as well as local climatic conditions relevant to length of the dry season, prevent the correlation of changes at all the sites within a single event. The proximity of a lake or rivers could maintain edaphic forests. Although a reduction in the hydrological budget and lowered lake levels have been documented by geological studies (Servant and Servant-Vildary, 2000), Late Holocene aridity was not an irreversible climatic event. Many sites indicate the return of wetter conditions during the last millennium, creating favorable conditions for a new forest expansion between 0.9 and 0.6 kcal yr BP (Vincens, 1996a, b; Elenga, 2004).

On the other hand, the synchronous expansion of grasslands at *c*. 2.2 kcal yr BP in the lowlands, on the eastern side of Mount Cameroon, nearby lakes Barombi Mbo (Maley, 1992), Mboandong (Richards, 1986), and Ossa (Reynaud-Farrera,, 1996), in the northern tropics, is in good correspondence with the Iron Age. However, whether such expansion was climatically controlled or human-induced does not reach a consensus among different specialists and remains a matter of speculation (Maley, 1992; Schwartz, 1992). High-resolution diatom analysis of the Ossa core provides new, interesting data for the climatic interpretation of that event. In striking correspondence with the 2.7 kcal yr BP North Atlantic cold event (Bond, 1997), in Africa an increase in lake level and rainfall is bracketed by two strong amplitude shifts towards drier conditions. The first was interpreted as a decrease in rainfall. The second lasted a few hundred years when a decrease in water level, and stronger input of allochthonous diatoms transported from Lake Chad, indicate reinforced northern winds responsible for stronger aridity between 2.3 and 2 kcal yr BP. The high-amplitude oscillations registered at Ossa suggest that a further high-resolution study of the nearby Bambili Lake, located at higher elevation (Stager and Anfang-Stutter, 1999), would be worthwhile. Synchronous vegetation change between a Caesalpiniaceae/*Lophira*-dominated forest before 2.5 kcal yr BP replaced by an *Alchornea*/*Macaranga* open forest after 2.3 kcal yr BP could well be explained by an increased length in the dry season and possible effect of low subsidence and storms following movement of the ITCZ (Nguestop, 2004). Such an interesting hypothesis might receive more support when higher resolution pollen data have been obtained. An increased proportion of *Elaeis guineense* (oil palm) in the Ossa pollen record occurred simultaneously, which brings to the fore the fact that several dry episodes—also expressed at Kitina and Sinnda—created consecutive openings through the equatorial forest. These gaps offered a possible direct route for the Bantu migrations from Cameroon to the south.

A recent study from southern Cameroon provides a high-resolution pollen sequence spanning the interval 3.1 to 2.35 kcal yr BP (Ngomanda *et al*., 2009). Located at the inland border of the coastal evergreen forest, close to its contact with the drier semi-evergreen, Nyabessan swamp, now occupied by *Musanga*/*Raphia* forest, is surrounded by secondary forests of different ages with pioneers in the alluvial plain of the Ntem River (Figure 5.1). Fossil pollen was found preserved only in the lower 2 meters of the core, and five radiocarbon dates provide a reliable chronology of the past 700 years. The pollen sequence is documented at a resolution interval varying between 10 to 30 years. The dynamic of the coastal evergreen forest is illustrated in Figure 5.13. Starting at the bottom part (3.1 kcal yr BP) the forest succession shows the development of Moraceae, followed by *Pycnanthus*, *Trema*, and later by a significant increase in Caesalpiniaceae. The Nyabessan pollen sequence indicates a rich and diversified association of pioneer trees, together with various components of secondary and mature evergreen (rain) forests. *Lophira alata* and Caesalpiniaceae are the most abundant pollen, followed by *Nauclea*, *Uapaca*, Sapindaceae, Flacourtiaceae, Moraceae, Combretaceae, and *Milicia*. The most significant change, occurring during the 3.1 to 2.45 kcal yr BP period, stands as an important increase in percentages of *Raphia*, lasting over 250 yrs (2.85–2.6 kcal yr BP), in response to higher ground water level. Composition of forests of *terra firme* remains fairly stable until 2.45 kcal yr BP. At that time, the most important change concerned the *Lophira*/Caesalpiniaceae association. After they had progressively decreased, pollen percentages of these trees remained very low during more than fifty years after 2.4 kcal yr BP. Simultaneously high values of *Trema*, *Tetrochidium*, *Alchornea*, and *Musanga* are registered as fast growing colonizers of two forests types. *Musanga* characterizes modern surface soil samples with monthly rainfall values above 50 mm. Distribution of *M. cecropioides* is restricted to the evergreen forest proper. *Trema orientalis*, largely distributed in the semi-evergreen forest, has seeds that can resist 6 months desiccation without loosing germination power. Strong change at the top of the Nyabessan pollen diagram at 2.4 kcal yr BP is interpreted as an indication of an increase in dry season length (or intensity) due to a much southern position of the ITCZ at that time (Ngomanda *et al.*, 2009). The timing is consistent with the record for domestication of pearl millet (*Pennisetum glaucum*) in archeological sites from southern Cameroon (Figure 5.14). However, no direct evidence (e.g., charcoal or fossils of cultivated plants) attest to human disturbance at the Nyabessan site. Synchroneity with drier episodes registered at Lake Ossa and Barombi Mbo points to a significant climatic change in the whole Cameroon region at a time when conditions were favorable for introduction and migrations of ceramic-producing, and farming, populations.

5.4.4 The oil palm, evidence for human impact?

Abundant pollen from cultivated plants in lake sediments (e.g., *Dioscorea* (the yam), *Elaeis guineensis* (oil palm), and *Canarium schweinfurthii* (an oil producing forest tree)) can provide evidence of human activity (Shaw, 1976). *Dioscorea* pollen has been identified in modern surface samples at the contact between the forest and the savanna at Kandara (Vincens, pers. commun.), but no fossil pollen evidence for it has been found yet. At Mboandong (Cameroon), a forest decrease associated with a significant grass increase, and followed by a well-marked increase in oil palm pollen (up to 20%) at 2.4 kcal yr BP, has been interpreted as evidence for human impact on the basis that this date was close enough to that of the Nok archeological Iron Age site. It was suggested that forest clearance could be attributed to iron technology (Richards, 1986). However, in the pollen diagram itself, opening of the forest occurred first, before the appearance of *Canarium schweinfurthii*. Pollen of *Canarium schweinfurthii*, clearly distinguished from other Burseraceae—notably *Aucoumea* (Harley and

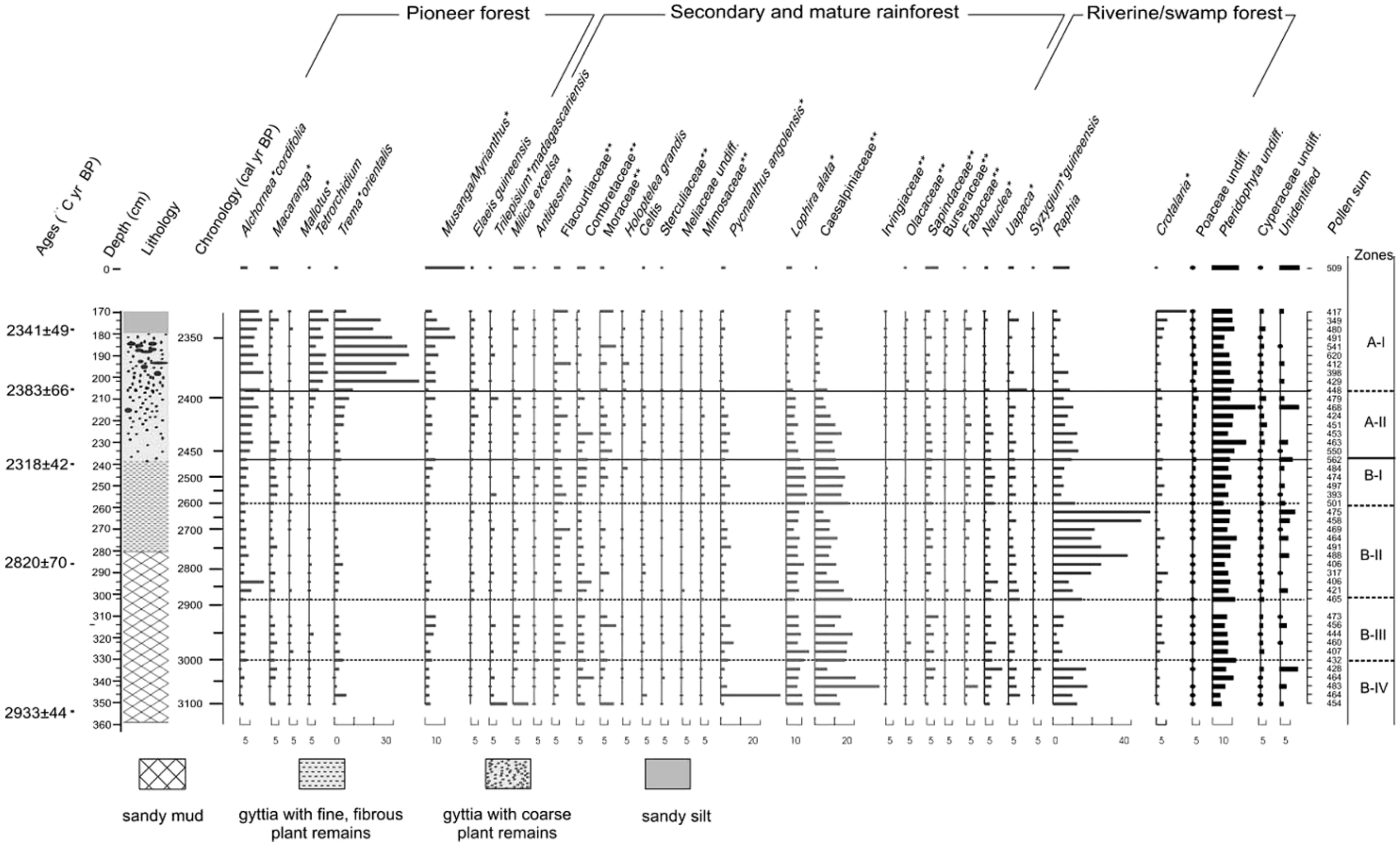


Figure 5.13. Pollen diagram of a core (3.1–2.35 kcal yr BP) recovered from the Nyabessan swamp, south Cameroon (after Ngomanda *et al.*, 2009). * Identification at the genus or species level. ** Groups genera with similar ecological requirements.

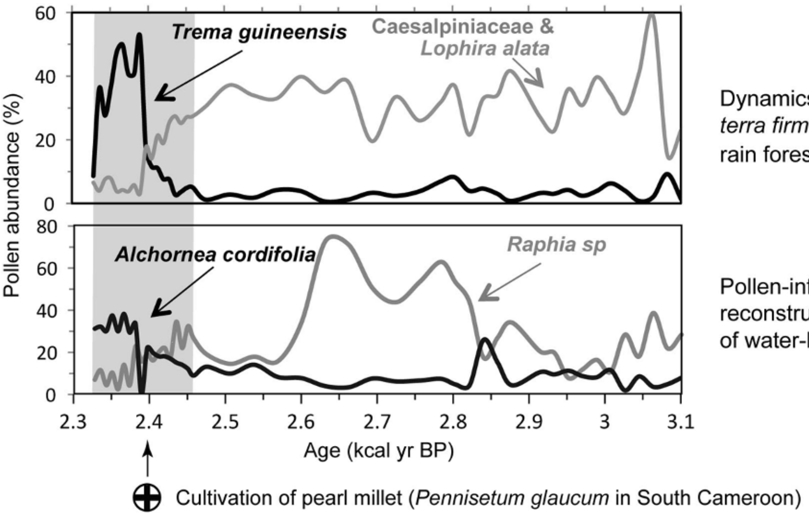


Figure 5.14. Comparison of percentage distribution of mature evergreen pollen taxa (Caesalpiniaceae and *Lophira alata*) versus pioneer taxa *Trema guineense*, *Alchornea cordifolia*, and swamp forest taxa (*Raphia*)—evidence for pearl millet at archaeological sites Bwambé Sommet and Abang Minko'o (Eggert *et al.*, 2006) (after Ngomanda *et al.*, 2009).

Clarkson, 1999; Sowunmi, 1995)—was recorded at *c.* 5 kcal yr BP, suggesting an earlier presence of humans nearby the fossil pollen site. Fossil pollen from *Elaeis guineensis* has been reported at many sites in west and central Africa. Early evidence of oil palm pollen is available since the Tertiary in the Niger Delta (Zeven, 1964), and was reported in Upper Pleistocene marine sediments offshore the Niger River (Dupont and Weinelt, 1996). However, it is only during the last 3,000 years that the proportion of *Elaeis guineensis* pollen reached significant values (up to 24%) in the Niger Delta (Sowunmi, 1999). As a "palm belt", present day natural distribution of the oil palm follows the Gulf of Guinea and largely penetrates inside the Congo Basin. *Elaeis guineensis* is a heliophytic pioneer species, also fire-resistant (Swaine, 1992), which occurs naturally in a great variety of habitats inside the rainforest, and at its periphery, including swamp (Letouzey, 1978). All these characteristics largely contribute to the difficulty of interpreting their fossil record. The pattern of occurrences and abundance of *Elaeis guineensis* pollen through time is not similar at all the investigated sites, and this led to a controversial interpretation. In Ghana, archeological remains indicate an earliest use of oil palm nuts at 5.8 kcal yr BP (Shaw, 1976), but its fossil pollen became abundant only after 3 kcal yr BP in the Niger Delta. The common pattern observed in the three Cameroon sites, starts with scattered *Elaeis guineensis* occurrences from *c.* 4 to 3 kcal yr BP, followed by a significant increase at *c.* 2 kcal yr BP (Richards, 1986; Reynaud Farrera, 1996; Maley and Brenac, 1998) in remarkable synchroneity. At Barombi Mbo, the peak of oil palm pollen (2.9 to 2.4 kcal yr BP) corresponds to the 2.75 kcal yr BP crisis (Van Geel,1998) or "dramatic forest decline". It occurs a few hundred years earlier than the peak of grasses (2.7 to 2.2 kcal yr BP) and much earlier than the Bantu invasion (2.2 to 2 kcal yr BP) (Schwartz, 1992; Maley, 2001). Therefore, *Elaeis guineensis* increased in response to increased aridity in the rainforest a few centuries before the spreading of oil palm by Bantu speakers. By contrast, several papers discussed the past record of *Elaeis guineensis* in West Africa (see Sowunmi, 1995 for an exhaustive literature), possibly enhanced by Bantu speakers (Schwartz, 1992; Maley, 2001). In Gabon, Neolithic populations had occupied the savanna of the Ogoue Valley since *c.* 3.7 kcal yr BP and the main expansion of iron-smelting dates at *c.* 2.2 kcal yr BP (Oslisly and Fontugne, 1993; Oslisly, 2001). Abundance of oil palm pollen happened at a coastal site around 3 kcal yr BP, following forest reduction 1,000 years later. Inland at Kamalete it is registered much later, from 1.2 to 0.3 kcal yr BP. There, the oil palm phase is registered simultaneously within the pioneer forest phase, showing a significant peak at 0.9 kcal yr BP, during a gap in human occupation (Ngomanda, 2007). At the Songolo mangrove site (Congo coastline), scattered occurrences of *Elaeis guineensis* pollen have been found from 3.6 kcal yr BP onward (Elenga, 2001), but no significant increase has been observed until the last centuries, neither at Ngamakala and Bilanko nor Kitina and Sinnda (Vincens, 1998). At inland sites, climatic conditions may have been too dry for the development of oil palm (Elenga, 1996, 2001). Occurrences of oil palm are apparently associated with increased grass pollen or a more deciduous character of the forests (Vincens, 1996a,b). However, their peaks in abundance are not synchronous events and the geographical distribution pattern through time is far from being spatially and geographically consistent. Our available knowledge can be summarized by the following conclusions. First, there was a greater evidence of oil palm pollen during the last 3,000 years over the Guineo-Congolian rainforest. Second, simultaneous forest openings and increased evidence of use of oil palm by human populations is not demonstrated at all the sites with sufficiently accurate time controls or fine-resolution intervals. Third, geographical progression of the use of oil palm, following Bantu migration, remains to be demonstrated. The oil palm has a very short reproductive cycle, and it can indicate simultaneous use by humans following—by a few years—anthropogenic or natural forest perturbation. Fourth, proof of anthropologically enhanced modifications of the rainforest, prior to the last few centuries, has yet to be provided.

5.4.5 The last historical period (Gabon)

Important past vegetation changes inside the moist evergreen Guineo-Congolian rainforest have been evidenced in the historical period within core sediments obtained from Lake Kamalete in central Gabon (Ngomanda *et al.*, 2005). Within the forest of the Lope National Park, Lake Kamalete is located inside a 60 km long strip of savanna interrupting the Maranthaceae forest, whereas the closed canopy forest stands at *c.* 20 km west of the lake (Figure 5.1). Situated at the end of a valley, not far from the Ogooue River, the shallow Lake Kamalete is surrounded by a mosaic of savanna and isolated fragments of Marantaceae forest. Sedges (Cyperaceae) and ferns colonize its shoreline. In this area, precipitation oscillates around 1,500 mm yr^{-1}, a low value for Gabon due to the rain shadow effect of the Cristal Mounts on the western side. But, present day meteorological values show great inter-annual variability related to variable timing and duration of the dry summer season (June to September) when the ITCZ moved to the northern hemisphere. During the dry season, dense cloud cover maintains high relative humidity and slightly lower temperature when sea surface temperature drops out.

A *c.* 4 m core recovered from Lake Kamalete (0°43″S, 11°46″E, 350 m a.s.l.) was dated by four conventional radiocarbon dates, providing a basal age of *c.* 1.3 kcal yr BP. Fine-resolution pollen analysis of the order of one or two decades documents important past vegetation changes and detailed composition of the moist evergreen Guineo-Congolian rainforest (Ngomanda, 2005). The original fossil pollen sequence includes 80 samples and counts of 124 identified pollen taxa. A simplified version is presented here (Figure 5.15). In this context, fern spores, grasses, and sedges produced the highest quantities of pollen. Grass pollen percentages average 70% of the total pollen sum (after spores, aquatics, and sedges had been excluded) indicating the persistence of a forest–savanna mosaic at the site. Because significant pollen counts had been achieved at each level, a detailed diagram could be drawn for forest AP (Figure 5.16). Among palynologists it is assumed that pollen abundance is related to abundance of trees, rather than to yearly pollen production, although this might deserve consideration when 1 cm sampling represents 2 or 3 years of pollen deposition. Significant changes in abundance and floristic composition of the regional forest occurred at Kamalete during the last *c.* 1.5 kcal yr BP. Successive fluctuations in dominant taxa are documented by trends that lasted a few hundred years or more. Before *c.* 1325 to 1240 cal yr BP, the first forest phase included a high representation of *Cnestis* (Connaraceae), *Celtis*, *Bosqueia* (Moraceae), Caesalpiniaceae, and *Lophira alata* pollen. It ended rather abruptly, being replaced by a disturbed forest dominated by pollen from trees—such as *Tetrorchidium*, *Macaranga*, *Musanga*, *Alchornea*—that dominate in opening gaps within forests today, whereas mature forest trees simultaneously decreased. The disturbance phase lasted about 700 years (*c.* 1,250 to 550 cal yr BP) and may have been caused by stronger winds, changes in rainfall regime, or human impact. Indeed, Iron Age settlements occupied the Lope region since 2.6 kcal yr BP—that is, long before the disturbed forest phase documented at Kamalete. However, from 1,400 to 800 yr BP the number of archeological sites in Gabon declined, a reduction attributed to a "population crash" (Oslisly, 2001). If there was any significant human impact on vegetation due to Iron Age population, one would expect it to be less important when the population was smaller than before or after. The opposite pattern being observed, Iron Age impact was considered not responsible for the observed disturbed forest (Ngomanda, 2005). The period of maximum forest disturbance includes the time span of the "Medieval Warm Period" (MWP, 900–600 cal yr BP), although the disturbed forest phase in Gabon (*c.* 1.25 kcal yr BP to 550 cal yr BP) started before the beginning of the MWP climatic anomaly. Well-known in the northern hemisphere (Bradley, 2000), the "Little Ice Age" (*c.* 600–200 cal yr BP) that followed the MWP had a major effect on the evergreen forest of Gabon (Ngomanda *et al.*, 2005), and is probably present in records from Cameroon (Nguetsop, 2004), Congo (Elenga, 1996), East Africa (Verschuren, 2000), and Lake Victoria (Stager, 2005). In Gabon, a re-expansion of the forest took place at *c.* 550 cal yr BP, after the disturbance phase. At this time *Celtis* and *Raphia* dominated,

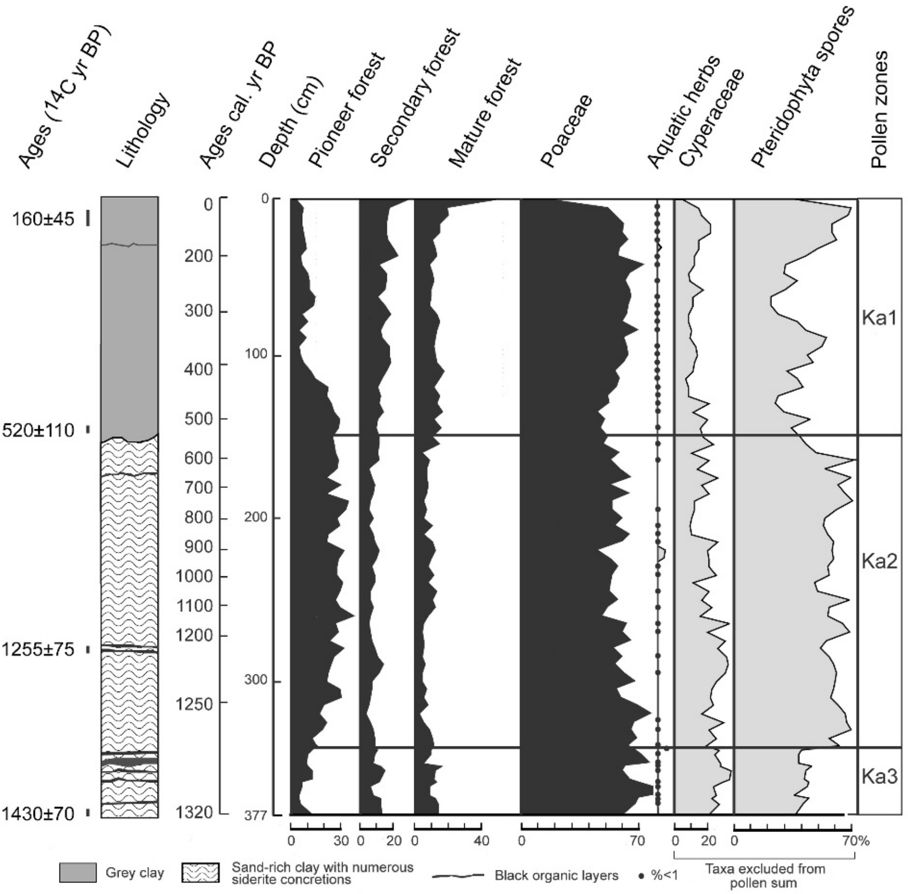


Figure 5.15. Synthetic pollen diagram from Kamalete, Gabon (after Ngomanda *et al.*, 2005), presented according to depth with corresponding timescale (% calculated versus pollen sum including all identified taxa, Cyperaceae, and spores).

indicating a colonizing stage resembling the modern one described for Kandara (Vincens, 2000). Two hundred years later, the site was both a ‘‘secondary forest’’ and a well-diversified mature forest occupied by *Lophira*, *Fagara* (Rutaceae), *Pycnanthus*, *Irvingia*, *Plagiostyles*, Caesalpiniaceae, and Burseraceae—bearing floristic affinities with the present day forest in the region (Jolly, 1996). At Kamalete the ‘‘Little Ice Age’’ period was favorable for forest development. In Gabon the re-establishment of a well-diversified mature forest dates from 400 years at most. Since 250 years ago, *Aucoumea* pollen frequencies exhibit three sharp peaks, indicating significant recoveries after forest cutting for timber. We have already discussed that the origin of mature forest seems no older than a few hundred years, in strong contradiction with the long-standing belief of rainforest stability over time. Past hydrological changes across the equatorial tropics are partly explained by amplified shifts in mean latitude of the ITCZ (Haug, 2001). The sensitivity of the rainforest to short-term, past climatic

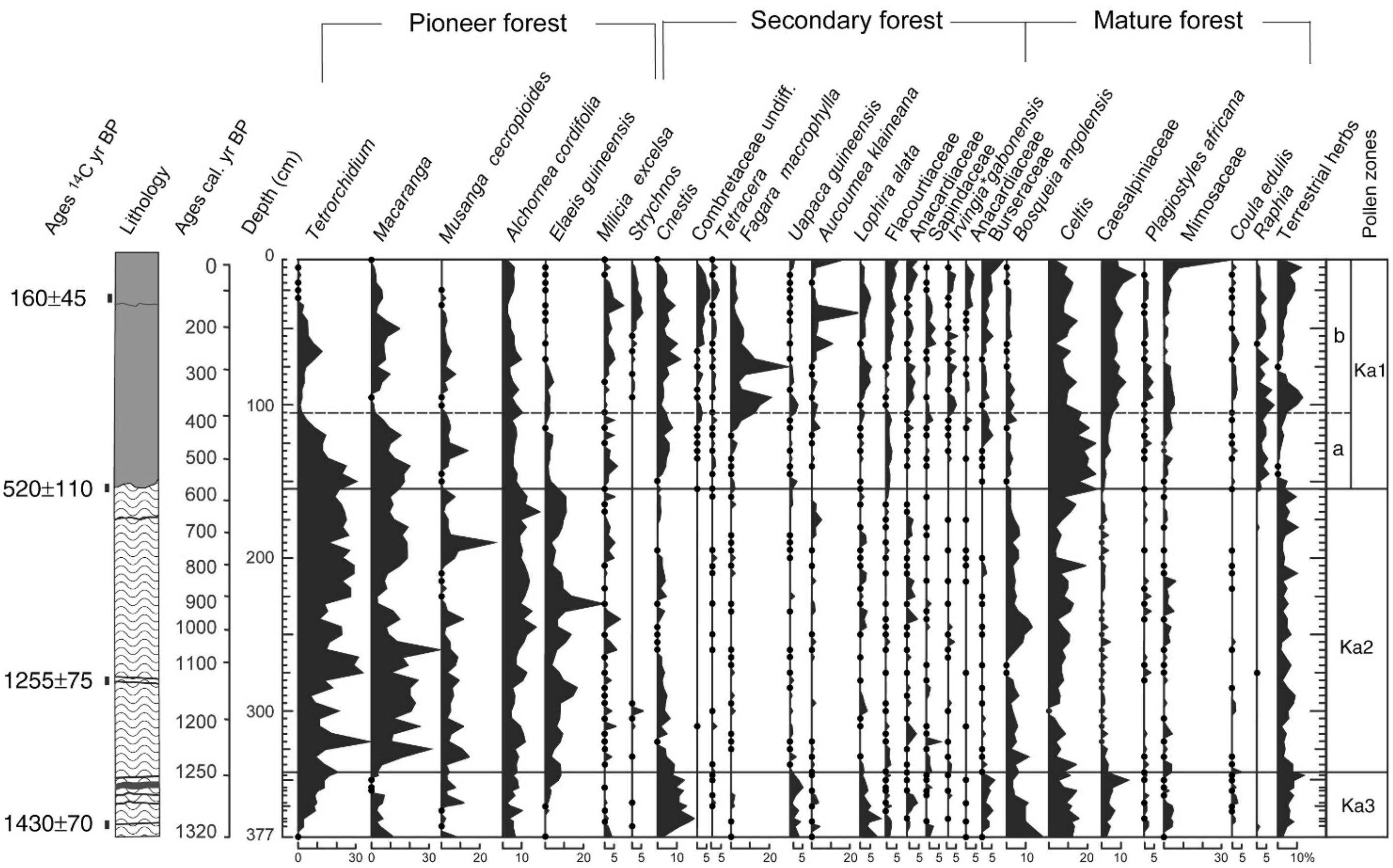


Figure 5.16. Pollen diagram of the forest trees from Kamalete, Gabon (after Ngomanda *et al.*, 2005) (% calculated versus pollen sum after excluding Cyperaceae and spores, and Poaceae). Symbols for lithology as in Figure 5.15.

forcing is clearly demonstrated and suggests that greenhouse warming can have a great impact in the future on the rainforest in Gabon.

5.5 CONCLUSIONS

For many decades, palynological studies in the tropics were limited by the lack of knowledge in tropical pollen morphology. Important reference collections of African tropical plants have been made in Durham (NC), Montpellier and Marseille (France), Germany, Nigeria (Africa), the United Kingdom, etc. A description of the pollen morphology for most common trees is available in several publications and pollen atlases (Maley, 1970; Bonnefille 1971a, b; Sowunmi, 1973, 1995; Caratini, 1974; Bonnefille and Riollet, 1980; Salard-Cheboldaeff, 1980, 1981, 1982), from which some pollen photographs are now being included in the African Pollen Data Base. Therefore, pollen analysis in the African tropics is feasible, although it still requires lengthy training. The bias between pollen assemblages and plant associations will remain. But, interpretation of fossil data will be facilitated by modern pollen rain studies concerning many types of rainforest, encountered under different ecological conditions. Taxonomic composition and taxa frequencies of pollen assemblages can be used to characterize habitat types, despite the absence of pollen from important tropical families. Modern pollen assemblages help us to interpret tropical forest dynamics in the past, as forced by climatic changes. They have also been successfully used in elaborating a biome approach for modeling past global vegetation (Jolly, 1998), the quality of which depends upon homogeneity in sampling and completeness along continuous climatic gradients. With the major threat of rainforest disappearance in mind, completing modern pollen data from all the African forests constitutes an urgent task.

Fossil pollen data from different vegetation types inside the Guineo-Congolian rainforest of the African continent—now available—document strong modifications in the floristic composition of both evergreen, semi-evergreen, and associated mixed types of forests through time, the most important occurring during the LGM. Proof exists that rainforest persisted during glacial time, at two investigated sites, although glacial forests included more semi-evergreen taxa, a few highland taxa (*Olea* and *Podocarpus*), and were more open. Site-based maps of global vegetation at the LGM including Africa (Elenga, 2000c) were used for a comparison between different vegetation models (Kohfeld and Harrison, 2000) addressing land surface feedbacks (Clausen, 1997) or the effect of lower CO_2 in global modeling. Although it has been generally considered that “tropical forests in Africa, Australia and Asia were partly replaced by more open vegetation” (Harrison and Prentice, 2003), the persistence of rainforest during the last glacial period, even when lower CO_2 content in the atmosphere was not favorable to tree growth, is clearly attested at two tropical sites located within the rainforest region. A greater extension of forest can even be postulated from abundant fossil wood remains. Lowlands on the eastern side of Mount Cameroon and near the Congo River have been proved to be rainforest refuges during the LGM. Clearly, forest refuges were not geographical areas or spots covered by forests of similar composition to those of today. Also there may have been many other refuges of different species or groups of species that remain to be found. Throughout the intertropical region ecological constraints related to hydrological constraints may have varied. Following the example illustrated here for *Olea*, different species may have found refuge in different localities. Direct evidence can be provided by further research on fossil pollen or macrobotanical remains.

During the Holocene, significant variations in tree pollen assemblage percentages have also been observed at all of the ten investigated sites presented in this chapter. These are not induced by variations in the CO_2 content of the atmosphere, which stayed fairly stable throughout this period. Replacement of dominant taxa or fluctuations in pollen abundance continuously occurred, suggesting the dynamic behavior and successive replacement and dominance within the rainforest forced by variations in the hydrological system. Some of these modifications reflect changes in the amount and distribution of rainfall in the tropics during the last 10,000 years, a pattern determined by several causes, not unanimously explained yet. Simultaneity of these forest changes at different localities is far from being established until homogeneity in time resolution of the fossil pollen sequences is reached and until the lower Holocene will be documented at sites other than Barombi Mbo. A strong-amplitude, century-scale arid/humid/arid oscillation in the interval 2.5 to 2 kcal yr BP is only found north of the equator. This change corresponds fairly well to the Iron Age, but its reversal character seems to be reflecting natural climatic change rather than being attributed to human impact. Evidence for disturbed vegetation in Central Gabon during the warm medieval period, when the influence of the Iron Age decreased, is followed by a different forest composition from 600 to 200 cal yr BP when wetter conditions seem to have been a response to the "Little Ice Age". That the tropical world was not a stable environment in the past is now amply demonstrated. Permanent changes in ecological conditions may have triggered speciation leading to high floristic diversity. The great sensitivity of the rainforest to any short-term global climatic changes draws attention to the consequences of future climatic changes induced by the greenhouse effect. The modern composition of the different types of rainforests only dates from a few centuries or 1,000 years at most, at all the investigated sites. This bears some consideration to rainforest conservation and biodiversity issues.

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6

Prehistoric human occupation and impacts on Neotropical forest landscapes during the Late Pleistocene and Early/Middle Holocene

D. R. Piperno

6.1 INTRODUCTION

This chapter presents a review of the evidence for human occupation and modification of the lowland neotropical forest during the pre-Columbian era. It examines some of the most important factors relating to the occupation and use of tropical landscapes by prehistoric human societies and updates the information presented in the 2006 edition of this book. Late Pleistocene through early and Middle Holocene temporal frames (*c.* 16 to 5 kcal yr BP) were covered most extensively in the first edition, as these were the periods during which humans colonized both hemispheres of the Americas and agricultural societies emerged and spread throughout the lowland tropical forest. Prehistoric agricultural practices, which often included types of swidden or slash and burn cultivation, sometimes resulted in profound landscape alteration and forest clearing. This chapter will deal more extensively with certain Later Holocene aspects of prehistoric land usage, including providing some comments on the recently advanced viewpoint that most of the Amazonian landscape was severely impacted by human populations in the thousand or two millennia before European arrival. It is beyond the scope of this chapter to adequately summarize the information relevant to the Old World. Instead the chapter points to some recent work important for understanding early habitation and modification of tropical forest in Africa, southeast Asia, New Guinea, and on the Pleistocene continent of Sahul.

6.2 SOME BRIEF COMMENTS ON THE OLD WORLD

Even given the limited amount of data on the subject, available evidence seems clear in pointing to an occupation of tropical forest by archaic (non-*Homo sapiens*) human

M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

relatives and subsequently by our own species beginning deep in antiquity. When insular southeast Asia was colonized by *Homo erectus* more than 1.2 million years ago, tropical forest was probably widespread (e.g., Semáh *et al.*, 2003). Molecular studies on modern human populations together with fossil skeletal evidence continue to be concordant in indicating the emergence of our own species at a single time in Africa by about 150 kyr ago (Tattersall, 2009). It also appears from genetic evidence obtained from modern African and Eurasian human populations that some Pgymy groups of the African rainforest represent an ancient human lineage (Forster and Matsumura, 2005), implying possible rainforest occupation at or shortly after the dawn of human emergence. Available archeological and associated paleobotanical evidence from Africa robustly indicates a succession of human occupations of species-diverse tropical forest in Equatorial Guinea, Cameroon, and Zaire between about 35 and 19 kyr ago (Mercader *et al.*, 2000; Mercader and Martí, 2003).

The timing, routes, and climatic/ecological circumstances associated with the earliest dissemination of *Homo sapiens* out of Africa, together with patterns of early modern human expansions/migrations within the continent itself, are under active investigation (Cohen *et al.*, 2007; Macaulay *et al.*, 2005; Scholz *et al.*, 2007; Thangaraj *et al.*, 2005). Robust paleoecological evidence from lakes indicates that severe dry periods (more dry than during the Last Glacial Maximum (LGM)) characterized the interval between 135 and 90–75 kyr ago over much of the African tropics (Cohen *et al.*, 2007; Scholz *et al.*, 2007). It is hypothesized that the return to more humid conditions at 90–75 kyr, and with it more productive environments, enabled human population expansion within and out of the tropical zones (Cohen *et al.*, 2007; Scholz *et al.*, 2007). In concert with this view, there is evidence for an initial, rapid settlement of tropical coastal areas of southern and southeast Asia by early modern humans at sometime between 85 kyr and 65 kyr ago. This would also indicate successful adaptations to tropical forest by some of the first human colonizers of Asia (Forster and Matsumura, 2005; Thangaraj *et al.*, 2005).

Recent archeological evidence from Niah Cave, Sarawak, northern Borneo documents a 45-kyr-old human presence with persistent exploitation of diverse plant foods (yams, aroids, and palms plus various other fruit and nut species) in this reconstructed moist tropical forest context (Barton and Paz, 2007). The Sahul—the Pleistocene continent formed by the joining of New Guinea, Australia, and Tasmania during times of low sea level—was colonized 45 kyr ago and well-settled 35 kyr ago (O'Connell and Allen, 2007). Tropical forest grew over significant areas of the Sahul, and archeological evidence indicates people were exploiting it before the LGM (Kershaw *et al.* 2006; O'Connell and Allen, 2007).

Therefore, by about 16 kyr ago, when hunters and gatherers of the New World were first approaching tropical environments in what is now western Mexico, tropical forest on a number of Old World land masses had already been settled by people who possessed the technological mastery to effectively exploit its varied resources. It appears that far from posing an ecological barrier, tropical forest was an important biome supporting human occupation and diffusion from early times. The possibility is real that these ancient forest foragers may have been actively manipulating their resources through practices such as intentionally increasing the distribution of favored plants (*see* Barton and Paz, 2007). Definitive empirical evidence is often difficult to generate on this matter owing to the less intensive nature of pre-agricultural environmental modification, but the resource management capacity of early forest dwellers should not be underestimated.

Despite the fact that the neotropics were colonized far later than the Old World tropics, the transition from hunting and gathering to agriculture occurred around the same time, shortly after the Pleistocene ended, in some regions of both places. For example, at Kuk Swamp, Papua New Guinea, starch grain and phytolith evidence suggests that bananas (*Musa* spp.), probably taro (*Colocasia* spp.), and possibly yams (*Dioscorea*) were taken under cultivation by 10 kcal yr BP (Denham *et al.*, 2003; Fullagar *et al.*, 2006). Associated pollen, phytolith, and charcoal evidence indicates an onset of human modification of the forest around the Swamp at this time, along with alterations of the Swamp terrain itself for plant cultivation in the form of drainage ditches and stake holes for tethering plants (Denham *et al.*, 2003). By about 7 kcal yr BP, human clearance resulted in the dominance of grassland and secondary forest growth. Paleoecological sequences from intermontane valleys across New Guinea testify to a dramatic agricultural impact on forests and their diversity beginning during the early or Middle Holocene, depending on the region (Haberle, 2007). Indications for an ancient and substantial human impact on tropical forest elsewhere in the Old World tropical forest during the Holocene is reviewed by Willis *et al.* (2004).

6.3 HUMAN COLONIZATION OF NEOTROPICAL FORESTS: AN ICE AGE ENTRY

6.3.1 The evidence for early human occupation

As elsewhere, there are formidable holes in the archeological records relating to initial human entrance into the now-humid neotropics, and new evidence tends to accumulate slowly because early human groups were small and often highly mobile, leaving behind few tangible remains. A long and classic debate was recently concluded concerning the initial peopling of the Americas. Tom Dillehay's excavations at the site of Monte Verde, located in a wet temperate forest in southern Chile (Dillehay, 1997), overturned the "Clovis First" paradigm that had previously dominated archeology, most prominently among North American scholars, and held that humans entered North America no earlier than *c.* 1.3 kcal yr BP (Meltzer, 1997). The oldest radiocarbon dates at Monte Verde go back to *c.* 1.5 kcal yr BP. The site is accepted as convincing proof for an early human presence in South America by a strong consensus of archeologists. Therefore, human populations must have first moved through Central America at an earlier time, although no incontrovertible sites dating to before about 1.3 kcal yr BP have been found yet, probably in large part because their settlements are now underneath the Pacific Ocean. Figure 6.1 shows the localities with evidence of human occupation in Central and South America dating to the Late and terminal Pleistocene, between *c.* 15.2 kcal yr BP and 11.8 kcal yr BP.

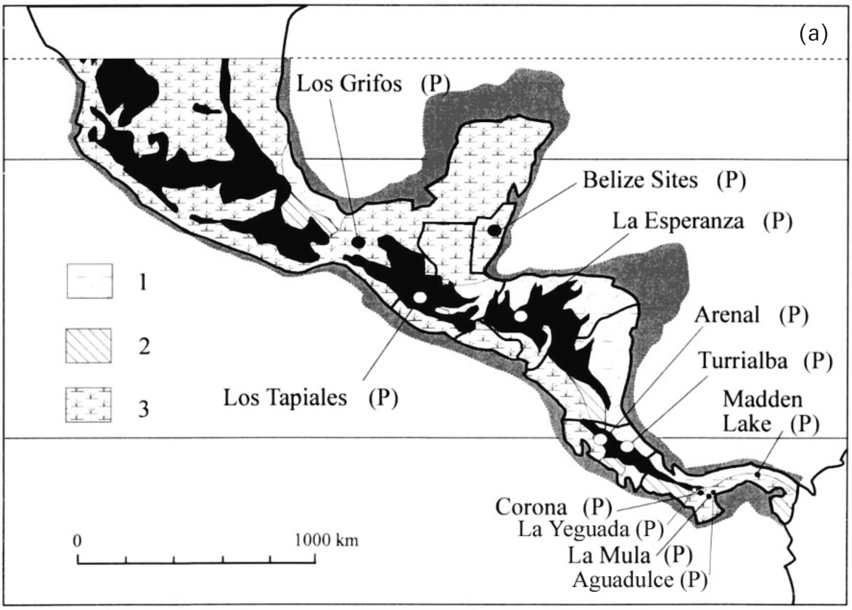
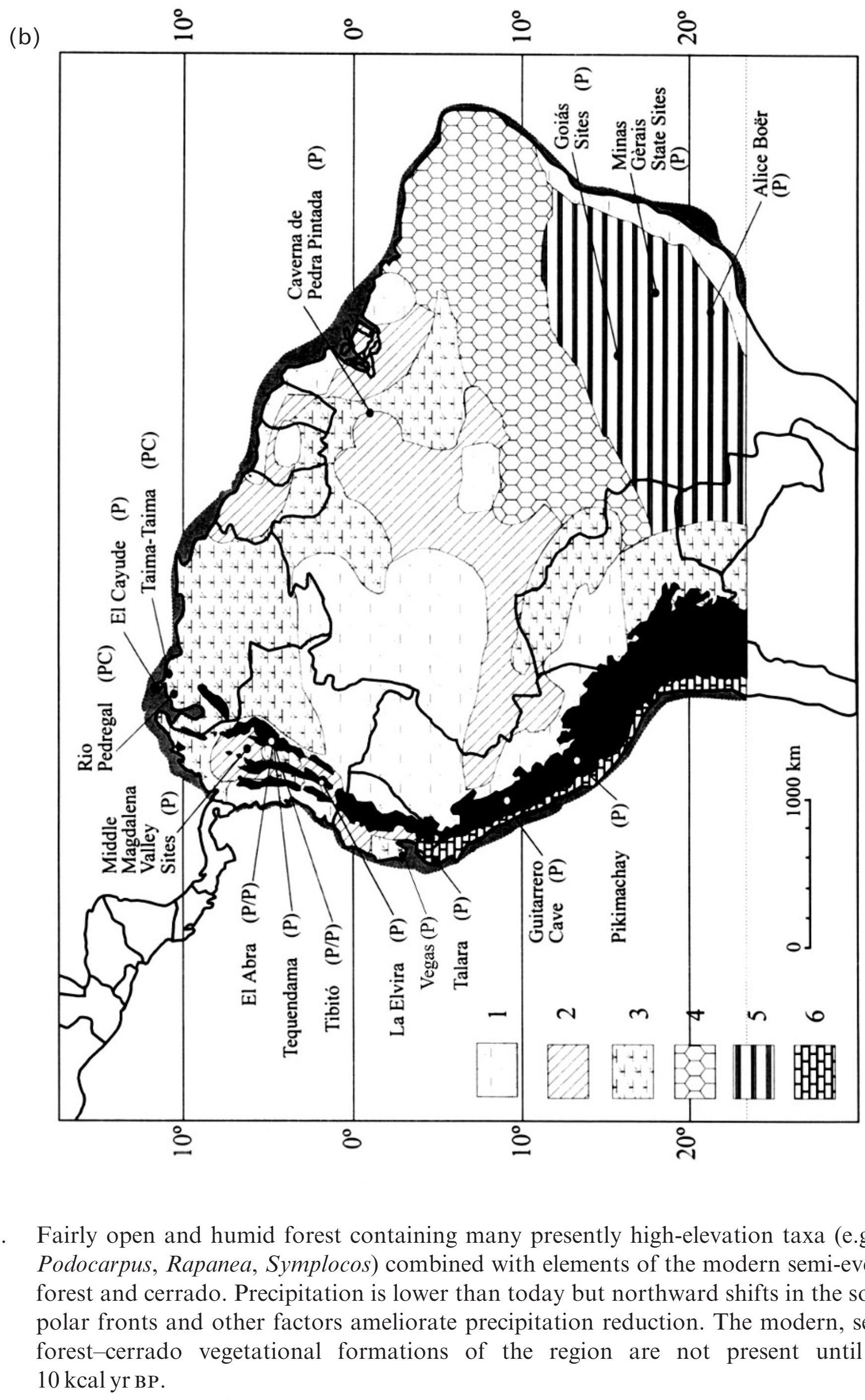


Figure 6.1. Locations of archeological sites in the Neotropics that date to between 13,000 and 10,000 BP placed against a reconstruction of (a) Central and (b) South American Pleistocene vegetation. Reprinted from Piperno and Pearsall (1998). PC = Pre-Clovis site; P/P = Pre-Clovis and Paleoindian site; P = Paleoindian site. More detailed information on the sites can be found in Cooke (1998), Dillehay *et al.* (1992), López Castaño (1995), Piperno and Pearsall (1998), Ranere and Cooke (2003), and Roosevelt *et al.* (1996). Black areas are mountain zones of 1,500 m a.s.l. and greater. Grey area along coastlines is land exposed by sea level drop; in most cases, exposed land probably contains vegetation similar to adjacent terrestrial zones. The vegetation reconstruction is based on available paleoecological sequences and, for regions where such information is not available, reasonable extrapolations of data. The reconstruction is intended to provide broad guides to late-glacial vegetation. For more information on the archaeological sites, see Piperno and Pearsall (1998, pp. 168–175). Explanation for the vegetational reconstruction:

1. Largely unbroken moist forest, often with a mixture of presently high-elevation and lowland forest elements. In some areas, montane forest elements (e.g., *Podocarpus*, *Quercus*, *Alnus*, *Ilex*) are conspicuous. Annual precipitation is lower than today, but sufficient precipitation exists to support a forest.
2. Forest containing drier elements than characteristic today. High-elevation forest elements occur, especially in moister areas of the zone. Areas near the 2,000 mm precipitation isohyet and areas with sandy soils may contain savanna woodland. The vegetation may be patchy.
3. Mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation. Some regions (e.g., Guatemala) have temperate elements (e.g., *Juniperus*). Areas receiving greater than 2,000 mm of rainfall today may still support a drier forest, as in 2. River- and stream-side locations support a forest.
4. Quite possibly, a drier vegetation formation than 5 (below), with fewer trees and more open-land taxa. Paleoecological data are lacking for the zone.



5. Fairly open and humid forest containing many presently high-elevation taxa (e.g., *Ilex*, *Podocarpus*, *Rapanea*, *Symplocos*) combined with elements of the modern semi-evergreen forest and cerrado. Precipitation is lower than today but northward shifts in the southern polar fronts and other factors ameliorate precipitation reduction. The modern, seasonal forest–cerrado vegetational formations of the region are not present until about 10 kcal yr BP.
6. Desert/cactus scrub.

Claims for a pre-15 kyr human presence in South America, including a cave in northern Brazil known as Pedra Furada, are not well supported because artifacts were not recovered from securely dated contexts, or pieces of stone attributed to human manufacture do not display convincing signs that they were altered and used by people (e.g., Meltzer *et al.*, 1994; Piperno and Pearsall, 1998, p. 169). Thus, there is no convincing evidence at the present time that people occupied the neotropics during the LGM or for the *c.* 4 kyr immediately following it.

The best studied lowland regions are often those of seasonally dry areas of southern Central America and northern South America, where focused archeological research has been of longer duration and broader scale (e.g., Cooke, 1998; López Castaño, 1995; Mora and Gnecco, 2003; Ranere and Cooke, 2003; Stothert *et al.*, 2003). A related, significant factor is that forests in many of these areas have unfortunately long been cleared, making it much easier for archeologists to find and excavate ancient human occupations. In Mexico, where native Americans first encountered tropical forest, more research directed toward documenting Late Pleistocene and early Holocene human adaptations has been carried out in the dry and cool highlands than in the warm and humid lowlands. This situation is, however, changing. Recent archeological research revealed evidence for human occupation together with maize and squash agriculture (Section 6.3.3) dating to at least 8.7 kcal yr BP (Piperno *et al.*, 2009; Ranere *et al.*, 2009). In addition, undated stone tools found at another archeological site in the same region appear to be Paleoindian (*c.* 1.3–1.1 kcal yr BP) in age (Ranere *et al.*, 2009). Pollen and phytolith records from nearby lakes make it clear that the ecological context of these activities was a lowland seasonal tropical forest (Piperno *et al.*, 2007).

Early human presence in the Amazon Basin is convincingly dated to 1.3 kcal yr BP at the site of Caverna de Pedra Pintada, located near Santarem just 10 km north of the main Amazon River channel (Roosevelt *et al.*, 1996). Human settlements were present in the wet forests of the western Amazon Basin (middle Caquetá River area of Colombia) before 1.0 kcal yr BP (Cavelier *et al.*, 1995; Mora and Gnecco, 2003). The Amazon Basin is so vast, about the size of the continental U.S.A., and often well-forested that it will be many years before any consensus is reached concerning the timing, passage routes, and possible ecological foci of early human settlement there. These questions are particularly important with regard to the cultural and environmental history of the terra firme forests (those not under the influence of watercourses), which occupy 98% of the land area of Amazonia, and contain some of the poorest soils and lowest concentrations of plant and animal resources found anywhere in the tropics (Piperno and Pearsall, 1998).

There has been a long-term and vocal dichotomy of views over whether terra firme forests were well-occupied and farmed in prehistory, which will only be resolved with much more archeological research (see Neves, 1999 for an excellent review of these and other issues in Amazonian archeology). The most recent iteration of this debate is discussed at more length in Section 6.4. In the seasonal forests of Bolivia and southwestern Brazil, where it appears that famous staple crops such as manioc (*Manihot esculenta* Crantz) (Olsen and Schaal, 1999) were domesticated, archeological research is presently underdeveloped and very little information is available on early human settlement and economic systems.

6.3.2 Pleistocene landscapes and early human modification of them

Of course, showing that people were living at tropical latitudes during the Pleistocene is not the same as proving they were living in tropical forest and surviving off of its resources. In fact, early scholars assumed that the earliest hunters and gatherers of the New World preferentially exploited the numerous, now-extinct large game animals that were available to them. These investigators proposed that because megafauna and other sizeable animals would have been rare in tropical forest, humans migrating from north to south would have largely avoided densely wooded areas, living instead in the more open landscapes they believed characterized the Pacific watershed of Central America, northern South America, and the intermontane valleys of the Andes (e.g., Sauer, 1944; Lothrop, 1961; see Ranere, 1980 for one of the first robust counter arguments based on archeological excavation and analysis). Some scholars writing later would agree with this assessment, going so far as to argue that Holocene hunters and gatherers could not have survived for long in tropical forest without access to a cultivated food supply because wild food resources, especially carbohydrates, were scarce (e.g., Bailey *et al.*, 1989; see Colinvaux and Bush, 1991 and Piperno and Pearsall, 1998 for responses and further discussion).

The large corpus of paleoecological data accumulated during the past 25 years, discussed in detail in other chapters in this book, shows that Late Pleistocene environmental conditions were indeed significantly different from those of the Holocene in ways that could have influenced early human colonization and the specific kinds of habitats that early hunters and gatherers exploited. Reconstructions from lacustrine pollen and phytolith data demonstrate the presence of a variety of vegetation communities ranging from dense, species-diverse forest to open, shrub, low-tree, and grass-dominated formations. There is strong evidence indicating some regions were considerably drier than today during the last stages of the Pleistocene (between *c.* 18 kyr and 12 kyr ago); e.g., the Rio Balsas region of southwestern Mexico; Petén, Guatemala; much of Pacific-side Central America; and parts of northern and southern (e.g., Bolivia) South America. At the present time, these regions receive between 1.2 and 2.6 m of precipitation and their potential vegetation is deciduous or drier forms of semi-evergreen forest. During the Late Pleistocene, their vegetational formations were dominated by thorn scrublands, dry forest/savanna mosaics, and/or grassland (e.g., Burbridge *et al.*, 2004; Bush *et al.*, 2009; Leyden, 1985; Piperno and Pearsall, 1998; Piperno *et al.*, 2007). It was during the first 2,000 years of the Holocene that a diverse tropical forest developed on these landscapes. Recent evidence from the Petén indicates that the LGM in that region was not a dry interval as had been long thought, but rather a cool and relatively moist period when oaks, pines, and other trees were prevalent on the landscape (Bush *et al.*, 2009; Hodell *et al.*, 2008). These new findings do not affect interpretations of human/environmental relationships because human colonization didn't occur until after the LGM, when the climate became very dry. Therefore, when humans first penetrated tropical latitudes, forests did not cover landscapes to the extent they do today. Where, however, annual rainfall is above about 2.6 m today and the actual or potential vegetation is evergreen and semi-evergreen forest, the evidence is strong that Pleistocene landscapes were mostly forested. This is empirically demonstrated in Caribbean-side of Panama at the Gatun Basin (Bartlett and Barghoorn, 1973), and probably was the case throughout most of the Caribbean watershed of Panama, Costa Rica, Nicaragua, and Honduras. It is also demonstrated at Pacific watershed sites in Panama at elevations of between 500 and 700 m a.s.l., such as La Yeguada and El Valle (Bush *et al*., 1992; Bush and Colinvaux 1990), and at various locations in South America (see Colinvaux *et al*., 1996 and Chapter 3 of this book). Therefore, considerable portions of the Pleistocene neotropical landscape were forested.

How can we relate this corpus of data on environmental history to questions concerning early cultural adaptations to tropical latitudes? Arguably, one of the best ways is to correlate reconstructed Pleistocene vegetation with archeological sites of the same age located nearby. If, for example, human settlement before *c*. 11.4 kcal yr ago is largely confined to open areas, the implication would be strong that forests were not persistently lived in and that human populations were surviving for the most part off resources typical of non-wooded environments (e.g., large animal game and plants like cacti and tree legumes found in drier types of vegetation). Another way to assess the issue is to examine actual dietary evidence from archeological sites to directly determine what kinds of resources people were exploiting. There is presently more evidence to consider from the first than from the second option. Fortunately, some of the best documented archeological sites are located near lakes from which detailed paleoenvironmental information has been generated. Furthermore, in the cases where early archeological sites are not in the vicinity of old lakes, major characteristics of the Pleistocene environment can still be reasonably inferred for them by using paleoecological information recovered from zones with a similar modern potential vegetation.

When the relevant data are evaluated, the following patterns emerge (see Piperno and Pearsall, 1998, pp. 169–175, for more details) (Figure 6.1). The few available archeological sites where a pre-Clovis (pre-1.3 kcal yr BP) occupation is indicated are located in deserts/grasslands/open woodlands at low elevations in northern South America (two sites in Venezuela), and open environments (páramo) at two northern Andean locations. No incontrovertible human occupation is located so far in an area reconstructed as having supported tropical forest vegetation. However, the number of sites is still far too few to draw firm conclusions as to whether people of this time period were preferentially selecting one type of habitat and its plant and animal resources over another. Archaeological sites of later, Paleoindian age (1.3–1.1 kcal yr BP) are greater in number and more likely to be representative of habitat choices that people made; these sites were located in a diverse array of environments. (For purposes of simplicity, I call all human occupations dated to between 1.3 and 1.1 kcal yr BP Paleoindian, even though all of them do not contain characteristic Clovis culture types of tools.) They included alpine meadow (in Guatemala), low- and higher-elevation forest (e.g., in Panama, Costa Rica, Colombia, and Brazil), and open, thorny and/or temperate scrub/savanna types of vegetation (e.g., in Mexico, Belize, Panama, Ecuador, and Venezuela) (see Piperno and Pearsall, 1998, pp. 169–175; Cooke, 1998; and Ranere and Cooke, 2003 for further descriptions of these sites).

Out of the 24 Paleoindian localities included in this survey, 10 were located in some kind of tropical forest. Moreover, moving through southern Central America and entering South America without encountering and living in forest some of the time may not have been possible. Data on human dietary patterns recovered from the sites that can buttress arguments of tropical forest occupation and resource exploitation are often scant because people typically did not stay in one spot long enough for a sizeable midden of food and other remains to accumulate. However, the Caverna de Pedra Pintada in Brazil yielded abundant carbonized nut and seed fragments from a variety of trees such as palms and Brazil nuts, as well as faunal remains of large and small mammals that were clearly derived from the forest and were dietary items (Roosevelt *et al.*, 1996). The archeological phytolith and carbonized seed and nut record from central Panama also contains indications that tropical forest plants were being exploited and eaten between 1.3 and 1.1 kcal yr BP (Dickau, 2010; Piperno and Pearsall, 1998).

We should remember that Pleistocene forests were often considerably different in their floristic compositions when compared with forests that grow in the same areas today; few of them appear to have modern analogs. Therefore, we cannot expect to be able to directly compare potential plant and animal resources of modern forests with those that existed during the Late and terminal Pleistocene periods. In many areas, seasonal forest probably expanded at the expense of evergreen formations, and forests in general may well have had more open canopies due to reduced precipitation and lower atmospheric CO_2 concentrations (Cowling, Chapter 13 of this book; Cowling and Sikes, 1999; Sage, 1995). A number of pollen and phytolith studies add empirical weight to these inferences (e.g., Piperno *et al.*, 1992; Mayle, 2004). For example, the Gatun Basin phytolith records, located very near the Madden Lake Paleoindian archeological sites (Figure 6.1), indicate that prior to 11.4 kcal yr BP arboreal associations contained more trees characteristic of modern deciduous forests than today, such as the Chrysobalanaceae (Piperno *et al.*, 1992). The pre-11.4 kcal yr BP phytolith records are, in fact, a very good match with those constructed from directly underneath modern deciduous forest in Guanacaste, Costa Rica. In contrast, plants that are significant components of modern semi-evergreen forests of the area (e.g., the Annonaceae (*Guatteria*), bamboos (*Chusquea*), and palms) do not enter the Gatun Basin record until after 11,000 BP (Piperno *et al.*, 1992).

Therefore, these records appear to reveal a significant change in forest composition over the Pleistocene/Holocene boundary characterized by increases of trees and understorey plants that were likely responding to rising precipitation levels. Many of the Pleistocene forests that humans occupied were likely to have been drier and more open—and possibly contained a higher animal biomass—than those that grow in the same regions today.

We should also remember that some early human populations appear to have been actively modifying on their own the new landscapes they were encountering, largely, it seems, by fire. For example, phytolith and charcoal records from

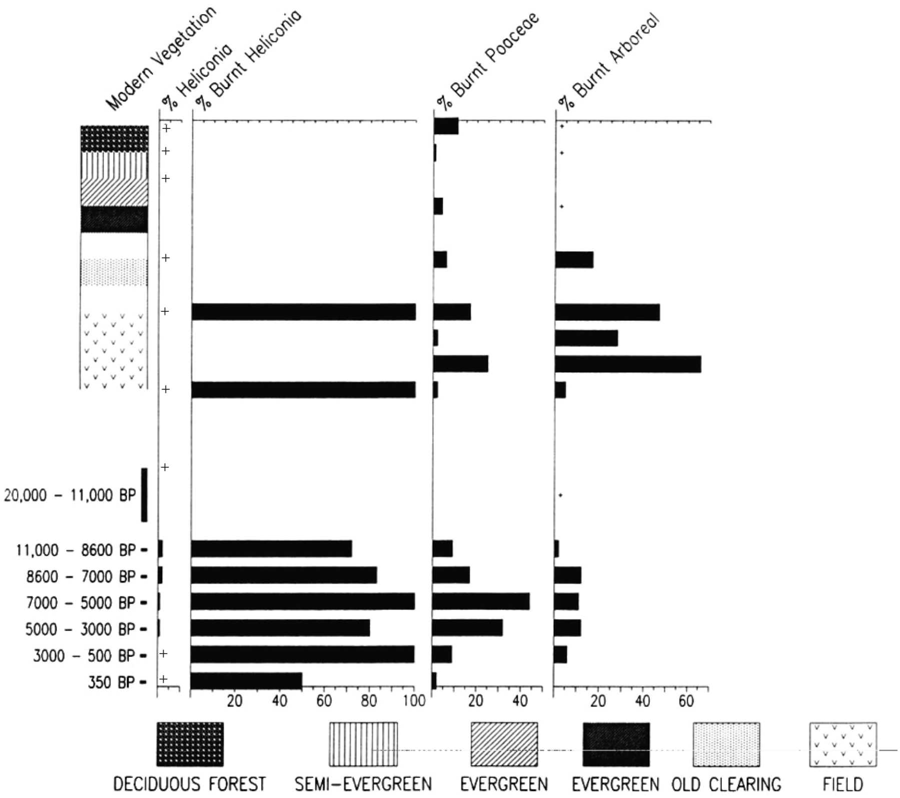


Figure 6.2. The frequencies of early successional phytoliths and burnt successional and arboreal phytoliths in modern tropical forests and through time at Lake La Yeguada. The data profiles from the Late Pleistocene period at El Valle, where human disturbance was not detected, are also displayed for comparison. At *c.* 12.9 kcal yr BP at La Yeguada, charcoal levels also increase by several orders of magnitude, and pollen and phytoliths from grasses and other invasive taxa increase substantially. Reprinted from Piperno and Pearsall (1998, figure 4.4).

Description of modern vegetation in the figure: Evergreen forests are from El Cope, Panama (hatched symbol) and north of Manaus, Brazil (black symbol). Semi-evergreen forest is Barro Colorado, Panama. Deciduous forest is Guanacaste Province, Costa Rica. Old clearing (cleared from forest and planted with banana 50 years ago) is from Guancaste, Costa Rica. Fields are present day slash and burn agricultural plots from Panama planted in manioc and maize. Phytolith frequencies for each modern site are averages from a series of soil transects or "pinch samples" taken from the upper soil surface at the sites (see Piperno, 1988 for details). Circa 23.9–12.9 kcal yr BP records are from El Valle and La Yeguada. Circa 12.9–0.35 kcal yr BP records are from La Yeguada. + = Observed at a frequency of less than 1%.

sedimentary records of lakes located in the central Balsas region of Mexico, indicate vegetational disturbance by humans near the lake shore during the earliest Holocene (Piperno *et al.*, 2007). At Lake La Yeguada, Panama multiproxy data also indicate that human firing of the vegetation around the 16,000 year-old lake began at about 12.9 kcal yr BP and continued without pause through the early and middle Holocene periods (Piperno *et al*., 1990, 1991 a,b; Bush *et al*., 1992) (Figure 6.2). Archeological data directly document initial human colonization of the lake's watershed when the vegetational disturbances are first apparent; a projectile point that dates to sometime in the 12.9 to 11.4 kcal yr BP period was found on the La Yeguada shoreline (Ranere and Cooke, 2003).

In summary, there is a substantial amount of evidence that successful adjustments to tropical forest and their subsistence resources, sometimes enhanced by cultural modification of landscapes through fire and the creation of forest clearings, were made by some of the earliest colonizers of low latitudes in the Americas. Evidence is still too scant to draw conclusions about the range of habitats and resources pre-Clovis populations may have lived in and exploited. However, the location of Monte Verde in a temperate rainforest in southern Chile and the wide range of plant and animal resources that its human occupants used, including wild potatoes (Dillehay, 1997), should give pause to scholars pre-disposed to argue that the ancestors of the Monte Verdeans avoided tropical forest on their way south.

6.3.3 After the Pleistocene: The origins and spread of tropical forest agriculture during the early Holocene

As in several other areas of the world, the lowland neotropical forest witnessed an independent emergence of plant food production and domestication not long after the Pleistocene ended (Piperno and Pearsall, 1998; Piperno, 2006a, in press). Combined information from archeological, molecular, and ecological research tells us that out of the more than 100 species of plants that were taken under cultivation and domesticated by native Americans before Europeans arrived, more than half probably came from the lowland tropical forest (Piperno and Pearsall, 1998; Piperno, in press). Both hemispheres of tropical America were involved. A variety of archeobotanical data from mostly microfossil plant remains (phytoliths, starch, and pollen), which are better preserved than macrofossils in many tropical contexts, and also some macrofossil data, documents the domestication and spread of important native crops like maize (*Zea mays*), manioc (*Manihot esculenta*), at least two species of squash (*Cucurbita moschata* and *C. ecuadorensis*), and possibly *C. argyrosperma*, arrowroot (*Maranta arundinacea*), yams (*Dioscorea trifida*), and leren (*Calathea allouia*) between 10,000 and 5,800 years ago (e.g., Bray, 2000; Dickau *et al*., 2007; Dillehay *et al*., 2007; Mora and Gnecco, 2003; Mora *et al*., 1991; Pearsall *et al*., 2003, 2004; Piperno, 2006a,b, in press; Piperno and Pearsall, 1998; Piperno and Stothert, 2003; Piperno *et al*., 2000 a,b, 2009; Pope *et al*., 2001; Pohl *et al*., 2007; Zarillo *et al*., 2008).

Recent archeological research in the Central Balsas region of Mexico indicates that maize was domesticated by 8.7 kcal yr BP, the earliest date recorded for the crop, and paleoecological studies indicate domestication occurred in an ecological context that was seasonally dry tropical forest (Piperno *et al*., 2007, 2009; Ranere *et al*., 2009). Molecular studies of modern maize and its wild ancestor teosinte predicted that maize, whose wild ancestor is native to that region, was probably domesticated 9,000 years ago (Matsuoka *et al*., 2002). Interestingly, further joining of the evidence from

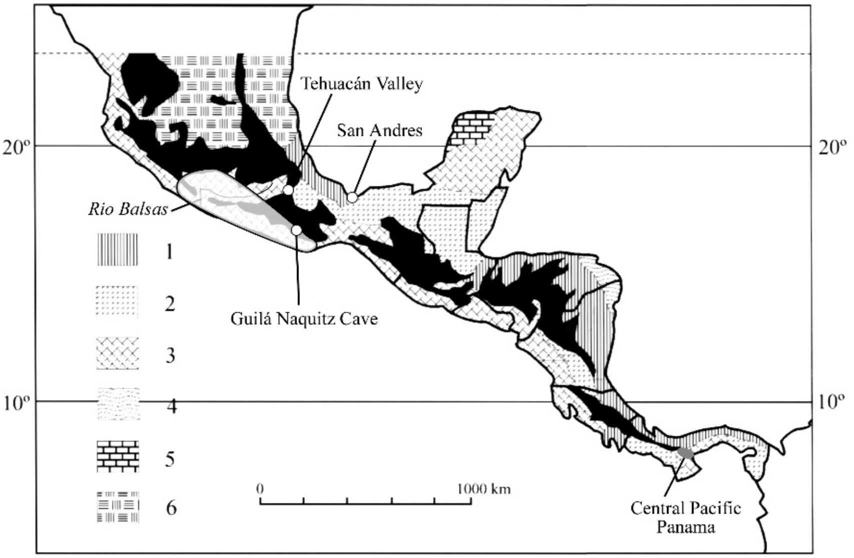


Figure 6.3. Postulated domestication areas for various lowland crop plants as indicated by present molecular, archeological, and ecological evidence. The ovals in the figure opposite labeled D1–D4 designate areas where it appears that more than one or two important crops may have originated. Arrows point to approximate domestication locales. Also shown are the locations of archeological and paleoecological sites in Central America and South America with early (11.4–5.7 kcal yr BP) domesticated seed and root crop remains. Detailed information on the sites can be found in Bush *et al.* (1989), Cavelier *et al.* (1995), Flannery (1986), MacNeish (1967), Monsalve (1985), Mora *et al.* (1991), Pearsall *et al.* 2003, 2004; Piperno and Pearsall (1998); Piperno *et al.* (2000, 2000b, 2007); Piperno and Stothert (2003), Piperno, in press; Pope *et al.* (2001), Pohl *et al.* (2007), Ranere *et al.* (2009), and Smith (1997).

Domestication areas for Mesoamerica: Mexico: maize (*Zea mays*) and squash (*Cucurbita argyrosperma*); sieva beans (*Phaseolus lunatus*) and jícama (*Pachyrhizus* spp).

Domestication areas for South America:

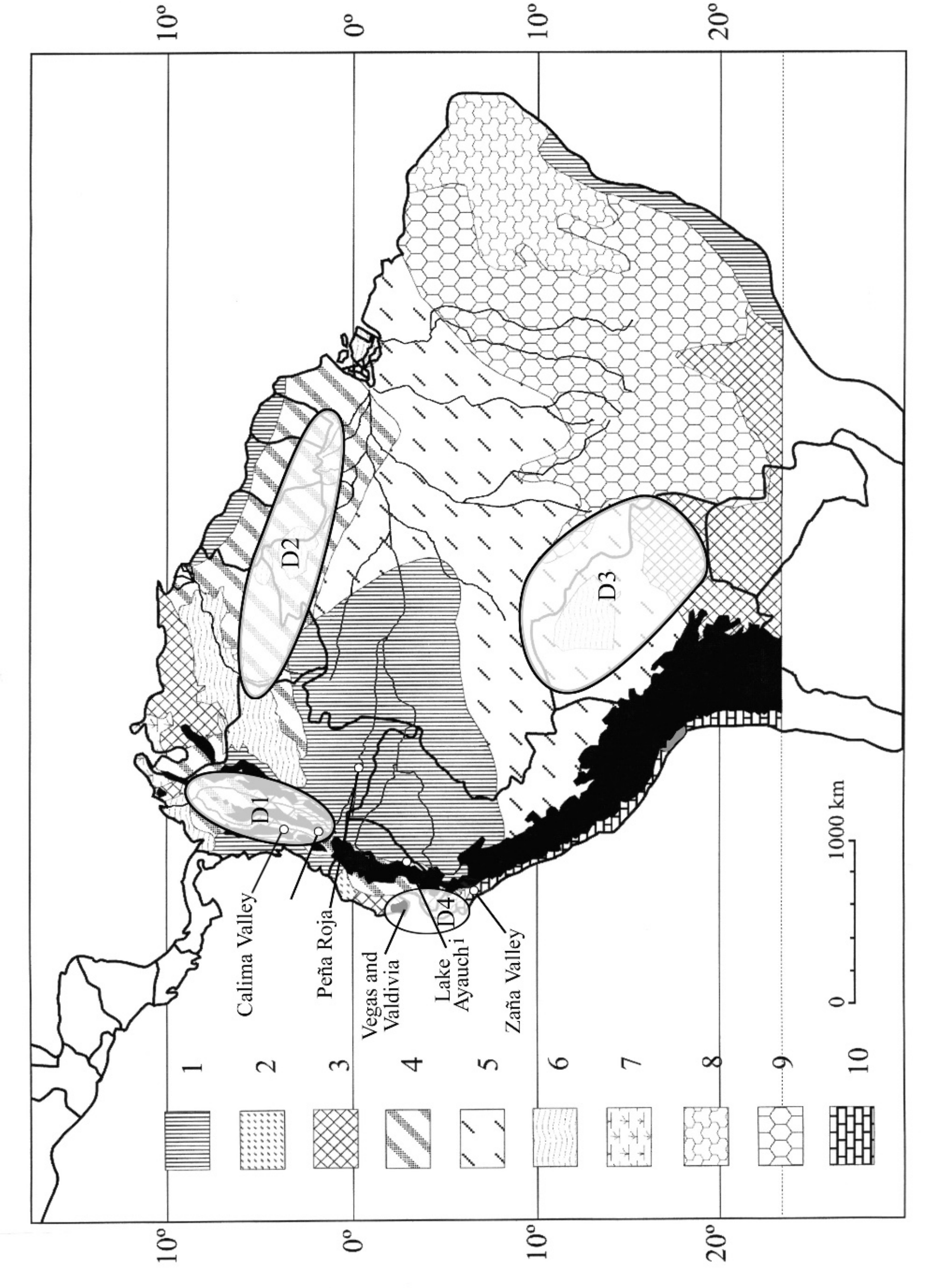
D1. Sweet potato (*Ipomoea batatas*), squash (*Cucurbita moschata*), arrowroot (*Maranta arundinacea*), achira (*Canna edulis*—lower, mid-elevational in origin); also possibly *yautia* or cocoyam (*Xanthosoma saggitifolium*), and leren (*Calathea allouia*).

D2. Yam (*Dioscorea trifida*); also possibly yautia (*Xanthosoma saggitifolium*) and leren (*Calathea allouia*).

D3. Manioc or yuca (*Manihot esculenta*), peanut (*Arachis hypogaea*), chile pepper (*Capsicum baccatum*), and possibly squash (*C. maxima*).

D4. Cotton (*G. barbadense*), *Cucurbita ecuadorensis*, and possibly jack bean (*Canavalia plagiosperma*).

Notes: Probable areas of origin for other lowland, pre-Columbian cultivars include the Yucatan Peninsula (*G. hirsutum*, cotton), wet forests of the western Amazon Basin (*Bactris gasipaes*, the peach palm and *Capsicum chinense*, chili peppers), and the eastern Amazonian slopes (coca, *Erythroxylum* spp.). Explanation of modern vegetation: (a) 1. Tropical evergreen forest (TEF). 2. Tropical semi-evergreen forest (TSEF). 3. Tropical deciduous forest (TDF). 4. Savanna. 5. Low scrub/grass/desert. 6. Mostly cactus scrub and desert. (b) 1. TEF. 2. TSEF. 3. TDF. 4. Mixtures of TEF, TSEF, and TDF (TSEF and TDF grow over substantial areas of the southern parts of the Guianas and south of the Orinoco River). 5. Mainly semi-evergreen forest and drier types of evergreen forest (floristic variability can be high in this zone). 6. Savanna. 7. Thorn scrub. 8. Caatinga. 9. Cerrado. 10. Desert.


10°
0°
10°
20°
D1
D2
D3
D4
Calima Valley
Peña Roja
Vegas and Valdivia
Lake Ayauchi
Zaña Valley
0
1000 km
1
2
3
4
5
6
7
8
9
10

archeology, molecular biology, and botany tells us that many important lowland food crops in Central and South America were originally brought under cultivation and domesticated in the seasonal tropical forest (e.g., Olsen and Schaal, 1999; Piperno and Pearsall, 1998; Piperno, 2006a, in press; Sanjur *et al*., 2002; Westengen *et al*., 2005). Figure 6.3 provides a guide to the geography of origins for various crops and shows the locations of archeological sites with early (11.4–5.7 kcal yr BP) remains of domesticated plants. Particularly important were regions such as the Balsas River Valley, southwestern Mexico (domesticated there were maize, probably the lowland Mesoamerican squash *Cucurbita argyrosperma* (the cushaw and silver-seeded squashes), and possibly the sieva (small-seeded) lima bean); the Cauca and Magdalena Valleys of Colombia and adjacent mid-elevational areas; southwestern Brazil/eastern Bolivia (the probable birth place of manioc and peanuts), and southwestern Ecuador/northwestern Peru (for a species of *Cucurbita*-*C. ecuadorensis*, South American cotton—*Gossypium barbadense*, and the South American jackbean—*Canavalia plagiosperma*).

The Amazon Basin has long been an area of interest for crop plant origins. However, although crops such as manioc and peanuts were domesticated on the periphery of the Basin, few that would become widespread staple foods, with the exception of the peach palm (*Bactris gasipaes*), appear to have been domesticated within its core area (Piperno and Pearsall, 1998). And as Harlan (1971) predicted, there appears to be no single, major center of agricultural origins in South America at all. Even after plants were domesticated and dispersed out of their geographic cradles of origin, peoples in other regions continued to experiment, modify, and significantly change them phenotypically. One prominent example of this is maize. There are hundreds of different varieties adapted to a wide range of ecological conditions. Paleoecological and archeological evidence indicates that the crop was dispersed into, and well-established in, South America by *c*. 6.3 kcal yr BP (e.g., Bush *et al*., 1989; Iriarte *et al*., 2004; Monsalve, 1985; Mora *et al*., 1991; Pearsall *et al*., 2003, 2004; Piperno and Pearsall, 1998; Zarillo *et al*., 2008).

A significant number of investigators interested in the origins of agriculture, including this one, believe that considerations of the dynamic ecological circumstances at the end of the Pleistocene combined with how efficiently (in calories obtained per person per hour) full-time hunters and gatherers could exploit their post-glacial landscapes, can provide cogent explanations for why and when agriculture arose (e.g., Kennett and Winterhalder, 2006; Piperno and Pearsall, 1998; Piperno 2006a, in press). The end-Pleistocene ecological transitions have often been depicted as a kind of environmental amelioration for human populations in the literature on cultural adaptations during this period. In all likelihood, however, subsistence options for low latitude hunters and gatherers, and perhaps those of other areas of the world, became a great deal *poorer* when the Ice Age ended.

For example, during the Pleistocene more than 30 genera of now-extinct, large- and medium-sized grazers and browsers, including horses, mammoths, and giant ground sloths, roamed the tropical landscape, and it is clear that humans routinely hunted some of them (Cooke, 1998; Piperno and Pearsall, 1998; Ranere and Cooke, 2003). The animals were gone by *c*. 11.4 kcal yr BP, at which point hunting and gathering became a far different enterprise. When compared with the Pleistocene fauna, animals that were available to human hunters by 11.4 kcal yr BP occurred at much lower biomass and were typically small-sized. Moreover, because tropical forest was expanding into the considerable areas where tree cover had previously been sparse or more discontinuous, hunters and gatherers had to more routinely exploit forest plants, but would find them to be a generally poor source of calories and widely dispersed in space. The most starch-dense examples (roots, rhizomes, and tubers), often contained high amounts of toxic chemicals and other defenses that made them time-consuming and difficult to convert into food (Piperno and Pearsall, 1998).

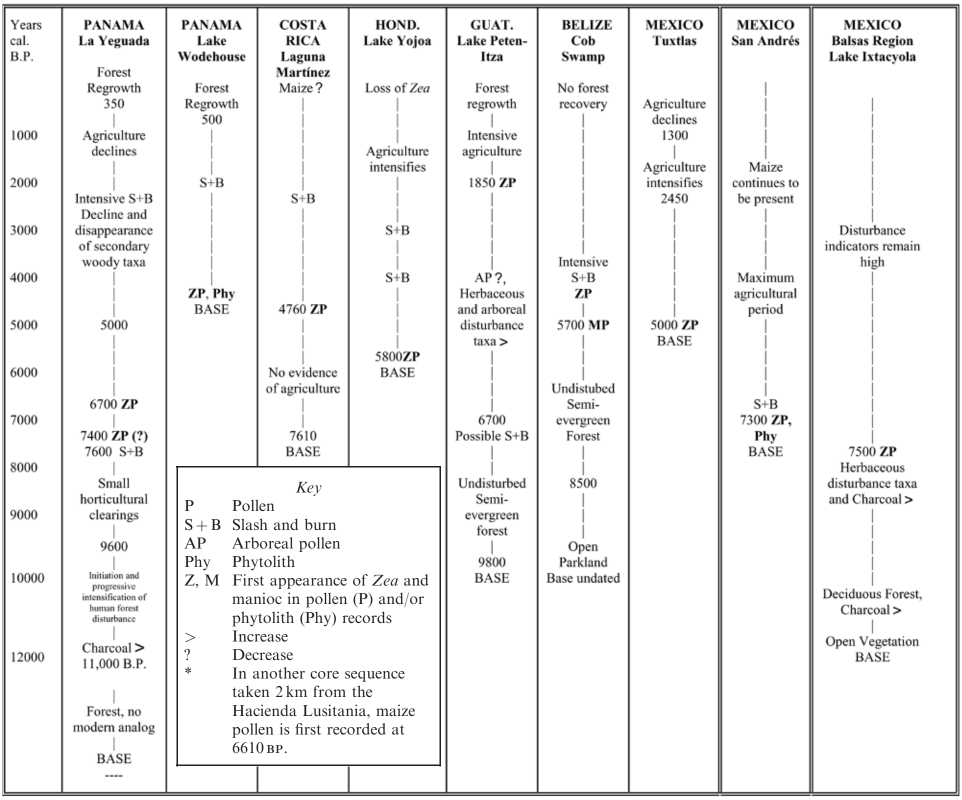
Empirical data generated recently on how modern hunters and gatherers chose their diets from the resources available to them, and on the relative energetic efficiencies of foraging and farming in various modern tropical habitats, have also proved to be significant illuminators of subsistence change at the transition to agriculture (see Kennett and Winterhalder, 2006). These data can be used to predict that in contrast to the situation that existed during the Late Pleistocene, plant cultivation in the early Holocene forest was probably a *less* labor-intensive and *more* energetically efficient strategy than was full-time hunting and gathering (Piperno and Pearsall, 1998; Piperno, 2006a). Thus, nascent farmers were very likely at a competitive advantage over people who were not growing their food, a factor that led to the establishment and rapid spread of agricultural systems (for a complete discussion of these issues and the utility of using evolutionary ecology, especially foraging theory, as an explanatory framework for agricultural origins, see Piperno and Pearsall (1998) and Piperno (2006a)). Explanations such as these for agricultural origins and other major transitions in human lifeways are not environmental determinism, at least not the form of it that a fair number of anthropologists are prone to deriding. They are acknowledgments that ecological factors and evolutionary biology matter deeply in human affairs, and that scientists need not shy away from nomothetic explanations for human behavior if available empirical evidence indicates that such kinds of generalizing explanations are supportable.

6.4 HUMAN MODIFICATION OF FORESTS BY PREHISTORIC FARMERS

6.4.1 Lake records and detecting human disturbance in them

There is now a considerable amount of paleoecological data available on the last 11,400 years of neotropical forest environmental history. The data increasingly go hand-in-hand with the discovery and investigations of nearby archeological sites, which provide direct information about which plants and animals of tropical forest were most frequently exploited and manipulated by people. The research indicates that the development and spread of agriculture in the American tropics exerted profound influences on the structure and composition of the vegetation. Many regions far removed from ancient centers of civilizations experienced systematic interference with, and sometimes removal of, tropical forest thousands of years ago. The records show that fire was an important instrument of vegetational modification for people practicing agriculture in tropical Central and South America. Figures 6.4 and 6.5 contain summaries of this information from a representative sample of the paleoecological sites that have been examined.

Although a fuller spectrum of the available paleobotanical techniques (e.g., pollen, phytoliths, and microscopic charcoal analyses) is being increasingly applied



Years cal. B.P.	**PANAMA La Yeguada**	**PANAMA Lake Wodehouse**	**COSTA RICA Laguna Martínez**	**HOND. Lake Yojoa**	**GUAT. Lake Peten-Itza**	**BELIZE Cob Swamp**	**MEXICO Tuxtlas**	**MEXICO San Andrés**	**MEXICO Balsas Region Lake Ixtacyola**
	Forest Regrowth 350	Forest Regrowth 500	Maize ?	Loss of *Zea*	Forest regrowth	No forest recovery	Agriculture declines 1300		
1000	Agriculture declines			Agriculture intensifies	Intensive agriculture				
2000	Intensive S+B Decline and disappearance of secondary woody taxa	S+B	S+B		1850 **ZP**		Agriculture intensifies 2450	Maize continues to be present	
3000				S+B					Disturbance indicators remain high
4000		**ZP, Phy** BASE	4760 **ZP**	S+B	AP ?, Herbaceous and arboreal disturbance taxa **>**	Intensive S+B **ZP**		Maximum agricultural period	
5000	5000					5700 **MP**	5000 **ZP** BASE		
6000	6700 **ZP**		No evidence of agriculture	5800**ZP** BASE		Undistubed Semi-evergreen Forest			
7000	7400 **ZP (?)** 7600 S+B		7610 BASE		6700 Possible S+B			S+B 7300 **ZP, Phy** BASE	
8000	Small horticultural clearings				Undisturbed Semi-evergreen forest	8500			7500 **ZP** Herbaceous disturbance taxa and Charcoal **>**
9000	9600				9800 BASE	Open Parkland Base undated			
10000	Initiation and progressive intensification of human forest disturbance								Deciduous Forest, Charcoal **>**
12000	Charcoal **>** 11,000 B.P.								Open Vegetation BASE
	Forest, no modern analog BASE ----								

Key

P	Pollen
S + B	Slash and burn
AP	Arboreal pollen
Phy	Phytolith
Z, M	First appearance of *Zea* and manioc in pollen (P) and/or phytolith (Phy) records
>	Increase
?	Decrease
*	In another core sequence taken 2 km from the Hacienda Lusitania, maize pollen is first recorded at 6610 BP.

Figure 6.4. Summary of charcoal, pollen, and phytolith data for vegetational history and human impacts on tropical forests in Central America from various paleoecological sites. *Sources*: Lake Ixtacyola (Piperno *et al.*, 2007); La Yeguada (Bush *et al.*, 1992; Piperno *et al.*, 1991a, b); Monte Oscuro (Piperno and Jones, 2003); Laguna Martínez (Arford and Horn, 2004); Lake Wodehouse (Bush and Colinvaux, 1994; Piperno, 1994); Lake Yojoa (Rue, 1987); Lake Peten-Itza (Islebe *et al.*, 1996); Cob Swamp (Pohl *et al.*, 1996); San Andrés (Pope *et al.*, 2001; Pohl *et al.*, 2007).

in paleoecological studies, the records were not all examined by the same methods. Detailed pollen information is available for all of them but fewer contain phytolith information, meaning that the resolution of the data is not the same for every one. Phytoliths, for example, are sometimes of greater utility than pollen for documenting shifts in taxa of primary and older types of forest, whereas pollen data can usually more accurately document increases and decreases of secondary forest growth. This all has to do with differences in production characteristics and taxonomic specificity (see Piperno, 1993, 2006b). Charcoal data were accumulated for most of the sequences considered here. Charcoal frequencies were not all computed in exactly the same manner, but all provide a direct perspective on fire history.

A commonality of views has emerged among paleoecologists working in the tropical forest about how to interpret charcoal, pollen, phytolith, and other lacustrine data sets, making it possible for trends recognized from sequence to sequence to be meaningfully compared and evaluated. For example, in a long depositional sequence

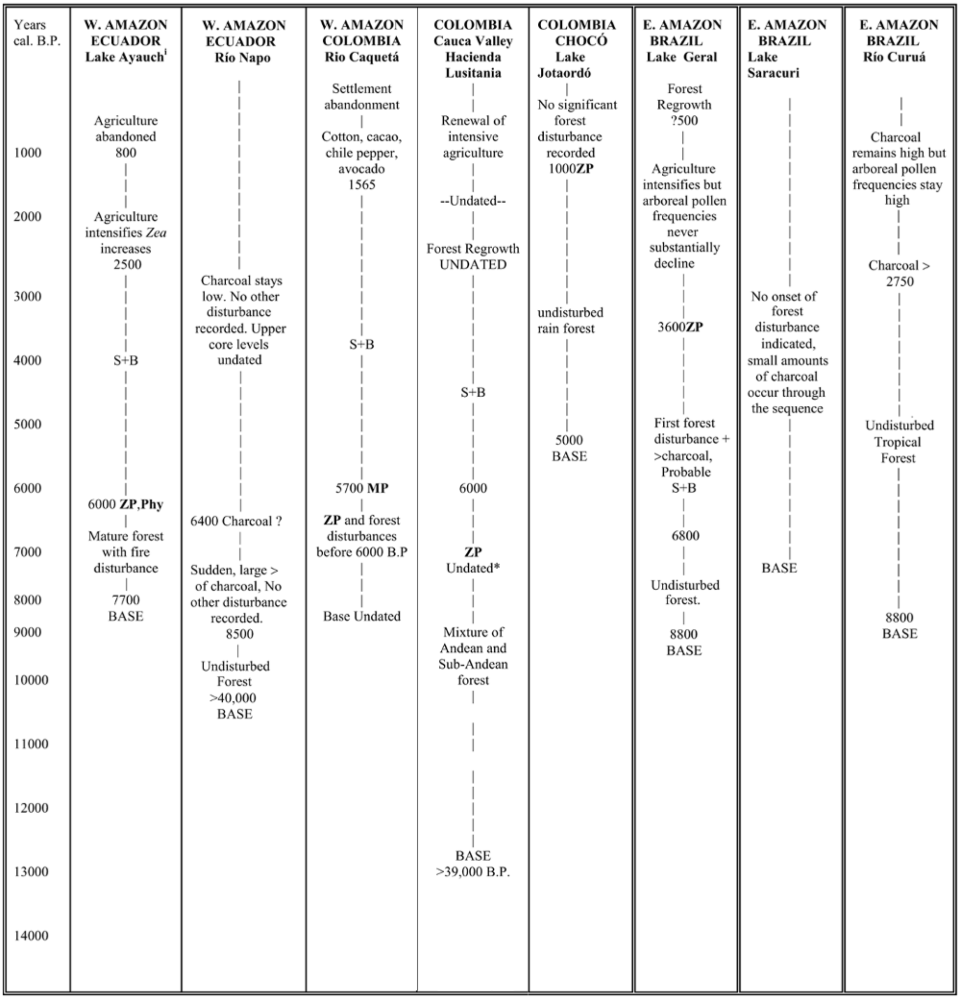


Figure 6.5. Summary of charcoal, pollen, and phytolith data for vegetational history and human impacts on tropical forests in South America from various paleoecological sites. *Sources*: Lake Ayauch^{i} (Bush *et al.*, 1989; Piperno, 1990); Río Napo (Athens and Ward, 1999); Río Caquetá (Mora *et al.*, 1991); Hacienda Lusitania (Monsalve, 1985); Lake Jotaordó (Berrío *et al.*, 2000); Lake Geral (Bush *et al.*, 2000); Lake Saracuri (Bush *et al.*, 2007); Río Curuá (Behling and Lima de Costa, 2000). See Figure 6.4 (opposite) for key.

sampled at an appropriate resolution, most investigators interpret the continual presence of high frequencies of charcoal over thousands of years of a lake's history as being indicative of human-set fires. This is because the high humidity, moisture, and shaded understorey of forests make the likelihood of natural ignitions occurring that frequently nearly impossible (e.g., Hammond and Steege, 1998). Similarly, when large proportions of phytoliths from early successional herbaceous plants such as the Poaceae and *Heliconia* are continually burned over long periods of time, human interference is indicated. It is hard to imagine a natural process that would create and then ignite significant areas of early successional plant growth that often. Burnt phytoliths are easily recognizable because they obtain charred surfaces when exposed to fire while retaining their diagnostic morphological features (see Piperno, 2006b).

Relying on pollen and phytolith profiles constructed from modern, old growth forests where vegetational censuses and other detailed plant inventories are available, as well as vegetation currently experiencing varying types of anthropogenic pressure, investigators have also developed pollen and phytolith population markers of human disturbance and agricultural activity for different types of neotropical forest (e.g., Bush, 1991; Bush and Rivera, 1998; Clement and Horn, 2001; Piperno, 1988, 1993, 1994; Piperno and Jones, 2003; Rodgers and Horn, 1996). These efforts went hand-in-hand with those dedicated to constructing large modern reference collections of neotropical pollen grains and phytoliths (references above; see also Colinvaux *et al.*, 1999). More recent studies continue to improve identifications of different major vegetational associations as well as individual tree and shrub taxa in tropical paleoecological sequences (e.g., Burn and Mayle, 2008; Gosling *et al.*, 2009).

The identification of pollen and phytoliths from cultivars can provide another important source of information for documenting past human influences and agricultural practices. New information has recently come to the fore concerning some aspects of these lines of investigation. For example, it once was thought that maize pollen could be distinguished from that of its wild ancestor, Balsas teosinte (*Zea mays* ssp. *parviglumis*), on the basis of maximum pollen diameter, providing a straightforward way of identifying a major domesticated plant in paleoecological sequences. However, a recent study indicates that pollen from Balsas teosinte and other wild members of the genus *Zea* frequently overlaps in size with maize (Holst *et al.*, 2007). This introduces a complicating factor for the identification of maize in paleoecological records in Mesoamerica, where a number of different wild *Zea* taxa grow naturally.

It is still importantly the case that phytoliths and starch grains can provide a straightforward means of discriminating maize and teosinte (Holst *et al.*, 2007); the latter's utility in lake sediment research has yet to be evaluated but should be studied. *Zea* phytoliths can be expected to routinely occur in lake sediments (e.g., Piperno, 1990, 1994; Piperno *et al.*, 2007). Because maize pollen can be distinguished in both size and morphological attributes from other larger-sized grass pollen, such as from the genus *Tripsacum*, it still can be identified outside of teosinte's natural distribution, meaning Central America south of Nicaragua and all of South America (Holst *et al.*, 2007).

Few other important crop plants can be definitively identified (i.e., separated from wild congenerics) through their pollen grains. The list of crops that can be firmly identified on the basis of size, morphology, or both through their phytoliths is somewhat longer (e.g., squashes (*Cucurbita* spp.), arrowroot (*Maranta arundinacea*), leren (*Calathea allouia*)), but these phytoliths do not appear to routinely occur in lacustrine records. There is a greater chance of finding them if prehistoric fields were located on, or very near the edges of, lakes (e.g., Piperno *et al.*, 2007). Furthermore, maize pollen grains are heavy and most fall to the ground near their plant sources, so that when the pollen is recovered from lake sediments it may also be reflecting local cultivation at distances of no more than 50 to 60 m from the lake edge (Clement and Horn, 2001). Most root crops that were significant components of prehistoric agricultural systems from ancient times in South America produce neither productive pollen nor phytolith records (e.g., sweet potato, yams, achira [*Canna edulis*]).

The end result is that there may be strong indications of forest disturbances and clearing in lake records without evidence of the crops that caused the clearing. Phytolith and starch grain records from archeological sites located in or near lake watersheds may help to fill in these lacunae, as they have already done in areas of Central America and northern South America (e.g., Pearsall *et al*., 2004; Perry, 2002; Piperno and Pearsall, 1998; Piperno *et al*., 2000b; Piperno *et al*., 2009).

6.4.2 Major trends and patterns of prehistoric tropical forest modification

Very significant to moderate human impacts can be identified on the full spectrum of neotropical forest vegetation—evergreen, semi-evergreen, and deciduous formations—from Mexico to the Amazon Basin (Figures 6.4 and 6.5). In some regions, the impacts were intense and a significant number of arboreal taxa were reduced to low levels by agricultural activity. This is especially true in the highly seasonal forests of Central America, but is not the case in other regions, such as the Amazon Basin. This situation is discussed in more detail below. Starting in Mexico, recent evidence from the Central Balsas River region, the presumed cradle of maize domestication, indicates slash and burn cultivation beginning at 7.2 kcal yr BP (Piperno *et al*., 2007). *Zea* pollen present at this time could not be unequivocally identified as maize for reasons discussed above, but both phytolith and starch records from a nearby archeological site indicated maize presence by 8.7 kcal yr BP. Records from the Caribbean coast of Mexico also indicate slash and burn cultivation with maize starting at *c*. 7.3 kcal yr BP (Pope *et al*., 2001; Pohl *et al*., 2007). Both of these Mexican records demonstrated the value of analyzing pollen and phytoliths in tandem, not only for firmly identifying maize but also for achieving greater clarity in the overall vegetational reconstruction.

Moving south, two pollen and charcoal records studied by John Jones from swamps called Kob and Cobweb, located about 55 km apart in northeastern Belize, show an early phase of intensive deforestation resulting from slash and burn agriculture starting at 4.6 kcal yr. BP (Jones, 1994; Pohl *et al*., 1996). At Lake La Yeguada, Panama, the initiation of slash and burn agriculture at 7.6 kcal yr BP resulted in a significant decrease in primary forest trees and increases in early secondary woody growth (Piperno *et al*., 1991b; Bush *et al*., 1992). Agriculture intensified at 4.7 kcal yr BP, as demonstrated by a significant decline of secondary growth woody taxa and associated charcoal. This sequence showed that microscopic charcoal frequencies sometimes are not persistently high under slash and burn agriculture, if there is no longer enough woody growth to sustain high levels. This region of Panama has also seen long-term archeological research and its pre-Columbian cultural records are among the best in the lowland neotropics (e.g., Cooke, 2005; Piperno and Pearsall, 1998). Archaeological foot surveys and excavations document types of settlements—small hamlets or hamlet clusters—during the 7.6 kcal yr BP to *c*. 3.0 kcal yr BP period near La Yeguada that are very similar in size and other aspects to those of modern shifting cultivators.

When the picture moves to South America another aspect of the paleoecological records that draws particular attention is the considerable variability evident in human land use patterns. For example, forest disturbance resulting from human agricultural pressure starts in the eastern and western Amazon Basin (Geral and Lake Ayauch^{i}, respectively) during the seventh to sixth millennium BP, and intensifies during the next few millennia (Bush *et al.*, 1989, 2000; Piperno, 1990; Piperno and Pearsall, 1998, pp. 280–281). However, during the periods of maximal agricultural intensification recorded in the Amazonian pollen and phytolith records, which occurred between *c.* 3.6 kcal yr BP and the Conquest period, arboreal pollen and phytolith frequencies never decline and frequencies of pollen from grasses and other weedy herbs never increase to the point indicating a large-scale destruction of the forest (compare Figures 6.4 and 6.5).

Bush *et al.* (2007) recently examined two more lakes in eastern Amazonia located near Geral and three in the western Amazon region, again finding an uneven picture from site to site regarding indications of fire and human disturbance. Once again, there were no signs of wholesale forest clearance in any site. In a long sequence from the Río Napo region of the Ecuadorian Amazon, charcoal is common during certain periods, but neither maize nor signs of forest clearing are recorded at all (Athens and Ward, 1999). There are a number of lake and other paleoecological sequences (e.g., Piperno and Becker, 1996) in which a definitive human modification of the regional forest through burning, cultivar presence, or tree felling cannot be detected at all using any of the available markers developed for this purpose.

The available Central American sequences contain evidence for significant to severe forest clearing more often than do existing Amazonian and other South American records. These differences may relate to the following factors; presence of smaller populations of shifting cultivators, smaller scale agricultural systems with longer fallow periods, and a greater importance of root crops such as manioc and sweet potato than of soil-demanding crops such as maize in Amazonian and other South American lake regions. One or all of these could have resulted in less expansive and destructive agriculture. It may also be significant that many Central American lakes are in areas whose real or potential vegetation is deciduous or otherwise highly seasonal tropical forest. The seasonal tropical forest offers less heavily leached and more highly fertile soils for agriculture, and the vegetation can be effectively cleared and prepared for planting using simple, slash and burn techniques that do not require the use of stone axes.

Denevan (e.g., Denevan, 2006) believes that typical forms of slash and burn cultivation practiced today in the tropics, whereby fields are planted and used for a few years and then abandoned to fallow for dozens of years, were little-used during the prehistoric era in Amazonian terra firme forests, primarily because making and maintaining the stone axes that he considers essential to this type of farming was too labor intensive to be worthwhile. As noted above, where and when fires could be easily set and maintained, slash and burn cultivation would have been far easier. Furthermore, long fallow types of slash and burn cultivation seem to be particularly suited to the poor soils of Amazonia. The confluence of high amounts of charcoal and pollen/phytolith signals for disruption of mature forest that are evident in some of the Amazonian lake records appears to strongly indicate that some type of long-fallow slash and burn system was being practiced. However one views these issues, it is no accident that population densities today in the lowland tropics are higher and agriculture is more developed and sustained in areas of former drier forest, and that far less of these forests remain than of semi-evergreen and evergreen formations. Although they do not carry the distinction enjoyed by their rainforest relatives, highly seasonal forests likely have been of greater use to humans for a longer period of time.

6.4.3 The Amazon as a human-built landscape?

The accumulated information on prehistoric agriculture and associated land usage summarized above also adds to an emerging debate about the past and future of the Amazon, which contains the largest contiguous area of remaining tropical forest in the New World. The older idea that prehistoric Amazonia supported only small and highly mobile human populations who exerted little impact on their environments has been largely abandoned by scholars, as data increasingly indicate that people in some areas extensively managed and/or farmed landscapes over millennia (e.g., Bush *et al.*, 1989; Neves, 1999; Erickson, 2000; Heckenberger, *et al.*, 2003; Lehman, *et al.*, 2003). And there is no doubt now that during the final 2 kcal yr BP to 3 kcal yr BP of the prehistoric era, numerous, densely populated villages—some of them parts of urban centers—were present along the main Amazon River channel and other major water courses and tributaries, and that advanced societies in these and other regions brilliantly utilized the productive capacity of their landscapes in various, sometimes unique, ways—extensively modifying them (Neves, 1999; Erickson, 2000; Heckenberger, *et al.*, 2003; Lehman, *et al.*, 2003).

However, as first discussed by Bush and Silman (2007), these data should not be extrapolated to Amazonia at large to argue that lowland forests throughout the Basin were densely inhabited and significantly altered by pre-Columbian cultures. It appears that a few prominent archeologists and anthropologists may be pointing their arguments exactly in that direction, referring to Amazonia as a "cultural parkland", "human created", or "built landscape" (e.g., Heckenberger *et al.*, 2003; Erickson, 2000; Mann, 2005). One leading popular science writer, Charles Mann, is already sympathetic to that view, injecting it into the public discourse (Mann, 2005) when no broad scholarly consensus one way or another is close to being reached. As reviewed above, existing paleoecological data indicate considerable variation in human occupation and land usage in the Amazon, and the clearing of terra firme forest at an intensity and scale leading to very low visibility of trees in pollen and phytolith spectra is not seen anywhere to this point.

These arguments, of course, have implications far beyond archeology and anthropology. Ecologists would like to know if past vegetation and fire are affecting the current state of the vegetation and carbon balances in the forests they study. Furthermore, conservation biologists and planners will need to rely on realistic, preferably empirically based, projections of past human land usage and forest resiliency after major disturbances in their efforts to promote sustainable development, or the consequences could be serious for future Amazonian biodiversity (Bush and Silman, 2007). Clearly, much more research is needed on the prehistoric human occupation of Amazonia. Suggestions or inferences that dense pre-historic human populations and associated landscape alterations may have existed on a basin-wide scale seem far from persuasive at this time.

6.5 SUMMARY

Neotropical forests were first settled during the final phases of the last ice age by hunters and gatherers who in short order began to modify some of them, especially with fire. Not long after the Pleistocene ended, humans created systems of plant cultivation that, during the following 5 kyr, would result in the widespread development of slash and burn agriculture. The changes wrought to the lowland forests by early neotropical farmers and other landscape managers were often more severe and of more widespread extent than had been inflicted by the extreme physical elements of the late-glacial period, when intense drying, cooling, and lower levels of atmospheric CO_2 impacted the vegetation forcefully in some regions by reducing forest cover. In other areas, late-glacial conditions had not caused forests to retract, just to change their floristic compositions. Humans then burned, cut, and eventually in some regions removed large tracts of these wooded landscapes not long after they settled them. Beliefs that pre-Columbian human populations frequently exploited tropical landscapes in ways that fostered conserving or protecting most of the natural flora (see Piperno, 2006c for a discussion of this issue) must be considered against the evidence presented here.

On the other hand, although prehistoric human impacts on the tropical forest can be identified in many regions of Central and South America, the geography, chronology, and trajectory of these impacts appear to have varied considerably. The spatial extent of significant human settlement and modification of the neotropical forest before Europeans arrived is a largely answerable, empirical question on which information will be steadily accumulated through continuing archeological and paleoecological explorations.

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7

The past, present, and future importance of fire in tropical rainforests

M. A. Cochrane

7.1 INTRODUCTION

The tropics bring to mind picturesque beaches and idyllic visions of seemingly endless tropical rainforests. Often overlooked, however, is that the tropics are also comprised of vast areas of savanna, montane grasslands, dry deciduous and dry thorn forests, as well as mangroves, deserts, wetlands, and a multitude of other ecosystems; many of these ecosystems burn frequently. The tropics cover one-third (33.7%) of the planet's land surface. They contain over 40% of the world's forests, the vast majority of all species, and are home to over 35% of the human population (Cochrane, 2009a). Satellite detections of thermal anomalies also show that the tropics experience more fires per year than anywhere else on Earth (Figure 7.1). In this region, where fire dominates many landcover types, sit the world's richest storehouse of biodiversity within what appear to be nearly fire-immune tropical rainforests.

The tropics experience the most intense solar radiation on the planet. This leads to substantial heating of the land surface, evaporation of moisture, cloud formation, and heavy rainfall. Plentiful moisture and sunlight have allowed the resultant rainforests that cover large portions of the region to grow lush foliage that almost completely obscures the forest floor from direct sunlight. Sunlight intensity beneath these canopies can be reduced to only 2% or so of that above the canopy. Competition for light forces adaptations that have led these forests to develop closed canopies with multiple layers of leaves. Each square meter of surface can have more than six square meters of foliage. As a result, the subcanopy environment is much cooler and moister than non-forest land cover types. Botanists, biologists, and ecologists have studied many aspects of tropical rainforests from drip tips on leaves that are specially adapted for shedding rainfall to models attempting to explain the riotous abundance of rainforest species that are packed into each hectare of forest, but little thought has gone into the adaptations of rainforests to fire.

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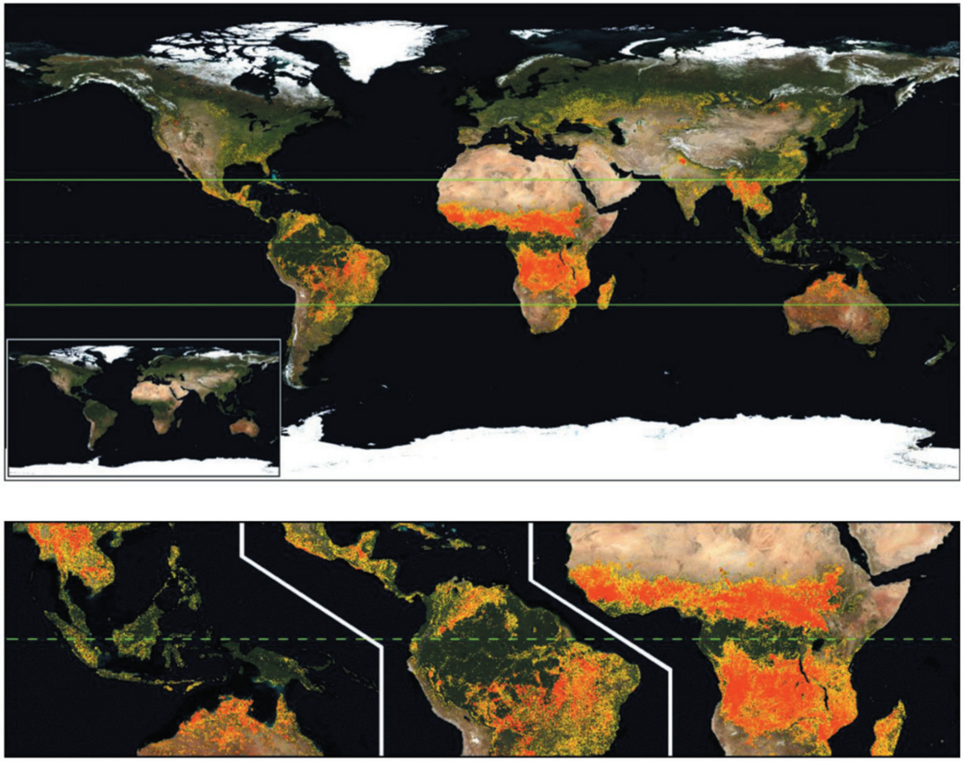

Figure 7.1. World fire in 2007. (a) Image illustrates the global distribution and density of fires in 5 × 5 km squares for the entirety of 2007. The background landcover image is the Blue Marble from NASA's Earth Observatory while the fire data are from FIRMS (Fire Information for Resource Management System, University of Maryland, *http://maps.geog.umd.edu/firms/*). Color provides the density range of between 1 (yellow) and 12 (red) fire events on each grid square. (b) Detailed panels illustrating fire distribution in specific regions of the tropics. Left panel shows the Australian and Southeast Asian tropics; center panel illustrates the Central and South American tropics; right panel shows the African tropics (Figure created by C. P. Barber).

7.2 RAINFOREST FIRE IN THE PAST

Rainforest adaptations to fire? Scientists, including myself, have pointed out that the trees of these forests are poorly, if at all, adapted to surviving fire (Uhl and Kauffman, 1990; Pinard and Huffman, 1997; Cochrane *et al.*, 1999; Cochrane, 2003). The bark thickness of most species is insufficient to protect the underlying cambium from lethal heating by all but the most transient of flames, post-fire seed mortality is extremely high (Van Nieuwstadt *et al.*, 2001) and no serotiny is observed. Although many species can resprout after fire (Kauffman, 1991), this is likely an adaptation to wind or treefall—induced breakage and not specifically fire. In short, these forests seem bereft of what have been called fire-life histories (e.g., scheduling reproduction and mortality around fire occurrence) (Bond and van Wilgren, 1996). How then are these forests adapted to fire?

Simply put, while the individual tree species are not adapted to fire, the ecosystem as a whole maintains conditions that are inimical to propagating flames. The canopy of an intact closed forest shades the forest floor and keeps air temperatures 10°C cooler during the day than that experienced in nearby fields or selectively logged forests with fractured canopies (Uhl and Kauffman, 1990). More importantly, the thick layers of foliage evapotranspire water and trap this moisture under the canopy. This moisture pump results in the subcanopy environment maintaining forest fuels too moist to burn during all but the most extreme droughts (Messina and Cochrane, 2007; Cochrane, 2009b). For this reason, even though the tropics experience more potential fire ignitions from lightning strikes than any other region (Stott, 2000), evidence of fire in these ecosystems prior to the arrival of *Homo sapiens* seems to have been very rare and restricted to times of extreme drought (Bush *et al.*, 2008; Sanford *et al.*, 1985).

Although tropical rainforests are often lumped together as a single forest type, they actually span a range from true rainforests that experience high precipitation levels during all months of the year to those, such as tropical moist forests that experience greater degrees of seasonality. In the parlance of tropical seasonality, seasons are either wet or dry depending on whether rainfall exceeds or falls below 100 mm per month—this is the amount necessary to balance expected evapotranspiration. Practically speaking, what this means is that the rooting depth needed to maintain evergreen foliage throughout the year increases with increasing dry season length. Areas experiencing dry seasons of 1–2 months, 3–4 months, and 5–6 months only supported evergreen forest if they had soil depths of 1–3, 3–5, and 5–10 m respectively (Ichii *et al.*, 2007). Many tropical tree species of everwet forests are renowned for having shallow root systems, but these are adaptations to recovering rapidly cycled nutrients (Jordan, 1982). Where moisture is regularly or periodically limiting to growth, roots have been found to exceed 10 m in depth within the Amazon (Nepstad *et al.*, 1994) and have been shown to grow deeper as water levels fall (Jipp *et al.*, 1998).

Fire in tropical rainforests can largely be divided into two periods; pre-human and post-human presence. For the three main tropical forest formations this translates into differing timelines, corresponding to human migration patterns, as fire has become more than an anomalous occurrence. In the wetter forests of the Neotropics (Central and South America), fire has only become a significant presence within the last 8,000–15,000 years (Bush *et al.*, 2007) and became more widespread in the last 1,000–2,000 years (Bush *et al.*, 2008). The Indo–Malaysian forests (west coast of India, Assam, southeast Asia, New Guinea, and Queensland, Australia) may have been subjected to anthropogenic fire for tens of thousands of years, with charcoal evidence from 37,000–52,000 years postulated as being from human impacts (Kershaw *et al.*, 2007). Conversely, African tropical forests (Congo/Zaire River Basin, West Africa) may have been experiencing humanoid-derived fires for hundreds of thousands of years. While there is no evidence for intentional landscape application of fires back that far, fire has been part of the human legacy since before we became a species, with inferred dependence upon fire use extending as much as 1.8 million years into our past (Wrangham, 2009). Interestingly, in simulations of tree cover without the presence of global fires, African rainforest areas would be expected to expand greatly, with Southeast Asian and Neotropical forests increasing to lesser degrees (Bond *et al.*, 2005). Similarly, Bowman (2000) finds that recurrent fires are the primary explanatory factor for the archipelago-like distribution of rainforests in Australia. Whether anthropogenic or not, fire appears to greatly limit the expanse of global rainforest into more seasonally dry regions, however, there is little evidence that fire is frequent within those rainforests that currently exist.

7.2.1 The rise of anthropogenic fire

Slash and burn agriculture has been practiced for thousands of years in the tropics (Pyne, 1997). It is still the most effective way to convert forests to agricultural lands. It is nearly impossible to burn a standing forest due to the ever present moisture so, within a desired plot, most or all of the trees are felled and then left to dry for several weeks or months. Seasons are variable across Earth's tropical rainforests, but in most regions one or more dry seasons determine when the practice of slash and burn can take place. The dry season is also the fire season. Once the slashed materials are judged to be sufficiently dry for burning, the farmer will light the felled vegetation in the late morning or early afternoon. The objective for the farmer is to reduce the pile of debris as much as possible, while simultaneously releasing the contained nutrients. Crops are planted soon after the fire to take advantage of the newly available nutrients. On the nutrient-poor oxisols and entisols, typical of Africa and Amazonia, crop yields of nitrogen-hungry crops (e.g., maize or cotton) can only be sustained for a few years. Consequently, the slash and burn agriculturalist is forced to continually open up new patches of forest for agriculture.

Human land use has increasingly changed the nature of fire in tropical rainforests. Land cover is changing rapidly, albeit for different land uses around the planet (Achard *et al.*, 2002; Hansen *et al.*, 2010). In recent decades, new road construction has allowed millions of people to settle previously remote and inaccessible forests (Laurance *et al.*, 2001). Deforestation has necessarily followed. Forest clearance has fragmented the remaining forests. Resultant forest edges are buffeted by winds and desiccating sunlight. These edge effects lead to structural changes including increased mortality of trees, decreased living biomass (Laurance *et al.*, 1997), and increased fuel loads (woody debris) (Nascimento and Laurance, 2002). In Southeast Asia, tropical peatlands (Page *et al.*, 2009) and other wetlands (Chokkalingam *et al.*, 2009), have been logged and drained to establish agricultural lands; drying immense amounts of organic soils. These changes predispose tropical forests to fire (Cochrane, 2001a; Page *et al.*, 2002; Cochrane and Laurance, 2002).

Within many remaining tropical forests, selective logging acts as another major landscape modifier. Logging in tropical forests is often selective in that only a few valuable trees are extracted, leaving most of the forest in place. Millions of hectares of tropical forests have already been logged and millions more are being logged each year (Siegert *et al.*, 2001; Nepstad *et al.*, 1999; Matricardi, 2007; Asner, 2005). Impacts of selective logging vary with extraction intensity and management practices (Uhl *et al.*, 1997; Jackson *et al.*, 2002; Sist and Nguyen-Thé, 2002), but can be substantial. Selectively logged forests can recover to pre-harvest levels of biomass if left undisturbed for 30–70 years (Barreto *et al.*, 1998; Cochrane and Schulze, 1999), but if these forests burn, recovery times are projected to be at least 100–150 years (Cochrane and Schulze, 1999). However, many forests are revisited several times when loggers return to harvest additional tree species as regional timber markets develop. The combination of human access provided by logging roads (Veríssimo *et al.*, 1995) and the forest damage caused by logging activities (Kauffman and Uhl, 1990) make logged forests extremely vulnerable to fire (Holdsworth and Uhl, 1997) and deforestation (Figure 7.2). This vulnerability may last for decades after the logging activities have ceased (Siegert *et al.*, 2001).

7.3 RAINFOREST FIRE IN THE PRESENT DAY

Currently, fire is an integral part of most agricultural practices in the tropics. Given the juxtaposition of damaged fire-prone forests and fire-dependent agricultural lands, forest fires are almost inevitable. In new frontier areas, with relatively low quantities of cleared land, extensive undamaged forests make large forest fires nearly impossible. However, as fire-prone agricultural land development continues, the forest becomes increasingly fragmented and the whole landscape becomes conducive to fire propagation (UNEP, 2002). The forest fires that do occur are often edge-related, moving into forests from deforested lands (Cochrane, 2001a; Bucini and Lambin, 2002). These fires can significantly alter fire regimes kilometers from forest edges (Cochrane, 2003). Fire frequency becomes a function of distance from deforested forest edges (Cochrane, 2001a; Cochrane, 2001b) and fire severity increases with frequency (Cochrane *et al.*, 1999). In the absence of other modifying disturbances, these forests will continue to erode, with isolated fragments collapsing, unless future fires can be prevented (Gascon *et al.*, 2000). This is a long-standing process in the African tropics (Aubréville, 1947).

7.3.1 Fire within tropical rainforests

Fire susceptibility in tropical forests occurs largely because of moisture stress, during periods of extensive drought, when normally moist fuels dry and become potentially

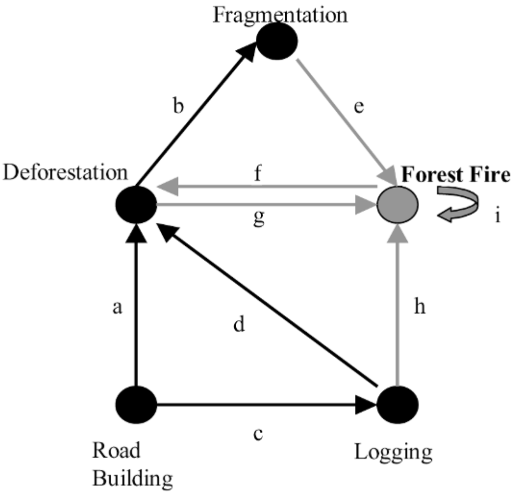

Figure 7.2. System linkages. Conceptual model of land cover change in the Amazon (adapted from Cochrane (2003)). Fire related processes (e–i) are shown in gray. Linkages such as road building or logging and fragmentation are considered to be linked only through the deforestation that they cause.

(a) Road building results in forest access which is strongly associated with deforestation (Laurance *et al.*, 2001). Subsequent deforestation is most strongly associated with previous deforestation (Alves *et al.*, 1999).
(b) Deforestation fragments the remaining forests creating increasing amounts of edge (Achard *et al.*, 2002; Laurance *et al.*, 1997).
(c) Road building and paving provide forest access to loggers, reduce transportation costs, and increase economic accessibility (Verı́ssimo *et al.*, 2002).
(d) Logging results in deforestation for roads and log landings (Souza and Barreto, 2000). Post logging colonization frequently leads to settlement and deforestation (Verı́ssimo *et al.*, 1995).
(e) Forest edges are subject to biomass collapse and microclimate changes (Laurance *et al.*, 1997) making them susceptible to frequent anthropogenic fires (Nepstad *et al.*, 1999). Greater than 90% of all forest fire occurrences have been explained by their distance from edges where spatial analyses have been conducted (Cochrane, 2001a).
(f) Repeated forest fires, especially in previously logged forests, can lead to unintentional deforestation by fire. Accidental deforestation can be responsible for half of the total deforestation in some regions during some years (Cochrane *et al.*, 1999).
(g) Deforestation fires and pasture/land maintenance fires result in many accidental forest fires that predominate along forest edges (Cochrane, 2001a).
(h) Logging degrades forests and can increase susceptibility to fire (Uhl and Buschbacher, 1985; Holdsworth and Uhl, 1997). This can lead to extensive fires even several years after the logging operations (Siegert *et al.*, 2001). In the Amazon, logged forests burn 1.5 to 2 times more frequently than unlogged forests. Fires in logged forests spread faster, allowing them to penetrate much more deeply into the forest than the slower moving fires in intact forests (Cochrane *et al.*, 2004).
(i) Forest fires create a positive feedback cycle where recurrent fires become more likely and severe with each occurrence (Cochrane *et al.*, 1999). Canopy degradation allows the forest to dry more quickly and post-fire tree mortality increases fuel loads making subsequent fires more severe for several cycles until deforestation occurs.

flammable. However, closed-canopy rainforests are remarkably resistant to drought. Even after months without rain, these forests can maintain an evergreen canopy and high sub-canopy humidity levels, making sustained combustion impossible (Uhl *et al.*, 1988; Kauffman and Uhl, 1990). This apparent fire immunity results from the effective trapping of transpired moisture such that most of the ambient forest humidity is derived from the trees themselves (Moreira *et al.*, 1997). Resilience to climatic stress through moisture recycling (Aubréville, 1947; Salati and Vose, 1984; Eltahir and Bras, 1996), enhanced by the deep-rooting capacity of many forests (Nepstad *et al.*, 1994), allowed many tropical forests to persist through severe droughts of previous glacial periods (Kleidon and Lorenz, 2001). Despite adaptations to drought conditions, rainforests can and do burn. Both natural and anthropogenic disturbances to forest canopies decrease the ability of forests to maintain moisture, making them more vulnerable to fire. In anthropogenic landscapes, fire is a continual presence making it only a matter of time until a sufficiently intense drought opens up the forest to fire (UNEP, 2002).

Fire occurrence in tropical forests is largely associated with forest edges (Uhl and Buschbacher, 1985; Cochrane, 2001; Cochrane and Laurance, 2002; Bucini and Lambin, 2002) and not randomly located throughout. Although tropical regions have the highest density of lightning strikes (Stott, 2000) and some associated tree mortality, these events are usually associated with heavy rainfall and rarely lead to forest fires (Tutin *et al.*, 1996). Other natural causes of fire such as volcanic eruptions and burning coal seams (Goldammer and Seibert, 1989) may be regionally important but, as in most locations throughout the world, fire in the tropics is primarily associated with human activity (Goldammer and Seibert, 1990; Vayda, 1999) and influence on land cover (Cochrane, 2003).

Although they are deadly to much of the forest, the initial fires in relatively intact rainforests do not appear severe. Known as "surface fires", they generally progress slowly in creeping ribbons of flame, 10 cm or so in height (Figure 7.3). The fires burn little besides fallen leaf litter, however, these fires are still capable of killing 23–44% of trees > 10 cm diameter at breast height (DBH) and are even more deadly to saplings (Cochrane and Shulze, 1999; Gerwing, 2002; Van Nieuwstadt *et al.*, 2001; Woods, 1989; Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997). Fire propagation in tropical forests is largely controlled by variations in ambient relative humidity (Cochrane *et al.*, 1999; Siegert and Ruecker, 2000; Kauffman and Uhl, 1990). Although fire intensity is very low (4–55 $\mathrm{kW\,m^{-1}}$), slow spread rates result in considerable contact time with spreading flames, heating tree-bark surfaces of contacted trees (Cochrane *et al.*, 1999). Most species in closed canopy evergreen forests have thin bark that poorly insulates against rising temperatures, so fires effectively girdle and kill them. Larger, thicker-barked trees and others without vulnerable cambium layers (e.g., palms) may survive (Woods, 1989; Kauffman and Uhl, 1990; Cochrane *et al.*, 1999). Fires such as these kill ~40% of all trees (> 10 cm diameter) but this corresponds to only 10% of the standing biomass because mortality is primarily among trees < 30 cm DBH (Cochrane and Schulze, 1999). Delayed mortality due to fire damage and falling trees may persist for at least the following 2–3 years (Cochrane *et al.*, 1999; Barlow *et al.*, 2003). After the initial fire, canopy cover is

Figure 7.3. Photo by the author of an initial fire in an unburned closed canopy forest. Forest fuels are very moist and the fires spread slowly and with low variability in fire behavior. Little or no wind reaches beneath the forest canopy. Fires continue to spread until temperatures drop, relative humidity rises, and the leaf litter becomes too moist to burn. Fires can smolder over night or through moist periods for several weeks until fire spread is again possible. Fires can spread like this for weeks or months during periods of extensive drought.

reduced below 65% and fuel loads rapidly increase as the dying vegetation rains to the ground.

Subsequent fires are far more severe if they occur before forest recovery. In recurring fires, flame lengths, flame depths, rates of spread, residence times, and fire-line intensities are all far greater than in initial burns (Cochrane *et al.*, 1999). Secondary fires can kill another 40% of the remaining stems, corresponding, this time, to 40% of the live biomass, because large trees have no survival advantage over smaller trees during these more intense fires. Canopy cover is reduced sharply to

$<35\%$ and the forest dries even more quickly. Weedy vines and grasses, some of which are quite flammable even when green, quickly colonize twice-burned forests (Cochrane and Schulze, 1999). In some forest types with root mats or deep organic layers, ground fires can accompany surface fires and persist long after. While surface fires consume the fallen litter, ground fires may consume everything down to the mineral soil, which in many forests includes much of the root mass, and cause near complete mortality (Woods, 1989; Uhl *et al.*, 1988; Page *et al.*, 2002; Page *et al.*, 2009).

Burning greatly alters forest composition and structure (Barlow and Peres, 2008). Common tree species suffer the greatest mortality but rare species are most likely to be locally extirpated (Cochrane and Schulze, 1999). Prospects for species recovery are diminished because surface fires sharply reduce seed availability in the litter and upper soil layers (Van Nieuwstadt *et al.*, 2001), while flowering and fruiting of trees in and near burned forests decreases (Kinnaird and O'Brien, 1998; Barlow and Peres, 2006). Such conditions strongly favor windborne, light-demanding pioneer species. Within burned forests, unburned patches and gallery forests are key seed sources for post-fire recovery, but recurring fires quickly reduce the size and number of unburned areas (Cochrane and Schulze, 1999) and kill regenerating vegetation. Taking all these factors together, fire produces a synergy of effects that diminishes prospects for recovery of mature-forest plant and animal species while encouraging invasion by exotic species (Barlow and Peres, 2004; Chokkalingam *et al.*, 2009; Barlow *et al.*, 2009).

Surface fires can create a dangerous positive feedback whereby each successive fire becomes more likely (Cochrane and Schulze, 1999) and severe because of higher fuel loads and fire intensities (Cochrane *et al.*, 1999). Fire severity in selectively logged forests are also high (Siegert *et al.*, 2001; UNEP, 2002; Gerwing, 2002) due to the large amount of available fuel in the form of slash piles and collateral damage caused by the logging operations (Kauffman and Uhl, 1990; Uhl *et al.*, 1997). Logged or burned forests near forest edges may not be more likely to burn than unlogged edge-forests, but burn severity and fire spread rates can be higher, leading to deeper penetration and increased damage by fire (Cochrane *et al.*, 2004).

The crux of the fire problem in tropical rainforests is not so much the introduction of fire into these ecosystems but the frequency with which they are being burned. Historical records (Tate, 1932; Barber and Schweithelm, 2000; Goldammer and Seibert, 1990) and charcoal in soil profiles (Bush *et al.*, 2007; Bush *et al.*, 2008; Uhl *et al.*, 1988; Sanford *et al.*, 1985; Goldammer and Seibert, 1989; Hammond and ter Steege, 1998) show that tropical forest fires, even in the wetter forests, are not unprecedented. Fire can be considered endemic but rare in tropical rainforests (Swaine, 1992) with return intervals of hundreds if not thousands of years (Kauffman and Uhl, 1990). Wetter forests burn less frequently but are more vulnerable to fire than dryer forests because they have thinner protective layers of bark (Uhl and Kauffman, 1990) and suffer much higher mortality rates from fires. Infrequent fire disturbance has left tropical rainforests evolutionarily ill-adapted to current patterns of burning (Mueller-Dombois, 1981; Uhl and Kauffman, 1990). In landscapes heavily impacted by logging and fire, the relationship between fire frequency and distance from deforested edges can decrease or disappear completely since the entire forest will have similar fire-return-intervals, often less than 10 years (Cochrane, 2001a). Such destabilizing dynamics are common in fragmented landscapes where frequent burning in nearby pastures and farms is a source of recurring ignition. Under such circumstances, the margins collapse in response to a withering recurrence of surface fires (Gascon *et al.*, 2000; Cochrane and Laurance, 2002). Neither deforestation, fire use, nor selective logging alone, is likely to create severe fire problems in tropical landscapes but the synergy and interaction between these land uses when present together can promulgate fire throughout the landscape and rapidly degrade forests (Cochrane, 2003).

7.3.2 Regional conditions of rainforest fires

At present, fire has differing levels of impact across the world's tropical rainforests, closely mirroring the amount of development pressure and intensity of commercial exploitation in each region.

7.3.2.1 Neotropics

In terms of area of tropical rainforest being burned, both intentionally for deforestation and accidentally through wildfires, the Amazon, and in particular Brazil, leads the way with an estimated loss of 164,000 km^2 of forest cover between 2000 and 2005 (Hansen *et al.*, 2010). Fires are intentionally set for deforestation purposes as well as maintenance of existing cleared lands. Several million hectares of land are intentionally burned in the Amazon each year, with an increasing number of fires escaping into the surrounding forests (Cochrane, 2003). There are no official statistics for wildfire occurrence but extremely large fires have been recorded throughout the region with up to 90% of burning occurring in El Niño years (Cochrane *et al.*, 1999; Alencar, 2006). However, large fires are actually the accumulated burning of potentially hundreds of locally set fires that have escaped their intended purposes. Such fires are dependent on intense and long-duration droughts which may or may not be associated with El Niño. In 2005, southwestern Amazonia experienced an intense drought that resulted in rivers and lakes nearly running dry during a non El Niño year, apparently due to climate teleconnections with warming sea surface temperatures in the tropical North Atlantic Ocean (Marengo *et al.*, 2008a, b). During this drought, massive wildfires impacted vast areas of Acre state in the Brazilian Amazon. Other large forest fires have occurred throughout the Neotropics. For example, in 1998, huge tracts of standing tropical forests in Central and South America were burned, including Roraima, Brazil ($>$5,000,000 ha), Bolivia (3,000,000 ha), Nicaragua (900,000 ha), Guatemala (650,000 ha), Honduras (575,000 ha), and Mexico (850,000 ha) among others (UNEP, 2002).

7.3.2.2 Southeast Asia

Within Southeast Asia, Indonesia has had the greatest amount of forest cover loss in recent years—35,000 km^2 (2000–2005; Hansen *et al.*, 2010). This region suffers intense droughts during El Niño events and as human settlement has spread in recent decades, so has the incidence of fire during these times. Particularly hard hit are the peat swamp forests of southern Sumatra and Kalimantan (Page *et al.*, 2002; Chokkalingam *et al.*, 1999; Page *et al.*, 1999). In these regions, the combinations of logging, settlement, and drainage of large peatland areas have led to immense and intensely smoky fires that have burned across millions of hectares of forested land (Tacconi, 2003) and deep into the organic soils. These fires annually create a haze that impacts travel and economies across much of Southeast Asia (Cochrane, 2003) but also leads to the death of thousands from respiratory and cardiovascular difficulties among other illnesses (Kunii, 1999). In the last decade, total carbon emissions from peatland fires have conservatively been estimated at 2–3 GT (Page *et al.*, 2009). In contrast, tropical evergreen forests of insular Southeast Asia and South Asia experience greater seasonality and have had a longer standing presence of fire-wielding humans. Many of the remaining evergreen forests are intermixed with deciduous and thorn forests as well as grasslands. These evergreen forests experience a relatively high frequency of fire incursions (Johnson and Dearden, 2009; Kodandapani *et al.*, 2009). Although tree species in the evergreen forests are sensitive to fire damage, they seem to have much lower levels of mortality than aseasonal forests of insular Southeast Asia (Baker and Bunyavejchewin, 2009).

7.3.2.3 Africa

Within the African tropics, between 2000 and 2005, the Democratic Republic of Congo experienced the greatest loss of forest cover, with a reduction of 10,000 km^2 (Hansen *et al.*, 2010). Every year, the African continent has more fires and area burned than anywhere else on the planet. It has been postulated that the remaining tropical rainforests in Africa may be remnants of more extensive forests eroded by human activity (Aubréville, 1947). In fact, climate conditions alone would allow rainforests to greatly expand in the absence of fire (Bond *et al.*, 2005). Whether due to human land use or natural ignitions, fire appears to have a role in constraining current rainforest extents. Humans have been clearing and burning forests in the region for thousands of years with much more extensive burning occurring during drier climate conditions (Brcnic *et al.*, 2009). Both natural (Tutin *et al.*, 1996) fires ignited by lightning and anthropogenic fires (Brncic *et al.*, 2007) have been reported from the region but individual fires do not appear to have been extensive. There are no recent reports of large wildfires penetrating into standing Central or West African tropical rainforests, however, the expansion of industrial logging operations, with more than 600,000 km^2 under concession in Central Africa alone, could be increasing fire risk over large regions (Laporte *et al.*, 2007).

7.4 RAINFOREST FIRE AND FUTURE CLIMATE CHANGE

7.4.1 Local and regional-scale phenomena

Major changes in land cover could have important effects on local and regional climates, which in turn may increase the likelihood of forest fires (Cochrane and

Laurance, 2008). The basic physics are the same in all tropical forests around the world, but the great majority of research of these phenomena has been conducted in the Neotropics. The loss and fragmentation of forest cover can alter local and regional climates in several ways.

First, habitat fragmentation can promote forest desiccation via a phenomenon known as the vegetation breeze. This occurs because fragmentation leads to the juxtaposition of cleared and forested lands, which differ greatly in their physical characteristics. Air above forests tends to be cooled by evaporative cooling (from evapotranspiration of water vapor), whereas such cooling is much reduced above clearings (this increases the Bowen Ratio, which is the ratio of sensible to latent heat). As a result, the air over clearings heats up and rises, reducing local air pressure and drawing moist air from surrounding forests into the clearing. As the rising air cools, the moisture it carries condenses into convective clouds that may produce rainfall over the clearing. The air is then recycled—as cool, dry air—back over the forest (Silva Dias and Regnier, 1996; Baidya Roy and Avissar, 2000).

The net effect of the vegetation breeze is that forest clearings promote local atmospheric circulations that may increase rainfall but, paradoxically, draw moist air away from nearby rainforest. In regions with prevailing winds, some rain generated by the vegetation breeze may fall on downwind forests, not just in clearings, with desiccation being most severe in upwind forests. In the Amazon, vegetation breeze effects have been observed in clearings as small as a few hundred hectares, but appear to peak when clearings are roughly 100–150 km in diameter (Avissar and Liu, 1996). The vegetation breeze is essentially a large-scale edge effect; satellite observations in Rondnia, Brazil suggest that the desiccating effects of major clearings can extend up to 20 km into adjoining forests.

Second, the conversion of forests to pasture or savanna reduces the rate of evapotranspiration because grass and shrubs have far less leaf surface-area than forests (Jipp *et al.*, 1998). Declining evapotranspiration could potentially decrease rainfall and cloud cover and increase albedo and surface temperatures. Moisture recycling via evapotranspiration is probably especially important in the hydrological regime of the Amazon, and potentially the Congo Basin, because they are both vast and relatively far from the ocean. Forests of Southeast Asia, Central America, and West Africa are within a few hundred kilometers of the sea and may suffer less desiccation due to deforestation-caused reductions in evapotranspiration. However, the regional effects of large-scale deforestation are far from fully understood. For example, several simplistic modeling studies, assuming complete Amazonian deforestation, predict basin-wide precipitation reductions of roughly 20–30% (Nobre *et al.*, 1991; Dickinson and Kennedy, 1992; Lean and Rowntree, 1993). Model results based on actual (*c.* 1988) deforestation patterns in Brazilian Amazonia have been less dramatic, with deforested regions predicted to experience modest (6–8%) declines in rainfall, moderate (18–33%) reductions in evapotranspiration, higher surface temperatures, and greater windspeeds (from reduced surface drag) that could affect moisture convergence and circulation (Walker *et al.*, 1995; Sud *et al.*, 1996). It is even possible that moderate forest loss and fragmentation could *increase* net regional precipitation, as a result of the vegetation breeze, although the main effect

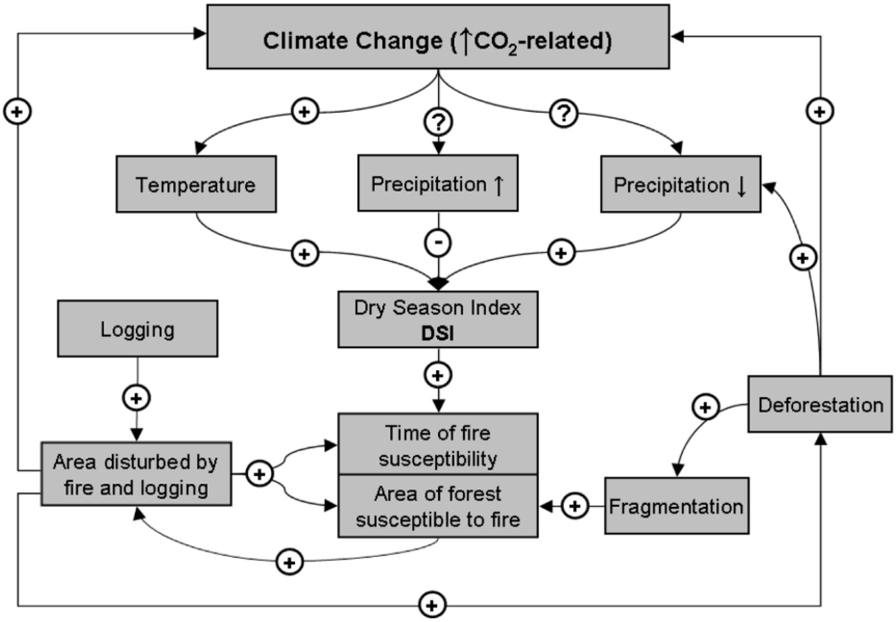

Figure 7.4. Schematic relationships between climate, land use, and fire.

would be to remove moisture from forests and redistribute it over adjoining clearings. The greatest concern is that if deforestation reaches some critical but unknown threshold, Amazonian rainfall could decline abruptly as the regional hydrological system collapses (Avissar *et al.*, 2002; Baida Roy and Avissar, 2002).

Two further effects of forest loss are caused by the massive smoke plumes (Figure 7.4) produced by forest and pasture fires. Smoke hypersaturates the atmosphere with cloud condensation nuclei (microscopic particles in aerosol form) that bind with airborne water molecules and thereby inhibit the formation of raindrops (Rosenfeld, 1999). In addition, by absorbing solar radiation, smoke plumes warm the atmosphere, inhibiting cloud formation. As a result of these two phenomena, large fires can create rain shadows that extend hundreds of kilometers downwind (Freitas *et al.*, 2000). Moreover, because tropical fires are lit during the dry season, both phenomena reduce rainfall during the critical dry season months, when plants are already moisture stressed and most vulnerable to fire.

7.4.2 Global-scale phenomena

Although much remains uncertain, all tropical rainforest regions are expected to experience altered climates, with substantial warming, due to ongoing and forecast atmospheric changes. By 2100, regional mean temperatures are projected to rise by between 1.5–5.1°C across the tropically forested regions (A1B scenario, Table 7.1). Median increases in temperature vary by region, with Southeast Asia (SEA) expected

Table 7.1. Tropical regional averages of temperature and precipitation projection from 21 global climate models for the A1B emissions scenario (derived from Table 11.1; IPCC 2007). Values represent differences between the 1980-1999 and 2080-2099 time periods for the 20th Century Climate in Coupled Models (20C3M) simulations. The table provides the minimum, maximum, median (50%) and 25% and 75% quartile values among the 21 models, for temperature (°C) and precipitation (%) change. Seasons correspond to four three month periods, December, January, February (DJF), March, April, May (MAM), June, July, August (JJA), and September, October, November (SON).

		Temperature response (°C)					*Precipitation response (%)*				
Region	*Season*	*Min*	*25*	*50*	*75*	*Max*	*Min*	*25*	*50*	*75*	*Max*
West African Tropics											
WAF	DJF	2.3	2.7	3.0	3.5	4.6	*−16*	*−2*	*6*	*13*	*23*
12S, 20W	MAM	1.7	2.8	3.5	3.6	4.8	*−11*	*−7*	*−3*	*5*	*11*
To	JJA	1.5	2.7	3.2	3.7	4.7	*−18*	*−2*	*2*	*7*	*16*
22N, 18E	SON	1.9	2.5	3.3	3.7	4.7	*−12*	*0*	*1*	*10*	*15*
	Annual	*1.8*	*2.7*	*3.3*	*3.6*	*4.7*	*−9*	*−2*	*2*	*7*	*13*
East African Tropics											
EAF	DJF	2.0	2.6	3.1	3.4	4.2	*−3*	*6*	*13*	*16*	*33*
12S, 22E	MAM	1.7	2.7	3.2	3.5	4.5	*−9*	*2*	*6*	*9*	*20*
To	JJA	1.6	2.7	3.4	3.6	4.7	*−18*	*−2*	*4*	*7*	*16*
18N, 52E	SON	1.9	2.6	3.1	3.6	4.3	*−10*	*3*	*7*	*13*	*38*
	Annual	*1.8*	*2.5*	*3.2*	*3.4*	*4.3*	*−3*	*2*	*7*	*11*	*25*
Southeast Asian Tropics											
SEA	DJF	1.6	2.1	2.5	2.9	3.6	*−4*	*3*	*6*	*10*	*12*
11S, 95E	MAM	1.5	2.2	2.7	3.1	3.9	*−4*	*2*	*7*	*9*	*17*
To	JJA	1.5	2.2	2.4	2.9	3.8	*−3*	*3*	*7*	*9*	*17*
20N, 155E	SON	1.6	2.2	2.4	2.9	3.6	*−2*	*2*	*6*	*10*	*21*
	Annual	*1.5*	*2.2*	*2.5*	*3.0*	*3.7*	*−2*	*3*	*7*	*8*	*15*
Central American Tropics											
CAM	DJF	1.4	2.2	2.6	3.5	4.6	−57	−18	−14	−9	0
10N, 116W	MAM	1.9	2.7	3.6	3.8	5.2	−46	−25	−16	−10	15
To	JJA	1.8	2.7	3.4	3.6	5.5	−44	−25	−9	−4	12
30N, 83W	SON	2.0	2.7	3.2	3.7	4.6	−45	−10	−4	7	24
	Annual	*1.8*	*2.6*	*3.2*	*3.6*	*5.0*	*−48*	*−16*	*−9*	*−5*	*9*
South American Tropics (Amazon)											
AMZ	DJF	1.7	2.4	3.0	3.7	4.6	−13	0	4	11	17
20S, 82W	MAM	1.7	2.5	3.0	3.7	4.6	−13	−1	1	4	14
To	JJA	2.0	2.7	3.5	3.9	5.6	−38	−10	−3	2	13
12N, 34W	SON	1.8	2.8	3.5	4.1	5.4	−35	−12	−2	8	21
	Annual	*1.8*	*2.6*	*3.3*	*3.7*	*5.1*	*−21*	*−3*	*0*	*6*	*14*
North Australian Tropics											
NAU	DJF	2.2	2.6	3.1	3.7	4.6	−20	−8	1	8	27
30S, 110E	MAM	2.1	2.7	3.1	3.3	4.3	−24	−12	1	15	40
To	JJA	2.0	2.7	3.0	3.3	4.3	−54	−20	−14	3	26
11S, 155E	SON	2.5	3.0	3.2	3.8	5.0	−58	−32	−12	2	20
	Annual	*2.2*	*2.8*	*3.0*	*3.5*	*4.5*	*−25*	*−8*	*−4*	*8*	*23*

to increase the least (2.5°C) and West Africa (WAF) and the Amazon (AMZ) the most (3.3°C). Expected changes in precipitation vary substantially by region, season, and whichever coupled global climate model is used. Median values of annual precipitation change indicate that the Central American tropics (CAM) are the most likely to become substantially drier (−9%) while East Africa (EAF) and SEA may become even wetter (+7%) over the next 100 years. The impacts of changing precipitation patterns on rainforests will depend strongly on seasonality and year-to-year variance. Within the 20th Century Climate in Coupled Models (20C3M) simulations, extreme changes in precipitation are defined as being the top or bottom 5% of precipitation amounts throughout the 100 years simulated by 21 different coupled global climate models. West Africa, East Africa, and Southeast Asia are all expected to have substantial increases in the likelihood of extremely wet years, roughly 4-, 6-, and 8-fold increases, respectively. The Amazon is expected to have greater likelihood of extremely wet seasonal periods (DJF, MAM) but not annual precipitation amounts while Northern Australia shows little change in chance for extreme seasonality. The simulations show little if any significant change in the chance of extremely dry years for any of these regions. The only region expected to have a substantial increase in the chance for extremely dry years is Central America. Climate simulations for this region show increasing chances for extreme drought in all seasons and a sixfold increase in the likelihood of extreme annual drought by 2100 (IPCC, 2007).

While global climate model simulations are informative for individual regions, it is important to keep in mind that these are average changes over large areas that may mask significant variability in climate change within these regions. Similarly, potentially important local weather phenomena may not be included in the global climate models. More appropriately scaled Regional Climate Models (RCMs) that can accurately address local land cover and topography are needed to improve predictions of climate change in tropical regions and their resultant impacts on rainforests.

7.5 TROPICAL RAINFOREST RESPONSE TO FUTURE CLIMATE CHANGE: AMAZONIA

Due to its large size, widespread deforestation, biodiversity, and carbon stocks, the Amazon has been closely studied for evidence of potential responses to global climate changes. Given the multitude of Global Climate Models (GCMs) and the large number of possible greenhouse gas emission scenarios, the IPCC (Intergovernmental Panel on Climate Change) has agreed upon several standard greenhouse emissions scenarios to enable meaningful intercomparison of model results. All GCMs include the Amazon by definition. However, an influential GCM (HadCM3) study by Cox *et al.* (2000) galvanized attention on the Amazon by predicting that future climate change could cause rapid dieback of much of the forest by 2050. Using an innovative composite model that coupled a GCM to an ocean carbon-cycle model and a dynamic global vegetation model (DGVM) they predicted that global carbon-cycle feedbacks could exacerbate atmospheric CO_2 levels in the IPCC standard IS92a scenario (980 versus 700 ppmv). This would result in an additional 1.5°C (5.5°C versus 4°C) increase in global-mean warming by 2100. The study was one of the first to try to dynamically link global vegetation into a GCM and it should rightly be recognized for this accomplishment. However, the legacy of this study has become its regional predictions of massive dieback in the Amazon as the global climate changes.

Within the model, regional temperature increases (some $>9^\circ C$) and much reduced annual precipitation (64%) forced a simulated dieback of the Amazon forest after 2050 (Cox *et al.*, 2000). By 2100, modeled climate conditions are so extreme that over 50% of the Amazon is expected to be bare ground (i.e., a desert) (Cox *et al.*, 2004). The climate mechanism behind this catastrophic result is the predicted establishment of perpetual and severe El Niño–Southern Oscillation (ENSO) conditions. This is not a unique feature of the HadCM3 GCM but prediction of El Niño-like conditions is not a common feature of most GCMs (IPCC, 2007). Under ENSO conditions, much of the Amazon region is expected to have reduced precipitation and higher temperatures. This combination of factors is calculated to reduce photosynthesis and increase plant respiration costs to the point that net primary productivity (NPP) becomes negative, initiating rapid tree death. Given that precipitation recycling of evapotranspiration from Amazon forests is responsible for 25–50% of the region's rainfall (Eltahir and Bras, 1996; Li and Fu, 2004), the modeled dieback creates a positive feedback of ever lower rainfall as tree cover is reduced. This causes a domino effect of rapid forest retreat from the northeastern coast south and west toward the Andes, reducing modeled forest cover from 80% to 10% in the Amazon (Betts *et al.*, 2004). By way of comparison, Salazar *et al.* (2007) forced a potential vegetation model with climate scenarios from 15 GCMs and estimated a 9% reduction in forest cover during the same time period and similar emission scenario.

If forest dieback were to occur, it is likely that the Amazon's fire regime would become one of extensive fires with extreme fire behavior until the affected forests were replaced with more fire-resilient vegetation types (Cochrane and Barber, 2009). Prior to disappearance though, drought stress would make many Amazonian forests susceptible to burning every year. Recurrent fires would severely degrade forests and cause rapid unintentional deforestation. The permeability of the landscape to fire spread would likely devastate much of the region's agriculture. With each fire's occurrence, future control of landscape level burning becomes more difficult (Cochrane, 2003). Without major changes in land use and fire management, fires of unprecedented scale and severity could occur. The dieback of the Amazon, outlined by Cox *et al.* (2000), would be preceded by years with thousands of wildfires burning millions of hectares of forest. Whole regions of previously damaged forests on fire could set off mass fires (Quintere, 1993). These so-called firestorms create their own weather with hurricane force winds being sucked into the flames and can cause chaotic fire spread over large regions (Cochrane, 2003). The devastation from such fires would have global climate consequences. Such apocalyptic scenarios of environmental devastation make it necessary to critically examine the climate model simulation driving speculation about a massive dieback of the Amazon.

7.5.1 Modeled versus real climate

One obvious check of model simulations is to evaluate how well they recreate current climate conditions. Cox *et al.* (2000) predict substantially reduced precipitation in the Amazon. However, current period Amazonian precipitation amounts modeled by the HadCM3 GCM are inaccurate. Prior to initiating future climate change simulations, the HadCM3 simulations of annual Amazon precipitation are 25% too low (Huntingford *et al.*, 2004). This underestimate is not spatially uniform. The north-eastern Amazon, which has some of the highest rainfall rates in the world (3,000 mm yr^{-1}), is modeled as receiving only 700–1,000 mm yr^{-1} (Gandu *et al.*, 2004). These annual precipitation estimates are 60–70% too low (1,800 mm yr^{-1}) (Cox *et al.*, 2004) before climate change is taken into account. Actual rainfall data from 1960–1998 shows no significant change in annual rainfall amounts across the Amazon. The eastern Amazon, thought to be most at risk of large precipitation reductions, has gotten steadily wetter (Malhi and Wright, 2004). A comparison of future Amazonian climate change in 21 GCMs showed only 7 with reduced precipitation, while 13 predicted rainfall increases. The HadCM3 models were the most extreme, predicting Amazon rainfall reductions twice as large as any other models (Covey *et al.*, 2003; Cox *et al.*, 2004).

The seasonality implied by the HadCM3 GCM raises additional concerns. Although it does a good job of recreating the spatial pattern of dry season length differences across the basin, the model overpredicts dry season length by approximately 1 month and substantially underpredicts monthly dry season rainfall. Modeled rainfall is near zero for June–August and is 1–2 mm day^{-1} lower than gauge observations in May (Li *et al.*, 2006). In short, HadCM3 predicts longer and more intense dry seasons than actually exist in the Amazon for the current climate.

Establishment of a perpetual El Niño state is the driving force behind the HadCM3 predictions of future Amazonian rainfall reductions. Should this occur, it would be a great concern in many regions and would potentially devastate the rainforests of Southeast Asia.

One way of evaluating the reliability of GCM predictions of future El Niño events is by examining how well historical ENSO variability (i.e., timing of El Niño and La Niña periods) is modeled. The Coupled Model Intercomparison Project (CMIP) looked at the realism of 20 GCM (including HadCM3) representations of ENSO variability. While some models predicted changes in climate to either a mean El Niño or La Niña state, most showed little or no change in ENSO variability. The CMIP results showed that the models that predicted the largest ENSO-like climate changes (El Niño or La Niña climate state) were the poorest at simulating historical ENSO variability. The most likely future ENSO climate scenario was concluded to be similar to today's climate, with no trend towards either mean El Niño or La Niña climate states (Collins, 2005), which is also the position of the IPCC (2007).

7.5.2 Modeled versus real vegetation distribution

Coupling the Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) DGVM to the HadCM3 GCM was a significant innovation (Cox *et al.*, 2000). Previous models had run asynchronously, with GCM and DGVM components running sequentially at each time step to generate parameters for input to each other (climate and land cover respectively). This approach may result in inconsistencies because the separate models may represent common processes, such as surface water balance, in different ways. There is also an implicit assumption that climate and vegetation are in equilibrium (Cox, 2001). Fully coupling the GCM and DGVM models better represents carbon-cycle feedbacks between model components.

Vegetation responses in DGVMs, such as TRIFFID, are based on sets of simplifying assumptions to facilitate global-scale model calculations. TRIFFID reduces the world's vegetation to five generic plant functional types (PFTs), specifically, broadleaf tree, needleleaf tree, C_3 grass, C_4 grass, and shrub (Cox *et al.*, 2000). PFTs compete against one another following a simple tree–shrub–grass dominance hierarchy (Betts *et al.*, 2004). The entire Amazon forest is classified as being a single type, broadleaved forest.

Northeast Amazonian vegetation is simulated by Cox *et al.* (2000) to be dominated by 50 million hectares of grass in areas that are currently broadleaved forest due to the model's erroneously dry regional climate conditions (Betts *et al.*, 2004). The expediency of the top-down DGVM approach is adequate for global modeling of vegetation effects on climate, since vegetation acts upon climate collectively. However, the converse is not true. Climate changes result in individual responses by plants that vary as functions of species, age, soils, topography, microclimate and a host of other factors (Korner, 2000). The crude simplifying assumptions for global modeling make regional estimation of vegetation responses tenuous at best.

Regional Climate Models (RCMs) have much higher spatial resolutions that can better represent local topography, geographic features and land cover changes at this scale (Cook and Vizy, 2006). Regional modeling studies have shown the Amazon to be highly resistant to climate change, with little vegetation change for reductions in rainfall as high as 60% (Cowling and Shin, 2006) and low variability in vegetation assemblages whether the ecosystem gained or lost carbon (Levi *et al.*, 2004). In intercomparisons, most models with dynamic vegetation components fail to predict an Amazon dieback (Friedlingstein *et al.*, 2006). Even the fully coupled HadCM3LC GCM, as developed by Cox *et al.*, (2000), shows no evidence of future Amazon dieback if the climate change simulation is initiated with current climate conditions (Huntingford *et al.*, 2004).

7.5.3 Modeled and real responses of vegetation to drought and temperature increases

Drought is a potential threat to tropical forests. Extreme drought conditions during the El Niño of 1997–98 are known to have increased mortality of large emergent trees on upland slopes in Indonesia. Similar findings have recently come from a simulated drought experiment in the Amazon where, after 3.2 years of 60% reduction in wet season rainfall, mortality of emergent canopy trees increased substantially (Nepstad *et al.*, 2007). Although large trees are impacted by severe drought, smaller trees appear to be more resistant.

The constraints of the TRIFFID DGVM mandate that the Amazon responds as a monoculture of constant height and universal rooting depth (3 m). A key ecophysiological driver of Amazon dieback is widespread depletion of soil water. This effectively shuts off photosynthesis, making the net carbon balance negative. TRIFFID has no capacity to emulate the drought deciduous behavior of many tropical trees (Cox, 2001), so severely drought stressed trees are all assumed to die. The Amazon basin is a vast network of rivers. Discharging 20% of the globe's riverine fresh water, the Amazon has over 1000 tributaries. A large percentage of the forest has direct access to groundwater and is therefore not adequately modeled by fixed soil water limits.

In the more extensive upland terra firme forests where the model could apply, forests have been shown to access much deeper soils (>10 m; Nepstad *et al.*, 1994). A blanket 3 m rooting depth is a poor analog for Amazonian forests, which extend rooting depths in response to dropping water table depths (Jipp *et al.*, 1998) and derive 75% of soil water uptake from depths below 2 m during the dry season (Nepstad *et al.*, 1994). Through direct comparison with 8 flux towers in the Amazon, Hasler and Avissar (2007) show that current GCMs and RCMs overestimate dry season water stress. Ichii *et al.* (2007) constrained rooting depths of Amazonian forests using the BIOME-BGC terrestrial ecosystem model and satellite imagery (MODIS). Using observed weather data, they modeled gross primary production and varied rooting depth model parameters to more closely match observed patterns of the MODIS Enhanced Vegetation Index (EVI). They found that areas experiencing dry seasons of 1–2 months, 3–4 months, and 5–6 months required soil depths of 1–3, 3–5, and 5–10 m, respectively.

Temperature increases may also impact the carbon retention capacity of tropical forests. Site limits to biomass accumulation and temperature sensitivity may exist for Amazonian vegetation and soil carbon storage (Cowling and Shin, 2006). Clark *et al.* (2003) found that forest tree growth rates in Costa Rica were negatively correlated with increased annual mean daily minimum temperatures. They inferred large CO_2 releases during the record hot 1997–1998 El Niño. They postulate the potential for a positive feedback process of CO_2 release from tropical forests as tropical climates continue to warm. To date, this scenario has been controverted by evidence from widespread long-term plot studies that continue to show net increases in biomass across the tropics (Phillips *et al.*, 1998; Baker *et al.*, 2004) and physiological models that show that potential photosynthetic productivity declines due to temperature increases should be more than offset by photosynthetic rate increases at higher CO_2 concentrations (Lloyd and Farquhar, 2007). Modeling studies of the effects of CO_2 increases on Amazonian forests show that biomass, and hence carbon storage, of these ecosystems is tied to atmospheric CO_2 levels and has probably been rising since the LGM (Beerling and Mayle, 2006). In a meta-analysis of temperature effects on carbon fluxes in mature tropical moist forests from around the world, Raich *et al*. (2006) found no detectable effect of temperature on total carbon storage. Net primary productivity increased with mean annual temperature, however, decomposition rates of soil organic matter also increased. It was concluded that temperature increases would prompt a shift in structure. Relatively low-biomass forests with larger accumulations of detritus would transition to large-biomass forests with less onsite detritus, but no net change in site carbon storage would occur. Reduced detritus levels would mean less potential surface fuels to carry fire. In principle, fire susceptibility of these forests could be further reduced but this is uncertain because type, size, and decomposition rates of the detritus are unknown variables.

7.6 CONCLUSIONS

By their very nature, rainforests are extremely resistant to the propagation of fire. Some of this resistance is fortuitous given the location of many of these forests in regions of high rainfall and little seasonality, but a large fraction of the world's tropical evergreen forests experience seasonal dry periods of several months. The physical structure of tropical rainforests, with dense multilayered foliage, blocks out sunlight and maintains a moist subcanopy environment that is only flammable after extended droughts or if the canopy is fractured by some disturbance. Although the tropics experience more lightning ignitions and more area burned than anywhere else, the closed canopy rainforests have persisted and maintained an environment with little or no fire. For these reasons, tropical rainforest tree species are extremely sensitive to even low-intensity fires should they occur. It is likely that significant amounts and frequencies of fires have only become prevalent within interior forests as a byproduct of anthropogenic activities in the last several thousand years. At present, many tropical rainforests are suffering due to the combination of several human land uses. Deforestation, fragmentation, drainage of wetlands, and selective logging combine to make remaining forests vulnerable to the ever present fires that accompany human settlement and land use. Unless alternatives to current fire management practices are found, tropical rainforests within several kilometers of human land use will continue to be at risk of burning. Global climate change could exacerbate or diminish the fire problems in the various tropical forest regions depending primarily on how precipitation amounts and seasonality are altered (Figure 7.4). If future climate changes bring unprecedented droughts, they could prove to be the catalyst for fire events so extreme as to make the traumatic conditions during the El Niño of 1997–1998 pale by comparison. At present, the majority of climate models do not indicate either imminent global shifts to more frequent El Niño conditions or higher frequencies of extreme drought years in most of the world's tropics. However, the extreme Amazonian drought of 2005 may be a harbinger of more frequent regional droughts if North–South Atlantic Sea Surface Temperature (SST) (Marengo *et al*., 2008a, b) and aerosol (Cox *et al*., 2008) gradients worsen with climate change. Central America is the one tropical region that the vast majority of global climate models agree will experience increased incidence of extreme drought. Consequently, the fire regimes of these forests are of growing concern. Central American countries should closely monitor both changes in their climates and the incidence of forest fires. While managing global climate change is beyond the capability of any single nation, active pursuit of better fire and forest management practices is a reachable objective.

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8

Ultraviolet insolation and the tropical rainforest: Altitudinal variations, Quaternary and recent change, extinctions, and the evolution of biodiversity

J. R. Flenley

8.1 INTRODUCTION

Ultraviolet light occurs in three wavebands. UV-A is the longest waveband (> 315 nm) which is close to visible light and is of limited biological significance. UV-B (280–315 nm) is damaging and mutagenic to living organisms. UV-C (< 280 nm) is lethal to all life, but is fortunately absorbed in the stratosphere, so does not reach the surface of the Earth in sunlight. It is therefore to UV-B that we must turn our chief attention. This, like UV-C, is also partly absorbed by ozone in the stratosphere, but some reaches the Earth's surface. Recent concerns about the ''Ozone Hole'' have focussed attention on polar regions, but in fact tropical regions have fairly low ozone concentrations in the stratosphere above them (Smith and Warr, 1991). The result is that, given their high overall insolation resulting from the low latitude, tropical regions have rather high UV-B levels.

UV-B insolation is greater at high altitudes because of the less atmosphere being traversed (Caldwell, 1971). It therefore follows that UV-B is particularly significant to vegetation on the tropical mountains, which are the highest altitude vegetated surfaces in the world. UV-B is known to be particularly high in the Alpine Zone of tropical mountains (Caldwell *et al.*, 1980; Sullivan *et al.*, 1992).

8.2 ALTITUDINAL VARIATIONS

On tropical mountains, there are marked altitudinal changes of vegetation (Troll, 1959). The concept of an actual zonation is rather too strict to be useful, but there is no doubt that as one ascends a mountain, there are gradual changes. Most tree species have an ecological amplitude in terms of mean annual temperature (MAT), of about

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M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

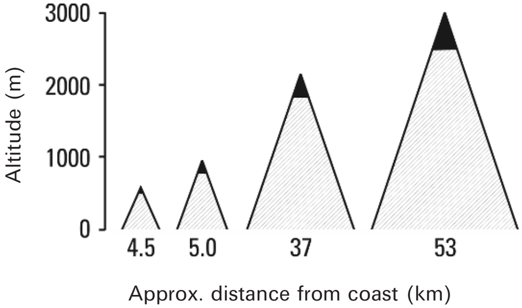

Figure 8.1. The Massenerhebung (mass elevation) effect illustrated by the occurrence of dwarf forest on mountains in Indonesia. From left to right: Mount Tinggi (Baurean), Mount Ranai (Natura Island), Mount Salak (W. Java), and Mount Pangerango (W. Java) (after van Steenis, 1972).

6°C (van Steenis, 1934–1936). There are some conspicuous exceptions to this, but it applies to many species. There is thus a continuum of change seen as the climber ascends to cooler altitudes. In New Guinea, for example, lowland trees start to be replaced around 1,000 m by the tropical oaks (*Lithocarpus* spp. and *Castanopsis* spp.), and at a higher altitude by the tropical beeches (*Nothofagus* sect. *brassii* spp.) which continue up to about 2,800 m on the main ranges. Above the "beech" forest we find the dwarf forest. This is also known as the mossy forest, cloud forest, or upper-montane forest, but the term dwarf forest is adopted in this chapter to avoid assumptions about causation. It is characterized not only by abundance of epiphytic bryophytes, but also by morphological peculiarities: stunted tree growth; small, thick leaves with a hypodermis and presence of extra pigments (Grubb, 1977). Above this we approach the altitudinal forest limit, usually marked by sub-alpine forest or shrubbery, over a vertical extent of *c.* 200 m, before the "alpine grassland" begins. These changes all tend to be lower on isolated peaks near the sea or on islands (the Massenerhebung effect, Figure 8.1).

What are the controlling factors of these variations? It has always been assumed that temperature must exert overall control. Mean annual values decline at about 0.6°C per 100 m, with increasing altitude, and the Alpine Grassland begins at about 6°C mean annual temperature (Walker and Flenley, 1979). Diurnal variation is extreme, so that the grassland experiences nightly frost and high temperatures in the day. Even the Massenerhebung effect may partly be explicable by temperature, for temperature lapse rates are steeper on isolated mountains near the sea than on large ranges which provide their own geothermal heat (Hastenrath, 1968; Flenley and Richards, 1982). How temperature operates other than by frost action is not well understood. Various workers (e.g., Brass, 1964; Grubb and Whitmore, 1966) have suggested that the dwarf forest is associated with cloudiness. It has also been suggested that temperature could operate via the soil (Grubb, 1977), lower temperatures leading to greater accumulation of organic matter and to changes in nutrient status.

It may well be that the extreme diurnal temperature variation is partly responsible. Many tropical mountains, although cloud-covered in the afternoons, lose their cloud cover during the night and early morning. Given the low atmospheric pressure resulting from the elevation, out-radiation is very high, resulting in extreme day/night temperature differentials (DIF). This thermo-periodicity has been studied in a number of cultivated plant species (Atwell *et al*., 1999). In general, a small positive DIF (i.e., day temperature a few degrees higher than night temperature) encourages growth. For instance, in *Chrysanthemum*, there is a strong positive correlation between stem elongation and positive DIF (Carvalho *et al*., 2002). In *Begonia*, however, growing the plants with a day temperature of 22°C and a night temperature of 16°C, and adding in a 2-hour temperature drop to 12°C after sunset led to inhibition of total plant height and width (Son *et al*., 2002). In general, a DIF of 20°C in several species can discourage growth, leading to stunting (Atwell *et al*., 1999), which is a feature of the trees of the dwarf forest. As it is likely that few, if any, species from this forest have been investigated in this regard so far, further consideration of the role of DIF must await research. It remains, however, a distinct possibility that it is a factor of importance on tropical high mountains, where the "summer every day and winter every night" environment is normal (Troll, 1959). It seems surprising that modelers of tropical climate (e.g., Farrera *et al*., 1999) have chosen to use mean annual temperature and mean temperature of the coldest month, indicating seasonality, as parameters in their models while apparently ignoring DIF.

Most of the explanations of altitudinal variation so far offered are based mainly on association. Experimental evidence of causation is usually scanty, or rather inconclusive. Alternative possible causative factors, such as the decline in atmospheric pressure with altitude, or the increase in ultraviolet light with altitude, have rarely been considered.

This section investigates the hypothesis that the variation of vegetation on the upper parts of tropical high mountains (above *c*. 2000 m) is related to insolation by ultraviolet light. This hypothesis was advanced by the late Francis Merton (pers. commun.) in 1973, but there was no serious consideration given to it at the time because of lack of evidence. Since then, however, discoveries have justified a revival of the hypothesis. These data relate to the effects of UV-B on plant growth.

Controlled experiments which simulate natural conditions are difficult with UV-B, for artificial light sources do not correctly reproduce the solar spectrum, and species differ widely in their response to individual wavelengths. Nevertheless, it has been possible to experiment on a range of plants (Lindoo and Caldwell, 1978; Teramura, 1983; Murali and Teramura, 1986a,b). In general the plants became stunted and developed small, thick leaves with a hypodermis: precisely the characteristics of the upper montane and sub-alpine forests. They also developed extra flavonoid pigments, which is also a common characteristic of the dwarf forest and shrubbery. In fact the puña of Peru (a sub-alpine scrub) has a distinct yellowish appearance possibly caused by such pigments. The sub-alpine scrub of New Zealand has a similar color.

The correspondence between the features induced in crop plants, and the features present in the dwarf forest and shrubbery, is rather striking. It must be remembered, however, that the former is phenotypic and the latter (presumably) genotypic. This need not be an insuperable difficulty. Probably genetic fixation of an initially induced feature would happen by natural selection. Is it possible, therefore, that the upper woody vegetation of tropical mountains is genetically adapted for resistance to UV-B? It would be good to test this idea by considering the Massenerhebung effect, since this involves the occurrence of dwarf forest at anomalously low altitudes.

8.3 THE MASSENERHEBUNG EFFECT

As usually defined, the *Massenerhebung* (or mountain mass elevation) effect means the occurrence of physiognomically and sometimes floristically similar vegetation types at higher altitudes on large mountain masses than on small isolated peaks, especially those in or near the sea. Although the effect was first reported in the European Alps (Schroeter, 1908) and in North America (where it is known as the Merriam effect; Martin, 1963), it is best known in the tropics. Perhaps its clearest expression is the occurrence of dwarf forest at lower altitudes on isolated peaks than on the main mountain masses, which are taken as the norm (Figure 8.1).

Some explanations of this phenomenon have involved mean temperatures and cloud formation. Cloud formation is often observed on isolated peaks at quite low altitudes, and it was shown by Hastenrath (1968) using radiosonde balloons in Mexico that lapse rates were somewhat steeper over lowlands than over large mountain masses. Similarly, a steep lapse rate (0.74°C per 100 m) was recorded on the 735 m high island of Krakatau in Indonesia (Forster, 1982); the regional average is 0.61°C per 100 m (Walker and Flenley, 1979). Presumably the afternoon clouding seen on isolated peaks is related to this temperature regime, and also, in the case of islands, to the greater evaporation from the sea (M. Bush, pers. commun.) The clouding does have pronounced ecological effects. For instance, it increases humidity to 100 percent and reduces total insolation received by about 30 percent compared with unclouded sites in Sabah, Malaysia (Bruijnzeel *et al.*, 1993). The difficulty comes in relating these changes to the morphological peculiarities of the vegetation. Usually, if plants are grown in high humidity and low insolation, they become etiolated (i.e., they are tall, have long internodes, and large, thin, pale green leaves). This is the exact opposite of the attributes of tropical mountain dwarf forest, which have stunted growth, short internodes, small, thick leaves (with a hypodermis), and often extra pigments (anthocyanins or flavonoids).

Now let us consider the UV-B hypothesis as an explanation for the Massenerhebung effect. UV-B light, like visible light, may experience total reflection at water or cloud surfaces. Total insolation may thus be increased by up to 70 percent through reflection from clouds (Figure 8.2). In the early morning, low peaks are surrounded by a sea of clouds (Figure 8.3), which will reflect sunlight strongly up onto vegetation. Islands receive similar reflection from the sea surface. Rayleigh scattering of light from the air molecules in the sky will also be particularly effective in the clear morning and favours UV above all other wavelengths (Dave and Halpern, 1976).

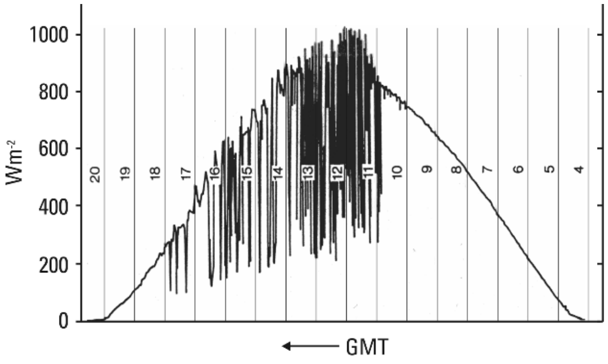

Figure 8.2. Solar radiation on a day of broken cloud (June 11, 1969) at Rothamsted (52°N, 0°W) taken directly from recorder charts. Note very high values of irradiance immediately before and after occlusion of the sun by cloud (after Monteith, 1973).

Later in the day the clouds move uphill and envelop the upper forests, reducing them almost to darkness (Hope, 1986). This later reduction of insolation may serve to exacerbate the effects of any UV-B damage caused earlier in the day. This is because of photo-reactivation, a process by which plants repair themselves from UV-damage. Photo-reactivation is strongly dependent on visible light insolation (Caldwell, 1971). The daily tropical regime of a heavy dose of UV-B in the morning, followed by semi-darkness, may therefore be particularly harmful to plants that are not adapted to it.

There have been several attempts to relate the Massenerhebung effect to soil attributes. Among the more successful of these was that by Bruijnzeel *et al.* (1993), who found a correlation between the occurrence of stunted forest and phenolic compounds in leaf litter. The latter were thought to cause stunting by harmful effects on plant physiology. This theory is complementary to the UV theory, however. The usual response of plants to excess UV-B is to produce protective compounds that absorb UV-B. These are usually flavonoids or alkaloids (Caldwell, 1981), or anthocyanins (Lee and Lowry, 1980b). Many of these compounds are phenolic or are likely to break down into phenolic compounds in litter. They could provide a reinforcement mechanism, exaggerating the original stunting caused by the UV-B (Bruijnzeel and Proctor, 1993).

I conclude, therefore, with the tentative hypothesis that the Massenerhebung effect could be partly the result of a high dose of UV-B due to reflection from clouds or the sea in the mornings. Obviously further research is needed to test this idea, although there is little doubt that the full explanation will be a multivariate one. Some factors may be more important in one location, while other factors may dominate elsewhere.

8.4 QUATERNARY VARIATIONS OF VEGETATION

Palynologically based paleoecology has given strong evidence in recent years about the altitudinal variations in the period *c.* 25,000–15,000 years ago, the coldest period

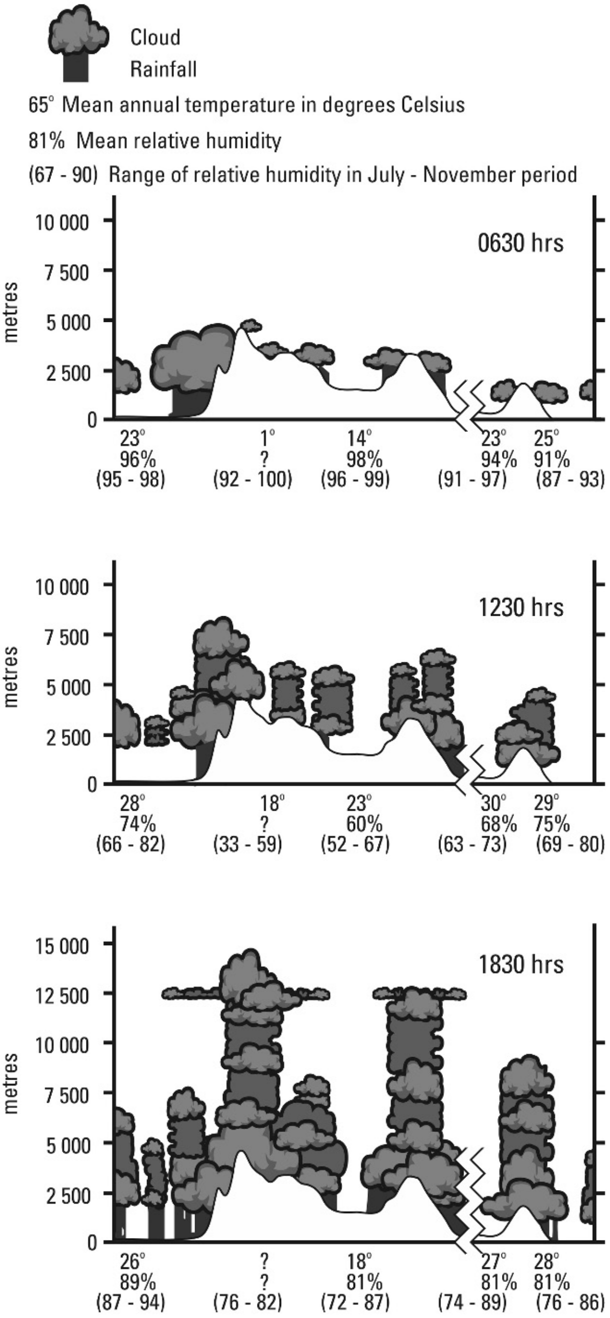

Figure 8.3. The daily weather regime in the New Guinea Highlands (modified after Brookfield, 1964). Note especially the cloud below the peaks at 6.30 a.m. followed by heavy clouding at 12.30 PM and later.

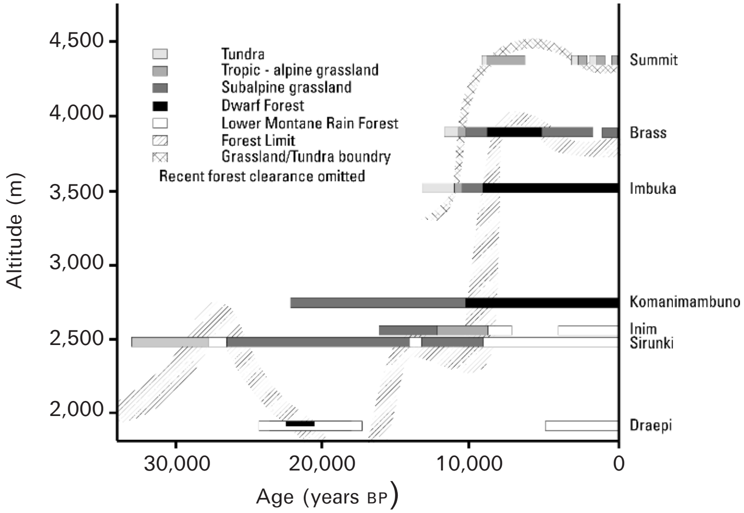

Figure 8.4. The Late Quaternary changes in vegetation on New Guinea mountains (inferred age at Sirunki), as evidenced by palynology (after Flenley, 1979).

of the last glaciation. The evidence from the New Guinea Highlands consists of pollen diagrams from a variety of altitudes between 1,900 m and >4,000 m (Flenley, 1979). These are consistent with a lowering of the altitudinal forest limit to *c.* 2,000 m in the Late Pleistocene (Figure 8.4). This could be explained by a lowering of temperatures.

There is, however, an anomaly which cannot be explained by temperature change alone: the fact that in the Late Pleistocene the dwarf forest apparently disappeared almost completely (Walker and Flenley, 1979). Its constituent taxa must have survived somewhere, presumably as rare individuals near the altitudinal forest limit. In its place, the alpine grassland was greatly expanded, and was apparently rich in tree ferns. This phenomenon has now been reported to be repeated during each glacial phase (see Chapter 4).

If this absence of the dwarf forest in New Guinea in the Late Pleistocene had been an isolated instance, one could perhaps have ignored it. A similar phenomenon has, however, been reported from the Colombian Andes (Salomons, 1986). In this case it was the sub-páramo, the sub-alpine shrubbery of the Andes, which was discontinuous in the Pleistocene. Both cases amount, however, to a great reduction in the Late Pleistocene of the upper woody formations which are characterized by stunted growth, small thick leaves, and a hypodermis.

The usual explanation advanced for this is that the climate of the Last Glacial Maximum (LGM) was somewhat drier than the present one, as well as cooler. Thus, the dwarf forest disappears. However, since desiccation is more likely to favor stunting than to discourage it, this explanation does not appear completely satisfactory. If, however, the UV-B hypothesis advanced in the last section has any credibility, the occurrence of dwarf forest is related, at least partially, to high UV-B. The disappearance of the dwarf forest during the glaciation can then be explained in the following way (Figure 8.5). In the Holocene, at lower altitudes, below *c.* 3,000 m,

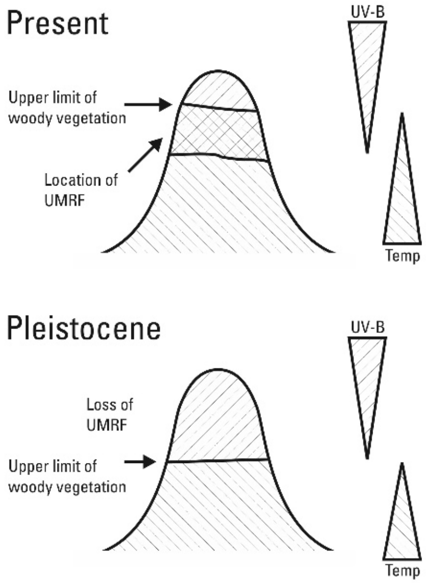

Figure 8.5. The hypothesis that lack of upper montane rainforest in the Pleistocene may be explained by absence of a habitat with a suitable combination of mean annual temperature and UV-B insolation (diagram by G. Rapson, unpublished).

the genetically stunted trees of the dwarf forest would be at a selective disadvantage compared with the larger trees of the lower altitude forest. Above *c.* 3,000 m they would be at an advantage, because of greater UV-B insolation there. In the Late Pleistocene, lower temperatures brought the forest limit below 3,000 m, therefore the stunted species became rare. In the Holocene, warmer temperatures allowed forests to expand uphill, but only those species genetically adapted to the high UV-B insolation could take advantage of this. The present forest limit thus could be controlled by temperature or UV-B, or a combination of both.

8.5 PRESENT AND POSSIBLE FUTURE TRENDS IN UV INSOLATION AND THEIR EFFECTS

Since the discovery of the Ozone Hole, there has been much interest in the elevated levels of UV-B experienced by natural ecosystems. Each southern spring, as the Ozone Hole that develops over Antarctica at the end of winter is filled in, this results in a depletion of stratospheric ozone in middle southern latitudes, and to a rise in UV levels there. It might have been expected that a knock-on effect would then lead to a rise of UV in the tropics, but measurements show little or no change there (Stolarski *et al.*, 1992; Madronich *et al.*, 1995; Gleason, 2001).

The possible effect of global warming on UV insolation has also been studied. More greenhouse gases lead to a warmer atmosphere, but this leads to a cooler stratosphere (Austin *et al.*, 1992; Shindell *et al.*, 1998a). This might be expected to lead to more widespread conditions favouring the destruction of ozone. If this were to happen, it could result in a rise in UV levels in temperate regions, and possibly in the tropics also. Mathematical modeling shows, however, that this is unlikely. A model simulation did indeed suggest a decrease of ozone in middle latitudes, but a small increase (2–6%) in the tropics (Shindell *et al.*, 1998b).

It thus appears that the tropical UV-climate is rather stable. One possible exception to this could be the effect of volcanic eruptions. For example, the eruption of Mount Pinatubo in the Philippines in 1991 resulted in the release of sulphur dioxide aerosols which destroyed stratospheric ozone and led to an observed increase in ground level UV of 15% for two years on a global scale (Gleason *et al.*, 1993). The Pinatubo eruption was, on a geological scale, brief and small.

Possible increases in tropical UV have been blamed for two major phenomena: the bleaching of tropical corals, and the decline and extinction of many Amphibia. Corals are indeed very sensitive to UV-A and UV-B, and many cases of coral bleaching and death have been reported. Corals have been shown to possess powerful UV-screening compounds, some of which are of commercial importance. It now appears, however, that a more likely cause of coral bleaching and death is a rise of water temperature. Even a rise of 1°C can be effective in this way (Gleason, 2001).

The Amphibia story is more complex, since the reported decline of Amphibia is world-wide. Many Amphibia are indeed sensitive to UV-B, which may significantly reduce the hatching of eggs, or may induce abnormalities (Blaustein *et al.*, 2001, 2003). Some 427 species of Amphibia (7.4% of known species) are critically endangered and 1,856 species (32.5%) are globally threatened. A high proportion of these (76.5%) are from the neotropics, Afrotropics, or Australasia (Stuart *et al.*, 2004). Nevertheless, the latest evidence suggests that increasing UV-B is unlikely to be the major single factor, and a fungal disease is now being investigated as the likely principal cause (Daszak *et al.*, 2003). The complete answer may involve many interacting factors (Collins and Storfer, 2003; Kats and Ferrer, 2003; Carey and Alexander, 2003; Storfer, 2003).

The possibility of investigating past ultraviolet radiation environments by the record of fossil pigments in lakes (Leavitt *et al.*, 1997) is an interesting development which may prove to be of considerable value.

8.6 EVOLUTION OF BIODIVERSITY: THE TROPICAL MONTANE UV-B HYPOTHESIS

Over the past 30 years, the principal research problem in ecology has been the explanation of biodiversity. More specifically, the aim has been to explain the gradient of diversity from its high values near the equator to the very low values in sub-polar regions. Most hypotheses about this assume that the present situation is in equilibrium with the environment, and thus try to explain matters in terms of currently operating processes. Although the complete explanation may well be multivariate (i.e. involving the interaction of many separate factors), there has still been a tendency to search for an underlying mechanism.

One such mechanism that has been popular in the last 20 years is the refuge theory (Haffer, 1997; Haffer and Prance, 2001), which was one of the first ideas involving paleoecology. If the tropical rainforest was divided into many separate blocks by dry Pleistocene climates, this could have isolated populations for long enough to allow allopatric speciation. In fact repetition of this by multiple Milankovitch cycles could have produced a "species pump" leading to many closely related species, which is what we find in the tropical rainforest. Despite the fact that the refuge theory had no explanation as to why it operated only in the tropics, and not also in temperate regions (Flenley, 1993), it remained popular even after it was found that there was little palynological support for the existence of the supposed dry phases (e.g., Bush, 1994; Bush *et al.*, 1992). The theory only foundered completely when it was demonstrated that the Quaternary had not been a time of great speciation in the tropics at all. In fact, using palynological richness as a proxy for diversity (Flenley, 2005), it could be suggested that diversity had actually declined during the Quaternary (Morley, 2000; Bennett, 2004; Flenley, 2005). It seems that mutation rates were too low to produce the required genetic isolation in the time available (Willis and Niklas, 2004).

The opportunity therefore exists for promulgation of a new hypothesis, which might retain some of the attractive features of the refuge hypothesis, such as the species pump concept, related to cyclical climatic change, while avoiding the pitfalls of the earlier hypothesis. This is the aim of the present section.

To be at all plausible, the new hypothesis must account for the origin and survival of large numbers of closely related species, now living in close proximity with each other. Assuming normal evolutionary processes, the most likely procedure for achieving this is allopatric speciation (i.e., the original population of a species must be split up and the sub-populations isolated). There must then be mutation at a sufficient rate within each sub-population that when the sub-populations are recombined, they remain reproductively isolated.

Referring again to the geological record, and using palynological richness as a proxy for diversity (Morley, 2000; Flenley, 2005) we find that the times of rapidly increasing diversity were the Eocene and the Early Miocene, especially the former (Wilf *et al.*, 2003). A similar result was obtained using DNA evidence for the date of branching of the evolutionary "tree" in the Leguminosae (Willis *et al.*, 2009). This family is abundant in the tropics, and out of five "bursts" of evolution in the last 50 million years, two were in the Eocene, two in the Early Miocene, and only one in the Oligocene. There is good evidence that both the Eocene and the Early Miocene were exceptionally warm. In the Eocene, megathermal forests spread well beyond their present limits (Morley, 2000). For instance the tropical palm *Nypa* occurred in Britain. Even allowing for continental movement, world climates must have been much warmer than now, and this could have been the result of either greater insolation, or higher concentration of greenhouse gases, or both (Morley, 2000; Willis and Niklas, 2004). Since the altitudinal temperature lapse rate is dependent on the amount of atmosphere above the surface, it is difficult to see how the lapse rate could have differed very much from the present rate found in the wet tropics, of *c.* 6°C per 1,000 m. At the peak of Eocene warmth, the sea surface temperature in the tropics rose as high as 32°C (Pearson *et al.*, 2001). This is about 5°C higher than now. The Late Paleocene thermal maximum may have been even warmer (Zachos *et al.*, 2001; Willis and Niklas, 2004).

Thus, using the above lapse rate, we might expect a MAT of 27–21°C (the present range of the lowland forest species) to occur at *c.* 800 m to 1,800 m altitude, and thus what are now lowland species could have grown at that altitude, assuming that their climatic tolerances have not changed. Since the usual MAT tolerance of a species has a range of about 6°C (van Steenis, 1934–1936), other species would have occurred at lower altitudes, although they might well have been congeners of the present-day lowland species.

At 800 m to 1,800 m we might expect the UV-B insolation to be slightly above that at sea level. This altitude effect is usually quite small, with values around 15% per 1,000 m (Blumthaler *et al.*, 1997). Since, however, there were major volcanic eruptions in Greenland during the Eocene (Aubry *et al.*, 1998) there might have been a considerably greater temporary rise in UV radiation (see Section 8.5). It must also be remembered that UV insolation will vary in line with Milankovitch cycles of thermal insolation. Therefore the warm phases of the cycles will tend to cause higher UV-B levels (Willis *et al.*, 2009; Bjorn and McKenzie, 2007). However, UV light also helps to create ozone, which then acts as a filter to remove UV-B. Mathematical models suggest, therefore, that the tropical UV-B environment may remain stable through Milankovitch cycles (Shindell *et al.*, 1998b).

UV-B is a well-known mutagen. Its effect in producing human skin cancer has been well researched (Lodish *et al.*, 2000) and it is clear that skin cancer is more common in the tropics (Smith and Warr, 1991). The latitudinal gradient of UV-B is well established (Caldwell *et al.*, 1980). UV-B is widely used by geneticists and plant breeders to promote mutation (Jansen *et al.*, 1998; Atwell *et al.*, 1999). Since plant reproductive apparatus is necessarily exposed to the atmosphere (for pollination, whether by wind, insects, or other means) it seems possible that UV-B induced mutations in the reproductive DNA would occur at an enhanced rate. The effect of elevated UV-B on plant reproductive apparatus has already been reported (van der Staaij *et al.*, 1997). Extreme elevation of UV-B in the geological past is thought to have caused world-wide dieback of woody plants (Visscher *et al.*, 2004).

It is relevant to consider why pollen is usually yellow in colour, or occasionally purple, red, or other colours. The colours are caused by the presence of flavonoids (which include anthocyanins). The coloration is generally regarded as an adaptation to attract insects (Wikipedia, 1 November, 2009). This cannot, however, be a complete explanation since the pollen of wind-pollinated taxa (e.g., *Pinus*, *Corylus*) is also yellow. Flavonoids may be classified into several different types, but a remarkable feature of all of them is their ability to absorb UV-B (Gould and Lister, 2006). It therefore seems more likely that a major significance of pigments in pollen is to protect the DNA against excessive mutation, which would be damaging or lethal. An exception which tests the rule is *Selenicereus grandiflorus*, the night-flowering cactus, in which the pollen is white, and may therefore lack flavonoids. In this species, however, the flowers open only at night and are pollinated by moths, so the pollen is not exposed to UV-B.

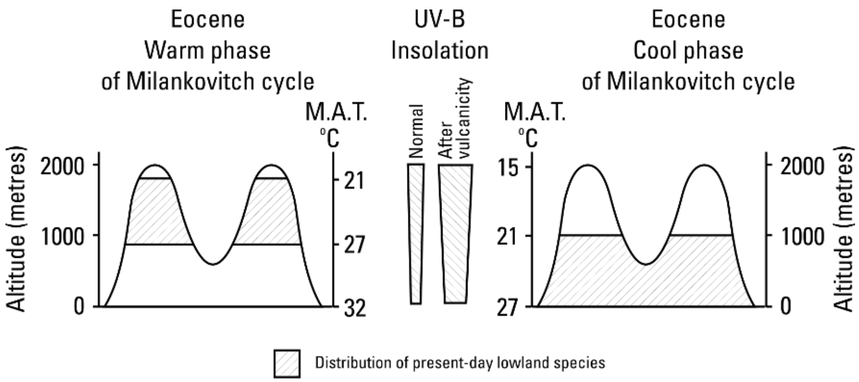

Figure 8.6. Diagram to show how a combination of appropriate topography, Eocene warmth, and enhanced UV-B after volcanicity could lead to isolation, mutation, allopatric speciation, a species pump, and increased biodiversity.

In some species it has proved possible to culture entire haploid individuals from grains. Thus, Ahmed *et al.* (1991) cultured *Brassica napus* after exposing some grains to extra UV-B. They proved to be very sensitive, and in many cases were killed. The survivors showed, in some cases, heritable resistance to the fungus *Alternaria brassicicola* which would be an advantageous mutation.

There is evidence that Milankovitch cycles have affected world climate throughout geological time (Willis and Niklas, 2004; Bennett, 1990; Pietras *et al.*, 2003). The effect of such cycles on Eocene megathermal forest taxa would have been to drive them up and down hills. In warm phases, what are now lowland taxa (already adapted to a MAT of 27–21°C) would have migrated into the hills. The possibility of isolation on individual peaks would occur and this would be repeated with each cycle (Figure 8.6). Thus, we have all the requirements for allopatric speciation and a species pump: mutation, geographic isolation, and cyclic change. Furthermore, this process would work preferentially in the area then covered by megathermal vegetation, which included mid-latitudes as well (Morley, Chapter 1 of this book). Outside that area, strong seasonality would have restricted tree growth to low altitudes.

It would support this hypothesis if present-day tropical montane taxa were experiencing similar high speciation rates, since they experience high UV-B and the possibility of isolation on mountain peaks during interglacials. One does not have to look far for examples. The case of *Espeletia* in the Colombian Andes is well known: while some species are widespread, others are restricted to single peaks (van der Hammen, 1974). It is likely that *Rhododendron* may provide another example, in New Guinea and the Himalayas (Sleumer, 1966; Leach, 1962). Interestingly, many *Rhododendron* species are epiphytes, and thus are exposed to strong insolation in the canopy. Possibly many epiphytic orchid genera would be another set of examples (e.g., *Cymbidium*) (Du Puy and Cribb, 1988). The possible origin of varieties of *Leptospermum flavescens* on Mt. Kinabalu (Borneo) by the action of UV-B has already been proposed (Lee and Lowry, 1980a). The abundance of endemic species in several genera on individual peaks in the Andes has already been noted by Gentry (1989).

In summary, the hypothesis presented here (first proposed by Flenley, 2007, 2008, 2011) is that major speciation in the tropics may have occurred especially in warm periods in the past (Eocene and Early Miocene), because in those times lowland taxa were able to live at higher altitudes where they experienced enhanced UV-B induced mutation rates (increased further by intermittent volcanicity), and isolation on individual mountain peaks. Cyclical climate changes could have led to a species pump. Occasional major volcanic eruptive phases could have provided the "punctuated equilibrium" which is the pattern of evolution accepted by many (Eldredge and Gould, 1972). It is not suggested that this is a complete explanation for biodiversity. While it could apply to some insects and some other animals, it is unlikely to apply to marine life or to nocturnal or soil animals. Probably the full explanation will turn out to be multivariate, but it is hoped that this hypothesis may make a contribution. Certainly the enormous diversity of tropical insects must be closely related to the diversity of the trees upon which they depend, directly or indirectly.

The idea that UV-B at low latitudes was of significance to evolution recently received support from Willis *et al.* (2009). These authors draw attention to the molecular phylogenics of plant groups centred on the Qinghai–Tibetan Plateau which, at 5,000 m receives about twice as much UV-B as land at sea level. The groups investigated, in the Asteraceae, have yielded molecular phylogenics which indicate rapid speciation over the past 50 myr in a series of "bursts" (Liu *et al.*, 2002, 2006; Wang *et al.*, 2005). These are probably linked to successive phases in the uplift of the plateau. In this case, however, the lack of variation in surface topography could suggest sympatric rather than allopatric speciation.

8.7 CONCLUSIONS

Generalizing, it may be said that the role of ultraviolet insolation (especially UV-B) in the tropics is still largely a matter of speculation and hypothesis. It may well be much more significant in sub-tropical regions, where total solar radiation is so much greater than in the tropics (Landsberg *et al.*, 1966). Nevertheless, there do seem to be some grounds for considering UV-B to be significant. This could be especially so after large volcanic eruptions, when sulphurous aerosols may damage the ozone layer. Even in normal conditions, UV-B appears to be a significant factor in the tropical high mountains, especially where cloud conditions are intermittent on a daily basis. It seems meaningful that the unusual features of the dwarf forest (stunting, small thick leaves with a hypodermis, and presence of extra pigments) can be produced in a range of cultivated plants by applying additional UV-B radiation. Nevertheless, it must be borne in mind that some of these symptoms are typical of stress in plants from various causes. For instance stunting can be induced by water shortage, nutrient deficiency, or by very cold night-time temperatures. The last of these is a known factor on tropical mountains.

There is little evidence of a change in UV-B insolation during the Quaternary. This stability of the UV environment, while temperature change was occurring, could account for the near-disappearance of the dwarf forest in successive cold phases of the Pleistocene, as the required combination of high UV-B and cool temperatures was much reduced.

The possible role of UV-B as an agent of extinction or endangerment of amphibian species since recent ozone depletion is discussed, but other factors seem to be involved.

Finally, the possible significance of UV-B as a mutagen is discussed. It would be easy to overestimate the importance of this as an evolutionary mechanism, but it seems possible that it could have contributed to the appearance of high tropical biodiversity during the Tertiary. This would only have been likely during periods of enhanced UV-B resulting from volcanic eruptions, but could have led to a "punctuated equilibrium" type of speciation. It could have been aided by a species pump mechanism involving allopatric speciation in hilly topography. This hypothesis has the advantage of being more effective in tropical than in temperate regions, which is in accordance with biogeographic reality. It could only have worked in hilly topography. In fact, however, the alpine orogeny occurred mainly during the Tertiary and affected tropical regions in the Americas, South East Asia, Australasia, and the African Rift Valley. The orogeny often involved considerable volcanicity in all those regions. The African activity was somewhat later than that in other regions, which could relate to the relatively low biodiversity in Africa, compared with the Americas and Southeast Asia/Australasia.

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8.9 REFERENCES

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9

Climate change in the Amazon Basin: Tipping points, changes in extremes, and impacts on natural and human systems

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9.1 INTRODUCTION

The Amazon River system is the single, largest source of freshwater on Earth and its flow regime is subject to interannual and long-term climate variability, which translate into large variations in downstream discharge (Richey *et al.*, 1989; Marengo and Nobre, 2001; Marengo 2004, 2005, 2006, 2007; Milly *et al.*, 2005, Marengo *et al.*, 2008a, b; Cox *et al.*, 2008; Zeng *et al.*, 2008). To predict future climate (rainfall) change and consequent river variability an understanding of the physical mechanisms related to regional and large-scale atmospheric–oceanic–biospheric forcings is required. The temporal and spatial nature and impact of any variability in the hydrometeorology of the Amazon Basin must be considered in this context.

Today the Amazonian rainforest plays a crucial role in the global climate system via hydrological feedbacks. Amazonian forests absorb solar energy and recycle about half of the regional rainfall, thereby driving atmospheric circulation in the tropics. As it is readily recognized that climate change can affect the global distribution of vegetation it therefore seems likely that future climate change will affect vegetation distribution. Perhaps less obviously, changes in the distribution and structure of the vegetation may also influence climate. The two-way interaction between the climate and vegetation consequently creates the possibility of both positive and negative feedbacks. Human actions that influence vegetation could play an important role in these feedbacks according to the scale of the disturbance. Natural ecosystems in tropical South America have been modified by human land use for centuries, in some cases, millennia. Deforestation and conversion to bare ground or hydrologically simple systems (e.g. grass or soy plantations), have altered large areas of Amazonia and almost all the eastern seaboard of Brazil.

M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

The Amazon region can be categorized as being at great risk from climate variability and change. The risk is not only due to projected climate change but also through synergistic interactions with other threats, such as land clearance, forest fragmentation, and fire. Some model projections exhibit, over the next several decades, a risk of an abrupt and irreversible replacement of forests by savannah with large-scale loss of biodiversity and livelihoods for people in the region (Betts *et al*., 2004; Cox *et al*., 2004; Oyama and Nobre, 2003; Salazar *et al*., 2007; Sitch *et al*., 2008).

Today the Amazon forest is thought to act as a sink for atmospheric CO_2 (Phillips *et al*., Chapter 12 of this book). However, outputs from some climate models indicate that a climatic "tipping point" can be reached where the forest becomes a carbon source rather than a sink. After that point is reached, the forest collapses and is replaced by secondary or degraded vegetation. With the establishment of savanna-type vegetation, the soils continue to dry and lose carbon in a process that has been referred as "savannization" of the Amazon region. The resilience of the forest to the combined pressures of deforestation and climate change is therefore of great concern.

Temperature increases and disruption in the energy and water cycles have the potential to seriously hamper the functioning of the Amazon as a forest ecosystem. Increasing soil temperature and the reduction of the ecosystem's capacity to retain carbon could eventually force the Amazon through a gradual process of savannization. The issue of Amazonian dieback leapt from climate change projections to global environmental concern with the unexpected Amazonian drought of 2005. However, droughts and floods are part of the natural climate variability of the Amazon Basin, probably linked to the global climate system by El Niño events or sea surface temperature (SST) anomalies in the tropical Atlantic. This natural climate variability means that the drought of 2005 cannot be attributed directly to long-term climate change nor assumed to have resulted from large-scale deforestation in the basin.

The potentially catastrophic impacts of Amazonian dieback make it vital to assess the risk of such an event under scenarios of future climate change. Unfortunately, global climate models differ significantly in their precipitation predictions for regional climate change over Amazonia (Li *et al*., 2006). For instance, the probability of a dangerous climate change due to Amazon forest dieback and subsequent savannization as suggested by the HadCM3 model is not clear in other climate models. As an ecological process, savannization remains uncertain, but as a product of climate change scenarios combined with potential vegetation models, savannization appears to be a plausible outcome. These are projections only, and hardly reflect a definitive outcome of climate change and impacts in Amazonia. However, synergistic interactions with the effects of forest clearing, fragmentation, and fire could flip the ecosystems forest to savanna, having large impacts on biodiversity, human livelihoods, and economic development (Betts *et al*., 2008; Malhi *et al*., 2008).

In the following sections, we will review the current knowledge of climate change in the Amazon region due to the increase in the concentration of greenhouse gasses

(GHGs) and also as a consequence of human drivers. We discuss the extent to which those changes could cause the Amazon system to approach a tipping point that would lead to irreversible changes in the functioning of the tropical forest (Nobre and Borma, 2009; Sampaio *et al.*, 2007; Salazar *et al.*, 2007). In the context of this chapter, savannization has been defined as an environmental change in tropical South America that would lead to changes in the regional climate caused by either land cover change (Nobre *et al.*, 1991; Oyama and Nobre, 2003; Sampaio *et al.*, 2007) or global warming in such way as to increase dry season length, thereby shifting regional climate envelopes into those typical of savannas. Other aspects to be discussed in this chapter are the occurrences of extremes events, focusing on the drought of 2005 and the floods of 2009, and the possible impacts of climate change on natural vegetation and environmental services provided by Amazonian forest.

9.2 CLIMATE CHANGE AND TIPPING POINT IN AMAZONIA

The term "tipping point" commonly refers to a critical threshold at which a tiny perturbation can qualitatively alter the state or development of a system (Lenton *et al.*, 2008). The stability of the Amazon forest–climate equilibrium is being perturbed by a number of human drivers (e.g., deforestation, global warming, forest fires, higher atmospheric CO_2 concentrations, and increased frequency of droughts and floods) (Nobre and Borma, 2009; Malhi *et al.*, 2008; Betts *et al.*, 2008). In the case of the Amazon forest, if warming due to an increase in concentrations of GHG (either natural or anthropogenic) is above 3.5–4°C, there is a risk of passing a tipping point leading to savannization. Quantitative assessments for the maintenance of the tropical forest indicate that a tipping point may be passed if the deforested area exceeds 40% of Amazonia (Sampaio *et al.*, 2007) or if global warming results in a temperature increase $> 34^\circ\mathrm{C}$ (Cox *et al.*, 2000). The likelihood of crossing a tipping point can be greatly exacerbated by increases in forest fires and droughts, but quantification of those effects is still lacking (Figure 9.1).

Rainfall in Amazonia is sensitive to seasonal, interannual variations in SSTs in the tropical oceans (Marengo, 1992; Fu *et al.*, 2001; Liebmann and Marengo, 2001; Ronchail *et al.*, 2002; Marengo *et al.*, 2008a, b). The warming of the tropical east Pacific during El Niño events suppresses wet-season rainfall through modification of the (East–West) Walker Circulation. Teleconnections leading to simultaneous changes in the Northern Hemisphere extra-tropics alter the flow of moisture into Amazonia and instigate drought events such as those of 1962, 1983, and 1998 (Williams *et al.*, 2005; Ronchail *et al.*, 2002). However, variations in Amazonian precipitation are also known to be linked to SST in the tropical Atlantic (Liebmann and Marengo, 2001). A warming of the tropical north Atlantic relative to the south leads to a north-westward shift in the Intertropical Convergence Zone (ITCZ) and compensating atmospheric descent over Amazonia, sometimes producing intense drought, as in 1963 and 2005 (Marengo *et al.*, 2008a, b).

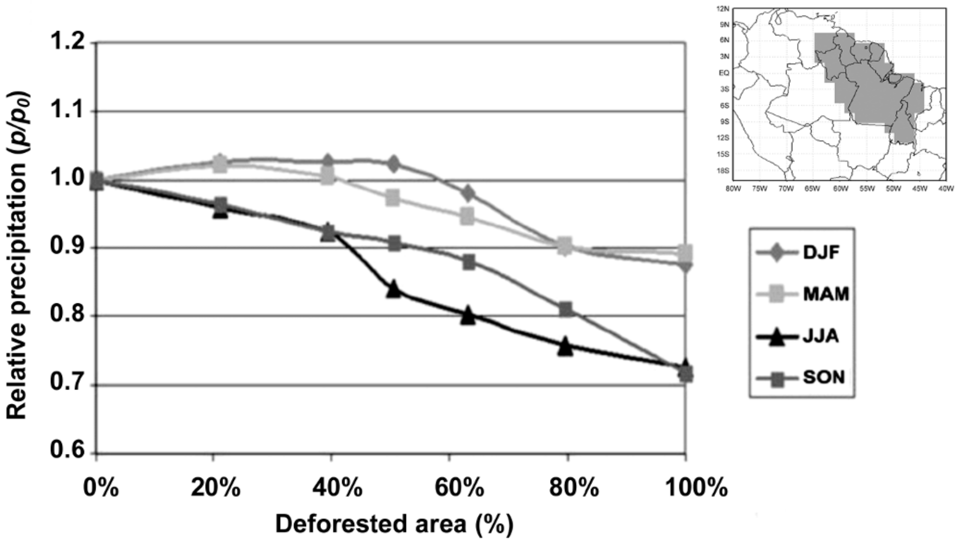

Figure 9.1. Simulated impacts of deforestation on rainfall in Amazonia. The curves show the fraction of rainfall in eastern Amazonia for different levels of deforestation across the whole of Amazonia, compared with the original forest extent, for each season. In the model, deforested land was converted to soybean plantations (Sampaio *et al.*, 2007).

A key question is whether a general long-term trend exists during recent decades toward drought conditions and, if so, whether it is associated with anthropogenic climate change or deforestation. Li *et al.* (2008) show that the Standard Precipitation Index (SPI), a measure of changes in precipitation normalized by the standard deviation, does indeed suggest a more pervasive drying trend over the southern Amazon between 1970–1999. Previously, tendencies studied by Marengo (2004, 2009) for the period 1929–1998 suggested that no unidirectional rainfall trend existed in the entire Amazon region, but a slight negative/positive trend was identified in northern/southern Amazonia. To understand discrepancies between the two studies it is necessary to evaluate the time scales over which the data were collected. Perhaps, the most important aspect of natural Amazonian precipitation change is the presence of interannual and interdecadal variability in rainfall. The negative trend detected by Li *et al.* (2008) for southern Amazonia during 1970–1999 coincided with the mid-1970s–1998 downward rainfall trend of the interdecadal rainfall variability in northern Amazonia (Marengo, 2004). This decadal variability seems to be linked to interdecadal variations in the SST in the tropical Atlantic (Wagner, 1996).

Projections of the Intergovernmental Panel on Climate Change (IPCC) AR4 and regional climate models suggest that the eastern Amazon may become drier in the future, and that this drying could be exacerbated by positive feedbacks with vegetation. At the broadest temporal and spatial scale, most Global Circulation Models (GCMs) predict that greenhouse gas accumulation, and associated increases in the radiative forcing of the atmosphere, will cause a substantial (> 20%) decline in rainfall in eastern Amazonia by the end of the century, with the biggest declines occurring at the end of the rainy season and in the dry season (Meehl *et al.*, 2007; Malhi *et al.*, 2008; Marengo *et al.*, 2009).

Investigation of the possible impact of Amazon deforestation on the regional climate and hydrology, prompted GCM simulations in which forest was replaced by grassland across the whole basin. The results suggested a possible change in both regional and global climates as a consequence of such tropical deforestation (see reviews in Salati and Nobre, 1991; Marengo and Nobre, 2001; Marengo, 2006; Sampaio *et al.*, 2007; Sampaio, 2008). Under a hypothesized Amazon Basin deforestation scenario, almost all models show a significant reduction in precipitation, decreased streamflow, and increased air temperature.

Observations and models suggest large-scale deforestation could cause a warmer and somewhat drier climate by altering the regional water cycle. Model results (Sampaio *et al.*, 2007; Sampaio, 2008) suggest that when more than 40% of the original extent of the Amazon forest is lost, rainfall will decrease significantly across eastern Amazonia. Complete deforestation could cause eastern Amazonia to warm by more than 4°C, and rainfall from July to November could decrease by up to 40%. Crucially, these changes would be in addition to any change resulting from global warming. Reducing deforestation could minimize these impacts as well as reduce emissions of greenhouse gases. It has been suggested that 40% deforestation (Figure 9.1) may be a tipping point beyond which forest loss causes climate impacts which cause further forest loss (Sampaio *et al.*, 2007). Global warming of 3–4°C may also lead to a tipping point. Although the existence of these tipping points still requires clarification, interactions between climate change and deforestation may make them more likely.

Climatic changes induced by deforestation may inhibit forest regeneration on fallowed lands. Contributing to this risk is the large fraction, perhaps as much as 50%, of precipitation in the Amazon Basin that is recycled via evapo-transpiration (Salati *et al.*, 1979). The importance of this hydrology is evident in GCM simulations, which suggest that the climate of Amazonia would dry by *c.* 20–30% and dry seasons would lengthen as summer temperatures increase. It can be presumed that changes to the cycles of water, energy, carbon, and nutrients that result from replacement of Amazonian forest will have consequences for the climate and the environment at local, regional, and global scales. Similarly, the biodiversity and the ecosystem services that forests offer would be negatively impacted. The conversion of primary tropical forest to agricultural areas, or secondary vegetation, represents one of the most profound changes to the natural environment of the present age.

While the large-scale effects of deforestation are relatively well substantiated (Gash and Nobre, 1997), heterogeneous patterns of sub-regional land cover change might result from increased local precipitation through the so-called "forest breeze" effect (Roy and Avissar, 2002; da Silva *et al.*, 2008). The outflowing forest breeze creates an effect of convergence between the forested and deforested patches and this can result in local increases in convection-driven rainfall at the boundary of the forested–deforested region.

On the other hand, modeling studies of surface hydrology suggest that these local responses depend on the scale of changes (D'Almeida *et al.*, 2007). If deforestation of the basin reaches 50%, models suggest evapo-transpiration could be reduced and runoff increased even in the absence of changes in rainfall (Coe *et al.*, 2009). Observations of change over deforested areas confirm increases of surface temperature and decreases in evapo-transpiration (Gash and Nobre, 1997); however changes in precipitation have been harder to detect. Recent analysis of satellite-based estimates of cloudiness and rainfall over deforested areas seem to confirm expectations (Cutrim *et al.*, 1995) of increasing non-precipitating cloudiness and decreasing dry-season precipitation (Wang *et al.*, 2009). Changes in the distribution of cloud condensation nuclei due to biomass burning may inhibit the formation of precipitating droplets in clouds (Andreae *et al.*, 2004) and thereby reduce precipitation.

If tropical climates can exist in multiple stable equilibria, one could ask how does a system get from one equilibrium state to another? Maybe such changes can occur if there is a change in the frequency and nature of extreme events as well as shifts in the mean. A shift in climate, due to natural or anthropogenic causes, can change the frequency and magnitude of disturbance. The change in relative system stability might make a vegetation change irreversible (e.g., Cox *et al.*, 2001; Oyama and Nobre, 2003)—however, it might take a disturbance for the shift to occur. This observation leads to the concept of instability and to the idea of a tipping point as a precursor to a non-linear change in an ecosystem's response to a forcing.

The paleoclimate records show that past climate changes have included both steady, linear changes as well as abrupt, non-linear changes (e.g., Bush *et al.*, 2010), where small increases in global warming produced large impacts once tipping points were passed. Climate scientists now warn that anthropogenic emissions are pushing the planet's climate system toward such a tipping point—sooner than previously expected—and that impacts could be catastrophic.

9.3 CLIMATE CHANGE IMPACTS ON AMAZON VEGETATION

9.3.1 Projected changes to the natural vegetation

Vegetation change in Amazonia is important for several reasons. Deforestation is a key land use change, affecting surface energy exchange through changing surface properties such as albedo, surface roughness, and evaporation. With more than 15% of the original Amazon deforested, substantial changes in precipitation and surface temperature are expected (Gash and Nobre, 1997). Changing vegetation may also alter the recycling properties of the original vegetation. As 30–50% of the precipitation within Amazonia consists of recycled evaporation (Molion, 1975; Salati, 1987; Eltahir and Bras, 1994), changing the evaporative properties of the vegetation will change the recycling potential.

Applying 2050 AD climate scenarios from 15 climate models for two emission scenarios (A2 and B1) from IPCC AR4 to the CPTEC Potential Vegetation Model (PVM) (Oyama and Nobre 2004), Salazar *et al.* (2007) demonstrated a probable reduction of tropical forest and replacement by savannas. The amount and rate of reduction of tropical forests increases with time through the 21st Century; with the greatest reduction occurring in southeastern Amazonia. The predicted decrease in tropical forest vegetation in South America, relative to potential modern vegetation cover under the A2 emission scenario, is 3% for the period 2020–2029, 9% for 2050–2059, and 18% for 2090–2099. The PVM is an equilibrium model (not a dynamic vegetation model), and this is vegetation that potentially would grow under optimum climate conditions. The model needs temperature and rainfall input, from which it calculates the water balance and soil moisture conditions. The vegetation seems to be more sensitive to temperature changes than rainfall, and while all models show warming, predicted changes in rainfall differ widely.

More recently, Salazar (2009) studied the consequences of regional projected climate change on biome distribution in South America in the time-slice 2070–2099, by forcing a regional potential vegetation model (CPTEC-PVMReg2.0) with climate scenarios from the three regional climate models of the CREAS project (RegCM3, Eta CCS, HadRM3; Marengo *et al*., 2009) under the A2 emission scenario. The CPTEC-PVMReg2.0 (Salazar, 2009), a regional version of the CPTEC-PVM2.0 model (Lapola *et al*., 2009), considered seasonality as a determinant factor for the delimitation of forest and savannas. It also took into account physiological responses of vegetation to seasonality (such as primary productivity) under variable atmospheric CO_2 concentrations. As a non-dynamic model, the CPTEC-PVMReg2.0 calculated only equilibrium solutions based on long-term mean monthly climate variables. The consequences of projected climate change on biome distribution in South America were analyzed through a PVM forced with the IPCC climate change scenarios. The results indicated the reduction of tropical forest cover and replacement by savannas mostly over southeastern Amazonia reaching a reduction of 18% for 2090–2099 (A2 emission scenario).

Figure 9.2 shows the current potential vegetation (biome distribution simulated by the CPTEC-PVM2.0Reg model under current climate) and the projected biome distribution for the A2 scenario and the 2070–2099 time-slices, for all the regional models analyzed—including the full fertilization effect. All models show loss of tropical forest in east Amazonia and replacement by savanna (most notably in RegCM3 model). The ETA CCS, output differs from the other models, showing the tropical forest being replaced by seasonal forest and savanna in southwestern Amazonia. The key difference of this output appears to be a greater increase in projected temperature compared with other models The biome changes are explained by the net effect of temperature and CO_2 concentration on net primary productivity and the precipitation decrease effect as dry-season length increases.

Precipitation decreases of 30% in southeastern Amazonia and 40% in the northeast and southwest could represent an increase of dry-season length to more than 4 months and shifts from forest to savanna vegetation. Lapola *et al.* (2009) identified this threshold of <4 months dry-season length as critical to maintaining tropical forest, even allowing for a CO_2 fertilization effect. Some areas in northeast Brazil are predicted to change from Caatinga to semi-desert in HadRM3P and RegCM3 models, due to decreased soil humidity (projections of temperature

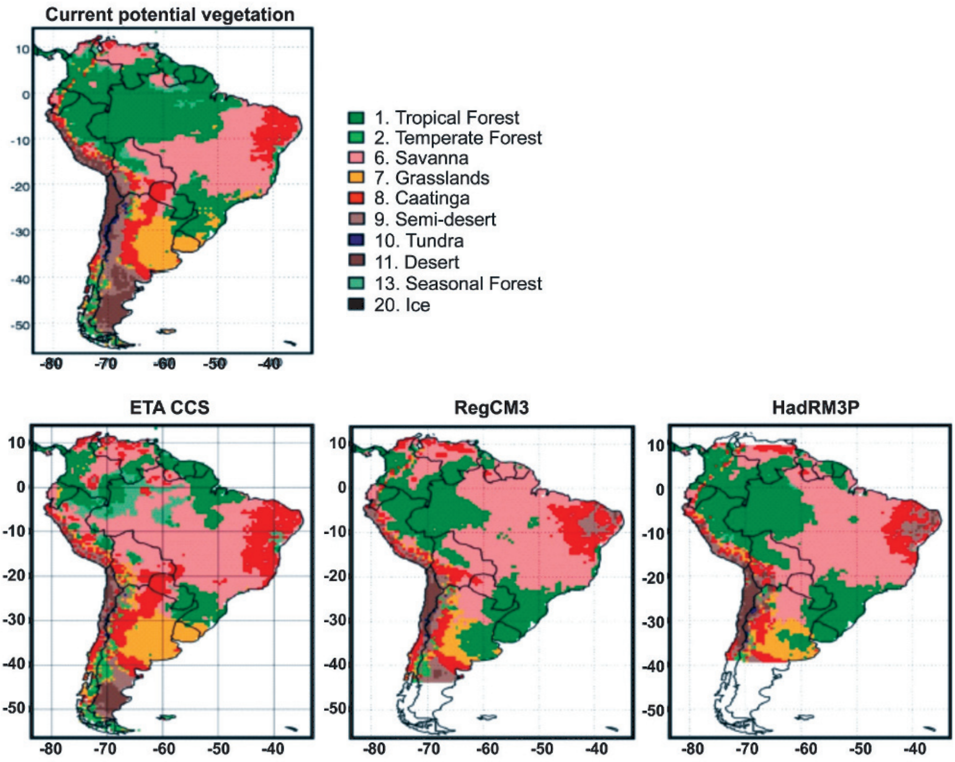

Figure 9.2. Projected distribution of biomes in South America for 2070–2099 from ETA CCS, RegCM3, and HadRM3P models under the A2 high-emission scenario. The top-left plot represents the current potential biomes (biomes in equilibrium with observed climatology) (Salazar, 2009).

increase and precipitation decrease) and net primary productivity. Both these models show an increase of tropical forest in southeast Brazil (Mata Atlántico) at the expense of grasslands in Uruguay and Argentina, due to the projections of increased precipitation and temperature in this region.

Nobre *et al.* (2010) performed analyses to quantify how deforestation, climate change, and fire may combine to affect the distribution of the Amazon forest biome. Changes in land use are modeled for deforestation scenarios of 0%, 20%, 40%, and 50%, with and without fires, under the two greenhouse gas scenarios—B1-low and A2-high—for the period 2015–2034 and 2040–2059 (“2025” and “2050” time-slices), from IPCC AR4. The results show that the area affected in scenario A2 is larger than in the climate scenario B1, and in both cases the effect is cumulative through time. Most important changes occur in eastern and southern Amazonia, with replacement of tropical forest by seasonal forest and savanna. The effect of fire in this region is important under both emissions scenarios (B1 and A2). The effect of 20% deforestation is smaller than the climate change only in the remaining tropical forest area in both emission scenarios. However, as deforestation exceeds 40% of the area its effect is larger than that of climate change alone. For the more extreme case (50% deforestation in the 2050 time-slice) the synergistic effects of climate change, fire, and deforestation reduce tropical forest area under both climate scenarios to between 36% and 38%. Northwestern Amazonia has the smallest changes in its area of tropical forest, indicating that even for substantial land use modifications and global climate change the resulting atmospheric conditions would still support tropical forest in the region.

The natural biome distribution derived from the global and regional climate change scenarios shows considerable uncertainty with respected to rainfall changes, mainly for Amazonia and northeast Brazil. The projected increase in temperature may elevate the rate of evapo-transpiration in tropical regions, which, in turn, could increase soil-moisture deficits, even when rainfall does not change significantly. Changes in rainfall are not consistent among models as some of them show increases and others show decreases in rainfall by 2050. As concluded by Salazar *et al.* (2007) and Salazar (2009), increased evapo-transpiration alone may be sufficient to trigger the replacement of the present-day potential biomes by other vegetation types that are adapted to drier soils. That is, tropical savannas replacing tropical forest in Amazonia.

Sitch *et al.* (2008) investigates changes in the future land carbon cycle, using five dynamic global vegetation models (DGVMs), forced with observed climatology and atmospheric CO_2, to model the contemporary global carbon cycle. The DGVMs are also coupled to a fast "climate analogue model", based on the Hadley Centre GCM, and run into the future for four IPCC emission scenarios: A1FI, A2, B1, and B2. Results show that all DGVMs are consistent with the contemporary global land carbon budget. Under the more extreme projections of future environmental change, the responses of the DGVMs diverge markedly. In particular, large uncertainties are associated with the response of tropical vegetation to drought, and boreal ecosystems to elevated temperatures and changing soil moisture status. Five DGVMs are considered here: the HyLand (HYL) model is based on the Hybrid DGVM (Friend *et al.*, 1997; Friend and White, 2000) with modifications as documented in Levy *et al.* (2004); the Lund–Potsdam–Jena (LPJ) DGVM (Sitch *et al.*, 2003), with the updated hydrology of Gerten *et al.* (2004); ORCHIDEE (ORC) as described in Krinner *et al.* (2005); Sheffield-DGVM (SHE) (Woodward *et al.*, 1995; Woodward and Lomas, 2004), and TRIFFID (TRI) (Cox, 2001).

There is a general consensus among the DGVMs in terms of the qualitative regional response of vegetation stocks to changing climate and atmospheric composition. All models simulate a decrease in vegetation carbon over Amazonia, in response to the reduction in precipitation predicted by HadCM3LC. TRI simulates the strongest Amazon dieback, with woody vegetation replaced by herbaceous plants. LPJ simulates only a moderate Amazon dieback, and a large reduction in boreal forest coverage and large, high-latitude losses in soil carbon. The high initial estimates of boreal forest carbon stocks in LPJ can partly explain the strong reduction in storage under very strong warming accompanied by severe summer drought. HYL simulates large carbon uptake in all ecosystems except over Amazonia, where, similar to TRI, the DGVM simulates a reduction in both vegetation and soil stocks. ORC and SHE both simulate only moderate decreases in vegetation biomass across Amazonia and small increases in soil carbon, the latter being a qualitatively different response to TRI, HYL, and LPJ. Note, the SHE model has fixed vegetation, and does not simulate changes in the coverage of plant functional types.

Biome projections for the first half of the century in tropical South America show a variety of results, depending not only on the climate scenario, but also on the effect of CO_2 fertilization on photosynthesis. In the Amazon, mostly in the east and southeast, projected increases in temperature and decreases in precipitation could support transitions to biomes where the vegetation is relatively sparse, such as transitions from tropical forest to savanna, from savanna to dry shrubland, or semi-desert replacing dry shrubland. On the other hand, CO_2 fertilization can minimize or even compensate for climate change effects on biome distributions.

9.3.2 Dieback of Amazon forest

In the most extreme scenarios GCMs (e.g., HadCM3) predict global warming to result in widespread forest dieback in the Amazon Basin (Cox *et al.*, 2000, 2004). Forest dieback has been explained in terms of sharp reductions of rainfall because of SST forcing from both the Pacific and Atlantic Oceans (Betts *et al.*, 2004; Cox *et al.*, 2000) and the role of vegetation–climate feedback (Betts *et al.*, 2008). Amazon forest dieback, in its turn, would induce a positive feedback as global warming transforms the large Amazonian carbon pool from supposedly being a carbon sink to a strong carbon source by 2050. However, there is uncertainty in climate projections of the hydrological cycle (precipitation) among IPCC AR4 climate models, where models failed to project a consistent change either for decrease or increase of rainfall in Amazonia through the 21st Century (Meehl *et al.*, 2007). One of the sources of uncertainty is the bias of the model in simulation of rainfall, and since models are validated against observations, the quality of the precipitation data used for validation may affect the identification and quantification of biases and systematic errors.

A review by Lenton *et al.* (2008) on tipping points and impacts on the forest shows that the dieback of the Amazon rainforest has been projected to occur with *c.* 3–4°C global warming. The apparent trigger for such a strong climate shift is a more persistent El Niño state that leads to drying over much of the Amazon Basin. However, whether such a state would reflect a more persistent El Niño-like behavior with stronger individual events or more frequent El Niño events, is not clear (Meehl *et al.*, 2007). Different vegetation models driven with similar climate projections also show Amazon dieback (Li *et al.*, 2006), but other global climate models (Salazar *et al.*, 2007) project smaller reductions (or increases) of precipitation and, therefore, do not produce dieback.

Vegetation models driven with a strong drying of the Amazon Basin have shown a dieback, but the magnitude of potential precipitation decrease over the Amazon remains controversial (Kriegler *et al.*, 2009; Sitch *et al.*, 2008). Figure 9.3 shows the simulations of the HadCM3 and the IPSL (Institute Pierre and Simon Laplace—University of Paris) models, for the carbon fluxes from ocean to air and

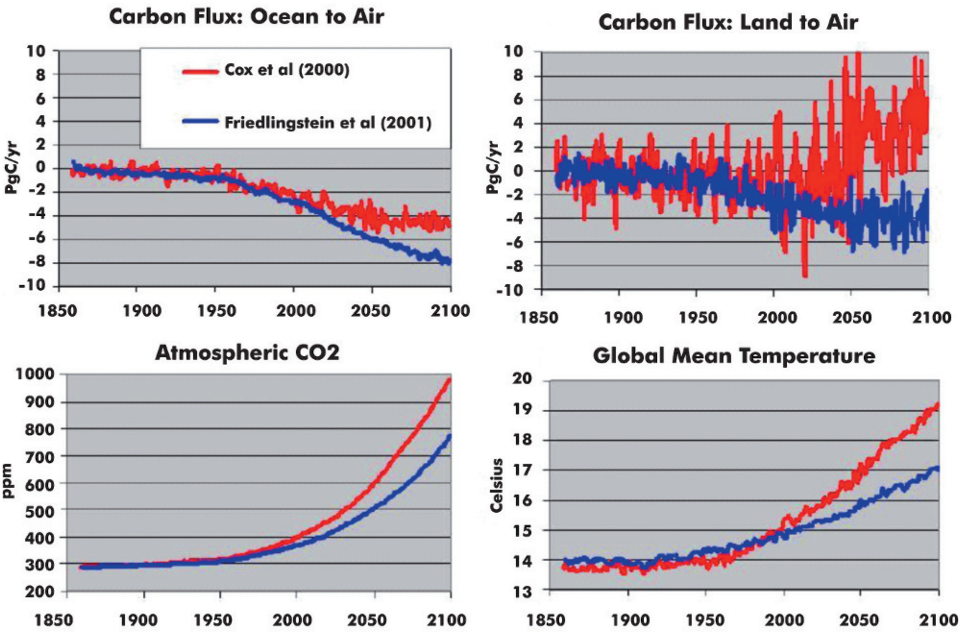

Figure 9.3. Carbon fluxes, CO_2 concentration, and global mean temperature as derived by the HadCM3 (red line) and IPSL (blue line) global coupled models until the end of the 21st century (Source: R. Betts)

land to air, together with the atmospheric CO_2 and warming increase. We notice that both coupled climate–vegetation models project dramatically different futures (CO_2, vegetation, temperature) using different ecosystem models. The HadCM3 model shows that near 2050 the Amazon regions become a net emitter of carbon as forests dry and dieback, while the IPSL model shows a more stable future.

The HadCM3 model projects that forest cover will begin to decrease in northeastern Amazonia by 2020 due to climate change, and that the changes will intensify after 2050. Between 2050 and 2090 forest cover in northern and central Amazonia will also decrease markedly. The loss of the forest biome in these simulations is purely attributable to climate change and does not include impacts of deforestation due to human activities.

The relative importance of the CO_2 fertilization effect versus altered precipitation was studied by Rammig *et al*. (2009). They "corrected" rainfall projections of 24 IPCC AR4 climate models by weighting functions derived from the performance of each model in representing the current climate. Rammig *et al*. (2009) concluded that the main source of uncertainty was in the effect of CO_2 fertilization and that differences in rainfall projections induced relatively small variances. Soil nutrients were another source of uncertainty, but were not analyzed here. The CO_2 fertilization effect was further studied by Salazar (2009) using three, high-resolution (50 km) regional climate models forced by HadCM3 global climate projections. They found that the maximum forest replacement would occur in eastern and southeastern Amazonia. In the absence of a CO_2 fertilization effect, a temperature increase of 2–3°C would be sufficient to change the moist tropical forest into seasonal forest or savanna. However, if a CO_2 fertilization effect is included, such changes would take place at temperature increases of 4–5°C. The potential effect of CO_2 fertilization on the tropical forests is clearly important, and is a factor that needs to be properly quantified.

An additional environmental driver of change in Amazonia is the increase in the occurrence of forest fires. Almost all modern fires in Amazonia are caused by human activities. However, natural fires have long played a critical role in determining the forest–savanna transition. Hirota *et al*. (2010) used a simplified climate–vegetation–natural fire model to assess the susceptibility of the forest–savanna transition to environmental changes in South America. Under current climate conditions, the modeling calculations suggest that the tropical forest would penetrate 200 km into the savanna domain in the absence of lightning-triggered fires.

Fire occurrence could increase the vulnerability of tropical forest ecosystems in Amazonia. Even a single fire can contribute to forest fragmentation and spread of fire-prone biomes (Barlow *et al*., 2003). With repeated fires the probability of progression toward savanna increases. Consequently, land-use change alone could potentially bring forest cover to a critical threshold. Thus, the fate of the Amazon may be determined by a complex interplay between direct land-use change and the response of regional precipitation, to forcing from El Niño and the tropical Atlantic.

Crucially, the impacts of deforestation are greater under drought conditions, as fires set for forest clearance burn larger areas. Reducing deforestation may help to maintain a more resilient forest under a changing climate. Forest fires, drought, and logging increase susceptibility to further burning while deforestation and smoke can inhibit rainfall, exacerbating fire risk. If SST anomalies (such as El Niño episodes) and associated Amazon droughts of the last decade continue into the future, approximately 55% of the forests of the Amazon will be cleared, logged, damaged by drought, or burned over the next 20 years (Nepstad *et al*., 2008).

Malhi *et al*. (2009) examine the evidence for the possibility that 21st Century climate change may cause a large-scale dieback or degradation of Amazonian rainforest by using 19 models from IPCC AR4. Most tend to underestimate current rainfall and also vary greatly in their projections of future climate change in Amazonia. Their analysis suggests that dry-season water stress is likely to increase in eastern Amazonia over the 21st Century, but the region tends toward a climate more appropriate to seasonal forest than to savanna. Such forests may be resilient to seasonal drought, but are likely to face intensified water stress caused by higher temperatures. Reduced leaf area index, increased seasonality, and episodic drought all increase the currently low risk of natural fire in Amazonia. Any increase in fire-frequency, whether associated with climate change, logging, or road construction is likely to trigger positive feedback mechanisms that promote establishment of fire-dominated, low-biomass forests (Barlow *et al*., 2003; Cochrane and Laurance, 2008). Conversely, deliberate limitation of deforestation and fire may be an effective intervention to maintain Amazonian forest resilience in the face of imposed 21st Century climate change.

Unlike the studies of Cox *et al.* (2000, 2004) and Betts *et al.* (2004), which project the diebacks, Mahli *et al.* (2009) fix the evaporation value at 3.33 mm day^{-1}, or 100 mm month^{-1}. This is the value used to define a dry month in Amazonia under present climates (Sombroek, 2001). By fixing this value, Mahli *et al.* (2009) do not allow large water deficits to develop and thereby constrain the extent of the dieback.

All these projected changes in Amazonia may have climatic, ecological, and environmental implications for the region, the continent, and Earth. A sound knowledge of how the natural system functions is thus a prerequisite to defining optimal development strategies. The complex interactions between the soil, vegetation, and climate must be measured and analyzed so that the limiting factors to vegetation growth and soil conservation can be established. New knowledge and improved understanding of the functioning of the Amazonian system as an integrated entity, and of its interaction with the Earth system, will support development of national and regional policies to prevent the exploitation trends from bringing about irreversible changes to it. Such knowledge, in combination with enhancement of the research capacities and networks between the Amazonian countries will stimulate land managers and decision makers to devise sustainable alternative land use strategies along with forest preservation strategies.

9.4 EXTREME EVENTS IN THE AMAZON BASIN

9.4.1 The drought of 2005

Tropical droughts may intensify and become more frequent this century as a result of anthropogenic climate change (Christensen *et al.*, 2007). In addition to affecting Amazonian peoples and biodiversity directly, such events appear capable of strongly altering the regional carbon balance and thereby accelerating climate change. The intense drought over the western and southwestern Amazon in 2005 gave rise to several studies analyzing the meteorological, ecological, and hydrological responses that arose from the anomalous warming of the tropical North Atlantic (Saleska *et al.*, 2007; Marengo *et al.*, 2008a, b; Zeng *et al.*, 2008; Arago *et al.*, 2008; Phillips *et al.*, 2009; Tomasella *et al.*, 2010a). Large sections of southwestern Amazonia experienced one of the most intense droughts of the last hundred years. The drought severely affected human population along the main channel of the Amazon River and its western and southwestern tributaries, the Solimões, and the Madeira Rivers. Water levels fell to historic lows forcing navigation along these rivers to be suspended. The drought did not affect central or eastern Amazonia, a pattern different from the El Niño-related droughts in 1926, 1983, and 1998. Figure 9.4(a) and (b) show rainfall anomalies in western and southern Amazonia reaching up to 70–100 mm lower than normal (normal being 200–400 mm month^{-1}), particularly at the beginning of the austral summer (Figure 9.4a).

The causes of the drought in 2005 were not related to El Niño but to the anomalously warm tropical North Atlantic, the reduced intensity in northeast trade wind moisture transport into southern Amazonia during the peak summertime

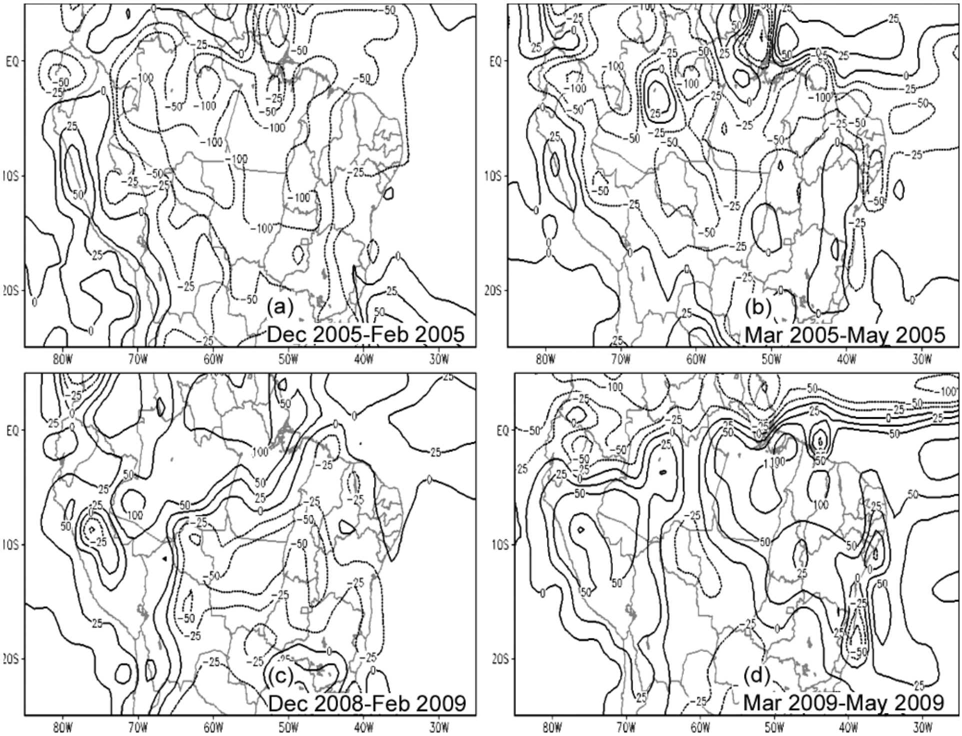

Figure 9.4. Seasonal rainfall anomalies (in mm) during (a) December 2004–February 2005, (b) February–May 2005, (c) December 2008–February 2009, (d) February–May 2009. Anomalies are relative to the 1961–2009 long-term mean (LTM1903–1986). Source: CPTEC/INPE.

season, and the weakened upward motion over this section of Amazonia. The net result of these influences was reduced convective development and rainfall. The drought conditions intensified during the dry season into September 2005 when humidity was lower than normal and air temperatures were 3–5°C warmer than normal. Due to the extended dry season, forest fires became unusually common in southwestern Amazonia.

During the drought period, there appears to have been a greening of the vegetation (Saleska *et al.*, 2007), a phenomenon often seen during the dry season in terra firme forests. This flush of growth is attributed to increased radiation and evapo-transpiration (it is often forgotten that tropical rainforests are light-limited systems) for areas with annual rainfall in excess of 1,700 mm and ecological adaptations such as deep roots and hydraulic redistribution mechanisms (Nepstad *et al.*, 2004).

Previously, the drought of 1998 in north and central Amazonia was generally considered to have been the most intense of the last 118 years (Kirchoff and Escada, 1998). However, Williams *et al.* (2005) suggested that the most severe drought in tropical South America during the 20th century occurred in 1926 during the El Niño of 1925–1926. They established that the drying in the northern portion of the Rio Negro Basin in 1925 also contributed to the overall drought in 1926, through both a depletion of soil moisture and possibly via negative feedbacks on rainfall from abundant smoke aerosols. The annual rainfall deficits were broadly consistent with the reduction in annual river discharge for 1926—estimated at 30–40%. The reduction in peak discharge during 1926 was closer to 50%. Sternberg (1987) describes an unparalleled drop in the floodwater levels of the Rio Negro at Manaus during the El Niño event in 1925–1926. During the severe dry season of that year a great fire blazed for over a month, scorching the vegetation along the main channel. The drought also affected the Orinoco Basin with widespread and drought-related fires in the savannas.

9.4.2 The flood of 2009

During austral summer and fall 2009, the Amazon Basin, drained by the Amazon River and its tributaries was hit by heavy flooding. Water levels rose higher, and stayed at flood stage for longer, than in the past several decades. According to national and international press coverage, almost 376,000 people were left homeless and 40 deaths resulted from the flooding. Communities living on the river banks and in urban areas (e.g., Manaus), suffered the impacts of the rising waters. Populations of already endangered species were adversely influenced. Damages are estimated in the order of US$200 million in the Brazilian state of Amazonas.

Total rainfall during the summer of 2008–2009 was very high across all of Amazonia (Figure 9.4(c,d)), with some areas doubling their normal precipitation. Initially (December–February) northern and northwestern Amazonia were especially wet, but by February–May, the strongest anomalies were evident in the transition region between eastern Amazonia and northeast Brazil. In central Amazonia, rainfall in April, May, and June was between normal and above normal. Rainfall anomalies reached values of about 100 mm above normal for most of central and eastern Amazonia in December 2004–February 2005 and over northeast Brazil in March–May 2009.

According to the measurements of the State University of Manaus (UEA), the abundant rainfall during January–February 2009 in northwest Amazonia caused high stands of the Solimões River at Tabatinga in March–April, with the levels reaching 12.5 m compared with the long-term pattern of 11.8 m. The higher levels of the Rio Negro at Manaus and the Amazonas at Òbidos were delayed by a few months. The Rio Negro at Manaus reached its maximum discharge between May and July. The measurements at the Manaus site reflect both the contributions of the Rio Negro and the Rio Solimões. It took about 4–5 months for rainfall that fell on the upper basin of the Rio Negro in northwest Amazonia to travel downstream to the Manaus gauge site. Therefore, the anomalously high levels measured during June and July were due mostly to the intense rainfall that fell during January and February 2009 over northwestern Amazonia. Rainfall in May and June over central Amazonia,

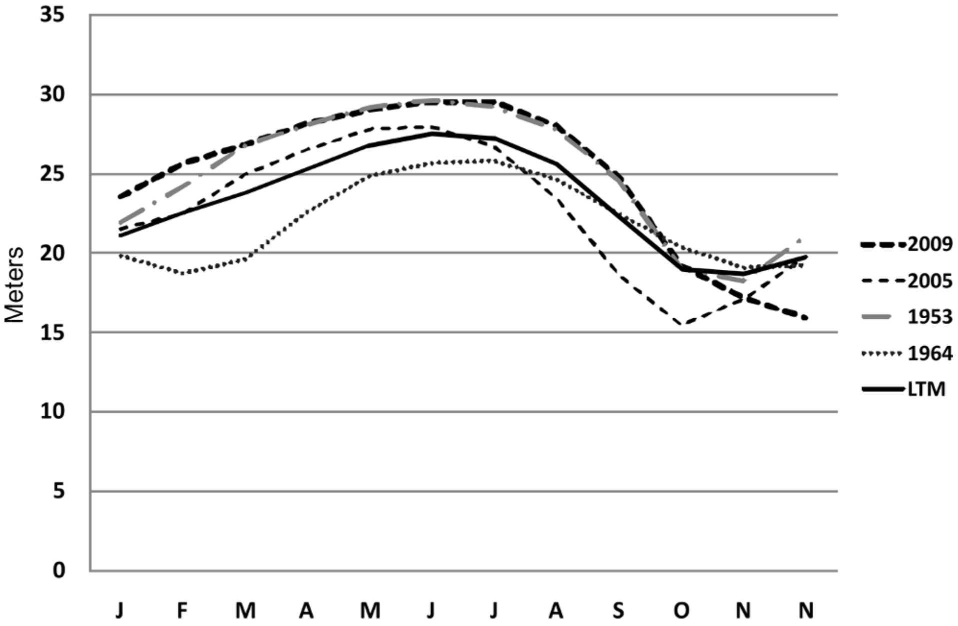

Figure 9.5. Annual values of the levels of the Rio Negro in Manaus, Brazil (in meters), for some extreme years: dry (1964, 2005), wet (1953, 2009), compared with the LTM for 1903–1986. Source: CPTEC/INPE.

where the rainfall takes 1 month or less to reach the gauge site at Manaus, was probably a relatively minor component of this discharge.

According to the Brazilian Geological Survey, the floods in Amazonia in 2009 were the highest in recorded history. The rise of the Amazon rivers began as early as March 2009. By July 2009, the levels of the Rio Negro in Manaus had reached 29.75 m, a new record high since the beginning of data collection in 1903. The five previous record highs observed in Manaus were: 1953 (29.69 m), 1976 (29.61 m), 1989 (29.42 m), 1922 (29.35 m), and 1908 (29.17 m). The Amazon River at Òbidos and the Tapajos River at Santarem also showed records high water levels since the beginning of data collection (Figure 9.5). Similarly, the levels of Peruvian rivers, the Amazonas, Marañón, Napo, and Corrientes Rivers also experienced record level/discharge highs, according to SENAMHI (the meteorological service of Peru).

The immediate cause of the unusually heavy rains across northern Brazil (Amazon and northeast Brazil regions) was associated with anomalously warm conditions in the tropical south Atlantic Ocean and a southward position of the ITCZ. Normally, the ITCZ, and its related rainfall, moves northward in April, but in 2009 it remained near its southern limit until May. Consequently, the moisture transport from the tropical Atlantic into the Amazon region was very intense. Almost simultaneously, La Niña conditions were detected in the tropical equatorial Pacific in 2009. Such mechanisms intensified the upward branches of the Walker and Hadley Cells, leading to persistent ITCZ episodes that caused very abundant precipitation conditions, sometimes concentrated over a few days, in most of the Amazon region. This pattern was especially evident in central and eastern Amazonia.

9.4.3 Climate change and extreme events in the Amazon Basin

Extreme droughts can lead to widespread forest fire regardless of whether they are caused by a very strong El Niño event or an anomalously warm tropical North Atlantic. Forest fires are exacerbated by man-made agricultural fires which run out of control and initiate fires in drought-stressed adjacent forest areas. In summary, land-use and land-cover change, droughts, and fire, reinforce each other through positive feedbacks (Nobre and Borma, 2009).

If severe droughts become more frequent in the future, which is a common projection for a warmer planet, then the process of savannization of eastern Amazonia may accelerate. Cox *et al.* (2008) suggest that intense droughts, such as those of 2005 could become more frequent and intense as climates warm in the second half of the 21st century. The probability of a "2005-like" year occurring in the HadCM3 run with aerosols, is approximately a 1-in-20-year event, but will become a 1-in-2-year event by 2025 and a 9-in-10-year event by 2060. These thresholds obviously depend on the rate of increase of CO_2, which is itself dependent on the emissions scenario chosen, resulting in a rapidly increasing risk of 2005-like droughts in Amazonia under conditions of reduced aerosol loading and increased greenhouse gases.

Phillips *et al.* (2009) used records from multiple, long-term monitoring plots across Amazonia to assess forest responses to the 2005 drought, and treated it as a possible analog of future events. Affected forest lost biomass, reversing a large long-term carbon sink, with the greatest impacts observed where the dry season was unusually intense. Therefore, the Amazon forests appear vulnerable to increasing moisture stress, with the potential for large carbon losses to exert feedbacks on climate change.

On the wetter side, even though model projections suggest drier conditions in central and eastern Amazonia for the future, the risk of intense rainfall events, especially in the western side of Amazonia is higher for the last 30 years of the 21st Century. While increased likelihood of flooding in northern Amazonia (Marengo *et al.*, 2009; Tebaldi *et al.*, 2006) is a qualitative projection, quantitative estimates of the probabilities of these events are lacking.

9.5 IMPLICATIONS FOR ECOSYSTEM AND ENVIRONMENTAL SERVICES IN AMAZONIA

In general, biodiversity plays an important role in ecosystem functions that provide support, provisions, regulations, and cultural services essential to human well-being. For example, people rely on biodiversity for food, medicine, raw materials, and ecosystem services such as water supply, nutrient cycling, waste treatment, and pollination. Forest ecosystems also provide a wide array of goods and services.

Human responses to a warmer climate are likely to increase demand for freshwater to meet urban and agricultural needs. Likely results will be decreased flow in rivers and streams, causing a loss of ecosystem services.

The Amazon forest is sufficiently large to have a significant impact on the regional and even global climate system, and provides a host of ecosystem services that are threatened by deforestation. As deforestation approaches this critical threshold, we can expect the marginal value of the forest ecosystem to rise rapidly, approaching the infinite if we believe that the loss of the Amazon ecosystem is unacceptable. Compounding the uncertainty of how much forest loss the climate system can tolerate before it can no longer generate adequate rainfall to sustain itself, are the regional effects of global climate change.

Studies of the hydrological cycle in the Amazon suggest that it recycles as much as 50% of its rainfall, and that if as little as 30% of the Amazon is cleared, it will be unable to generate enough rainfall to sustain itself, leading to a positive feedback loop of more forest loss and less rainfall. Rainfall in other words is essential for sustaining the Amazonian ecosystems and all the ecosystem services they generate. Indeed, the value of the Amazon as a water-regulating eco-utility becomes indistinguishable from the value of all ecosystem services generated by the Amazon. The Amazon forest releases water vapor to the atmosphere daily, transferring heat, moderating weather conditions and supplying Brazil and the La Plata Basin further south with rainfall on which US$1 trillion of agribusiness, hydro-power, and industry depend. Reduced rainfall in the Plata Basin would impact agriculture, industry, and hydro-electricity. These sectors are responsible for 70% of the GNP of five Latin American nations. Rainfall in the Plata Basin is derived from moisture from the Amazon Basin together with local evaporation in the Plata Basin, cold fronts from the south, and air masses from the South Atlantic. The major economic region of Latin America depends to an as yet unknown extent on rainfall from the Amazon.

These ecological services provided by the Amazon Basin may be threatened by global warming through a middle-century, climate-driven dieback and substitution of forests by savannah-like vegetation. Changes in rainfall and atmospheric moisture transport resulting from declines in Amazonian forest cover will need to be considered in addition to changes resulting from global climate change. Further research is needed to investigate the role of the forest in the economic well-being of the continent and to integrate this information into policies and practical activities to conserve the Amazon and provide benefits to its inhabitants. The introduction of payments for environmental services offers an opportunity for traditional and indigenous populations to be compensated for contributing to carbon sequestration in meeting the challenge of ameliorating global warming (Hall, 2008).

Besides the environmental impacts of expanding agribusiness and poor forestry practices, unsustainable development in the Amazon has also led to significant poverty and social inequality (Viana, 2009). Forests have historically been seen as valueless and forestry as backwards—neither of them worthy of inclusion in "development" strategies or in the usual set of policy instruments encouraging relevant investment, such as tax incentives and credit. Yet the significant problems deforestation causes now suggest that forests need to be regarded as valuable assets to individuals, families, businesses, and governments. In short, public, non-profit and private sector policies have to be guided by a simple message: ‘‘forests are worth more standing than cut’’. This paradigm shift has to be translated into broad cross-sectorial policies in areas such as finance, education, health, energy, and sustainable land use systems.

Tropical forests are ‘‘eco-utilities’’ providing critical ecosystem services that underpin food, energy, water, and climate security on local to global scales. Currently, these services are unrecognized and unrewarded in international policy and financial frameworks, causing forests to be worth more dead than alive. Some valuations of standing forests in the Amazon have produced very positive results. On the one hand are the results of public policies aiming to increase the value of forest products—such as honey and managed timber—supporting private sector investment and social–environmental entrepreneurship. On the other hand, environmental services such as carbon sequestration and storage have big potential and are a key part of the equation too. The more valuable environmental services are the more resources will be available for investment in improving local people’s quality of life and ability to generate income.

Trivedi *et al.* (2009) described the tropical forest eco-utility in the form of (a) carbon capture and sequestration—mitigating climate change, (b) water pumping moderating surface temperatures, (c) rainfall recycling—supporting energy and food security. The Amazonian eco-utility can be assessed in the form of standing forests, frontier forests, and deforested and degraded land. Standing forests support human populations that are not currently clearing large areas of forest. In contrast, frontier forests are under direct and immediate threat from human activities, as in the ‘‘arc of deforestation’’. In such areas, the eco-utility services are being replaced by other ecosystem services such as agricultural production and forestry operations. Finally, there are large areas that were once forest but have been converted to agriculture and are now degraded of their natural capital. Conservation and sustainable development activities should aim to support the standing forests, stabilize the frontier, and restore the degraded forests.

Looking to the future, the conservation of Amazonian forests may prove to be based in green economics, while the greatest threat may come from the brown economics of forest destruction and climate-changing pollution. Much attention is currently focused on REDD (Reducing Emissions from Deforestation and forest Degradation) and afforestation and reforestation as mitigation options (Trivedi *et al.*, 2009). In short, the more profitable sustainably harvested forest products become, and the more realistic the accounting of ecosystem-services offered by forests, the less attractive deforestation becomes.

9.6 SUMMARY

The dieback of Amazonian forest in the 21st Century remains a distinct possibility, even though the uncertainties are still high. As a consequence of this dieback, some model experiments predict a large-scale substitution of Amazon forest by savanna-like vegetation by the end of the 21st century. To minimize the potential risk of this dieback and savannization, a reduction in global greenhouse gas emissions is needed, and reducing land use cover change is one of the forms of mitigation. The stabilization of Amazonian deforestation and degradation would be an opportunity for local adaptation to climate change, as well as a potential global contributor toward mitigation of climate change. Maintaining forest cover would be the best strategy for climate change mitigation, regional development, and biodiversity conservation.

El Niño–Southern Oscillation (ENSO) and tropical North Atlantic feedbacks are likely to increase the severity and frequency of droughts and floods, as the Earth warms. The century-scale events of 2005–2010, in which severe droughts, floods, and fires, exerted pressure on Amazonian ecosystems, may become the norm rather than the exception by mid-century. Synergies of climate change and land clearance pose the greatest of all threats to Amazonia, threats that to some extent could be mediated by appropriate policy. Proper accounting of the benefits of ecosystem services offered by forests must be a priority for the development of forest conservation policy under climate change.

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10

Plant species diversity in Amazonian forests

M. R. Silman

10.1 INTRODUCTION

Looking at the Amazonian landscape from space one sees unbroken forest stretching from the eastern lowlands of Colombia south through Peru to Bolivia, and east from the Andes to the Atlantic Ocean. The expanse of trees—covering over half a billion hectares—is draped over a relatively flat landscape broken only by large rivers and human-induced habitat modification (Figure 10.1a).

Amazonian forests are the most diverse on the planet, estimated to harbor 30,000 species of vascular plants, with 5,000–10,000 species of trees alone (Henderson *et al.*, 1991; Thomas, 1999; Myers *et al.*, 2000). While we have a picture of Neotropical forests as spectacularly diverse, how diversity is distributed across the landscape is less well-known. The monotonous green sameness belies large changes in diversity and species composition of the forest. A hectare of Amazonian forest may harbor anywhere from 30 to 300 species of trees, and may be dominated by one of more than a dozen different plant families (Gentry, 1988). As one moves across the Amazon Basin, forest composition and diversity changes at all spatial scales (Campbell, 1994). Species lists of trees from an eastern Amazonian site on poor soils are bewilderingly unfamiliar to a botanist trained in western Amazonia. Go from upper Amazonian forest on predominantly rich soils to the poor soils of eastern Amazonia and the character and composition of the forests will be as distinct as those of the major forest classes in temperate areas. Changes in community composition on different soils at local scales can be equally dramatic (Balslev *et al.*, 1987; Duivenvoorden, 1996; Lips and Duivenvoorden, 1996; Tuomisto *et al.*, 2002; Phillips *et al.*, 2003; Masse, 2005). In a new set of 1 ha plots in western Amazonia, rich- and poor-soil plots have <5% overlap in species (N. Pitman, unpublished). Ecological interactions have been shown to underlie interspecific trade-offs in performance on distinct soils, and the diversification of certain clades shows repeated evolution of edaphic specialization (Fine *et al.*, 2004, 2005).

M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

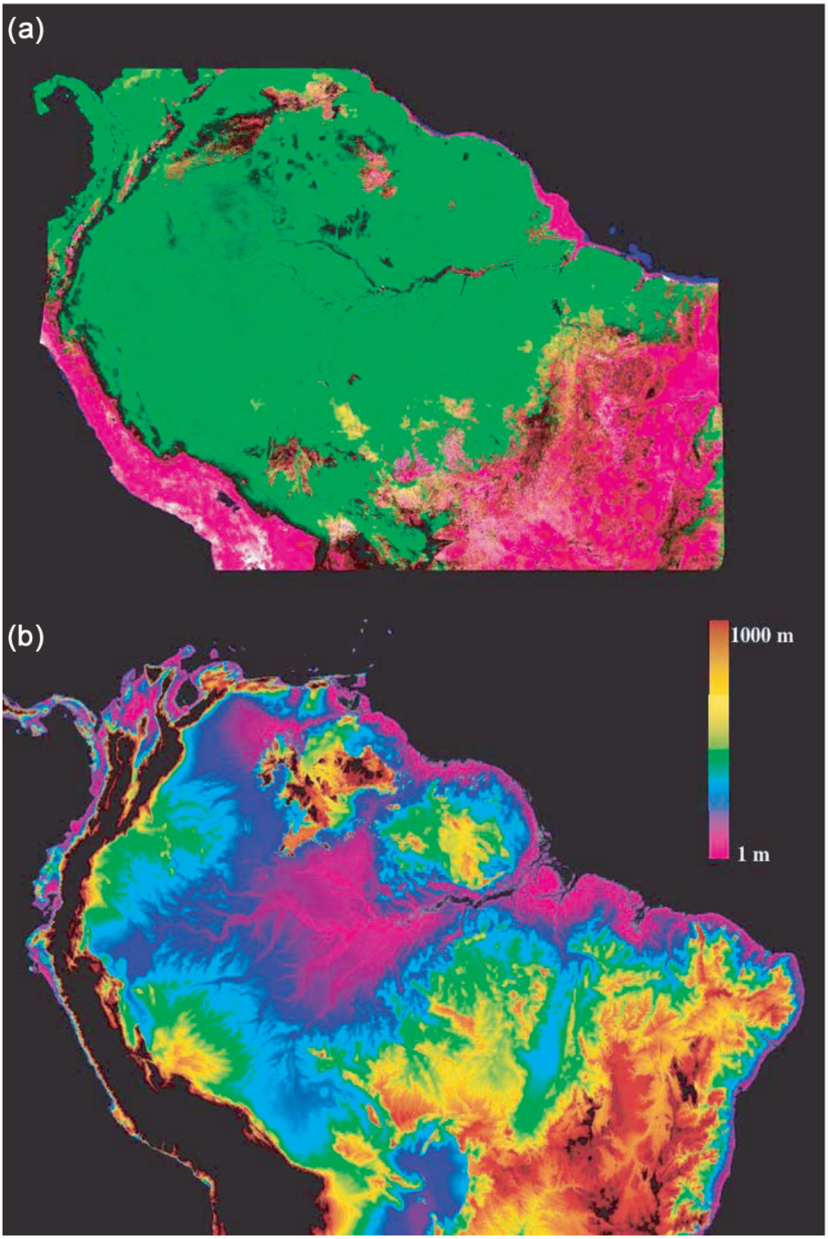
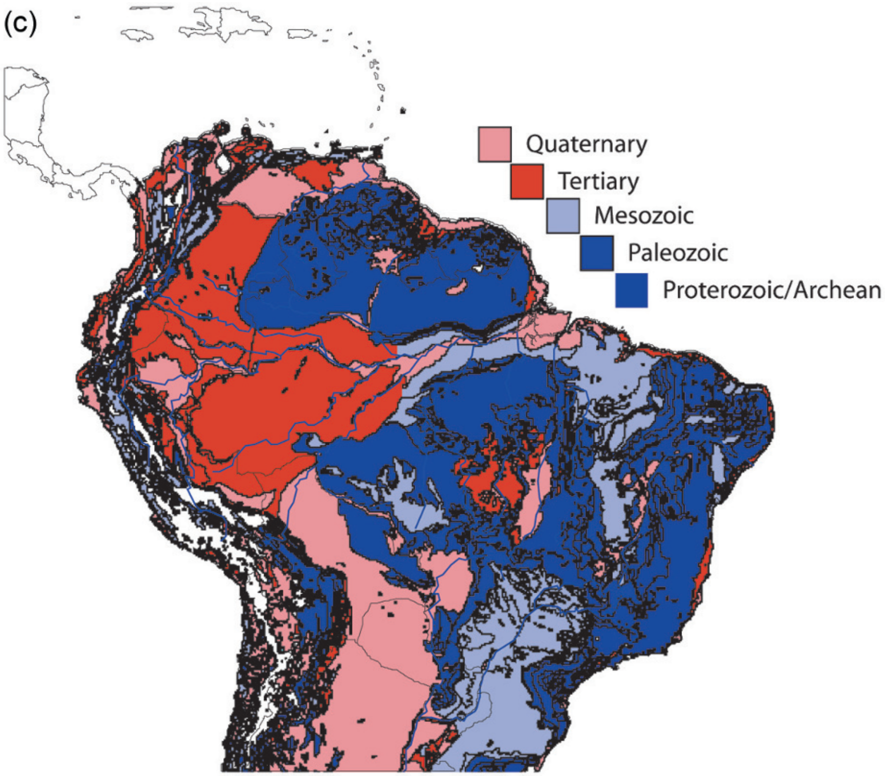


Figure 10.1. Overview of Amazonian geography: (a) Vegetation cover shown as false color composite of MODIS reflectance data. Areas from light to dark green represent open to densely covered forest, grasslands and woodland savannas appear pink to red, and areas of no vegetation including water and wetlands appear black. (b) Topographical variation across the Amazon Basin represented by SRTM (Shuttle Radar Topography Mission) elevation data. (c, facing page) Ages of surface geology.



Looking further into the environmental variables underlying changes in composition and diversity, it becomes clear that climates in Amazonian forests range from highly variable both within and among years to near absolute monotony, and that forests are underlain by geologies ranging from bleached and nutrient-poor metamorphics and granites from the earliest parts of the Earth's history to young sediments weathered from the Andes.

This suite of features of the Amazonian landscape—its immense size, variable climates, heterogenous geology and soils—has been pinpointed as the reason for its high plant diversity in the ecological literature (Willis, 1922; Terborgh, 1973; Rosenzweig, 1995), even though the low diversity in the vast expanses of Siberian forests or the high diversity of geographically-restricted South African plant communities provide poignant counter examples. Moving beyond the simple assumption that large areas, long timespans, and high environmental heterogeneity equal high species diversity, how each of those factors—gradients in soils, climate, and geological history—influence forest diversity at sites (alpha diversity), how diversity in a landscape accrues as one moves across sites (beta diversity), and how these combine to form regional (gamma) diversity is only recently becoming known and even more rarely integrated into explanations of diversity that treat both local and regional scales (e.g., Pitman *et al.*, 2002; Ricklefs, 2004) .

Nearly 20 years ago, Alwyn Gentry (1988) wrote the first quantitative paper on neotropical forest diversity and floristics, examining four environmental gradients: latitude, precipitation, soils, and elevation. Though providing empirical hypotheses for patterns of diversity across gradients, Gentry's paper was based on just 38 lowland and 11 montane 0.1 ha plots, and just a few preliminary hectare inventories in upper Amazonia. Since 1988, empirical work on Amazonian flora has exploded, including over 400 ha of tree inventories in the Amazonian lowlands (Ter Steege *et al.*, 2003; ATDN, 2006). New climatological tools, such as satellite-based measurement of rainfall and compilations of station data, paint a more complex picture of precipitation amount and variability—both within and among years—than previously known (Malhi and Wright, 2004; Marengo, 2004; Chiu *et al.*, 2006). In many cases the details of the gradients Gentry (1988) treated are only now becoming known due to advances in remote sensing and ongoing revisions of our understanding of Amazonian historical geology, climatology, and paleoecology. Geological surface and soil data were even sparser in the 1980s, particularly in western Amazonia, where ages were poorly constrained, and large expanses of terrain had never been visited by geologists. Consequently, soils were often classified simply through educated guesses based on aerial photos and satellite images. Andean uplift timing was relatively unconstrained, and the modern understanding of the complex history of the formation of the modern Amazon River from the Miocene through the present was a little-known hypothesis. How these new data on environmental gradients affect our understanding of diversity remains unexplored.

This chapter looks at patterns of within-site (alpha), between-site (beta), and regional (gamma) diversity in Amazonian forests. A goal is to update patterns of floristic composition and diversity given the current understanding of Amazonian climatology, geology, and history, revisiting Gentry's ideas in the light of new data.

10.2 STUDY SITE: OVERVIEWS OF AMAZONIAN GEOGRAPHY, GEOLOGY, AND CLIMATE

An overview of Amazonian geography is central to understanding the environmental gradients that influence Amazonian plant communities. The following sections give an overview of current empirical results and hypotheses regarding environmental gradients in the Amazon Basin.

10.2.1 Amazonian geography, geology, and soils

The Amazon Basin is largely in the southern hemisphere, with its bulk lying south of ~3°N in the west and ~1°N in the east. The Amazon Basin proper has its western border in the Andean highlands of Bolivia, Peru, Ecuador, and Colombia, where large white-water rivers—the Madeira, Ucayali, Marañon, Napo, and Caqueta—descend onto the large alluvial fans of upper Amazonia (Figure 10.1b). West of Manaus, Brazil, the *terra firme* habitats along the Amazon are a complex mix of young (Late

Tertiary and Quaternary) sediments derived from changing depositional environments (Räsänen *et al.*, 1992; Hoorn, 1994a, b; Potter, 1997; Hovikoski *et al.*, 2005; Rossetti *et al.*, 2005). Soils in the western lowlands range from rich soils on the higher elevations of the alluvial fans to a mosaic of rich and poor soils along the main stem of the Amazon from Iquitos eastward (Davis *et al.*, 1997). The northern limit of the Amazon Basin lies ~3°N on the highly weathered Paleozoic sandstones and Proterozoic/Archean metamorphic series of the Guianan Shield with soils that are largely podzolized and deeply acidic (Ducke and Black, 1956; Davis *et al.*, 1997; Johnson *et al.*, 2001; Malhi *et al.*, 2004). These ancient and nutrient-poor landscapes are drained in the west by the black-water rivers of the Río Negro system: the Vaupés, upper Negro, and Branco. The southern and south-eastern limits of the Amazon Basin lie on Proterozoic metamorphic rocks of the Brazilian Shield and are drained by the clear water Tapajos and Xingú river systems (for a general overview see Sioli, 1984; Schenk *et al.* 1997). As in Guianan Shield areas, soils are largely poor, particularly when compared with those on upper-Amazonian alluvium (Figure 10.1c).

The geology of the basin is such that there are relatively fertile soils on young alluvium and recently exposed rock formations of Andean orogeny in the western Amazon Basin, which are replaced by alluvial deposits weathered from the Guianan and Brazilian Shields along the main stem of the Amazon, and poor soils on some of the oldest rocks on Earth at the northern and southern limits of the Amazon (Schenk *et al.*, 1997) (Figure 10.1c). This pattern of origin leads to a broad correlation between substrate age and fertility in the Amazon, with soils derived from younger geological formations generally more fertile than those derived from old (Malhi *et al.*, 2004).

Studies on Amazonian historical geology show the basin to be dynamic, with modern Amazon drainage being a relatively recent (Late Miocene to Early Pliocene) geologic feature whose origin is concurrent with, or even later than, the divergence of many animal and plant taxa (Potter, 1997; Rossetti *et al.*, 2005). From the Paleozoic through the Cretaceous the non-shield areas of the Amazon were depositional environments (Potter, 1997). To the east of Manaus, deposition largely stopped in the Cretaceous, save for the Miocene fluvial deposits of the Barreiras Formation and Quaternary deposits along river banks (Irion *et al.*, 1995; Potter, 1997; Rossetti *et al.*, 2005). From the Paleozoic through the Miocene, waters drained west from shield areas onto a continental margin and then, with the uplift of the northern Andes in the Miocene, as series of lacustrine and transitional marine habitats. Late Tertiary tectonic changes in land elevation caused the Amazon to change flow from westward to eastward, adopting its current bed through the depression between the Guianan and Brazilian Shield areas at Santarem (Hoorn, 1994b; Hoorn *et al.*, 1995; Potter, 1997).

Direct correlations between plant diversity as derived from inventory data and geology require high-resolution maps of soils and surface geology. While several excellent country-wide campaigns are currently underway (e.g., the Peruvian INGEN-MET and Brazilian CPRM geological survey campaigns), geological maps of the Amazon Basin have spotty coverage (e.g., Rosetti *et al.*, 2005). The problem is compounded by nomenclatural differences in geological formations that span several countries.

Gentry (1988) hypothesized that diversity would be positively correlated with soil fertility, but that the effect would be subsidiary to precipitation amount and predictability. Subsequent research has found a large effect of soil fertility on productivity in Amazonian forests (Malhi *et al.*, 2004), but not diversity (Clinebell *et al.*, 1995). The present analysis looks at diversity as it relates to depositional age (which is correlated with substrate type) using a compilation of South American geology from the United States Geological Survey (Schenk *et al.*, 1997), updated with information from Brazil's CPRM and Rosetti *et al.* (2005).

10.2.2 Elevation

Except for its western and northern extremities, the Amazon Basin is marked in its flatness; 85% of the Amazon Basin, including its Andean headwaters, are under 500 m in elevation. Ninety-seven percent of rainforests lie below 500 m (S. Saatchi, pers. commun.). The main stem of the Amazon drops only 215 m from where the Marañón passes the final Andean foothill at the Pongo de Manseriche to its mouth 3,200 km away at Ilha de Marajó (Figure 10.1b). To the north and south of the Marañón, alluvial fans of Andean sediments rise to ~400 m at the base of the Andean foothills. The northern limit of Amazonia rises up to ~2,000 m in the Tepuis of the Guianan Shield, and the southern limit of the basin gradually rises up to ~1,000 m on the Brazilian Shield. The western border of the basin is found on the east Andean flank, with forests rising to 4,800 m in the *Polylepis* woodlands of the high Andes (e.g., Hoch and Korner, 2005). Given the measured moist air lapse rate of 5.6°C km^{-1} (Bush *et al.*, 2004), elevation *per se* will have little effect on lowland Amazonian forests, save for the transition from lowland to Andean forests at the basin's western margin.

10.2.3 Precipitation

The Amazon River discharges roughly 20% of Earth's river water that reaches the ocean, even though its basin occupies just 2% of continental land area. The spectacular discharge rate is due to the deep convection that forms over the Amazon Basin, the moisture brought in from the Atlantic by easterly winds, and the huge amounts of orographic rainfall generated as water vapor from the Atlantic is forced upwards by the Andean massif. While the mean annual rainfall is ~2,400 mm yr^{-1}, precipitation is not uniformly distributed over the Amazon Basin, either in space or in time (Sombroek, 2001; Malhi and Wright, 2004; Marengo, 2004). The number of dry months (months averaging <100-mm precipitation) at Amazonian sites ranges from 0 to 8, and annual precipitation over closed-canopy humid forest and rainforest varies from 1,200 mm yr^{-1} in the southeastern Amazon Basin to >8,000 mm yr^{-1} in the Andean foothills.

Total rainfall in the Amazon Basin is high in a large region of upper Amazonia in northeastern Peru, eastern Ecuador, eastern Colombia, and western Amazonas state in Brazil, as well as near the mouth of the Amazon in eastern Pará and Amapá states. High-rainfall areas are also found along the base of the Andes to from ~5°N to ~16°S. Rainfall amounts drop rapidly south of ~6° to 8° in the western and central Amazon. A region of lower rainfall in central Pará state, the Roraima territory of Brazil, and adjacent Guayana and Surinam is known as the transverse dry belt (Nimer, 1977; Pires and Prance, 1977, Davis *et al.*, 1997), though total annual rainfall in this area is as high as much of the upper-Amazonian forests in southeast Peru and Acre, Brazil.

Precipitation varies temporally in the Amazon Basin on all time scales, even though the effects of super-annual variation on diversity have been little studied. Variability ranges from daily cycles and anomalies in rainfall rate due to local climatic processes, to intra-annual variation in rainfall, to among-year variation in rainfall driven by changes in sea surface temperature—such as ENSO and the North Atlantic Oscillation (Marengo *et al.*, 2001; Pezzi and Cavalcanti, 2001; Marengo, 2004). On even longer time scales, precipitation changes are driven by the orbital parameters of Earth and their interaction with proximate climate drivers—such as the South American Low-Level Jet and the South American Convergence Zone (Baker *et al.*, 2001; Cruz *et al.*, 2005). Far from being static, detailed paleoclimatological reconstructions show that the main atmospheric and oceanic features influencing climate in the Amazon Basin show large variations through time. Indeed, modern studies correlating these drivers with historical weather patterns show that temporal variation also translates into differential spatial effects across the Amazon Basin (Giannini *et al.*, 2001; Cruz *et al.*, 2005; Vuille and Werner, 2005).

Previous empirical hypotheses of tree diversity suggested that tree diversity increased with precipitation amount and decreased with the number of months having <100-mm precipitation, a figure where evapotranspiration exceeds precipitation in a typical lowland ecosystem (Gentry, 1988; Clinebell *et al.*, 1995; ter Steege *et al.*, 2003). Annual precipitation amount and dry-season length are also inversely correlated with each other (Figure 10.2a).

Precipitation regimes have traditionally been characterized in terms of monthly and yearly averages interpolated from existing gauges, with varying degrees of quality and duration (e.g., Sombroek, 2001). Much of the Amazon Basin remains wilderness, and large areas are without rain gauges, particularly in upper Amazonia. In the present analysis we use satellite measurements of total monthly precipitation on a $0.25^\circ \times 0.25^\circ$ grid collected over 7 years by the Tropical Rainfall Monitoring Mission (Chiu *et al.*, 2006). These data give complete temporal and spatial coverage for precipitation across the tropics in grid-cells just less than 30 km per side, or for every ~900 km^2, and allow examination of precipitation trends in the Amazon with unprecedented clarity.

From these data we derive four measures of precipitation amount and variability: average annual precipitation; average dry-season length, taken as the average number of months with precipitation below 100 mm (Clinebell *et al.*, 1995; Sombroek, 2001; Ter Steege *et al.*, 2003); inter-annual variability, taken as the coefficient of variation of rainfall among years; and total variability, taken as the coefficient of variation among months over the 7-year period.

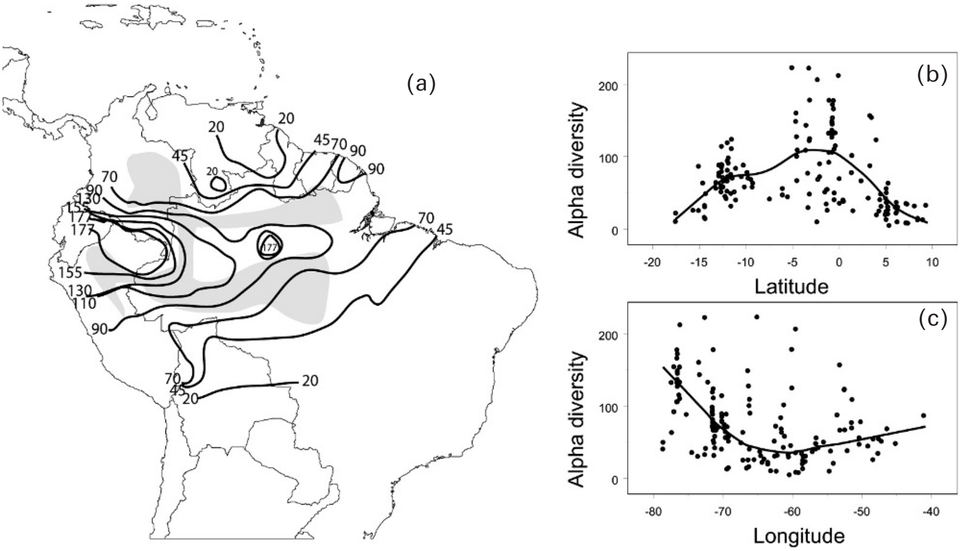


Figure 10.2. (a) Local (alpha) diversity derived from 423 1 ha Amazonian tree plots. Isoclines drawn from universal kriging fit for 1° grid-cells. Figure adapted from *Amazon Tree Diversity Network*. Shaded regions show areas with no inventory plots. (b) Local diversity versus latitude. (c) Local diversity versus longitude.

10.2.4 Species diversity and environmental gradients

To look at the influence of these environmental gradients on species diversity, we looked at alpha and gamma diversity in Amazonia (Whittaker, 1972). Alpha diversity was measured as both species density ($\mathrm{N\,ha^{-1}}$) and also Fisher's alpha (Fisher *et al.*, 1943). Fisher's alpha has been used extensively in comparisons of neotropical forest diversity as it is relatively independent of plot size (Condit *et al.*, 1996; Leigh, 1999; Ter Steege *et al.*, 2003). Gamma diversity was estimated as the total number of species that include a given latitude and elevation within their range (Silman *et al.*, unpublished).

Data on tree species diversity from individual locales were taken from compilations of Ter Steege *et al.* (2000) and Pitman *et al.* (1999, 2001), as well as unpublished data of J. Terborgh, P. Núñez and N. Pitman. Basin-wide estimates of tree alpha diversity were taken from universal kriging estimates based on 423 plots in moist *terra firme* forest in Amazonia and the Guianan Shield (Ter Steege *et al.*, 2003, as updated by the ATDN, 2004). Gamma diversity estimates for upper Amazonia and the adjacent eastern Andes are derived from 263,000 collections of vascular plants from 0 to 23°S in Ecuador, Peru, and Bolivia, housed in the Missouri Botanical Garden TROPICOS database (Silman *et al.*, unpublished).

Many of the analyses are simple correlations or graphical comparisons of empirical patterns of diversity with environmental gradients. In cases where multiple factors are compared quantitatively, relationships were modeled non-parametrically using generalized additive models (GAMs; Hastie and Tibshirani, 1990). GAMs make no assumptions about the form of the relationship among variables, letting the data present empirical hypotheses.

10.3 RESULTS

10.3.1 Precipitation: patterns

Patterns of precipitation amount and variability in Amazonia change with both latitude and longitude. Analysis of TRMM data shows average annual precipitation in the Amazonian lowlands peaks at ~2–4°S latitude, with a broad plateau from ~4°N to 4°S of the equator. Precipitation decreases steadily to the south and north (Figure 10.3e). Precipitation at low latitudes can be either high or low, while sites to the north and south have more uniformly low rainfall. Precipitation variability, measured as dry-season length and total variability, reaches a minimum between ~1°N and 4°S (Figures 10.3a and 10.3c, respectively). Large areas of upper Amazonia have almost no variability in rainfall from month to month and year to year. Near the equator at Yasuní, Ecuador, maximum monthly rainfall has occurred in every month of the year (Pitman *et al.*, 2001). Precipitation variability increases as one moves away from the equator, with dry season length increasing through 20°S, and precipitation variability reaching a peak ~15°S (Figures 10.3a, c).

In contrast to latitude, mean annual precipitation shows little relationship to longitude, though areas of high rainfall are more common in western Amazonia, causing a slight decrease in average rainfall as one moves from west to east (Figure 10.3f). Dry season length is on average shorter in western Amazonia and increases to the east, though the main cause of the trend is the absence of areas with no dry season in eastern Amazonia (Figure 10.3d). Total variability in rainfall is lowest in western Amazonia and increases consistently as one moves east (Figure 10.3b).

As noted by other authors, precipitation variables are correlated (e.g., Gentry, 1988; Clinebell *et al.*, 1995; Ter Steege *et al.*, 2003). Mean dry-season length decreases with increasing rainfall, though areas with the highest rainfall can have dry-season lengths that vary from 0 to 4 months (Figure 10.4a). Total variability in precipitation is on average lowest in areas with high rainfall and increases with decreasing rainfall down to ~1,800 mm yr^{-1}, below which it is approximately constant (Figure 10.4b). At precipitation levels above ~1,800 mm yr^{-1}, however, one can find sites with either high or low total variability in precipitation. Variability among years shows little trend with annual precipitation above 1,500 mm yr^{-1}, save for a slight tendency for areas with high annual precipitation to have fewer sites with high inter-annual variability. Total variability in precipitation is highly correlated with dry-season length ($r_s = 0.80$), but the increase in variability with dry-season length is slight until dry seasons exceed 5 months in length.

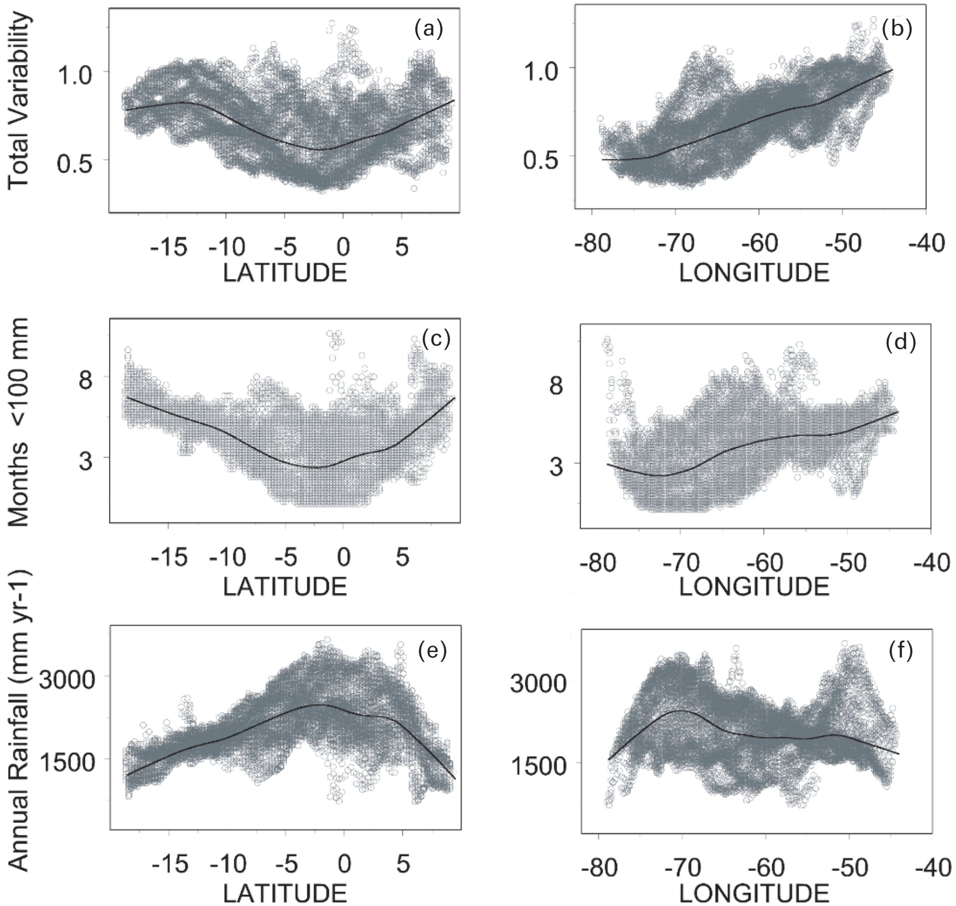


Figure 10.3. Latitudinal and longitudinal variation in Amazonian precipitation variability (a) and (b), dry-season length (c) and (d), and total amount (e) and (f) derived from TRMM measurements. Average dry-season length and precipitation variability reach a minimum centered at ~2–3°S latitude. Dry-season length and precipitation variability are lowest in western Amazonia and incease to the east. Precipitation also peaks ~2–3°S, but shows little trend from west to east.

10.3.2 Latitudinal and longitudinal gradients in Amazonian diversity

Even within the tropical forests of South America there are large gradients in plant species diversity (Gentry, 1988, figs. 2a–c). For both tree alpha diversity and vascular plant gamma diversity, diversity has a broad peak between ~1°N and 5°S. South of 5°S, tree alpha diversity decreases steeply and nearly linearly with latitude (Figure 10.2b). Regional (gamma) diversity of all vascular plants peaks at ~4°S and remains fairly constant from ~5°S to 10°S, decreasing rapidly south of ~14°S. To the north, Amazonian forests *sensu stricto* end at ~3°N. Even so, diversity in extralimital forests,

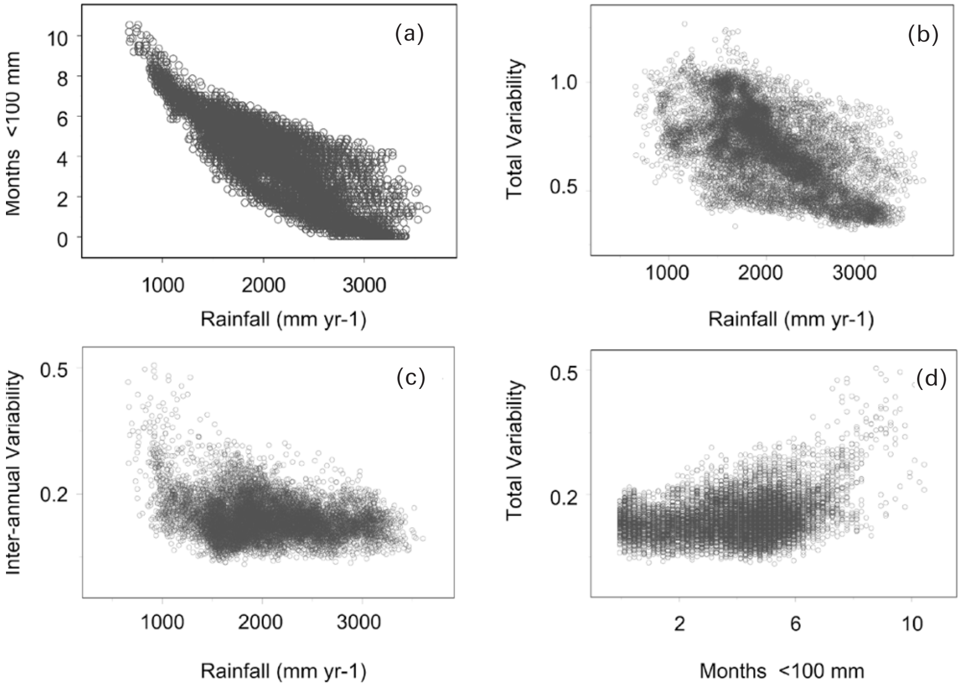


Figure 10.4. Amazonian rainfall and three measures of variation in rainfall derived from 7 years (1998–2004) of satellite measurements from the Tropical Rainfall Monitoring Mission (TRMM). (a) Total precipitation versus length of dry season as measured by months having <100-mm precipitation (Spearman's rho, $r_s = -0.85$). (b) Total variability in rainfall (measured as the coefficient of variation) among 94 months of precipitation versus accumulated rainfall ($r_s = 0.60$). (c) Inter-annual variability versus accumulated rainfall ($r_s = -0.17$). (d) Total variability versus dry-season length (Spearman's rho, $r_s = 0.86$). In all cases measures of variability in precipitation decrease with increasing rainfall. There is substantial variability in the trend, however, with sites at any given precipitation having short or long dry seasons, and predictable or unpredictable rainfall amounts from month to month or year to year.

which certainly are Amazonian in taxonomic composition, continues to decline rapidly.

The pattern of decrease in tree alpha diversity with increasing latitude is clearest in western Amazonia. Tree plot data from four inventories—Yasuni at ~0°, Loreto at ~4°S, Madre de Dios at ~12°S, and Madidi at ~15°—show that diversity remains constant from 0° to 4°S, with plots averaging ~240 spp ha^{-1} (Gentry, 1988; Pitman *et al.*, 2001; Phillips *et al.*, 2003). Between 4°S and ~12°S, however, species diversity falls to an average of 176 spp ha^{-1}, a decrease of ~27% in species diversity over 8° of latitude, or ~7 spp per degree. Between Manu and Madidi, species diversity drops to ~118 spp ha^{-1}, a drop of 36% over 2.5° of latitude, or a loss of ~23 species per degree.

In eastern Amazonia the area of highest diversity is not centered on the equator, but rather occurs to the north and to the south of it, though overall diversity remains fairly constant across a broad range of latitude (Figure 10.2a).

The longitudinal (west–east) decrease in species diversity is nearly as great as the latitudinal change (Figure 10.2b). Diversity is highest in upper Amazonia and decreases as one moves east. While exceptionally diverse forest has been found at ~60°W near Manaus, the general trend is a decrease as one moves east at any give latitude (Figure 10.2c). The decrease is highest in the band from 0 to 4°S, with high-diversity forest extending to the central Amazon near the equator (De Oliveira and Daly, 1999; De Oliveira and Mori, 1999; De Oliveira and Nelson, 2001). The longitudinal gradient in species diversity becomes much less pronounced beyond 6°N or S of the main stem of the Amazon River (Figure 10.2a).

An important result is that areas central to understanding the gradients of tree diversity in Amazonia remain largely unsampled (Figure 10.2a; see also Ter Steege *et al.*, 2003). In addition to the large areas without inventory shown in Figure 10.2a, certain habitats—such as swamp forest (Ancaya, 2000), bamboo forest (Nelson *et al.*, 1994; Griscom and Ashton, 2003; Silman *et al.*, 2003), and upper Amazonian dry forest (e.g., Gentry, 1995; Pennington, 2000, p. 265)—remain poorly sampled, reinforcing the point that this chapter presents empirical hypotheses of patterns of diversity that can be tested and updated with more sampling.

10.3.3 Diversity in relation to precipitation and geology

In the current analysis, alpha diversity shows broad correlations with both precipitation patterns and geology (Figure 10.5a–d). Total precipitation amount is positively correlated with diversity (Figure 10.5a) and average length of dry season negatively correlated (Figure 10.5d). Both reproduce the basic pattern of high average diversity in central and western Amazonia, and along the main stem of the Amazon, though with notable discrepancies. Strong gradients in alpha diversity are found across areas of high rainfall, particularly in northwest Amazonia, and, conversely, areas of low diversity are found in areas of high average annual rainfall (Figure 10.5a). Manaus, in particular, has diversity as high as western Amazonian forests, but has much lower rainfall. High rainfall areas at the mouth of the Amazon and in Guianan forests show similar diversity to much drier forests in the western Amazon. Average dry-season length, while having its minimum at areas of highest diversity in western Amazonia, also has strong gradients in diversity across areas of short average dry-season length, particularly in northwest Amazonia (Figure 10.5c).

Total variability in monthly precipitation and diversity shows a closer correspondence to the basic patterns of alpha diversity (Figure 10.5b). Isoclines in total variability largely follow isoclines in alpha diversity, particularly in southern and northwest Amazonia. The transverse dry belt, separating central and western Amazonian forests from Guianan forests, is clearly visible in these images (Figures 10.5a–c) as an area of not only relatively low rainfall, but also an area of highly variable rainfall. Species diversity in this area, and to the east, is correspondingly lower than one would expect from a forest with similar total precipitation, but lower intra- and inter-annual variability.

Geologic age also shows broad correspondence to patterns of alpha diversity, with the highest diversity forests all falling on the Tertiary and Quaternary sediments west of Manaus, and the area of high diversity extending east along a narrowing tongue of Miocene and younger-aged Tertiary sediments (Figure 10.5d). Forests on the Proterozoic- and Archean-aged rocks of the Guianan and Brazilian Shields have relatively uniformly low diversity, even in areas of high rainfall and stable precipitation regime. Geologic age remains correlated with diversity, even after accounting for the association between total variability in precipitation and geologic age (residuals from local regression fit of total variability in precipitation and alpha diversity versus geologic age, Kruskal–Wallis $\chi^2 = 14.5509$, $df = 3$, $p = 0.002$).

Because of the relatively homogeneous Middle- to Late Cenozoic sediments, patterns of diversity in central and western Amazonia present a test of precipitation's influence on diversity while minimizing variability in geologic age. Focusing on areas $\geq 60^\circ$W, where Amazonian tree plot density is highest, average alpha diversity of forest trees shows a broad peak from the equator south to $\sim 5^\circ$ with a nearly linear decrease to the south and a steeper decline to the north (Figure 10.6). Looking at the maximum diversity (*sensu* Ter Steege *et al.*, 2003) one sees broadly the same pattern, the exception being a slower rate of decrease to the north of the equator. Both of these patterns correspond well to patterns of dry-season length and total precipitation variability in the southern hemisphere. North of the equator, maximum diversity follows precipitation, while average diversity decreases more rapidly than precipitation amount or either measure of precipitation variability. Another notable feature of this figure is the paucity of plots from 0 to 5°N and 6 to 10°S (see also Figure 10.2a).

Southern hemisphere vascular plant gamma (regional) diversity increases to $\sim 4^\circ$S, then decreases slowly to $\sim 12^\circ$S, falling off rapidly as one moves farther south. Gamma diversity remains high much farther south than alpha (local) diversity (Figure 10.6). While this trend appears to be discordant with predictions based on precipitation, it is understandable in terms of how underlying species abundances change as their ranges cross the precipitation gradient. Gamma diversity in this analysis is based on range data with a species only having to include a particular latitude/elevation combination in its range to be counted. The species can be present in the landscape, but be at low abundance near the edge of its range and therefore not likely to contribute to alpha diversity (*sensu* Holt *et al.*, 1997). This influence on diversity will be particularly true when species outliers are found in local areas of suitable habitat outside its central range (Levin, 1995; Holt and Keitt, 2000).

10.3.4 Elevation and diversity

There are not enough hectare inventories from the Andes to look at changes in diversity with elevation, much less patterns of changes in diversity along the elevational gradient with respect to latitude, geology, and climatic variability (though see Boyle, 1996). However, data from neotropical inventories of all woody plants ≥ 2.5 cm d.b.h. (diameter at breast height) in both the Andes (Gentry, 1988) and Mexico (Vazquez and Givnish, 1998) show a linear decrease in diversity with elevation (Figure 10.7a). Inventories of tree alpha diversity from 1 ha plots in Costa Rica (Lieberman *et al.*, 1996) and gamma diversity in South American collection data also show a linear decrease in species number with elevation (Figure 10.7b).

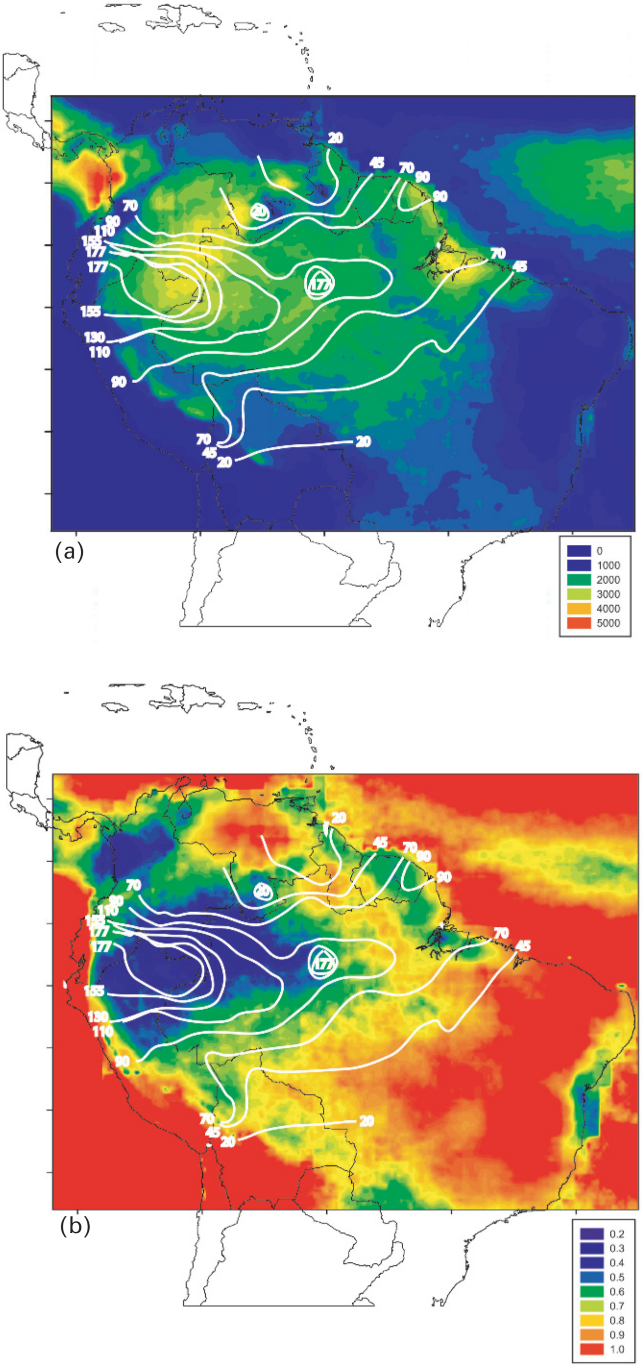
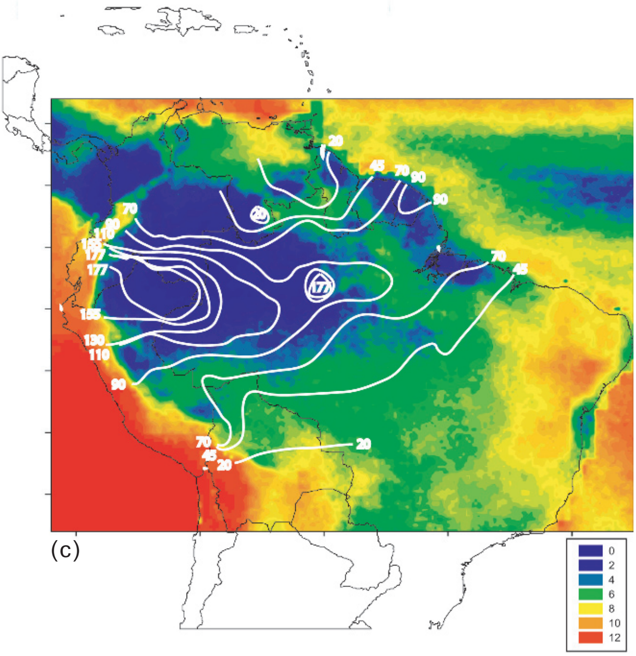


Figure 10.5. Local (alpha) diversity versus rainfall patterns and geologic age. (a) Accumulated precipitation. (b) Variability in precipitation. (c) Dry-season length. (d) Geologic age.


(c)
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45
70
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177
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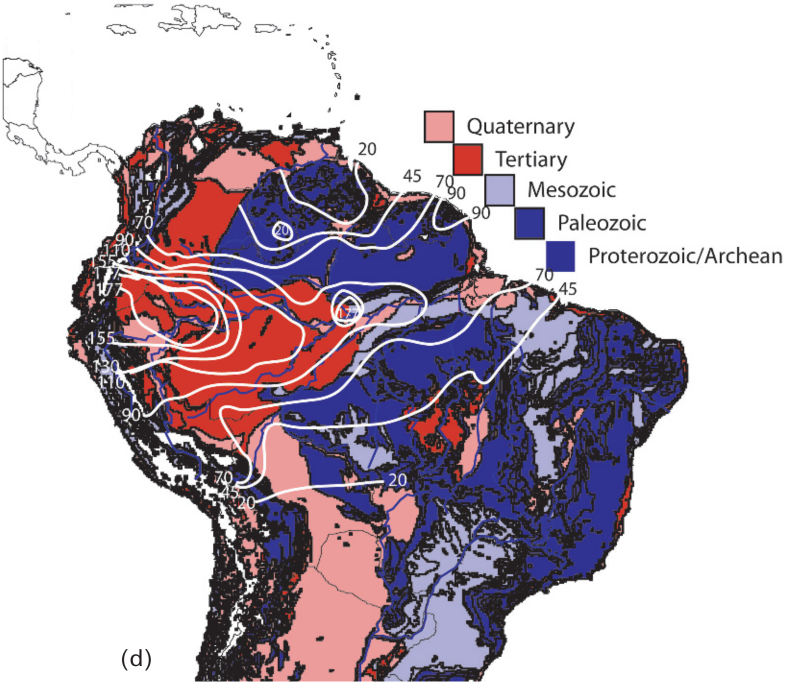
(d)
Quaternary
Tertiary
Mesozoic
Paleozoic
Proterozoic/Archean
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45
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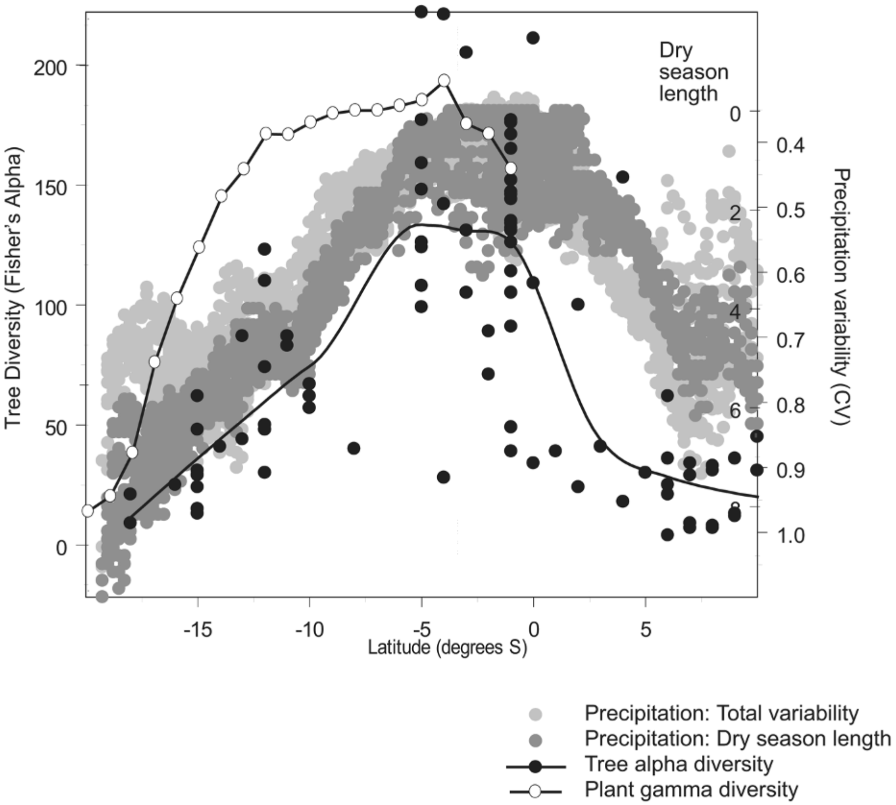

Figure 10.6. Changes in dry-season length, precipitation variability, tree alpha diversity, and vascular plant gamma diversity with latitude for western Amazonian forests. Dry-season length and precipitation variability are lowest ~2°N to ~5°S. Tree alpha diversity shows a plateau from the equator to ~5°S. Gamma diversity, measured for the southern hemisphere, peaks at ~4°S with a slow decline south to ~11°S, with a steep decline farther south.

10.4 DISCUSSION

10.4.1 Precipitation and diversity

Diversity is clearly correlated with climatic stability, and the plateau in Amazonian diversity from 1°N to 5°S falls squarely on the area with no predictable dry season, and the lowest variability in climate over time (Figures 10.5b, c). Both local and regional diversity in all data sets analyzed showed this trend. Diversity may also appear anomalously low in areas with a shorter dry season as calculated through the number of months that average below 100 mm, especially if the timing of rainfall is unpredictable and that area is subject to episodic super-annual drought that may not change average monthly figures in a systematic way. The correlation of diversity with seasonality and climate variability across latitude is seen clearly in western Amazonian

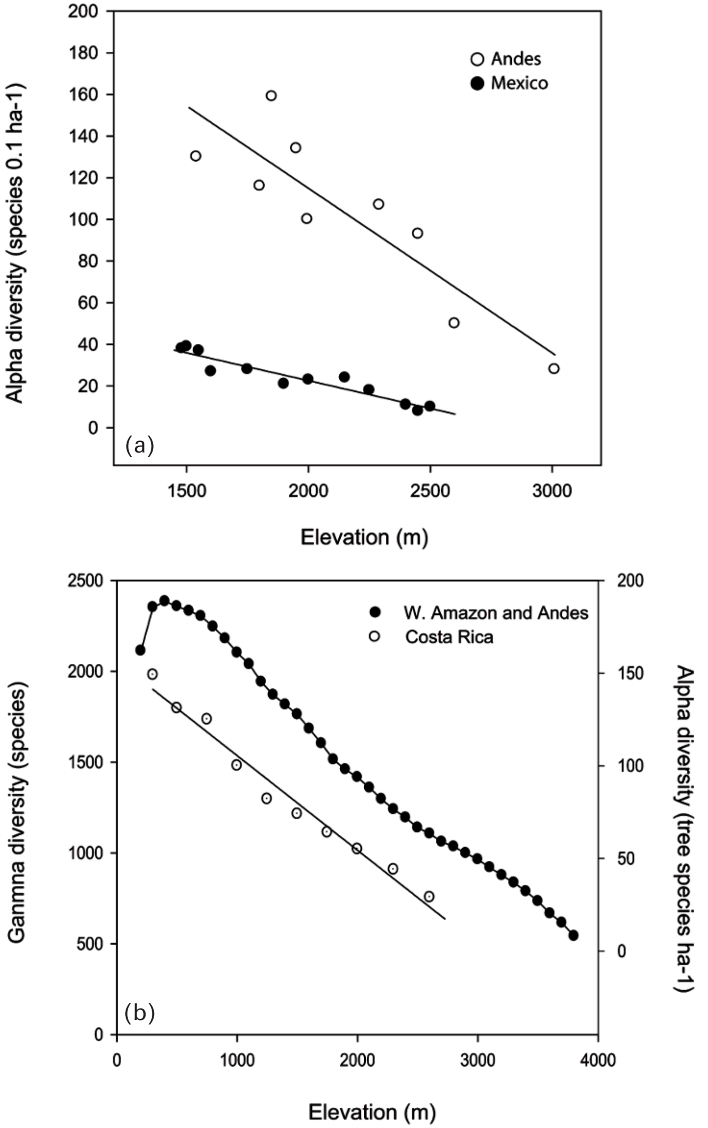

Figure 10.7. Change in species richness (N_{species}) with elevation in four Neotropical inventories (Andes: Gentry, 1988; Costa Rica: Lieberman *et al.*, 1996; Mexico: Vazquez and Givnish, 1998; western South America: Silman *et al.*, unpublished). (a) 0.1 ha diversity results for woody plants >2.5 cm dbh. Mexican results are from a single elevational transect, while Andean plots range from 11°N to 16°S. Mexico and the Andes show similar rates of change in diversity with elevation (Mexico ~70 spp km^{-1}; Andes ~60 spp km^{-1}), with a distinct number of species in the source pools (intercepts) in the two regions. (b) Results for gamma diversity (all species whose ranges include a given elevation) in western Amazonian and Andean vascular plants with ≥10 collections (left axis) and tree alpha (local) diversity from a transect of 1 ha plots in Costa Rica (right axis; replotted from Lieberman *et al.*, 1996, $r^2 = 0.99$).

plots, with the close correspondence between tree alpha diversity and climate standing in stark contrast to the patterns of vertebrate species diversity in western Amazonia, which remains nearly constant to ~14°S (Mares, 1992; Stotz *et al.*, 1996; Symula *et al.*, 2003). In addition to the latitudinal pattern, the longitudinal decrease in tree diversity in Amazonia also correlates well with both seasonality and climate variability. These data suggest that species are limited by physiological tolerances to drought, with areas of constant, wet climate decreasing water-use efficiency constraints and allowing species to occupy understory light environments that would be unprofitable in dry environments (Pitman *et al.*, 2002). Comparisons of forests along climatic stability and rainfall gradients support this hypothesis, with species diversity of forests in wet areas increasing disproportionately rapidly among understory taxa, and with certain families being much more diverse in wet areas (Gentry and Emmons, 1987; Pitman *et al.*, 2002). Givnish (1999) hypothesized that stable climate would increase distance- and density-dependence caused by moisture-loving plant pathogens. Though this complementary hypothesis remains untested, it would not necessarily predict the observed increase in specific plant families, or in understory plants. Indeed, it is unclear whether Janzen–Connell effects are stronger in the tropics than in the temperate zone (HilleRisLambers *et al.*, 2002).

Previous results have shown both absolute amount of precipitation and average dry-season length to be related to diversity (Gentry, 1988; Clinebell *et al.*, 1995; Ter Steege *et al.*, 2003). Gentry (1988) presented evidence that showed diversity to be strongly correlated with absolute rainfall. He noted, however, that it was likely seasonality, as evidenced by the strength of the dry season, which was the true cause of the increase in diversity, rather than precipitation *per se*. Clinebell *et al.* (1995; and others subsequently) demonstrated an inverse correlation between diversity and the length of the dry season, taken as the number of months with average rainfall below either 65 mm or 100 mm.

Because rainfall in the Amazon is variable on multiple time scales, precipitation stability may be a better indicator of moisture regime as it affects plants over their life-cycles. Places with high average monthly rainfall but subject to episodic drought may cause decreases in diversity belied by measures of climate means. Areas with the same "average" dry-season length can have a wide range of variability, from a very consistent dry season from year to year, to one that is highly variable among years (Figures 10.3a–d).

The main oceanic climate forcings on Amazonian forests—El Niño/Southern Oscillation and the North Atlantic Oscillation/South Atlantic Oscillation dipole—do not affect Amazonian forests equally (Pezzi and Cavalcanti, 2001). For example, the warm phase of ENSO causes drought in the northeastern Amazon and Bolivia, and increased raininess in the western Amazon in Ecuador and northern Peru and central and southern Brazil. Central and southern Peru and the central Amazon are transition areas for ENSO correlations, and can have either positive or negative rainfall anomalies depending on the event. The main effect of oceanic forcings on Amazonian precipitation is to change the length of the rainy season while not changing the daily rain rate (Marengo *et al.*, 2001). Because of this, the metric "dry-season length" varies across the Amazon. In areas of low variability the mean is representative of the long-term trend, while in areas of high variability the mean will over- or under-estimate dry-season length in any one year. Whether the variability affects forest structure and species composition awaits further study.

10.4.2 Geology and diversity

The current study shows that, for South American tropical forests, tree alpha diversity is also associated with geological age of substrate. While subsidiary to rainfall effects, alpha diversity tended to be higher on younger substrates, which in turn were more fertile substrates, even after accounting for precipitation variability (Figure 10.5d). This is almost certainly not an effect of age *per se*, but rather due to the correlation between age and fertility in Amazonian surface geology. This effect can be seen most clearly in Amazonas state of Venezuela and adjacent Brazil and Colombia, where forests on shield areas have much lower alpha diversity than those on adjacent Tertiary sediments, even though total precipitation and precipitation variability are similar. The result that the highest diversity forests in Amazonia are on some of the youngest substrates emphasizes the role of assembly through plant migration rather than *in situ* diversification (Wilf *et al.*, 2003; Ricklefs, 2004) (though Richardson *et al.*, 2001 present an interesting counterexample in the genus *Inga*). If tropical forests are museums of diversity, they are museums where the exhibits are constantly re-arranged.

Substrate also has a large effect on the floristic composition of Amazonian tree communities, and these effects are conserved at higher phylogenetic levels. At a local spatial scale, at our upper-Amazonian sites, tree plots can be reliably classified to floodplain or *terra firme* forest even if stems are only identified to family, and that result holds generally at localities across the Amazon Basin (e.g., Terborgh *et al.*, 1996). Terborgh and Andresen (1998) showed that at larger spatial scales, however, adjacent *terra firme* and floodplain sites were more similar to each other than either was to the same habitat type at a more distant site. Floodplain sediments by and large reflect local to regional sediment transport and suggest that trees are responding to soil characteristics. Another explanation would be that trees are highly dispersal-limited, and that floristic differences among regions reflect *in situ* evolutionary differences (Campbell, 1994). While biogeographic explanations cannot be completely discounted, collecting expeditions to areas of similar geologies, even areas separated by hundreds to thousands of kilometers, have surprisingly similar floras (Schulenberg and Awbrey, 1997; Neill, 1999; Holst, 2001; P. Núñez, unpublished). Conversely, juxtaposed areas of distinct geologies show distinct species compositions. At the southern limit of the Amazon Basin in Bolivia, rainforest in Madidi National Park shows more similarity to forests derived from Andean sediments ~2,000 km away in Ecuador than the Brazilian Shield forests at the same latitude in Noel Kempff Mercado National Park, a distance of ~500 km (Pitman *et al.*, 2001; Macia and Svenning, 2005; Silman *et al.*, 2006).

Soils and their underlying parent materials affect diversity in two ways. The first is in the total diversity at a point, or alpha diversity. Gentry (1988) presented empirical data that suggested that alpha diversity is highest on rich soils, though the difference in soil fertility was much less important than precipitation amount and seasonality. This result was borne out by Clinebell *et al.* (1995) and the results of the current study. A second way that soils and geology influence diversity is through their effects on species distributions through niche relations. In this case taxa have preferences for soil types, leading to different species composition among soil types, with this beta diversity increasing the total (gamma) diversity of a region. Thus, edaphic effects on diversity can act through ecological processes at the hectare scale, and through floristic (distributional) effects at larger spatial scales.

Changes in community composition and plot-to-plot similarity with geological substrate are well-known in both the Neotropics and Paleotropics (e.g., Duivenvoorden, 1995; Clark *et al.*, 1998; Potts *et al.*, 2002; Phillips *et al.*, 2003; Tuomisto *et al.*, 2003; Palmiotto *et al.*, 2004; Valencia *et al.*, 2004; Masse, 2005; Russo *et al.*, 2005). Tests of substrate effects will need to be carried out at multiple spatial scales because substrate geology can affect plots; both through species-level ecophysiological effects (the niche) and larger-scale and longer-term effects on local species pools. Physiological and related ecological niche effects are likely due to direct effects of nutrient status or water holding capacity on species ability to maintain a positive population growth rate on a certain substrate, or indirect effects of natural enemies mediated through physiological effects (e.g., Givnish, 1999; Fine *et al.*, 2004).

The role of the dynamic pre-Quaternary geological history of the area encompassed by modern Amazonia in generating modern patterns of plant diversity is only recently being integrated into studies of floristics and diversity (Fine *et al.*, 2005). However, phylogeographic explanations in light of the Andean orogeny and its associated effects on the continental margin and shield areas have become standard explanations of animal diversification in Amazonia. Much of the lower Amazon was under water until 2-5 Myr BP due to high Miocene and Pliocene sea levels, and western Amazonia was a sequence of depositional centers very different from today, with a mosaic of shallow lakes and seas (Potter, 1997; Kronberg *et al.*, 1998; Rossetti *et al.*, 2005). The rapid uplift of the Bolivian Andes, rising ~3 km in elevation between ~10.3 and 6.8 Myr BP (Lamb, 2004; Ghosh *et al.*, 2006), and the dynamism of the Amazonian forelands throughout western Amazonia (Räsänen *et al.*, 1992; Kronberg *et al.*, 1998; Hovikoski *et al.*, 2005; Roddaz *et al.*, 2005) certainly had profound effects on Andean and Amazonian phytogeography, though they remain unexplored.

10.4.3 Gamma diversity and range limits along environmental gradients

In the current analysis gamma diversity remains high much farther south in upper Amazonia than alpha diversity. When thought of in terms of species ranges, the result is not surprising. A general macroecological pattern is that species are more abundant, or frequently encountered, at the center of their ranges than at their periphery (Brown. 1984, 1995). Decreases in evenness in species abundances, whether due to local or regional effects, would decrease alpha diversity, even if local plant communities were assembled through random sampling from a landscape species pool. Rarer species would still occur in areas of the landscape that fit their ecological requirements, but would be included in communities less frequently, leading to lower alpha diversity. Examples of this are frequently observed when working along elevational gradients in the Andes where, on geological formations, tree taxa common in the lowlands are found infrequently over a kilometer above their "usual" range (R. Foster and P. Nuñez, pers. communs.; Silman, unpublished).

10.4.3.1 Beta diversity

The data in this chapter do not treat how habitat specificity translates patterns of local (alpha) diversity into regional (gamma) diversity. However, previous research suggests that, although substrate strongly influences floristic composition at a variety of spatial scales, it does not create a large number of absolute habitat specialists (Pitman *et al.*, 1999). If one samples enough area in *terra firme* forests, species common in other habitat types occur. This has led to an unproductive argument in the literature about the role of soils in influencing community similarity in Amazonian forests (Pitman *et al.*, 1999, 2001; Tuomisto *et al.*, 2003). The fact that species can be widely distributed and relatively abundant on different substrates is not incompatible with these same substrates causing substantial changes in community composition from site to site. Because most species occur at frequencies of one or two individuals in even the largest Amazonian inventories, both quantitative measures and presence–absence measures of community similarity can show apparently high beta diversity, while the nature of the forest from site to site remains largely similar. Understanding the effects of performance differences across climatic and edaphic gradients on species distributions, and the origins of these differences, will not be solved by correlative studies, but rather require experimental approaches (e.g., Fine *et al.*, 2004.)

10.4.4 Elevation and diversity

Gentry found that species diversity decreased nearly linearly with elevation in a small sample of 0.1 ha plots scattered at different elevations from 9°N to 22°S. This linear decrease in species diversity was also found in a comparable Central American sample taken in Mexico, and—when plotted on a log scale—shows that the rates of species loss with elevation are nearly the same in the two locales, but with the South American samples being nearly an order of magnitude more diverse (Figure 10.5a).

Data from the Andes to test this hypothesis remain scarce. In the current study, both the collections of all Andean vascular plants and Costa Rican hectare tree inventories show a linear decrease with elevation (Figure 10.5b). We have no comprehensive explanation of the decrease in diversity with elevation, and both niche-based hypotheses and biogeographically-based hypotheses are compelling. If one makes the simple prediction that diversity is related to area, the trends will basically agree, as area decreases regularly with elevation in the Andes up to ~3,600 m. Above that, however, area increases on the broad highland plateaus of the Andes, while diversity does not. The decrease in area with increasing elevation is accentuated when allowance is made for the relatively recent occurrence of the Andean uplift. However, western Amazonian lowland landscapes were undergoing large changes in the Late Tertiary as well (Hoorn, 1994b; Potter, 1997; Costa *et al.*, 2001; Rossetti *et al.*, 2005), yet they harbor the consistently highest diversity in the Amazon Basin.

More compelling are the large and steep environmental gradients across elevation in the Andes. Temperature changes with elevation at ~ 1°C per 175 m. Rainfall gradients along the Andean flank can be correspondingly steep. In southeastern Peru, rainfall varies from 1,700 mm yr^{-1} near the border with Bolivia and Brazil, to 6,900 mm yr^{-1} in the Andean foothills. Much of that change comes over just 20 km. That these factors and others correlated with them are known to drive plant distributions points to the importance of explanations for observed diversity centered on niche relationships and species interactions.

Importantly, no mid-elevational bulge is apparent in either the inventories of all vascular plants, or of trees. A mid-elevational bulge in epiphytes, both vascular and non-vascular, was expected due to the reliance of many of these taxa on persistent cloud, particularly when the spectacular radiation of Andean orchids is included. Still, the absence of a mid-elevational bulge is compelling in these data, and, if it does exist and was missed by this analysis, would occur low in the foothills (<1,700 m) where local climatic conditions allow Amazonian families to coexist with what are traditionally considered Andean families.

10.4.5 Long-term climate change and Amazonian diversity: A Holocene minimum in western Amazonia?

While Amazonia conjures up images of vast lowlands, Amazonian forest extends up the east slope of the Andes, gradually losing its lowland elements. Because modern temperatures are exceptionally warm compared with most of the Quaternary, forest tree species found today on the Andean flank up to ~1,700 m were likely members of lowland Amazonian forest communities for much of the last 2 million years, with many showing large altitudinal migrations with changing climate (Colinvaux *et al.*, 1996; Bush *et al.*, 2004). The non-equilibrium model of community structure makes the prediction that increasing regional species diversity would also increase within-site diversity (Hubbell, 2001). A prediction that emerges is that diversity, at least in upper-Amazonian forests, was even higher during the cooler periods of the Quaternary when lowland floras included taxa that are currently thought of as montane. Whether the Holocene is a diversity minimum for upper-Amazonian forests awaits further study.

10.4.6 The mid-domain effect

The idea that simple geometry explains many patterns of diversity (Colwell and Lees, 2000) has been advanced for taxa as disparate as small mammals (McCain, 2004), corals (Connolly *et al.*, 2003), and Andean epiphytes (Kessler, 2001). However, this study found no evidence for the mid-domain effect in Amazonian or Andean flora. Ter Steege *et al.* (2003) also suggested that the mid-domain effect was responsible for the peak in Amazonian diversity ~5° south of the equator. Results from the current study show that this peak falls in areas where climate is wet and stable, with a high degree of predictability both within and among years. Additionally, forests in Amazonia are clearly most diverse in central and western parts, with the highest consistent diversity falling in western South America (Figure 10.2a). Geometric constraints do not predict this pattern, with environmental effects and historical explanations providing more plausible and biologically satisfying answers (Hawkins *et al.*, 2005).

10.4.7 Discounting migration

This chapter has implicitly discounted dispersal limitation as a major factor limiting the distribution of tree species in the Amazon Basin, even though it has been demonstrated for small mammals and certain bird taxa. Both theoretical data on species dispersal ranges and empirical data on the paleo-distributions of species argue that in Amazonia migration *per se* has not limited the majority of plant taxa (Clark *et al.*, 1999, 2001, 2003; Higgins *et al.*, 2003). This same conclusion has been reached for North American forests, and we expect it to hold true for South American forests as well. At the continental scale, Pennington and Dick (2004) report that up to 20% of the taxa in Amazonian forests are likely long-distance immigrants from other continents. While these results do not discount the effect of dispersal limitation as being important in some taxa, particularly autochorous taxa, it does refocus investigations of species distributions towards edaphic and climatic explanations and the way these factors interact with processes of species formation and extinction. Given recent ecophysiological results on habitat limitation, the role of longer-term climate variability might leave imprints on species distributions that become clear when looking at community level data.

10.4.8 Future efforts

While tree inventory work in the Amazon has exploded, with the installation of large numbers of tree plots and the recent publication of several excellent local floras (e.g., Vásquez Martínez, 1997; Ribeiro *et al.*, 1999), large areas of the Amazon remain uninventoried. Ter Steege *et al.* (2003) used the imprecision of their extrapolations of Amazonian diversity to suggest where floristic inventories should be focused. In more simple terms, Figure 10.2a shows that large areas of Amazonia remain uninventoried, including important geological transitions, rainfall gradients, and areas of rapid change in tree diversity. Completing Amazonian forest inventories—such as those of the Amazon Tree Diversity Network—are imperative for an overview of Amazonian diversity. In addition to siting these plots on areas of high uncertainty in diversity from the predictions of extrapolative and interpolative models, plots should be stratified to include areas of changing geology with similar climate, and similar geology with changing climates. Indeed, areas with strong or weak dry seasons can have either predictable or unpredictable climates on either a within-year or among-year basis, giving one the ability to tease apart the effects of dry-season *per se* versus climatic variability at longer time scales. Doing so would allow us to start asking questions that get at historical factors influencing tropical forest diversity.

Though we have focused on diversity–environment correlations in explaining why diversity varies among Amazonian forests, these diversity–environment correlations are underlain by ecological, physiological, and historical mechanisms (Wright, 2002; Leigh *et al.*, 2004; Ricklefs, 2004). The results of this study show that even concepts like "dry-season length," though seemingly concrete, may have complicated links to diversity depending on the degree to which modern forest community membership reflects whether species are in equilibrium with climate and substrate and are simply limited by their physiological and ecological tolerances, or whether forests bear longer-term imprints of climatological variability.

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11

Biogeochemical cycling in tropical forests

M. E. McGroddy and W. L. Silver

11.1 INTRODUCTION

Increased inputs of greenhouse gases have altered the composition of the atmosphere over the past 150 years (IPCC, 2001, 2007), resulting in shifts in temperature and precipitation around the globe. The scientific community has put an enormous effort into understanding the causes of these changes, and predicting future climate and the interactions between climate and the biosphere that may moderate or accelerate current trends. Most of the research on climate change has focused on boreal and north temperate ecosystems where temperature shifts are predicted to be the largest (IPCC, 2001, 2007). These ecosystems are often characterized by deep organic soils that present the potential for a strong positive feedback to climate change (Oechel *et al.*, 1998; Vourlitis and Oechel, 1997; Hobbie *et al.*, 2002).

Our understanding of the potential ramifications of climate change on the structure and function of ecosystems in tropical regions is much less well developed (Körner, 1998; Silver, 1998; Chambers *et al.*, 2001; Chambers and Silver, 2004; Clark, 2004; Körner, 2004; Cramer *et al.*, 2004; Lewis *et al.*, 2004; Ometto *et al.*, 2005). Tropical forests play an important role in the global carbon cycle, accounting for an estimated 43% of global net primary production, and storing over 25 % of the carbon found in forest soils (Brown and Lugo, 1982; Melillo *et al.*, 1993). Long-term forest inventory plots in Amazonia show increasing tree biomass over the past 50 years, coupled with parallel trends in tree recruitment and, to a lesser degree, mortality (Phillips *et al.*, 1998; Baker *et al.*, 2004; Lewis *et al.*, 2004). While some suggest this results from increased atmospheric CO_2 concentrations (Phillips *et al.*, 1998; Baker *et al.*, 2004; Gloor *et al.*, 2009), others argue for alternative causal factors such as changes in disturbance regime or climate variation (Chambers and Silver, 2004; Lewis *et al.*, 2004; Clark *et al.*, 2010). Evidence from eddy flux towers

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suggests that mature tropical forests are at, or close to, equilibrium with respect to carbon on an annual basis (Miller *et al*., 2004; Rice *et al*., 2004). Changes in the ratio of net primary productivity (NPP) to decomposition of organic material, whatever the ultimate cause, could significantly affect the rate of increase of atmospheric CO_2 at a global scale due to the typically high annual rates of carbon cycling and large spatial extent of tropical forests (Brown *et al*., 1993; Wang and Polglase, 1995; McKane *et al*., 1995; van Noordwijk *et al*., 1997; Tian *et al*., 1998; Körner, 2004). Almost all efforts to model or predict the forest response to elevated atmospheric CO_2 and climate change are qualified by the caveat that nutrient limitations may restrict the ability of the vegetation to respond with increased productivity.

Long-lived perennial plants adapted to the fairly stable climates characteristic of tropical forest regions may have limited plasticity to respond to the changes in atmospheric composition and climate. For example, some biogeochemical properties, such as foliar stoichiometry, are subject to fundamental physiological constraints and thus have limited flexibility with climate change (McGroddy *et al*., 2004a). However, others, such as those dominated by microbes (Balser and Wixon, 2009) or related to phenology (Koltunova *et al*., 2009) may be able to rapidly and effectively change in response to changing environmental conditions.

11.2 CURRENT AND PREDICTED CLIMATE CHARACTERISTICS

Tropical climates are generally characterized by warm temperatures with little seasonal variation in temperature (Holdridge, 1967). Near constant warm temperatures throughout the year are likely to result in little cold temperature stress to organisms relative to that seen in temperate and boreal ecosystems, but may also make tropical systems particularly sensitive to even small changes in climate (Townsend *et al*., 1992; Silver, 1998). Rainfall is more variable in tropical forests, ranging from 1 to 8 $m\,yr^{-1}$ with a wide range in distribution patterns.

Atmospheric CO_2 concentrations have doubled over the past century and mean annual temperatures in most tropical forest regions have shown a strong warming trend over the past 40 years (Hulme *et al*., 2001; Malhi and Wright, 2004; Clark, 2007). Over the next century, mean annual temperatures in tropical regions are predicted to increase anywhere from 1 to 5°C (IPCC, 2001; Hulme *et al*., 2001; Lal *et al*., 2002; Cramer *et al*., 2004; see Table 11.1). Though tropical forest temperature sensitivity is poorly understood, photosynthetic rates will likely decrease at high temperatures (Goulden *et al*., 2004), and the productivity of some species has been shown to be negatively correlated to mean night-time temperature (Clark *et al*., 2010). Interannual and multidecadal rainfall variability in the tropics is quite substantial and while trends in rainfall are less clear than those of temperature it appears that in at least some regions the intensity and duration of dry seasons have increased over the past 30 years (Clark, 2007). Climate change induced patterns in precipitation may vary significantly across regions within the tropics. Thus, predicted changes in the volume of rainfall and changes in the seasonality or intensity of rainfall events may also be important on the regional scale (IPCC, 2001; Lal *et al*., 2001b, 2002; Hulme *et al*., 2001). Changes in

Table 11.1. Magnitude of predicted changes in regional climates in tropical regions. Data are from Cramer *et al.* (2004), based on output from four different climate models for the period 2081–2100 and are presented as anomalies relative to the period 1969–1998.

Region	*Temperature* (%)	*Rainfall* (%)
Neotropics	+3 to +5.5	−17 to +8
Africa	+3.7 to +7.7	−17 to +10
Asia	+3.1 to +5.6	+7.5 to +23

precipitation that lead to increased drought, drenching rains, or soil saturation are likely to have a significant impact on tropical forest form and function. Approximately 42% of tropical forests currently experience significant drought during part of the year (Brown and Lugo, 1982). In these ecosystems litterfall, decomposition, and nutrient uptake are synchronized with the timing and quantity of rainfall (Jarmillo and Sanford, 1995; Martinez-Yirzar, 1995; Lawrence, 2005; Wood *et al.*, 2005). Changes in the frequency and severity of drought in seasonal and aseasonal forests will feed back on the amount and distribution of above- and below-ground NPP, nutrient mineralization rates, and the frequency and severity of fires (Goldammer and Siebert, 1990; Davidson *et al.*, 2008).

In this chapter we discuss the potential effects of climate change on biogeochemical cycling and explore the possibility for nutrient limitation to alter the ecosystem's response to elevated CO_2 and climate change. It is important to keep in mind that current measures of nutrient dynamics reflect a system that is already responding to climate changes. We briefly review the basic attributes of tropical soils, and then focus our analysis on soil phosphorus (P) and nitrogen (N), internal ecosystem fluxes (litterfall, decomposition, plant nutrient uptake), and carbon (C) and N trace gas emissions. In tropical forests on highly weathered soils P is thought to be the primary limiting nutrient to NPP, and thus is the most likely to impact the ecosystem's response to global changes. In contrast, N is rarely thought to be limiting, but climate change coupled with increasing anthropogenic N deposition in tropical regions could have a significant impact on gaseous N losses, N leaching, and associated cation leaching. Recent work has also suggested trace nutrients may have significant roles in regulating nutrient cycles and productivity in tropical forests (Barron *et al.*, 2009; Powers, unpublished data). We focus on short-term (less than 100 year) effects of climate change on tropical forest biogeochemical cycling. Longer term changes are more likely to include significant shifts in species composition and forest structure confounding the effects of nutrient availability (Pimm and Sugden, 1994; Condit *et al.*, 1996; Bazzaz, 1998; Hilbert *et al.*, 2001; McLaughlin *et al.*, 2002; Enquist, 2002; Chambers and Silver, 2004; Jensen, 2004).

11.3 TROPICAL FOREST SOILS

The warm, and generally moist climate of the tropics combined with the lack of large-scale disruptions, such as the periodic glaciations of the boreal and temperate regions, has allowed soil development to continue undisturbed for millions of years. While most soil orders are represented in the tropics (Sanchez, 1976), the most common and extensive soil orders are the highly weathered oxisols and ultisols (McGill and Cole, 1981; Jordan, 1985; Vitousek and Sanford, 1986). These soils are generally characterized by fine textures, low charge density in the mineral fraction, and the dominance of variable, pH dependent charge (Sanchez, 1976; Sollins *et al.*, 1988). Changes in precipitation can stimulate shifts in pH, which in turn affect cation and anion retention in soils. For example, dry season irrigation in a moist forest in Panama resulted in increased permanent charge and cation retention in the surface soils (Yavitt and Wright, 2002).

With advanced weathering, most of the primary minerals in soils are absent, and iron (Fe) and aluminum (Al) oxides and hydroxides predominate. These minerals impart properties to soils that can decrease their nutrient holding capacity in the mineral fraction, increase organic matter storage and associated nutrient retention, and lower pH (Uehara, 1995). In highly weathered tropical soils, organic coatings on mineral surfaces control a significant proportion of nutrient availability and cation exchange capacity (Tiessen *et al.*, 1994). Thus, factors that influence rates of production and decomposition can feedback on nutrient cycling directly through mineralization of organically bound nutrients, and indirectly through changes in nutrient retention and storage associated with plant biomass and soil organic matter (Miller *et al.*, 2001; Porder and Chadwick, 2009).

11.4 SOIL PHOSPHORUS

Old tropical soils tend to have low exchangeable P pools (Cross and Schlesinger, 1995). In terrestrial ecosystems, P is primarily derived from the weathering of parent material; ecosystem P pools, and especially the available P fraction, reach a maximum early in ecosystem development (Walker and Syers, 1976; Crews *et al.*, 1995). Commonly used indices suggest that P availability generally declines over geologic time as fresh weathering inputs diminish and losses remain constant or increase (Walker and Syers, 1976). Geochemical reactions with Fe and Al oxides provide an additional sink for P, which is thought to function as a loss from the perspective of the biota. If P becomes occluded with Fe and Al, it forms secondary minerals that can require hundreds to thousands of years to weather into plant available forms (Walker and Syers, 1976; Tate, 1985; Stevenson and Cole, 1999). Supply of residual primary P through weathering usually occurs well below the surface layers of the soil where most of the active roots occur. The low total P pools, lack of primary mineral P, slow weathering of secondary P minerals, and low rates of P deposition provide the basis for potential P limitation to NPP in tropical forests (McGill and Cole, 1981; Galloway *et al.*, 1982; Vitousek, 1984; Vitousek and Sanford, 1986; Andreae *et al.*, 1990; Williams *et al.*, 1997).

However, the extent and importance of P limitation has recently come under scrutiny (Johnson *et al.*, 2003; Chacon *et al.*, 2006). While productivity and biomass have been shown to be positively correlated to soil P pools along natural gradients (Paoli *et al.*, 2008; Espeleta and Clark, 2007) in lowland tropical mature forests, fertilizer addition experiments have not shown a significant increase in biomass or stem growth as a result of P additions (Mirmanto *et al.*, 1999; Newbery *et al.*, 2002). The size of the plant-available P pool is sensitive to the soil environment and subject to both direct and plant biomass mediated effects of climate dynamics (Porder and Chadwick, 2009). For example, P availability increases under short-term anaerobic conditions. Some humid tropical forest soils experience fluctuating redox in surface horizons due to rapid rates of oxygen consumption that exceed diffusive resupply (Silver *et al.*, 1999). As soil oxygen declines, oxidized Fe forms are reduced releasing bound P and decreasing the bonding efficiency for new P (Peretyazhko and Sposito, 2005; Chacon *et al.*, 2006; Liptzin and Silver, 2009). Experimental studies have shown that P released during periods of low redox can be taken up by the microbial biomass (Liptzin and Silver, 2009). In Hawaiian soils, however, fluctuating anaerobisis has been associated with the leaching of non-crystalline metals and the organic and inorganic P compounds associated with them (Miller *et al.*, 2001). Increased temperature and/or rainfall may result in more frequent anaerobic events in humid tropical soils, potentially altering a number of important soil P pools (Silver *et al.*, 1999). In contrast, increased drought in humid regions could enhance the proportion of oxidized Fe forms and decrease plant P availability through strong P sorption and occlusion. Drought could also lead to decreased decomposition and associated P mineralization resulting in larger pools of organically bound P in the soil.

Elevated CO_2 could indirectly impact soil P availability in a number of ways. Increased plant demand for P due to a CO_2 fertilization response could result in increased plant production of phosphatases and/or organic acids resulting in increased mineralization of organically bound P. Additionally, increased plant production and soil organic matter density could result in decreased P sorption due to organic matter coating of Fe and Al oxide minerals (Lloyd *et al.*, 2001). At the landscape scale soil organic matter was positively correlated with exchangeable P in soils along a rainfall and temperature gradient in a subtropical forest in Puerto Rico (Figure 11.1) and in a Bornean rainforest (Burghouts *et al.*, 1998). Similarly, labile P in mineral soils was strongly positively correlated with soil C pools along a localized soil texture gradient in moist tropical forest in Brazil (Figure 11.2). Elevated CO_2 or climate changes that decrease the mass of soil organic matter could indirectly impact soil P pools, and feedback to decrease NPP. It is also possible, however, that the strong correlations between P and soil organic matter along natural gradients results from other factors that affect soil P availability and in turn stimulate organic matter production and P content (Lloyd *et al.*, 2001). In the Brazilian forest, forest floor P content was positively correlated with forest floor C (Figure 11.3). This could indicate a top down control of the soil C and P relationship. Alternatively, fungal colonization

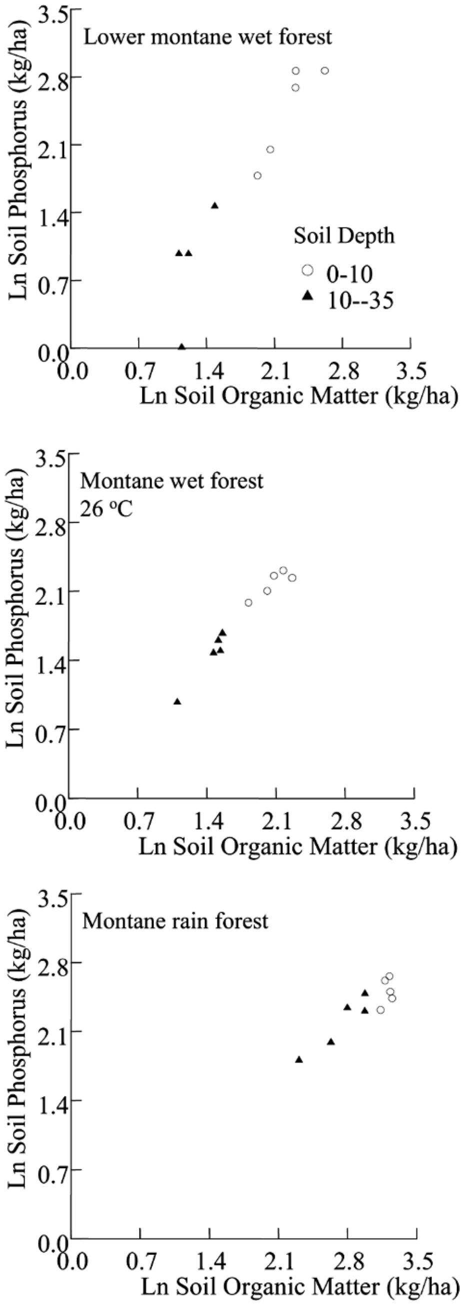

Figure 11.1. Relationships between soil organic matter content and exchangeable P in the 0–10 and 10–35 cm depths. Data are log transformed and are from Silver *et al*. (1999). For the lower montane wet forest $r^2 = 0.89$, $P < 0.01$; for the montane wet forest $r^2 = 0.96$, $P < 0.01$, and for the montane rain forest $r^2 = 0.82$, $P < 0.01$.

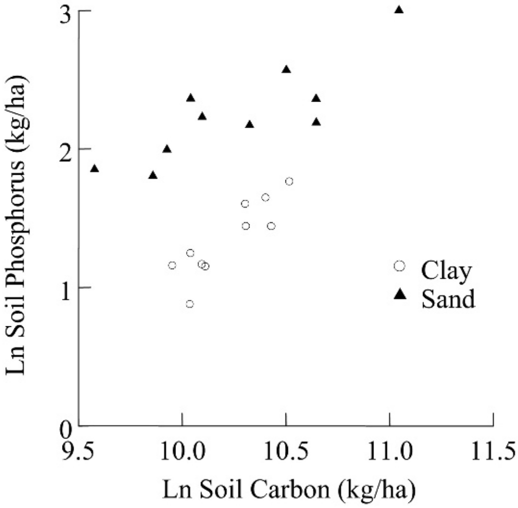

Figure 11.2. The relationship between total C and exchangeable P pools in sand and clay soils in a moist tropical forest in Brazil. Data are log transformed and are taken from the 0–10 cm soil depth in Silver *et al.* (2000). For sandy soils, $r^2 = 0.71$, $P < 0.01$; for clay soils $r^2 = 0.77$, $P < 0.01$.

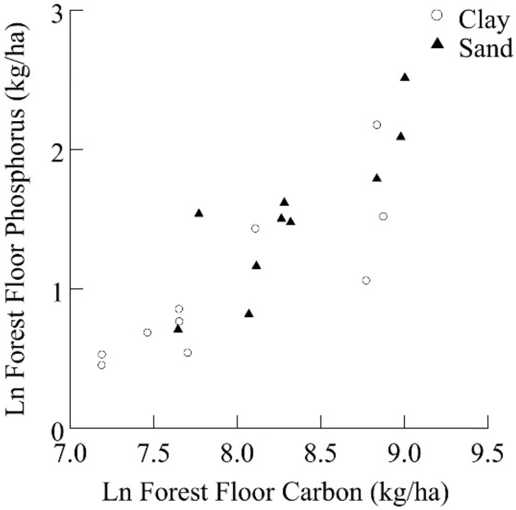

Figure 11.3. The relationship between forest floor C and forest floor P pools in sand and clay soils in a moist tropical forest in Brazil. Data are log transformed and are from Silver *et al.* (2000). For sandy and clay soils combined, $r^2 = 0.71$, $P < 0.01$.

of the forest floor may alter soil P concentrations (Lodge, 1993), leading to a narrow range of C : P ratios favorable during decay.

11.5 SOIL NITROGEN

In contrast to many temperate ecosystems, tropical forests on highly weathered soils tend to have adequate to high N availability (Vitousek and Howarth, 1991; Hedin *et al.*, 2009). While the mechanisms underlying the relative N abundance of tropical soils are not well understood, N accumulation via N fixation (Riley and Vitousek, 1995; Crews *et al.*, 2000; Cusack *et al.*, 2009), and internal N retention mechanisms that limit losses (Silver *et al.*, 2001; Silver *et al.*, 2005b; Templer *et al.*, 2008) are both potentially important factors. Even when it is abundant, N cycling in tropical forests can impact the availability of other nutrient cations and anions. Variable charge soils in high-rainfall environments can experience ammonium and associated anion leaching (Sollins and Radulovich, 1988). High nitrification rates coupled with abundant rainfall can stimulate nitrate and associated cation leaching from tropical soils (Silver and Vogt, 1993).

In temperate and boreal ecosystems, net N mineralization rates tend to increase with mean annual temperature and moisture, and generally increase with *in situ* warming (Rustad *et al.*, 2001). In laboratory studies, net N mineralization rates were insensitive to temperature changes along a tropical montane forest elevation gradient (Marrs *et al.*, 1988), as were soils from a Colombian cloudforest (Cavelier *et al.*, 2000). A recent review (Silver *et al.*, 2010) found no apparent effect of temperature on net or gross N mineralization and nitrification rates along tropical elevation and temperature gradients.

Nitrogen cycling is likely to be sensitive to changes in precipitation, particularly at the arid or very wet extremes. In dry tropical forests, pulses of precipitation can result in rapid rates of N mineralization, nitrification, and nitric oxide emissions (Davidson *et al.*, 1993; Lodge *et al.*, 1994). In wet forests, increased precipitation can enhance element leaching (Sollins and Radulovich, 1988), lower soil redox (Silver *et al.*, 1999), and lead to increased N losses via denitrification (Silver *et al.*, 2001). If increased precipitation lowers soil redox it could also decrease rates of nitrification, a strictly aerobic process, providing a potential negative feedback to cation leaching and gaseous N losses. In contrast, rainfall exclusion from a seasonal moist forest in the Brazilian Amazon found decreased rainfall resulted in decreased N_2O emissions over the course of several years with an increase in NO fluxes detected only in the fourth year of the study when the entire region was subject to severe drought (Davidson *et al.*, 2008).

Agricultural and urban development in the tropics is dramatically increasing the rate of N deposition to tropical ecosystems (Galloway *et al.*, 1995; Asner *et al.*, 2001). The interaction of N deposition and climate change, particularly increased duration or intensity of rainfall, could significantly alter C and nutrient cycling in these ecosystems (Figure 11.4). Nitrogen fertilization in N-rich Hawaiian forests led to increased nitric oxide (NO) and nitrous oxide (N_2O) fluxes (Hall and Matson, 1999),

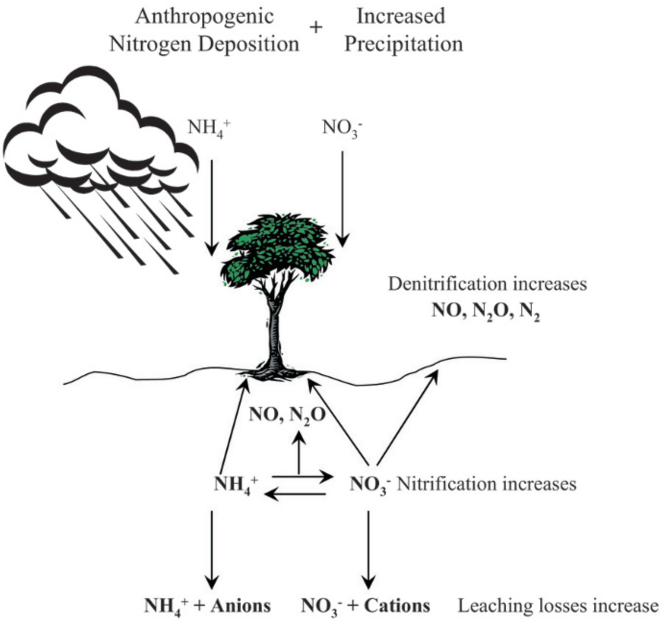

Figure 11.4. The potential effects of anthropogenic nitrogen deposition and increased precipitation in tropical forests. Increased inputs of ammonium could stimulate ammonium leaching in variable charge soils, and lead to associated anion losses. Ammonium deposition could stimulate nitrification enhancing nitric and nitrous oxide fluxes. Increased nitrate pools via nitrification or direct deposition could stimulate nitrate and cation leaching and denitrification. If soil redox declines with climate change, then nitrification rates could decrease partially offsetting the effects of nitrogen deposition.

and stimulated N leaching (Lohse and Matson, 2005). Increased N leaching could enhance cation and anion losses, leading to nutrient limitation to NPP.

Nitrogen deposition also affects C cycling in tropical forests. In Costa Rica, N fertilization stimulated soil respiration and fine-root production (Cleveland and Townsend, 2006), while it decreased soil respiration in tropical forests in China (Mo *et al.*, 2008) and Puerto Rico (Cusack *et al.*, 2010a, b). In Puerto Rico, the decrease in soil respiration corresponded to increased soil C storage. Soil C was lost from the labile fractions, but accumulated in the heavy, mineral associated fractions, which represented a larger proportion of the bulk soil C pool (Cusack *et al.*, 2010a). Carbon bound to the mineral soil fraction is likely to have a longer residence time than C in the lighter soil fractions (Cusack *et al.*, 2010b). The interactions of N deposition, elevated CO_2, and climate change are poorly understood for tropical forests.

11.6 ABOVE-GROUND BIOMASS AND LITTER PRODUCTION

For forest ecosystems on highly weathered soils, vegetation plays a key role in retaining and cycling essential nutrients through production and decomposition of plant biomass. Reports from a number of tropical forests showed significant increases in tree mortality linked with the El Niño associated droughts (Clark, 2004) as well as experimentally reduced rainfall regimes (Brando *et al*., 2008). Larger trees in wet and moist forests seem to be particularly susceptible to drought induced mortality, suggesting that shifts to drier climates or extended, more intense dry seasons may result in decreased biomass in these ecosystems. Work in Hawaiian forests suggests that the effectiveness of the vegetation in retaining essential nutrients is strongly related to precipitation patterns (Porder and Chadwick, 2009), with soil nutrients in excess of water-limited plant demand at the drier end of the gradient and redox-driven leaching more dominant at the wet end.

Alterations to the amount and timing of rainfall in tropical forests may significantly affect nutrient cycling via litter production, although the relationship between climate and litter dynamics is likely to be complex. Litter P concentrations have been found to correlate positively with rainfall seasonality and with inter-annual rainfall in moist and dry tropical rainforests (Read and Lawrence, 2003; Wood *et al*., 2005), but not spatially along larger scale elevation and rainfall gradients (Silver, 1998). The observed increase in litterfall P content during the wet season or wet years in seasonal environments may be due to increased soil P availability and/or decreased demand for the retranslocation of P during leaf senescence (Wood *et al*., 2005). Similarly, there may be significant changes in plant P demand associated with seasonal phenological activity (Lal *et al*., 2001a). Although foliar N may increase per unit leaf mass with increasing precipitation (Wright *et al*., 2001; Wright and Westoby, 2002; Santiago and Mulkey, 2005), leaf litter N concentrations do not appear to vary with precipitation in moist (Santiago and Mulkey, 2005; Read and Lawrence, 2003) or humid (Silver, 1998; Wood *et al*., 2005) tropical forests. Elevated atmospheric CO_2 has also been shown in some cases to increase the litter C : N and C : P ratios though again the effect is not consistent (Kanowski, 2001; Santiago and Mulkey, 2005).

Climate change impacts on litter inputs may also come from shifts in timing or amount of litterfall. In seasonal tropical forests litterfall and nutrient uptake are synchronized to the annual patterns in precipitation (Jaramillo and Sanford, 1995). Seasonality of litterfall has been shown to be negatively correlated to mean annual precipitation in gradient studies (Santiago and Mulkey, 2005; Read and Lawrence, 2003) but in a recent survey seasonality of litterfall was found to correlate with the seasonality of rainfall and not the total amount (Chave *et al*., 2010). Shifts in the duration of the dry season may lead to temporal separation between plant demands and nutrient availability (Silver, 1998). Increased duration and severity of droughts may also lead to an increase in drought deciduousness, or a decrease in the leaf area index of the canopy (Nepstad *et al*., 2002). This could decrease litter inputs and/or disrupt the synchronicity between nutrient inputs and plant demand (Lodge *et al*., 1994). Over the long term, a shift to a significantly wetter or drier environment could lead to a species composition shift with associated changes in both litter quality and quantity (Condit, 1998; Santiago *et al*., 2005).

Belowground litter inputs are difficult to study and few data are available. Elevated CO_2 may increase allocation to root tissues in tropical forests if nutrients are limiting (Arnone III and Korner, 1995), although this could be offset by increased root mortality and turnover; thus far the data from field and greenhouse experiments are very mixed (Norby and Jackson, 2000). At a global scale, there were no strong relationships between root turnover (below-ground NPP/fine root standing stocks) and temperature or precipitation in forested ecosystems (Gill and Jackson, 2000). In temperate forests, fine-root growth cycles appear to be regulated by temperature resulting in strong annual signals of productivity and mortality (Pregitzer *et al.*, 2000). In contrast, tropical soils experience little variation in soil temperature seasonally suggesting that any patterns in turnover are more likely to be dominantly controlled by soil moisture, nutrient supply, or internal regulation of root : shoot ratios. Dry season irrigation did not change overall root phenology in a moist tropical forest, but did alter the timing of root growth and mortality by increasing longevity of new roots while simultaneously increasing the mortality of older roots (Yavitt and Wright, 2002).

11.7 DECOMPOSITION

Actual evapo-transpiration is one of the strongest predictors of decomposition on a global scale (Aerts, 1997), although it's explanatory power is quite weak ($r^2 = 0.14$). Using elevation gradient studies within tropical forests, Silver (1998) found no predictive relationship between rainfall and decomposition rates. A 50% reduction in precipitation reaching the forest floor had no effect on litter decomposition rates in a partial throughfall exclusion experiment in a moist forest in Amazonia (Nepstad *et al.*, 2002), and dry season irrigation resulted in only a small increase in the decomposition rates of the forest floor in a moist forest in Panama (Wieder and Wright, 1995). In Hawaii, leaves decayed faster in moist forests than in wet forests (Schuur, 2001), but a common substrate showed a weaker trend suggesting an important interaction of plant characteristics with climate or site conditions. In contrast to the results from Hawaii, two recent multi-site studies in tropical forests suggest that climate decomposition index (CDI) is the strongest predictor of decomposition rates for common substrates (Cusack *et al.*, 2009; Powers *et al.*, 2009). In both of these studies rates of above- and below-ground decomposition were positively correlated with rainfall and most strongly with CDI, suggesting that rainfall seasonality as well as rainfall total are important regulators of decomposition rates. The wide variation among sites in these studies suggests that beyond the CDI, site specific characteristics are also key to understanding the rate of litter turnover. In addition to the role of climate, litter chemistry and in particular calcium, C : P, lignin : P, C : N, and lignin : N ratios are often inversely related to decomposition rates in tropical sites (Ostertag and Hobbie, 1999; Hobbie and Vitousek, 2000). In a multiple element fertilization study in Panama, P additions were found to increase rates of leaf decomposition while both P and potassium (K) additions increased rates of cellulose decomposition. As discussed above, both decreased rainfall and/or elevated atmospheric CO_2 might lead to increased C : nutrient ratios in litter. Significant immobilization of nutrients during the early stages of decomposition is commonly observed in tropical forest ecosystems

(Ostertag and Hobbie, 1999; McGroddy *et al.*, 2004b; but see Kitayama *et al.*, 2004). Increased C : nutrient ratios in leaf litter could increase immobilization of nutrients in the microbial biomass during decomposition, and decrease rates of decomposition in the litter layer (Baillie *et al.*, 2006).

Below-ground decomposition appears to be less sensitive to climate factors than above-ground litter, with tissue quality playing a key role in regulating the rate of decay (Silver and Miya, 2001). Across 5 tropical forest sites, Cusack *et al.* (2009) reported that mean annual temperature was positively correlated to initial rates of root decomposition (loss of 50% of initial mass), but overall, root tissue quality was a stronger predictor of decay rate than any climate factor.

11.8 ROOT AND MICROBIAL DYNAMICS

The below-ground portion of ecosystems is hidden from view and thus it is not surprising that the impact of climate change on below-ground ecology has received far less attention than above-ground effects. In order to stimulate more research, Norby and Jackson (2000) produced an excellent review of root responses to elevated CO_2 and climate changes. Plant uptake of essential nutrients is highly sensitive to soil temperature, moisture, and aeration and thus is likely to be affected by climate change, but measured changes in nutrient uptake kinetics are often not strongly correlated with changes in productivity (Chapin, 1974; Bassirirad, 2000). The rate of plant nutrient uptake depends in turn on the amount of active root surface area, the movement of nutrients to the active root surface, nutrient availability, and the transport rate across membranes into both the root itself and finally into the xylem system. All of these factors may respond to climate change in ways that magnify or mitigate the impacts.

Tropical forests are often characterized by high below-ground biomass (Jackson *et al.*, 1996) and root turnover (Gill and Jackson, 2000; Trumbore *et al.*, 2006). Both soil temperature and soil moisture have the potential to affect root architecture, root growth, and turnover (Gill and Jackson, 2000; Espeleta and Clark, 2007). Soil moisture and temperature can be positively correlated to fine-root length and root uptake (Bassirirad, 2000; Pregitzer *et al.*, 2000), although field studies have found that phenology and other constraints often weaken these relationships (Fitter *et al.*, 1998). Fine-root biomass is much more variable on both spatial and temporal scales than above-ground biomass in forests suggesting increased sensitivity to environmental dynamics. Effects of seasonal variation in rainfall and soil moisture on fine-root biomass have been mixed, but on the interannual scale El Niño events appear to cause both short- and long-term increases in fine-root mortality (Espeleta and Clark, 2007). Fine-root biomass tends to decrease as nutrient availability increases. A number of studies have found negative correlations between fine-root biomass and soil nutrient pools, particularly phosphorus, in tropical forests (Gower, 1987; Ostertag, 2001; Powers *et al.*, 2005; Espeleta and Clark, 2007), suggesting that any change that alters soil nutrient dynamics, especially in the surface soils is likely to change the allocation to fine roots as well.

Under elevated CO_2 some species increased their below-ground biomass suggesting that the additional available C is used to increase fine-root volume and water and nutrient uptake, particularly in deciduous forests (Norby *et al.*, 1999). Other studies, however, have shown no effect or increased root mortality resulting in higher turnover of fine-root pools and no measurable change in standing stocks (Tingey *et al.*, 2000; Arnone *et al.*, 2000; Pregitzer *et al.*, 2000). Based on work with crop plants and the regulatory role of simple sugars on cell division, Pritchard and Rogers (2000) suggested that under elevated CO_2 roots will be larger and more highly branched, but less efficient at nutrient and water uptake. They go on to suggest that this might amplify the impact of warmer, drier soil conditions predicted for some tropical regions. Fine roots are only one component of plant uptake, and for P uptake in particular, mycorrhizal associations are vital components (Bolan, 1991; Miyaska and Habte, 2001). Mycorrhizal hyphae increase the amount of soil volume explored and exude phosphatases and organic acids to increase P uptake (Bolan, 1991). Mycorrhizal associations are ubiquitous in tropical forest soils where up to 90% of tree species are thought to support associations with endomycorrhizae (Bolan, 1991).

One might hypothesize that elevated CO_2 increases C allocation below-ground and, in particular, to mycorrhizal associations—this could in turn increase plant nutrient uptake. Studies thus far, however, have not found support for this (Fitter *et al.*, 2000; Zak *et al.*, 2000b; Gavito *et al.*, 2003; Staddon *et al.*, 2004). It appears that elevated CO_2 on its own has little or no impact on mycorrhizal infection rates or production of mycorrhizal tissue, at least under experimental conditions (Staddon and Fitter, 1998). Mycorrhizae do appear to respond positively to increased soil temperature, though most studies have been done on temperature ranges more typical of temperate regions (Braunberger *et al.*, 1997; Fitter *et al.*, 2000; Staddon *et al.*, 2004). It is not clear if the relationship will continue to hold at the warmer temperatures typical of the tropics. Mycorrhizal infections are inversely related to soil P availability (Janos, 1983), and if plant P demand were to increase, it could result in increased mycorrhizal infection rates. Furthermore, responses of mycorrhizae to changes in soil temperature and moisture often appear to be species specific; thus, any shift in climate that results in a significant shift in mycorrhizal community composition has potentially wide-reaching implications for nutrient cycles (Fitter *et al.*, 2000).

The nutrients held in the microbial biomass represent a small but very rapidly cycled pool. Though soil microbial communities are widely considered to be C limited, work in highly weathered tropical sites suggests that microbial activity may be limited by P availability or co-limited by C and P (Vitousek and Matson, 1988; Cleveland *et al.*, 2002), although few data are available. The rate of mineralization of organically bound nutrients is closely linked to the rate of microbial activity and turnover of the microbial biomass. Field studies have found slightly positive, but highly variable responses of microbial biomass or microbial respiration to elevated atmospheric CO_2 in temperate forests (Zak *et al.*, 2000b). Under low-nutrient conditions, microbial immobilization of limiting nutrients increased in response to elevated CO_2 (Berntson and Bazzaz, 1997, 1998). This could lead to significant negative feedbacks to productivity in nutrient limited ecosystems.

Drought may also strongly affect microbial biomass and activity including nutrient immobilization and mineralization. In seasonal tropical forests microbial biomass and P pools have been found to increase in the dry season, presumably in response to decreased plant uptake (McGroddy *et al.*, 2008). As discussed above for litter inputs, there is a synchronous flush of nutrients released from the microbial biomass at the onset of the wet season in these seasonal forests coinciding with the onset of new root growth and increased plant demand (Perrott *et al.*, 1990). In contrast, aseasonal tropical forests do not have intra-annual patterns in microbial P pools (Yavitt and Wright, 1996; Luizão *et al.*, 1992). Shifts in the timing and length of dry seasons in seasonal forests and the introduction of drought into aseasonal forests could alter the competitive balance between microbial biomass and plant demand for nutrients. Drought or shifts in temperature can also lead to a shift in microbial community composition and function (Papatheodorou *et al.*, 2004; Sowerby *et al.*, 2005) with potential long-term effects on rates of nutrient cycling and productivity. Several studies have shown direct effects of elevated CO_2 on the composition and function of the microbial community, presumably through increased or altered carbon exudates into the rhizosphere, though this response may be moderated by soil nutrient or C availability (Zak *et al.*, 2000a).

11.9 TRACE GAS EMISSIONS

Tropical forests have the highest rates of soil respiration, which releases CO_2 back to the atmosphere (Raich and Schlesinger, 1992) and are important sources and sinks of greenhouse gases, particularly CO_2, N_2O, and methane (CH_4). Drought, fire, blow downs, clearing, and disease, are all factors that rapidly increase rates of tree mortality and can alter microbial activity or community structure, generally resulting in pulses of CO_2 and other greenhouse gases (Schimel and Gulledge, 1998; Keller *et al.*, 2005). Methane is produced under anaerobic conditions and tropical forests have generally been considered a weak sink (Keller and Reiners, 1994; Steudler *et al.*, 1996; Keller *et al.*, 2005). However, some upland tropical forest soils have been identified as a significant source of CH_4 at local (Keller *et al.*, 1986; Silver *et al.*, 1999; Teh *et al.*, 2005) and regional (Frankenberg *et al.*, 2005) scales.

Humid tropical forests are the largest natural source of N_2O globally (Lashof and Ahuja, 1990). Nitrous oxide is produced via nitrification and denitrification. Factors that stimulate nitrification such as the death of N-rich tissues and anthropogenic N deposition can increase N_2O emissions (Silver *et al.*, 2005a; Hall and Matson, 1999); similarly if soils become reduced denitrification rates to N_2O and dinitrogen (N_2) may increase (Firestone *et al.*, 1980; Silver *et al.*, 2001). In the humid tropics, denitrification is likely to be the dominant source of N_2O emissions from soils. The potential effects of climate change on the ratio of $N_2O:N_2$ are poorly understood. Theory suggests that denitrification to N_2 is favored under low NO_3^- and low redox conditions, so it is possible that if increased rainfall and temperature lead to more strongly reducing conditions, less NO_3^- will be available for denitrification and N_2 production will be favored. It is extremely difficult to accurately estimate N_2 fluxes from ecosystems, although this is an active area of research. Recent laboratory and modeling experiments using isotope mass balance approaches suggest that N_2 fluxes can be large from humid tropical forest soils, amounting to over five times the rate of N_2O losses in Hawaiian forests (Bai and Houlton, 2009).

There have been few controlled experiments looking at the effects of climate changes on greenhouse gas production in tropical forests. Throughfall exclusion experiments mimicking increase drought conditions decreased N_2O emissions and increased atmospheric CH_4 consumption in a seasonal forest in tropical Brazil (Cattanio *et al*., 2002; Nepstad *et al*., 2002; Davidson *et al*., 2004, 2008). Similar results were found during an induced drought in a tropical megacosm experiment (van Haren *et al*., 2005). Observational data along a tropical montane rainfall gradient showed increased N_2O emissions with increasing rainfall (Keller *et al*., 1986) and decreased soil O_2 availability (Silver *et al*., 1999).

11.10 SUMMARY AND FUTURE DIRECTIONS

In summary, nutrient cycling in tropical forests is likely to be sensitive to current and future global changes, in both the amount and distribution of precipitation (Table 11.2), and possibly in temperature. Existing research has focused on the effects of increased drought, which impacts P and N cycling primarily through changes in microbial processes and plant litter dynamics. From this review it is clear that predictions of the response of tropical forests to climate change and elevated atmospheric CO_2 are based primarily on extrapolation from other regions, observational changes along climate gradients, and a few direct experiments. Extrapolation from other regions, particularly north temperate and boreal ecosystems can be problematic because tropical forests occur on highly weathered, P-limited soils; support very diverse microbial, plant, and animal communities; and have high mean annual temperatures with low temporal variability. Similarly, while climate gradient research can provide insights into systematic changes across plant communities and habitats, they are generally poorly suited to explore climate changes within a given community or site. There have been some significant strides forward with the establishment of large-scale, *in situ* manipulations in the tropics such as the throughfall exclusion experiment in eastern Amazonia (Nepstad *et al*., 2002) and the irrigation of a seasonally dry forest in Panama (Wright, 1991; Yavitt and Wright, 1996). Clearly more experimentation is needed to determine the sensitivity of tropical forest flora, fauna, and biogeochemical cycles to elevated CO_2 and climate change.

Future research should be designed to capture ecosystem responses within a realistic range of temperature and/or precipitation change, and over a long enough time interval to determine if self-regulation or equilibration to a new condition occurs. As mentioned above, tropical regions are characterized by mean annual temperatures near the biological optimum. Under these conditions a small

Table 11.2. Summary of potential effects of climate change on nutrient cycling in tropical forests.

	Increased temperature	*Altered rainfall* (+/−)	*Other effects*	*Research directions*
Soil nutrient availability	Increase in mineralization rates for both N and P	+ Increased P availability due to shift in redox conditions, increased N losses via nitrification, denitrification, and increased N and P losses via leaching	Increased soil organic matter due as a result of elevated CO_2 could increase nutrient retention capacity and organic coatings could decrease P sorption capacity	What is the impact of increases in nutrient deposition due to urbanization and intensification of agriculture in addition to climate shifts and elevated CO_2 in these systems?
Litter nutrient inputs and decomposition		Data show both + and − correlations between rainfall and litter nutrient concentrations. Shifts in seasonality could decouple decomposition of litter from nutrient demand	Some evidence for increased C : nutrient ratios under elevated CO_2 potentially leading to decreased decomposition rates and/or increased nutrient immobilization during decomposition	What are the effects of climate change on belowground nutrient inputs and decomposition?

shift in temperature may have a stronger or different effect than a large increase in ecosystems that typically experience wide seasonal shifts in temperature (Townsend *et al.*, 1992). Collaborative research should be a key component of future climate change experiments, to better understand the linkages among population, community, and ecosystem processes. Future work needs to consider human drivers such as N deposition, landuse change, and invasive species in conjunction with climate factors to improve our ability to predict future conditions.

	Increased temperature	*Altered rainfall (+/−)*	*Other effects*	*Research directions*
Nutrient uptake	Root uptake kinetics are positively related to soil temperature. Mycorrhizal infection appears to be positively correlated to soil temperature	Stronger drought/dry season dynamics may reduce fine root and microbial biomass in surface soils thus reducing nutrient uptake	Shifts in relative and absolute belowground plant biomass under elevated CO_2 appear to be species specific thus hard to predict in a diverse tropical forest	Are changes in nutrient uptake dynamics translated into shifts in net productivity?
Trace gas emissions		N_2O emissions are sensitive to soil moisture conditions and have been found to positively correlate to rainfall. Under wet conditions upland tropical forests can switch from a slight sink to a net source of CH_4		Will trace gas dynamics in tropical forests under wetter and warmer or more strongly seasonal conditions lead to positive feedbacks for the global climate?

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12

The response of South American tropical forests to recent atmospheric changes

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12.1 INTRODUCTION

Ecosystems worldwide are changing as a result of anthropogenic activities. Processes such as deforestation are physically obvious, but others, such as hunting and surface fires, are subtler but affect biodiversity in insidious ways (cf. Lewis *et al.*, 2004a; Laurance, 2004). Increased rates of nitrogen deposition and increases in air temperatures and atmospheric CO_2 concentrations are altering the environment of even the largest and most well-protected areas (e.g., Galloway and Cowling, 2002; Malhi and Wright, 2004). Anthropogenic atmospheric change will become more significant during this century, as CO_2 concentrations reach levels unprecedented for the last 20 million or perhaps even 40 million years (Retallack, 2001; Royer *et al.*, 2001). Nitrogen deposition rates and climates are predicted to move far beyond Quaternary envelopes (Galloway and Cowling, 2002). Moreover, the rate of change in all these basic ecological drivers is likely to be without precedent in the evolutionary span of most species on Earth today (Lewis *et al.*, 2004a). This then is the Anthropocene: we are living through truly epoch-making times (Crutzen, 2002).

Given the scale of the anthropogenic experiment with the atmosphere–biosphere system, it is now self-evident that all ecosystems on Earth are affected by human activities in some sense. Recent research (Malhi and Phillips, 2005) suggests that tropical forests far from areas of deforestation are indeed undergoing profound shifts in structure, dynamics, productivity, and function. Here we synthesize recent results from a network of long-term monitoring plots across tropical South America that indicate how these forests are changing.

Changes in tropical forests are of societal importance for three reasons. First, tropical forests play an important role in the global carbon cycle and hence the rate of climate change, as ~40% of terrestrial vegetation carbon stocks lie within tropical forests (Malhi and Grace, 2000). Second, as tropical forests house at least half of all Earth's species, changes will have a large impact on global biodiversity (Groombridge

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M. B. Bush, J. R. Flenley, and W. D. Gosling (Editors), *Tropical Rainforest Responses to Climatic Change* (Second Edition).

and Jenkins, 2003). Finally, as different plant species vary in their ability to store and process carbon, both climate and biodiversity changes are potentially linked by feedback mechanisms (e.g., Cox *et al.*, 2000).

Evidence suggests that the remaining Amazonian rainforest has been a substantial carbon sink since at least the 1980s. The evidence is from long-term monitoring plots which show that forest stands are increasing in above-ground biomass (Phillips *et al.*, 1998, 2002a; Baker *et al.*, 2004a), and from inverse modeling of atmospheric CO_2 concentrations that indicate tropical ecosystems may contribute a carbon sink of 1–2 Gt (1 gigatonne = 1 billion metric tonnes) per year (e.g., Phillips *et al.*, 2009; Rodenbeck *et al.*, 2003). The existence of a substantial tropical carbon sink is consistent with modeling and laboratory studies that imply changes in the productivity of tropical forests in response to increasing CO_2 (e.g., Lloyd and Farquhar, 1996; Norby *et al.*, 1999; Lewis *et al.*, 2004a). Although these interpretations are still being debated (see Lewis *et al.*, 2004a), efforts to overcome limitations in each line of evidence have generally confirmed the presence of a sink. Thus, it is reasonable to suggest that tropical forests are providing a substantial buffer against global climate change. Indeed, the results from long-term forest-monitoring plots suggest that intact Amazonian forests have increased in biomass by ~0.3–0.5% per year, and hence sequester carbon at approximately the same rate that the European Union emits it by burning fossil fuels. Recent research shows that forests in Africa have also been sequestering carbon for the last few decades (Lewis *et al.*, 2009), indicative perhaps of a shared mechanism influencing both African and Amazonian systems.

Increasing atmospheric CO_2 concentrations and rising air temperatures will alter fundamental ecological processes and in turn will likely effect changes in tropical biodiversity. Changes in biodiversity as a consequence of anthropogenic climate change have in fact already been noted in better studied temperate areas (e.g., Parmesan and Yohe, 2003) and in a well-studied old-growth tropical forest landscape in Brazil (Laurance *et al.*, 2004). The interactive "balance" among tens of thousands of tropical plant species and millions of tropical animal species is certain to shift, even within the largest and best protected forest ecosystems, which are traditionally thought of as "pristine" wilderness. These areas are vital refugia—where global biodiversity may most easily escape the current extinction crisis—as they are large enough to allow some shifts in the geographic ranges of species in response to global changes, and are afforded some protection from industrial development, such as logging and agriculture. However, how most tropical forest taxa will respond to rising temperatures and CO_2 concentrations, among other global changes, is currently unknown (Thomas *et al.*, 2004).

Biodiversity change has inevitable consequences for climate change because different plant species vary in their ability to store and process carbon. One example of this is how shifts in the proportion of faster growing light-demanding species may alter the carbon balance of tropical forests. Long-term plots suggest that mature humid Neotropical forests are a net carbon sink of ~0.6 gigatonnes per year (Phillips *et al.*, 1998; Baker *et al.*, 2004a). However, tree mortality rates have increased substantially in recent decades, so causing a likely increase in the frequency of tree-fall gap formation (Phillips and Gentry, 1994; Phillips *et al.*, 2004). A shift in forests towards gap-favoring, light-demanding species with high growth rates, at the expense of more shade-tolerant species, is plausible (Körner, 2004). Such fast-growing species generally have lower wood-specific gravity, and hence lower carbon content (West *et al.*, 1999), than do shade-tolerant trees. An Amazon-wide decrease in mean wood specific gravity of just 0.4% would cancel out the carbon sink effect apparently caused by accelerated plant productivity. Whether such changes are occurring is currently poorly understood, but it is clear that the biodiversity and climate change issues are closely linked and merit further study.

In this chapter we present a summary of the latest findings from permanent plots monitored by a large network of Amazon forest researchers, known as "RAINFOR" (*Red Amazónica de Inventarios Forestales*, or Amazon Forest Inventory Network; *http://www.geog.leeds.ac.uk/projects/rainfor/*). Here we summarize findings from old-growth forests in terms of (i) structural change, (ii) dynamic process change, and (iii) functional change, over the period since 1980 to 2005, concentrating on the period 1980 to 2000 for which the most detailed analyses have been done.

12.2 THE PLOT NETWORK

For these analyses, we define a plot as an area of forest where all trees above 10 cm diameter at breast height (d.b.h., measured at 1.3 m height or above any buttress or other deformity) are tracked individually over time. All trees are marked with a unique number, measured, mapped, and identified. Periodically (generally every 5 years), the plot is revisited, and all surviving trees are re-measured, dead trees are noted, and trees recruited to 10 cm d.b.h. are uniquely numbered, measured, mapped, and identified. This allows calculation of: (i) the cross-sectional area that tree trunks occupy (termed "basal area"), which can be used with allometric equations to estimate tree biomass (Baker *et al.*, 2004a); (ii) tree growth (the sum of all basal area increments for surviving and newly recruited stems over a census interval); (iii) the total number of stems present; (iv) stem recruitment (number of stems added to a plot over time); and (v) mortality (either the number or basal area of stems lost from a plot over time). We present results from 50 to 91 plots, depending upon selection criteria for different analyses (most critically, the number of census intervals from a plot and whether only stem count data or the full tree-by-tree data set is available). The number of plots used for stem density changes is more than that used in the biomass study because full tree-by-tree data are required to calculate biomass (using Baker *et al.*'s, 2004a methods), whereas stem change data can often be obtained from published studies. The plots span the Amazonian forests of northern South America (Figure 12.1), including Bolivia, Brazil, Ecuador, French Guiana, Peru, and Venezuela. Most are 1 ha in size and comprise ~600 trees of ≥10 cm d.b.h. The smallest are 0.4 ha and the largest is 9 ha, all large enough to avoid undue influence by the behavior of an individual tree (Chave *et al.*, 2003). Many plots have been monitored for more than a decade, although they range in age from 2 to more than 25 years. The earliest plot inventory was started in 1971, the latest in 2002. Details of the exact

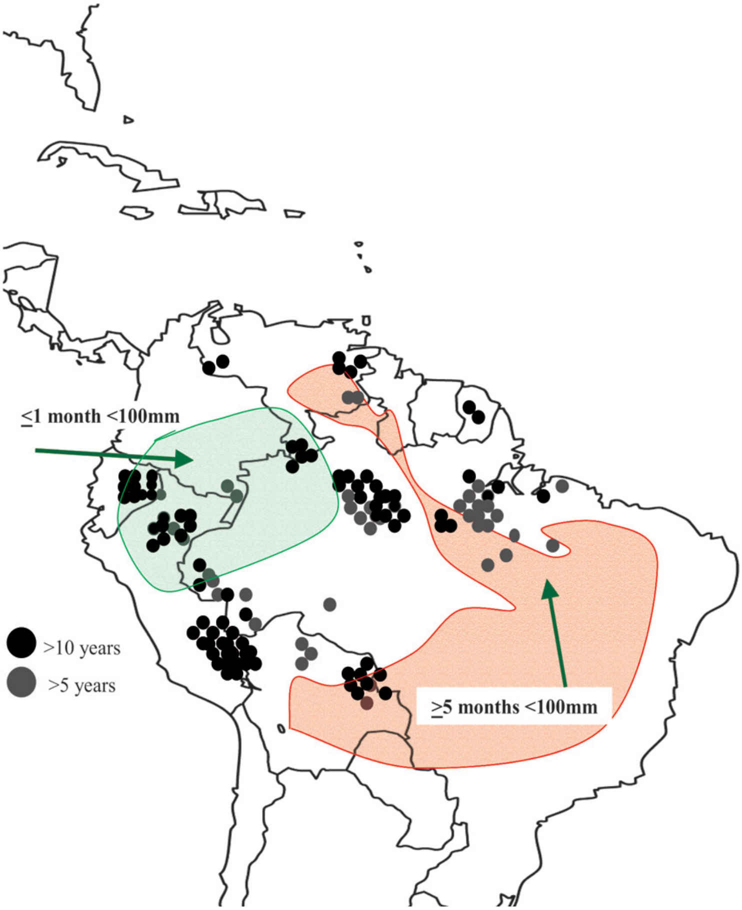

Figure 12.1. Plot locations used in this study. Symbols represent approximate locations of each plot; gray circle for plots monitored for 5–10 years, black for those with >10 years of monitoring. The approximate extent of seasonal and highly seasonal areas of tropical South America are indicated.

plot locations, inventory and monitoring methods, and issues relating to collating and analysing plot data are omitted from this chapter for reasons of space, but are discussed in detail elsewhere (Phillips *et al.*, 2002a, b, 2004, 2009; Baker *et al.*, 2004a, b; Malhi *et al.*, 2002, 2004; Lewis *et al.*, 2004b).

12.3 STRUCTURAL CHANGES

Among 59 plots monitored in old-growth Amazon forests with full tree-by-tree data, there has been a significant increase in above-ground biomass between the first and last time they were measured. Over approximately 20 years, the increase has been

0.61 ± 0.22 tonnes of carbon per hectare per year, or a relative increase of 0.50 ± 0.17% per year (mean ± 95% confidence interval; Baker *et al.*, 2004a). Across all 59 plots, the above-ground biomass change is normally distributed and shifted to the right of 0 (Figure 12.2a). The estimate of a net increase of 0.61 ± 0.22 t C ha^{-1} yr^{-1} is slightly higher than the 0.54 ± 0.29 t C ha^{-1} yr^{-1} estimated earlier for the lowland Neotropics by Phillips *et al.* (1998) using 50 sites up to 1996.

We estimate the magnitude of the South American carbon sink by multiplying 0.61 tonnes per hectare per year by the estimated area of mature Neotropical humid forest cover (c. 8,705,100 km^2; FAO, 1990), which yields a value of about 0.5 gigatonnes of carbon per year. If we further assume that the ratio of above-ground to below-ground biomass is 3 : 1 (cf. Phillips *et al.*, 1998), and that below-ground biomass is increasing in proportion to above-ground biomass, then the sink increases to 0.71 ± 0.26 gigatonnes of carbon per year. If other biomass components—such as small trees, lianas, and coarse woody debris—are also increasing in biomass, then the sink will be fractionally larger still. However, these estimates depend critically on (i) how representative the 59 tree-by-tree plots are of South American forests; (ii) assumptions about the extent of mature, intact forest remaining in South America; (iii) the extent to which we have sampled the regional-scale matrix of natural disturbance and recovery.

Clark (2002) raised two concerns about the original findings of Phillips *et al.* (1998) that Amazon biomass was increasing, suggesting that (i) some floodplain plots that Phillips *et al.* considered mature may still be affected by primary succession, and that (ii) large buttress trees in some plots may have been measured in error—that is, not above the buttress, as protocols dictate, but around them. However, Baker *et al.* (2004a) showed that the carbon sink remains when plots on old floodplain substrates and those that may have buttress problems are removed from the analysis.

Consideration of all 91 RAINFOR plots up to 2002 shows a small increase in stem density between the first and last time they were measured, of 0.84 ± 0.77 stems per hectare per year (Figure 12.2b; paired *t*-test, $t = 2.12$, $P = 0.037$), or a 0.15 ± 0.13% per year increase (Phillips *et al.*, 2004). Across all plots, stem change rates are approximately normally distributed and slightly shifted to the right of 0 (Figure 12.2b). The same test using 59 plots (from the Baker *et al.* 2004a study) shows a similar increase in stem density (0.16 ± 0.15% per year), while a smaller but longer term data set (50 plots from Lewis *et al.*, 2004b) shows a slightly larger increase (0.18 ± 0.12% per year). While still significant, these changes in stem density are proportionally not as great as the biomass changes. A more recent pan-Amazon analysis (Phillips *et al.*, 2009) spanned the 2005 drought, and found that the drought reversed the biomass carbon sink for at least a year, but did little to the quantity of biomass carbon accumulated net over the previous two decades.

12.4 DYNAMIC CHANGES

An alternative way of examining forest change is to look for changes in processes (growth, recruitment, death), as well as in structure (biomass, stem density). Are these

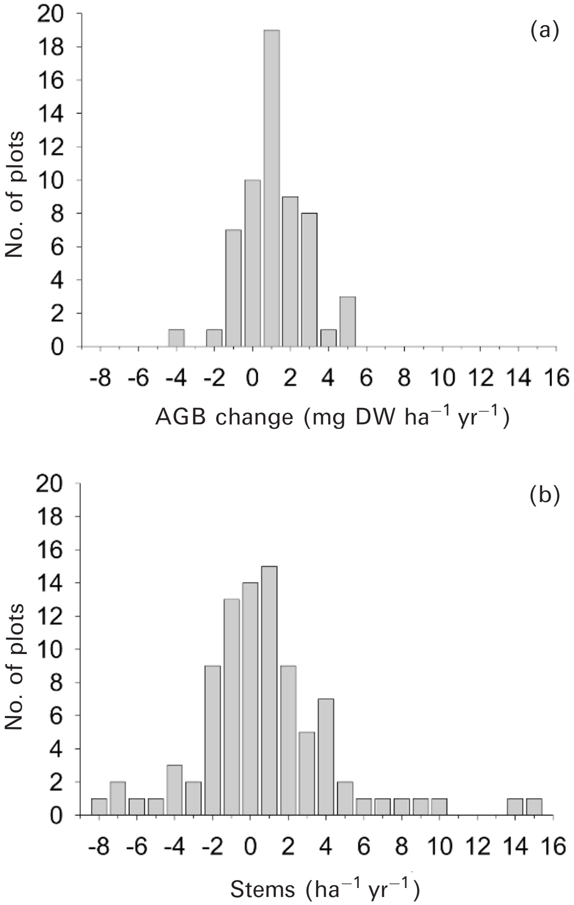

Figure 12.2. (a) Above-ground biomass change (dry weight) of trees greater than 10 cm diameter in 59 Amazon plots, based on initial and final stand biomass estimates calculated using an allometric equation relating individual tree diameter to biomass, and incorporating a correction factor to account for variation in wood density among species (from Baker *et al.*, 2004a). As would be expected in a random sample of small plots measured for a finite period, some sites show a decline in biomass during that period indicating that at that particular point in space and time tree mortality has exceeded tree growth. However, the mean and median are shifted significantly to the right ($P < 0.01$). (b) Stem number change in 91 plots from across South American tropical forests. Stems were counted during the first and final censuses of each plot (plots are the same as those used by Phillips *et al.*, 2004). The mean and median are shifted significantly to the right ($P < 0.05$).

forests getting more active or simply gaining mass? We measure the dynamics of forests in two ways. First, we can examine changes in stem population dynamics. By convention (Phillips and Gentry, 1994) we estimate stem turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees $\geq$10 cm diameter. Second, we examine changes in biomass fluxes of the forest—

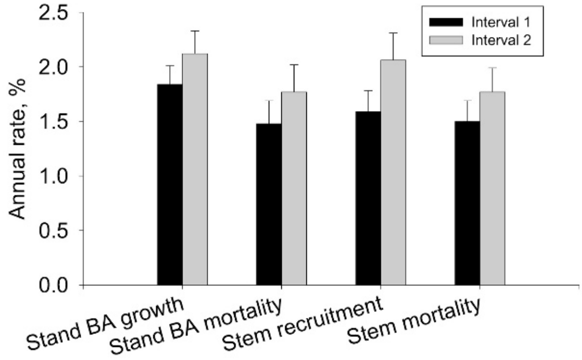

Figure 12.3. Annualized rates of stand-level basal area growth, basal-area mortality, stem recruitment, and stem mortality from plots with two consecutive census intervals (i.e., the subset of RAINFOR sites that have been inventoried on at least three successive occasions), each giving the mean from 50 plots with 95% confidence intervals. Paired *t*-tests show that all of the increases are significant. The average mid-year of the first and second censuses was 1989 and 1996, respectively (from Lewis *et al.*, 2004b).

in terms of growth of trees and the biomass lost with mortality events. These stand-level rates of "biomass growth" and "biomass loss" should be approximately proportional to the rate at which surviving and recruiting trees gain basal area and the rate at which basal area is lost from the stand through tree death (Phillips *et al.*, 1994).

Among 50 old-growth plots across tropical South America with at least three censuses (and therefore at least two consecutive monitoring periods that can be compared), we find that all of these key ecosystem processes—stem recruitment, mortality, and turnover, and biomass growth, loss, and turnover—are increasing significantly (Figure 12.3), between the first and second halves of the monitoring period (Lewis *et al.*, 2004b). Thus, over two decades, these forests have become, on average, faster growing and more dynamic. Notably, the increases in the rate of dynamic fluxes (growth, recruitment, and mortality) are about an order of magnitude larger than are the increases in the structural pools (above-ground biomass and stem density; Lewis *et al.*, 2004b).

These and similar results can be demonstrated graphically in a number of ways. In Figure 12.4, we plot the across site mean values for stem recruitment and mortality as a function of calendar year. This shows that the increase has not been short term (e.g., the result of a spike around a year with unusual weather), that recruitment rates have on average consistently exceeded mortality rates, and that mortality appears to lag recruitment (Phillips *et al.*, 2004).

Using data for the 50 plots with two consecutive census intervals, we can also separate them into two groups: one faster growing and more dynamic (mostly western Amazonian), and one slower growing and less dynamic (mostly eastern and central Amazonian). Both groups showed increased stem recruitment, stem mortality, stand basal area growth, and stand basal area mortality, with larger absolute increases in

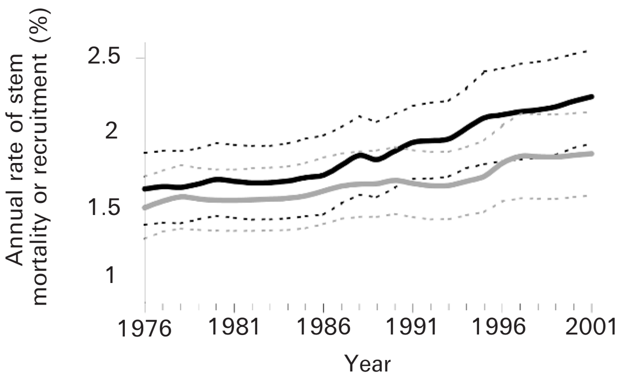

Figure 12.4. Mean and 95% confidence intervals for stem recruitment and mortality rates against calendar year, for plots arrayed across Amazonia. Rates for each plot were corrected for the effects of differing census-interval lengths, for "site-switching", and for "majestic forest bias". A detailed justification methodology for these corrections is given in Phillips *et al.* (2004); all trends are robust and hold equally if these corrections are not applied. Black indicates recruitment, gray indicates mortality, solid lines are means, and dots are 95% confidence intervals (from Phillips *et al.*, 2004).

rates in the faster growing and more dynamic sites than in the slower growing and less dynamic sites (Figure 12.5; Lewis *et al.*, 2004b). However, the proportional increases in rates were similar, and statistically indistinguishable, across both forest types (Lewis *et al.*, 2004b). This shows that increasing growth, recruitment, and mortality rates are occurring proportionately similarly across different forest types and geographically widespread areas.

12.5 FUNCTIONAL CHANGES

Changes in the structure and dynamics of tropical forests are likely to be accompanied by changes in species composition and function. There is, moreover, no *a priori* reason to expect that large changes in Amazon forests should be restricted to trees. Phillips *et al.* (2002b) studied woody climbers (structural parasites on trees, also called "lianas"), which typically contribute 10–30% of forest leaf productivity but are ignored in almost all monitoring studies except in most of our western Amazonian sites. Across the RAINFOR plots of western Amazonia there has been a concerted increase in the density, basal area, and mean size of lianas (Figure 12.6; Phillips *et al.*, 2002b). Over the final two decades of the 20th century, the density of large lianas relative to trees increased here by 1.7–4.6% per year. This was the first direct evidence that intact tropical forests are changing in terms of their composition and function. A long-term monitoring study from beyond Amazonia (Barro Colorado Island in Panama) has since reported a substantial increase in absolute and relative liana leaf-fall rates since the 1980s, indicating that lianas are both increasing and becoming more dominant there (Wright *et al.*, 2004). There is some experimental

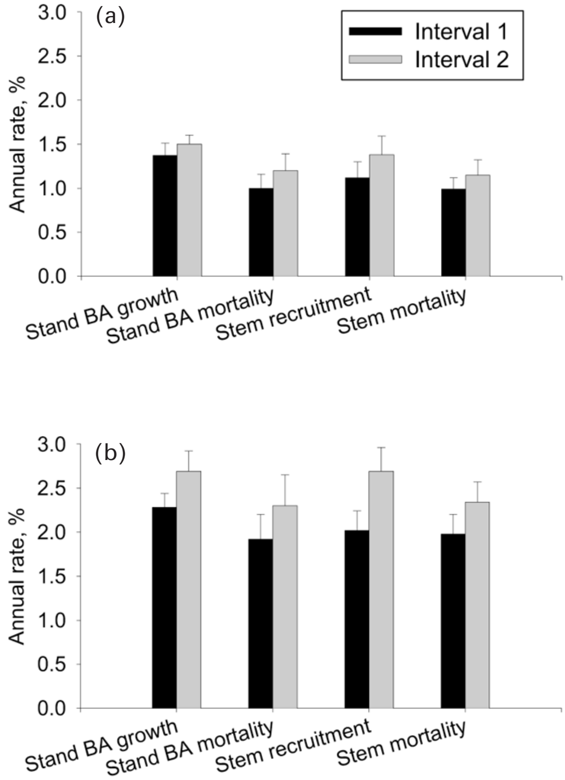

Figure 12.5. Annualized rates of stand-level basal area growth, basal-area mortality, stem recruitment, and stem mortality over consecutive census intervals for plots grouped into "slower growing less-dynamic" (a) and "faster growing more-dynamic" (b) forests. Of the slower dynamics group, 20 of 24 plots are from eastern and central Amazonia, whereas just two are from western Amazonia. Of the faster dynamics group, 24 of 26 plots are from western Amazonia, with just one from central Amazonia. The remaining three plots are from Venezuela and outside the Amazon drainage basin. Changes have occurred across the South American continent, and in both slower and faster dynamic forests (from Lewis *et al.*, 2004b).

evidence (Granados and Körner, 2002) for a very strong response of tropical lianas to elevated atmospheric CO_2 concentrations, much stronger than the normal experimental response of trees.

Finally, analysis from a cluster of plots in central Amazonia has shown consistent changes in tree species composition over the two decades up to the early 2000s (Laurance *et al.*, 2004). Many faster growing genera of canopy and emergent stature trees increased in basal area or density, whereas some slower growing genera of sub-canopy or understory trees decreased in density. Laurance *et al.* (2004) provide evidence of pervasive changes in central Amazonian forests: growth, mortality, and recruitment all increased significantly over two decades (basal area also increased, but not significantly so), with faster growing genera

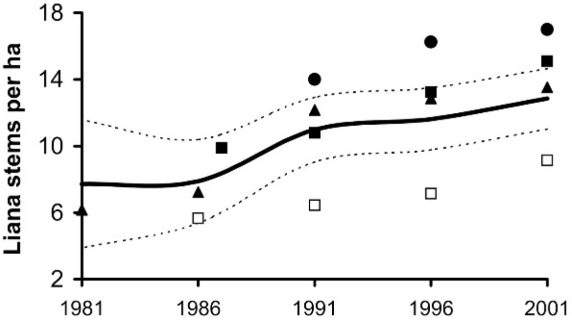

Figure 12.6. Five-year running means (solid line) with 95% confidence intervals (dashed lines) of liana stem density per hectare (>10 cm diameter at breast height), with values plotted separately for northern Peru (filled squares), southern Peru (filled triangles), Bolivia (filled circle), and Ecuador (open squares) (adapted from Phillips *et al.*, 2002b; see that paper for full details of field and analytical methodology).

showing much larger absolute and relative increases in growth, relative to slower growing genera. Further studies are urgently needed to determine whether comparably large shifts in tree communities are occurring throughout the tropics.

12.6 WHAT IS DRIVING THESE CHANGES?

What could be causing the continent-wide changes in tree growth, recruitment, mortality, stem density, and biomass? Many factors could be invoked, but there is only one parsimonious explanation. The results appear to show a coherent fingerprint of increasing growth—that is, increasing net primary productivity (NPP)—across tropical South America, probably caused by a long-term increase in resource availability (Lewis *et al.* 2004a, b). According to this explanation, increasing resource availability increases NPP, which then increases stem growth rates. Faster individual growth rates account for the increase in stand basal area growth and stem recruitment rates, and the fact that these factors show the ‘‘clearest’’ signals (statistically most significant) in the analyses (Lewis *et al.*, 2004b). Because of increased growth, competition for limiting resources—such as light, water, and nutrients—increases. Over time some of the faster growing, larger trees die, as do some of the ‘‘extra’’ recruits (the accelerated growth percolates through the system), resulting in increases in the rate of biomass mortality and stem mortality. Thus, the system gains biomass and stems, while the losses lag some years behind, causing an increase in above-ground biomass and stems. Overall, this suite of changes may be qualitatively explained by a long-term increase in a limiting resource.

The changes in composition can also be explained by increasing resource availability, as the rise in liana density may be either a direct response to rising resource supply rates, or a response to greater disturbance caused by higher tree mortality rates. The changing tree composition in central Amazonian plots (Laurance *et al.*, 2004) is also consistent with increasing resource supply rates, as experiments show that faster growing species are often the most responsive, in absolute terms, to increases in resource levels (Coomes and Grubb, 2000).

What environmental changes could be increasing the growth and productivity of tropical forests? While there have been widespread changes in the physical, chemical, and biological environment of tropical trees (Lewis *et al.*, 2004a), only increasing atmospheric CO_2 concentrations (Prentice *et al.*, 2001), increasing solar radiation inputs (Wielicki *et al.*, 2002), and rising air temperatures (Malhi and Wright, 2004) have been documented across Amazonia and could be responsible for increased growth and productivity. For none of these three changes, however, do we have overwhelming evidence that the driver has both actually changed and that such a change must accelerate forest growth (Lewis *et al.*, 2004a).

The increase in atmospheric CO_2 is our leading candidate, because of the undisputed long-term increase in CO_2 concentrations, the key role of CO_2 in photosynthesis, and the demonstrated positive effects of CO_2 fertilization on plant growth rates, including experiments on whole temperate forest stands (Hamilton *et al.*, 2002; Norby *et al.*, 2002; Lewis *et al.*, 2004a). At present, however, no experiments have assessed the effects of increasing CO_2 availability on intact, mature tropical forest stands, and this interpretation is still contested by some (e.g., Chambers and Silver, 2004).

Air temperature increases are also undisputed, and could conceivably be causing the changes we document. However, many authors expect that the 0.26°C per decade air temperature increase (Malhi and Wright, 2004) would actually reduce, not increase, forest growth, as respiration costs are likely to increase with temperature. However, increased air temperatures will also increase soil temperatures, which could in turn increase soil mineralization rates and thus nutrient availability (see review by Lewis *et al.*, 2004a). Whether recent rises in air temperature have increased or decreased tropical forest NPP requires further study.

Recent satellite data suggest an increase in incoming solar radiation across the tropics between the mid-1980s and late 1990s as a result of reduced cloudiness (Wielicki *et al.*, 2002). However, because stem turnover has increased across the tropics since the 1950s (Phillips and Gentry, 1994; Phillips, 1996), increasing solar radiation since the mid-1980s may not have occurred over a long enough period of time to explain the trends in forest plot data, at least in terms of stem turnover. Furthermore, as the *difference* between stand-level basal area growth and mortality was similar at the start (1980s) and end (1990s) of the study by Lewis *et al.* (2004b), the factor causing changes in growth, recruitment, and mortality was probably operating before the onset of the study, and hence before the observed increase in incoming solar radiation. The evidence for increased insolation in Amazonia is rather weak and there is a possibility that forest NPP may be greater under cloudy conditions (e.g., Roderick *et al.*, 2001: cloudiness increases the fraction of radiation that is indirect, which penetrates further into the canopy and could thus have a positive impact on whole forest NPP since canopy leaves overheat in midday tropical sun and may already be saturated with respect to light). Finally, while the 2005 drought was associated with increased insolation we found no evidence for increased growth (Phillips *et al.*, 2009). However, a clear response of temporarily elevated mortality risk was detected in the more severely dried locations, so any ecophysiological impacts of changing radiation were probably confounded with those resulting from increased moisture stress.

Determining which environmental change, or changes, has caused the long-term trends we document across South American tropical forest is very difficult. However, each environmental change is expected to leave a unique signature, or fingerprint, in forest data, as different environmental changes initially impact different processes, have different distributions in time and space, and may affect some forests more than others (e.g., depending upon soil fertility). Future analyses of forest plot data at finer spatially and temporally resolved scales should therefore allow a further narrowing of potential causes underlying rising productivity across South American tropical forests (Lewis *et al.*, 2004a).

12.7 THE FUTURE

For those concerned about future biodiversity losses and global climate change, our analyses suggest both worrying trends and some apparently "good news". The Amazon, the world's largest remaining tract of tropical forest, has shown concerted changes in forest dynamics. Such unexpected and rapid alterations—apparently in response to anthropogenic atmospheric change—raise concerns about other possible surprises that might arise as global changes accelerate in coming decades. Tropical forests are evidently very sensitive to changes in incoming resource levels and may show large structural and dynamic changes in the future, as resource levels alter further and temperatures continue to rise (Lewis *et al.*, 2004a). The implication of such rapid changes for the world's most biodiverse region is unknown, but could be substantial.

Moreover, old-growth Amazonian forests are evidently helping to slow the rate at which CO_2 is accumulating in the atmosphere, thereby acting as a buffer to global climate change—certainly "good news" for the moment. The concentration of atmospheric CO_2 is rising at a rate equivalent to 3–5 gigatonnes of carbon per year; this would be significantly greater without the tropical South American carbon sink of 0.5 to 0.8 gigatonnes of carbon per year—values that are doubled if the rest of the world's tropical forests are behaving similarly as already documented for Africa (Lewis *et al.*, 2009). However, this subsidy from nature could be a relatively short-lived phenomenon. Mature Amazonian forests may either (i) continue to be a *carbon sink* for decades (Chambers *et al.*, 2001, Cramer *et al.*, 2001), or (ii) soon become a *small carbon source* because of changes in functional and species composition (Cramer *et al.*, 2001; Phillips *et al.*, 2002b; Körner, 2004; Laurance *et al.*, 2004), or (iii) become a *mega-carbon source*, possibly in response to climate change (Cox *et al.*, 2000; Cramer *et al.*, 2001) as happened temporarily after the 2005 drought (Phillips *et al.*, 2009). Given that a 0.3% annual increase in Amazon forest biomass is roughly equivalent to the entire fossil fuel emissions of the European Union (in January 2004), a long-term switch of tropical forests from a moderate carbon sink to even a moderate carbon source would have profound implications for global climate, biodiversity, and human welfare.

Finally, it is important to emphasize that climate-based models that project the future carbon balance in Amazonia (and future climate change scenarios) have made no allowance for changing forest composition. This omission is likely to lead to erroneous conclusions. For example, lianas contribute little to forest biomass but kill trees and suppress tree growth (Schnitzer and Bongers, 2002), and their rapid increase suggests that the tropical carbon sink might shut down sooner than current models suggest. Large changes in tree communities could undoubtedly lead to net losses of carbon from tropical forests (Phillips and Gentry, 1994; Körner, 2004). The potential scope for such impacts of biodiversity changes on carbon storage is highlighted by Bunker *et al.* (2005) who explored various biodiversity scenarios based on the tree species at Barro Colorado Island. When slower growing tree taxa are lost from an accelerated, liana-dominated forest, as much as one third of the carbon storage capacity of the forest could be lost. Clearly, projections of future carbon fluxes will need to account for the changing composition and dynamics of tropical forests.

12.8 ACKNOWLEDGMENTS

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13

Ecophysiological response of lowland tropical plants to Pleistocene climate

S. A. Cowling

13.1 INTRODUCTION

Climate changes associated with the Last Glacial Maximum (LGM, 21 kyr) are probably the most extreme that terrestrial vegetation, including tropical lowland ecosystems, have been forced to respond in over the past 100,000 years. The degree of tropical cooling can be reconstructed by paleoproxies that generally indicate a minimal cooling of 3°C and a maximum cooling of approximately 7°C (Guilderson *et al.*, 1994; Stute *et al.*, 1995; Mix *et al.*, 1999; Behling and Negrelle, 2001; Mora and Pratt, 2001; Behling, 2002; Urrego *et al.*, 2005; Punyasena *et al.*, 2008; Blard *et al.*, 2009; Williams *et al.*, 2009). Some debate surrounds the degree of tropical decreases in glacial precipitation, primarily because precipitation patterns are strongly regional, and thus wide discrepancies in paleoprecipitation trends occur between different reconstructions. Despite this, a value of approximately 20% decrease in LGM rainfall is typically reconstructed from pollen-proxies in tropical catchments—such as the Amazonian Basin (Bush and Silman, 2004). Paleoclimate simulations of the South American monsoon during the LGM indicate an annual reduction in rainfall across Amazonia of between 25–35% relative to today (Cook and Vizy, 2006). Research also shows that glacial decreases in rainfall likely occurred in wet as opposed to dry seasonal months (Bush and Silman, 2004).

Less ambiguous with respect to paleoclimate reconstruction is the decline in atmospheric CO_2 that occurred at the LGM. Direct measurement of CO_2 gas trapped in Antarctic and Greenland polar ice provides us with a record of CO_2 for the past 420,000 years (Indermuhle *et al.*, 1999; Monnin *et al.*, 2001). Ice core studies indicate that atmospheric CO_2 at the LGM was on average 200 parts per million by volume (p.p.m.V) (relative to modern day values of >380 p.p.m.V), indicating an over 40% reduction in atmospheric levels during glacial periods.

A combination of climate cooling, decreasing precipitation, and low atmospheric CO_2 surely promoted changes in equatorial vegetation form and function, but in what

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way and to what extent is still a matter of discussion. There are far fewer palynological sites located in tropical regions relative to those in temperate North America and Eurasia, simply due to geological history. Discovery of new coring sites with good paleoecological reconstruction potential, however, is increasing (Mayle *et al.*, 2000; Bush, 2002; Gosling *et al.*, 2009; Behling and Safford, 2010; Urrego *et al.*, 2010).

As a result of the current shortage of tropical palynological records, dynamic global vegetation models (DGVMs) play a key role in filling knowledge gaps where no tropical pollen profiles currently exist (Harrison and Prentice, 2003; Cowling *et al.*, 2004; Wu *et al.*, 2007; Cannon *et al.*, 2009; Mayle *et al.*, 2009; Alba-Sanchez *et al.*, 2010). Vegetation models can also be important for elucidating the underlying mechanisms of vegetation change because models are built upon fundamental principles of plant physiology, biochemistry, and ecosystem ecology. Models differ in the way they emphasize or parameterize particular processes, but they address fundamental biophysical mechanisms nonetheless.

Research effort towards better understanding past vegetation changes is essential, for if we can't explain ecological changes that we know to have occurred within past climates, then how can we place confidence on our estimations about ecological responses to future changes in climate? By outlining knowledge on how plants physiologically and biochemically respond to different abiotic stresses, we can begin to hypothesize about how lowland vegetation may have looked in the past, and how it might be influenced in the future. Equipped with this knowledge, we are able to make more informed decisions concerning aspects of tropical conservation, as well as developing mitigation strategies before a time when unwanted ecological changes may occur.

In this chapter I introduce some of the biochemical and physiological plant processes (mechanisms) that are important in terms of ecosystem-level responses to climate change, focusing on those most influenced by Pleistocene climate. Due to the ability of models to deconvolve co-varying responses, I address the independent versus interactive effects of Pleistocene precipitation, temperature, and atmospheric CO_2 on lowland plant ecology. Whether or not C_4 plants (mostly subtropical and tropical grasslands) experienced widespread proliferation during glacials will be a topic of discussion, one that includes recent research highlighting the potential for over-prediction of C_4 plant abundance due to caveats associated with stable carbon isotope analyses. The latter sections of this review will contain more speculative discussions of the stratification of tropical lowland forests based on the results of different modeling experiments, and of the possible response of tropical soil processes to Pleistocene climate change.

13.2 ECOPHYSIOLOGICAL PRIMER

Natural vegetation can be divided into two broad categories (C_3 and C_4), named according to the number of carbon atoms in the first organic intermediate of photosynthesis. Most plants exhibit the C_3 photosynthetic pathway and include a vast range of herbaceous, woody, and grass species. On the other hand, C_4 species are nearly all grasses typically found in seasonally moist and semi-arid regions of the tropics (Sage, 1999).

In C_3 plants the enzyme that is responsible for initiating biochemical reactions involving CO_2 (called "carboxylation") is called "Rubisco" (ribulose-1,5-bisphosphate carboxylase-oxygenase). Rubisco is reactive with both CO_2 and O_2 at rates determined by concentrations of O_2 and CO_2, the catalytic properties of Rubisco, as well as leaf temperature (Pearcy and Ehleringer, 1984). Photorespiration (the oxygenation of Rubisco) causes an overall loss of fixed carbon in the leaf, and is a process that is highly sensitive to changes in leaf temperature. High temperatures reduce the affinity of Rubisco for CO_2 relative to O_2 (called the "specificity factor"), thereby elevating rates of photorespiration (Brooks and Farquhar, 1985).

Carboxylation in C_4 species occurs within structures surrounded by bundle sheath cells (called "Kranz morphology") (Pearcy and Ehleringer, 1984). The bundle sheath functions as a type of "CO_2 pump" in that it actively transports CO_2 across cell membranes to concentrate CO_2 at the site of carboxylation. The primary carboxylating enzyme in C_4 plants, phosphoenolpyruvate (PEP) carboxylase, is non-reactive with O_2, so that photorespiration is far less limiting to plant carbon balance than in C_3 species (Ehleringer and Bjorkman, 1977).

Plant carbon and water relations are tightly linked via the functioning of leaf pores called "stomata". The concentration of CO_2 in intercellular spaces (C_i) is sensed by plants, promoting subsequent feedbacks onto the shape and size of stomata as mediated by changes in stomatal conductance (Farquhar and Sharky, 1982). The ratio of the amount of CO_2 gained relative to the amount of water lost, called "water-use efficiency" (WUE), is a good indicator of plant–water balance and can have a strong influence on overall plant productivity.

^{13}C is a naturally-occurring stable isotope in the atmosphere. The diffusion of $^{12}CO_2$ through stomata is faster than $^{13}CO_2$ simply because $^{12}CO_2$ is a lighter compound. The concentration of ^{13}C in C_3 and C_4 plants, however, differs because ^{13}C is differentially discriminated against, primarily because of the photosynthetic pathway, but also from the plant–water status (Farquhar *et al.*, 1989). C_3 plants discriminate against ^{13}C more than do C_4 plants because Rubisco has a higher affinity for $^{12}CO_2$. Within C_3 plants themselves, the ratio of ^{13}C to ^{12}C (denoted $\delta^{13}C$) varies as a result of differences in plant–water balance, which can be initiated by changes in soil moisture content or atmospheric vapor pressure deficit (VPD) (Lloyd and Farquhar, 1994). When C_3 plants become water-stressed, they are less able to discriminate against ^{13}C, therefore become enriched with the heavier ^{13}C isotope.

Most of what has been speculated about how paleovegetation may have responded to Pleistocene conditions (primarily to low atmospheric CO_2) is based on the results of empirical research involving modern day plant genotypes treated with low atmospheric CO_2, either in isolation or in combination with other environmental stresses (Sage and Reid, 1992; Johnson *et al.*, 1993; Mayeux *et al.*, 1997; Sage and Cowling, 1999; Anderson *et al.*, 2001; Gill *et al.*, 2002). Experiments involving modern day genotypes could be biased because plants may be able to genetically adapt to climatic variations, in specific to long-term changes in atmospheric CO_2 (Ward and Strain, 1997; Ward *et al.*, 2000). In other words, we may be forcing plants adapted to relatively higher CO_2 concentrations to respond to lower CO_2, resulting in an over-sensitivity of plant processes to experimental reductions in the level of CO_2. Some researchers have tried to overcome this limitation by experimenting with plants having short life cycles (i.e., *Arabidopsis*) and growing several generations of plants under experimental growing conditions (Tonsor and Scheiner, 2007; Gonzalez-Meler *et al.*, 2009). In contrast, some have suggested that modern day plants may still be exhibiting adaptations to the lower atmospheric CO_2 levels of the past (Sage and Cowling, 1999), thus minimizing potential evolutionary bias. Tensor and Scheiner (2007) show that in Arabidopsis, the CO_2 concentration in which the plants were grown influences plastic responsiveness in concentrations of leaf nitrogen and carbon, leaf water-use efficiencies, and biomass production. They observed that the lowest CO_2 concentrations resulted in a wider range in ecophysiological sensitivities to environmental change (i.e., greater phenotypic plasticity) relative to those grown in higher CO_2 levels.

Generally, however, many of the studies involving plant responses to low CO_2 can be characterized by the following features: (a) experimental species that are annuals and highly genetically modified (i.e., crop species), (b) experimental designs that involve closed-environment chambers, and (c) short-term exposure to CO_2 or other climate treatment. Together, these factors could limit the extent to which empirical knowledge is transferable to growth-limiting environmental controls during the Pleistocene.

13.3 INDEPENDENT VERSUS INTERACTIVE CLIMATE EFFECTS

13.3.1 Global cooling

Paleoecological reconstructions of montane vegetation under glacial climate reveal a sensitivity of vegetation growing along altitudinal gradients (Colinvaux *et al.*, 1996a, b; Street-Perrott *et al.*, 1997; Olago *et al.*, 1999). Paleorecords of vegetation along the Andean flank and within the highlands of Central America and eastern Africa indicate that, in general, altitudinal vegetation ranges shifted down the mountainside in response to glacial cooling. Unique tropical ecosystems, containing non-analogous admixtures of highland and lowland forest species, have been reconstructed from tropical paleosediments (Street-Perrott *et al.*, 1997; Bush *et al.*, 2004).

The influence of glacial cooling may have not been as profound for tropical lowlands as it was for vegetation in montane regions. The average temperature optimum (the temperature at which photosynthesis is the highest) for C_3 plants is around 22–23°C (Collatz *et al.*, 1998). Adaptation to temperatures above the C_3 thermal optimum is possible, many examples of which can be found in plants thriving in very hot regions—such as desert (>40°C) and some tropical grasslands/croplands (>30°C; Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004). Not many studies have investigated the *in situ* thermal optimum of forest species growing in tropical lowlands. A survey of experimental and field data on thermal response of photosynthesis to changes in temperature indicate that woody species tend to exhibit less species-to-species variability in thermal optima than do herbaceous species (Medlyn *et al.*, 2002). Eddy covariance measurements of net ecosystem exchange (NEE) in an old-growth Amazonian forest near Pará (Brazil) show that hour-to-hour changes in temperature result in reduced photosynthetic uptake (Goulden *et al.*, 2004), showing that the thermal optimum of tropical forest species can be exceeded on a daily basis. Based on extrapolations from studies that have been performed (i.e., on seedlings or crop species grown in controlled environments; see Amthor, 1991), some lowland plant species are probably growing near or above their photosynthetic optimum in today's climate. Very little is known about the tolerance levels of tropical lowland forest to changes in temperature extremes. Alternatively, Lloyd and Farquhar (2008) have argued that tropical forest species are not growing above their thermal optima and are currently showing signs of enhanced growth due to the rise in CO_2 since the Industrial Revolution. Researchers generally agree that thermal extremes are more important for plant survival (growth) than monthly or annual climate means (Asner *et al.*, 2000; Tian *et al.*, 2000).

Supporting evidence that tropical forests are growing near their thermal optima comes in part from the results of modeling experiments that are able to isolate the effects of warm temperatures from those of dry atmospheres (i.e., climatic variables that often co-vary). These studies indicate a substantial increase in forest productivity when monthly temperatures are reduced from modern day (Kutzbach *et al.*, 1998; Cowling *et al.*, 2001, 2004; Harrison and Prentice, 2003). A decline in ambient temperature, particularly in the range of the last glacial maximum (between -3 and $-5^\circ C$) probably had little *direct* influence on lowland vegetation, except to perhaps force compositional changes depending on the ability of plant species to either adapt to changing climate or to alter species range. The aforementioned modeling studies show that tropical cooling during glacials could have been a benefit to lowland vegetation. A reduction of photorespiration in response to lowering ambient temperature promotes conservation of carbon in plants. In an already carbon-starved environment (i.e., due to low atmospheric CO_2; Ward *et al.*, 2005) conserved carbon could in turn be re-allocated to organs (i.e., roots, seeds, shoots) or to enable stress tolerance mechanisms.

13.3.2 Decreased glacial precipitation

Vegetation modeling studies performed for African tropical forest indicate that the reduction in potential evapotranspiration (PET) following reduced tropical temperatures could have acted to compensate for small decreases in glacial precipitation (Kutzbach *et al.*, 1998). This mechanism provides an explanation for why some paleovegetation modeling studies show that the area of tropical forest remains the same as today, or even increases, when only glacial temperature and precipitation values are included in LGM simulations (Harrison and Prentice, 2003).

Modern day tropical field and modeling studies, however, indicate that drought is responsible for inter-annual reductions in tropical ecosystem carbon balance, and that this decline is related to a complex interaction of temperature warming, drought, and drought-induced increases in fire frequency (Laurance and Williamson, 2001).

Analyses of remotely sensed data for the 1980s in the Amazonian region of northern Brazil indicate that forest stem density is significantly reduced during ENSO years (Batista *et al.*, 1997; Asner *et al.*, 2000) because of the heightened occurrence of drought (Williamson *et al.*, 2000; Laurance *et al.*, 2001; Potter *et al.*, 2001a; Nepstad *et al.*, 2004), with concomitant increases in forest fire frequency (Laurance *et al.*, 2001; Barlow and Peres, 2004).

The accuracy of scaling small-scale hydrological responses to the ecosystem level is problematic for modern day hydrological cycling, and thus becomes even more uncertain in paleoenvironments. Several paleo-precipitation reconstructions in tropical regions indicate local drying and wetting, unfortunately sometimes for the same region (Sylvestre, 2009). High-resolution marine paleosols off the shores of northeast Brazil indicate drier conditions at the LGM (Dupont *et al.*, 2010). In contrast, speleothem-based reconstructions indicate periods of enhanced summer monsoons over Brazil during the End Pleistocene (Vimeus *et al.*, 2009), with studies of the geomorphic stability of the Andean piedmont also showing wetter climate during this time (May *et al.*, 2008). Climate modelling experiments simulate reduced spring convection, resulting in greater rainfall on the piedmont region of the eastern Andes and a much drier high Andes (Vizy and Cook, 2007). Precipitation reconstructions of the Yucatan during the LGM indicate that climate was generally wetter than today (Hodell *et al.*, 2008; Bush *et al.*, 2009). Carbon isotope analysis of paleosediments in Lake Malawi (Africa) show a dry glacial followed by a wetter early Holocene (Castaneda *et al.*, 2009). Interestingly, Tierney *et al.*'s (2010) analysis of carbon isotope and pollen reconstructions of precipitation in Lake Tanganyika (east Africa) identify that vegetation shows signs of response before the reconstructed changes in paleohydrology, indicating that something other than drought (i.e., atmospheric CO_2) is driving glacial vegetation trends.

The response of lowland forest to drought may not be linear because of interactions with other ecosystem-level processes. Analysis of observed rates of rainfall, runoff, and evaporation in a seasonal forest in Amazonia indicate that tropical rainforest is able to take up and store excess water from year to year, showing lag-times in the response of rainforest to drought (Zeng, 1999). Eddy covariance studies of forest near Santarem (Brazil) indicate that ecosystem carbon—that is, net ecosystem exchange (NEE)—is lost in the wet season and gained in the dry season (Saleska *et al.*, 2003), a response opposite to intuition, but is likely the result of ecosystem-scale responses superimposed on long-term disturbance history.

13.3.3 Low atmospheric CO_2

A decrease in atmospheric CO_2 generally decreases C_3 photosynthesis because the concentration of CO_2 as a photosynthetic substrate is reduced and the competition between CO_2 and O_2 for active binding sites on Rubisco is greater. Reductions in atmospheric CO_2 also promote increases in stomatal conductance in C_3 plants, causing an increase in the rate of water lost to transpiration (Farquhar and Sharkey, 1982).

Closed-chamber experiments using a variety of crop species (wheat, oat, mustard, and bean) indicate that water-use efficiency (WUE) is significantly lower (up to 50%) at low (~200 p.p.m.V) relative to ambient (~360 p.p.m.V) CO_2 (Polley *et al.*, 1993, 1995; Cowling and Sage, 1998). In experimental low-CO_2 treatments, the combination of decreased photosynthesis and lower WUE often results in an overall decrease in C_3 plant productivity (Sage, 1995; Tissue *et al.*, 1995; Mayeux *et al.*, 1997; Sage and Coleman, 2001). On the other hand, responses of C_4 plants to changes in atmospheric CO_2 are different than C_3 responses because of dissimilarities in morphology and biochemistry (Pearcy and Ehleringer, 1984). Due to the insensitivity of PEP carboxylase to O_2 and because of C_4's active pumping of CO_2 into the bundle sheath, stomatal conductance in C_4 plants responds much less to CO_2 fluctuations than C_3. Consequently, C_4 plants exhibit substantially much higher water-use efficiencies than C_3, even when exposed to sub-ambient atmospheric CO_2 levels.

Leaf-level changes in WUE can be scaled to the level of plant and ecosystem. WUE averaged over the life-span of the plant is estimated from fossil organic matter using stable carbon isotopes (Farquhar *et al.*, 1989). WUE estimated from fossil leaves dating to the Mid Holocene (Araus and Buxo, 1993) and over the last two and a half centuries (Bert *et al.*, 1997) are significantly lower than in modern plant material, likely as a result of elevations in atmospheric CO_2 since the start of the Industrial Revolution. In summary, low atmospheric CO_2 results in low productivity because of low rates of photosynthesis and induced decreases in plant water-use efficiency.

In the last couple of years, there has been a sharp increase in the number of experimental CO_2 experiments being performed on both herbaceous and woody plant species (i.e., *Acacia*: Possel and Hewitt, 2009; *Acer*: Mohan *et al.*, 2004) as well as studies investigating genetic (Edwards *et al.*, 2009; Tonsor and Scheiner, 2007) and morphological (Izumo *et al.*, 2007) response to varying CO_2 levels. Rates of maintenance (night-time) respiration were lower in low CO_2 relative to high CO_2 for both Arabidopsis plants (Gonzalez-Meler *et al.*, 2009) and big blue-stem grass (Polley *et al.*, 2006), yet remained the same at low and high CO_2 in some common crop species investigated by Paernik *et al.* (2007). Alternatively, day-time respiration was higher under low CO_2 relative to high CO_2 in crop species including Triticum aestivum and Secale cereale (Tcherkey *et al.*, 2008). From a plant-level carbon balance perspective, low respiration rates at night can compensate for low rates of carbon fixation during the day (Gonzalez-Meler *et al.*, 2009).

13.3.4 Interactive effects of Pleistocene climate and atmospheric CO_2

Modeling studies can address research questions requiring the separation of interactive multiple factors because of the modular construction of models, a research objective that cannot be accomplished in "real-life" vegetation experiments. Several modeling studies show that it is specifically the *interactive* effects of Pleistocene climate and CO_2 that were likely responsible for most of the reconstructed changes in glacial vegetation form and function (Cowling, 1999; Harrison and Prentice, 2003). Perhaps the most profound illustration of this is found in Harrison and Prentice's (2003) study that incorporates 17 different paleoclimate reconstructions of the LGM in connection with one dynamic global vegetation model. The authors conducted factorial experiments promoting vegetation responses to a combination of climate stressors and were clearly able to show that the interactive effects of low atmospheric CO_2 are most important for vegetation dynamics in equatorial relative to high-latitude regions.

The most recent empirical research supports the occurrence of interactive CO_2 and climate effects in terrestrial plants. A C_4-plant (*Amaranthus retroflexis*) showed large increases in growth at low CO_2 relative to a C_3-plant (*Abutilon theophrasti*) grown at low CO_2; however, the extent of this increase decreased under lower temperatures (Ward *et al.*, 2008). Similarly, a C_4-plant exposed to low CO_2 increased biomass when grown at temperatures below the plant's thermal optimum (T_{opt}, 30°C), but remain unchanged when grown at temperatures above T_{opt} (Kakani and Reddy, 2007). The degree of light inhibition of photosynthesis was higher under low CO_2 relative to high CO_2 levels (Paernik *et al.*, 2007).

13.4 ECOLOGICAL RESPONSES TO PLEISTOCENE CLIMATE CHANGE

13.4.1 Expansion of C_4 grasslands

The distribution of modern day C_3 and C_4 plants is primarily governed by temperature, but may be modified by changes in atmospheric CO_2 (Ehleringer *et al.*, 1991, 1997; Sage *et al.*, 1999). C_4 plants, with their intrinsically higher WUE, have a strong competitive advantage in hot and arid regions, but the associated energetic costs of the C_4-syndrome (i.e., CO_2-pump) renders them less competitive in regions experiencing moderate to low temperatures. The point at which C_4 plant abundance drops below 50% is commonly referred to as the C_4–C_3 transition temperature. On average, transition temperature is between 20°C and 28°C in a variety of C_3 and C_4 plants surveyed across North America, South America, Asia, Australia, Africa, Europe, and Central America (Ehleringer *et al.*, 1997), and is mechanistically simulated in vegetation models (Cerling *et al.*, 1998; Collatz *et al.*, 1998).

Decreases in atmospheric CO_2, like that during the LGM, are thought as favoring C_4 grasses over C_3 herbaceous plants because of low CO_2 induced increases in C_3 photorespiration (Ehleringer *et al.*, 1997). Robinson (1994) argues that glacial reductions in global temperature would have restricted C_4 plant ranges more than low atmospheric CO_2 would have favored expansion; however, Collatz *et al.* (1998) demonstrate that low CO_2 causes a lowering of the C_4–C_3 transition temperature. A decrease in transition temperature could have expanded the geographical extent to which C_4 grasses are competitive against C_3 herbaceous species.

Analyses of $\delta^{13}C$ of organic fossil sediments can be used to determine the relative proportion of C_3 and C_4 abundance in the past because C_3-dominated soils contain less of the heavier isotope ($\delta^{13}C = -28$ per mil) than C_4 ($\delta^{13}C = -14$ per mil). Unfortunately, very few carbonate sediments in tropical lowlands dating to the LGM have been analyzed for relative C_3 versus C_4 presence, with most of these types of studies being performed in tropical highlands (Aucour *et al.*, 1994; Sukumar *et al.*, 1995; Liu *et al.*, 1996; Street-Perrott *et al.*, 2004). Both highland and lowland studies indicate contradictory trends with respect to the carbon isotope signature of paleosediments and their corresponding reconstruction of C_3 versus C_4 vegetation. Noticeable transformation of C_3 tree vegetation into C_4 glassland is observed in subtropical northeast Argentina (Zech *et al.*, 2009), glacial sediments from Lake Malawi (Castaneda *et al.*, 2009), much of South Africa (Scott, 2002), and at a site in Venezuela (Gonzalez *et al.*, 2008); although the authors of the latter study indicate that the increase in C_4 plant cover occurred in regions of expanding salt-water marshes. In contrast, no transformation of C_3 forests into C_4 grasslands was observed during the LGM on the Guianan Shield (northern South America) (Freycon *et al.*, 2010), in western Brazil (Bush *et al.*, 2004), and at a site in the montane rainforest of Sao Paulo, Brazil (Pessenda *et al.*, 2009).

Haberle and Maslin's (1999) analysis of pollen found in ocean sediments at the mouth of the Amazon River, and Kastner and Goni's (2003) study of organic matter composition of Amazonian deep-sea sediments support the hypothesis that C_4 or C_3 grasslands did not extensively expand their range in tropical lowlands such as Amazonia. Because the $\delta^{13}C$ of C_3 plants under water stress is similar to that of unstressed C_4 vegetation, Liu *et al.* (2005) caution that reconstructed abundance of LGM C_4 grasslands may be over-estimated. This is because research shows that some tropical C_3 grasslands (e.g., monsoonal China; Liu *et al.*, 2005) were drought-stressed during the LGM, and could have indicated a characteristic C_4–$\delta^{13}C$ sediment profile.

Although atmospheric CO_2 as a global phenomenon was not sufficient to force expansion of C_4 grasslands into much of the tropical regions of South America and Africa, regional patterns in LGM precipitation prove critical for understanding glacial C_3–C_4 vegetation transitions.

13.4.2 Rainforest versus seasonal forest

Based strictly on the physiological effect of low CO_2 in promoting low plant water-use efficiency, one might predict that the occurrence of seasonal forest (with adaptations to regularly-occurring drought) would have been more prominent during glacials relative to today, and that any expansion of seasonal forest may have occurred at the expense of tropical evergreen forest. In support, several palynological studies demonstrate the heightened presence of seasonal forest during glacials, in areas that are covered with rainforest today (Mayle, 2004). Modern day biogeographical studies of forest distributions in central Amazonia (Chaco Forest) indicate that seasonally dry forest was significantly more abundant in the past than at present (Pennington *et al.*, 2000), although species composition was probably much different than today (Mayle, 2004). A comprehensive collection of African pollen data dating to the LGM, for example, indicate that—although data for the lowlands are sparse—modern day tropical rainforest was largely replaced by tropical seasonal forest, while areas that are today dominated by seasonal forest were typically encroached upon by savanna (Elenga *et al.*, 2000). Modeling studies are in agreement with paleo-proxy data. Mayle and Beerling (2004) compare various paleodata with results from dynamic vegetation model simulations, and conclude that southern Amazonia was likely covered by deciduous (seasonal) forest rather than evergreen rainforest.

Some researchers suggest that the occurrence of fire was greater during the last glacial than at present, not only because of decreased moisture, but also because seedlings may not have been able to grow fast or tall enough to avoid death by fire (i.e., due to low plant carbon resources) (Bond *et al*., 2003; Power *et al*., 2008). The increased occurrence of seasonal forest, particularly seasonal forest having a thinner canopy, may have contributed to the ability of tropical lowland ecosystems to overcome persistent fire events. Research by Marod *et al.* (2004) in a seasonal forest in Thailand shows that seedling survival rates for plants grown in canopy gaps (i.e., experiencing high light levels) were greater than those established under dense canopy (i.e., shade). Thus, increased occurrence of open-canopied, seasonal forest at savanna–forest ecotones during glacial periods may have contributed to a decreased probability of grasslands invading forest, despite the catalyst of increased fire frequency.

13.4.3 Vertical stratification of glacial forests

The structure and stratification of tropical lowland forest may have been substantially different during the Pleistocene relative to today (Cowling, 2004). Canopy density, the vertical and horizontal stratification of forest canopies, implicitly encompasses various architectural traits—such as branching, crown depth, and tree height (Meir *et al*., 2000; Clark *et al*., 2004; Lalic and Mihailovic, 2004). The silvicultural and vegetation modeling communities tend to parameterize canopy density in terms of an index called "leaf area index" (LAI)—that is, one-sided leaf surface area (m^2) relative to ground cover (m^2). In general, LAI values $<3\,m^2\,m^{-2}$ are found in association with open vegetation types like tropical grasslands, with values between 4 and $8\,m^2\,m^{-2}$ associated with closed-canopied rainforests (Chapin *et al*., 2002).

A recent simulation of tropical Africa indicates that LAI declines from 5.2 to $4.1\,m^2\,m^{-2}$ in response to LGM climate relative to modern day (Cowling *et al*., 2004). Harrison and Prentice (2003) model a global decrease in LAI from 4.28 to approximately $4.03\,m^2\,m^{-2}$ as a result of cooler and drier LGM climate and lower atmospheric CO_2 conditions. Most vegetation–climate simulations indicate that vegetation canopy density was probably lower under glacial climate, although models disagree on the actual degree of reductions relative to today (Levis *et al.* 1999; Cowling *et al*., 2001; Harrison and Prentice, 2003). Modern day observations in the eastern, central, and southwestern regions of Amazonia indicate large differences in forest structure between permanent study plots (Vieira *et al*., 2004). Thus, landscape heterogeneity (i.e., of tree height and canopy density) may have been even more profound during glacials, where low concentrations of atmospheric CO_2 could have promoted further variations in canopy thickness and tree height.

An opened canopy in response to Pleistocene climate may have permitted a more developed understory layer of grass and herbaceous plants, although the functional types and dominant species were likely much different than today. A thinning canopy allows more solar radiation to reach the ground, causing surface temperatures to rise, but also cause greater diurnal variations in temperature (Leopoldo *et al.*, 1993; Potter *et al.*, 2001b; Thery, 2001; Montgomery, 2004). Species that are light-intolerant, or sensitive to wide fluctuations in temperature, would have been detrimentally affected by such canopy changes. Alternatively, understory seedlings adapted to high light environments and tolerant of relatively wider temperature ranges would have thrived in the new glacial forest (canopy) microclimate.

Thinner canopies also result in less moisture retention within forest strata because of the greater mixing of intra-canopy air, as well as from reduced rates of evapotranspiration (Costa and Foley, 1997; Albertson *et al.*, 2001). Understory fern species adapted to relatively high light levels and to wide-ranging atmospheric moisture levels, for example, may have been favored in open-canopied glacial forests. Tropical forest epiphytes that require high canopy humidity may have been severely disadvantaged in glacial forest microclimates. The tight coupling between canopy density and canopy microclimate holds strong implications for species phylogenies. Reconstructed low population size and narrow distribution of some species, for example, found in combination with larger population size and widening distributions of other species, may be indicators of changes in paleoforest structure.

13.5 SOIL PROCESSES AND PLEISTOCENE CLIMATE CHANGE

Within discussions of how tropical ecosystems may have adjusted to climate change during glacial periods, very little is said of below-ground processes, which is surprising considering the importance attributed to soil processes in modern day and future ecosystem studies (Ross *et al.*, 2002; Lenton and Huntingford, 2003; Sotta *et al.*, 2004; Fay *et al.*, 2009; Trumbore, 2009). Whether or not soil processes act as a negative or positive feedback to climate change depends on the balance of the response of net primary production of terrestrial vegetation, and of soil respiration and litter decomposition, to changes in temperature, soil moisture, and atmospheric CO_2 (Kirschbaum, 2000).

Tropical climate cooling may have reduced rates of heterotrophic respiration. Glacial changes in leaf tissue chemistry—such as plant litter with relatively more nitrogen-based complex molecules than carbon-based (i.e., one of the observed physiological effects of low CO_2)—may have resulted in slower rates of litter decomposition. The quantity of tannins (nitrogen-based compounds) is shown to relate directly to decomposition in *Cecropia* species in secondary forest in central Amazonia (Mesquita *et al.*, 1998). Changes in litter chemistry, therefore, could have promoted a continual build-up of tropical soil carbon throughout the duration of a glacial cycle. Most of the carbon stored in modern day tropical ecosystems is found in above-ground structures, but this may have been reversed during periods of glacial advance.

The effect of reduced plant productivity for lowering quantity of leaf litter has traditionally been considered the most important variable in modifying soil carbon, although there are few experimental data to verify this statement. A C_3 perennial shrub subjected to a range of CO_2 levels, from sub- (200 p.p.m.V) to super-ambient (550 p.p.m.V) CO_2 (and no other changes in climate), shows only a marginal (11%) reduction in bulk soil carbon over 4 years (Gill *et al.*, 2002). Rates of respiration, translocation, and nitrate reduction are observed in soybean grown in low-CO_2 growth chambers (Bunce, 2004). Modeling studies tend to indicate decreases in soil carbon storage at the LGM, primarily because model calculation of soil carbon is strongly dependent on the type of ecosystem present, as well as the productivity (NPP) of that ecosystem (Friedlingstein *et al.*, 1992; Prentice *et al.*, 1993; Kubatzki and Claussen, 1999; Levis *et al.*, 1999; Kaplan *et al.*, 2002). Kirschbaum (2000) highlights the problems associated with assuming that there is no difference in soil carbon storage for past and present biome types.

Another factor that may have influenced processes modifying soil carbon storage during glacials is the response of groundwater and water-table levels to decreases in sea level. Faure *et al.* (2002) believe that the 120-m glacial drop in current sea level could have increased hydrostatic pressure on continental water sources, causing an increase in groundwater flow to coastal regions, and a subsequent decline in regional water-table levels (Clapperton, 1993). Drier surface soils could have reduced microbial decomposition and contributed to an increase in tropical soil carbon storage during glacial periods. Without a better grasp of the relative strength of soil carbon processes to changes in climate, we will be unable to confidently predict how below-ground processes may have been altered during glacial and interglacial cycles of the Pleistocene.

13.6 CONCLUSION

It is specifically the *interaction* of low atmospheric CO_2 and global cooling and aridity that is critical for understanding the potential response of plants to changes in Pleistocene climate. The combination of modeling and palynological data should put to rest the notion that lowland tropical forests were severely restricted in glacial times by expanding C_4-dominated grasslands. Rather, evidence indicates that seasonal forest likely encroached on rainforest in lowland regions and that grasslands expanded at forest–grassland boundaries. Perhaps one of the potentially largest differences in the character of lowland tropical forests in the Pleistocene relative to today involves changes to canopy density, and subsequent changes in species composition of canopy strata. One of the greatest uncertainties with respect to tropical ecosystem responses to Pleistocene climate change involves below-ground soil processes. If we assume that decreases in vegetation productivity had the dominant effect on soil processes, then soil carbon storage was lower during glacials than present. Alternatively, if we assume that the temperature and moisture response of soil processes drives below-ground carbon storage, then tropical soil storage increased during glacials relative to today. As with modern day ecosystem research, much has to be learnt about the response of below-ground processes to biotic and abiotic stress in order to predict how they might have changed in the past, or how they might change in the future.

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14

Tropical environmental dynamics: A modeling perspective

R. Marchant and J. C. Lovett

14.1 INTRODUCTION

The impact of climatic change on tropical vegetation is of global and regional concern because of the high biodiversity and the feedbacks to the carbon, water, and nutrient cycles. Tropical ecosystem functioning is governed by complex systems, that, in spite of their diversities, share in common structures and characteristic states which can be modeled (Aassine and Jay, 2002). Records of fluctuating biotic and chemical characteristics from numerous sedimentary archives, including oceans (Guilderson *et al.*, 1994), continental lakes, bogs, swamps (Hooghiemstra and van der Hammen, 1998; Behling and Hooghiemstra, 2000; Haberle and Maslin, 1998), and ice caps (Thompson *et al.*, 1995), demonstrate that tropical environments change at a range of time scales. One of the most recent extremes of these variations concerns the 100,000 glacial–interglacial cycles associated with the Quaternary geological period (i.e., the past 2.6 million years). Climate change involves massive reorganisation of global climate systems with major impacts on ecosystem form and function giving rise to complex interactions between the atmosphere, geosphere, hydrosphere, and biosphere (Kohfeld and Harrison, 2000). Models are essential tools to assess the potential response of vegetation to climate change, particularly where large spatial and temporal scales are considered (Ostendorf, 2001). Such changes can also be documented by accessing sedimentary archives, whereas the nature and implications of such changes can be investigated through modeling. Models using a space for time substitution are based on rich and detailed spatial information and have a very high level of empiricism (Ostendorf, 2001).

There are numerous modeling approaches concerned with different components of the Earth system: the majority of these initiatives have been developed within the temperate regions, particularly North America and Europe, with relatively few studies focused on the tropics. Indeed, as we will see, the modeled environmental history of the tropics remains poorly resolved despite its increasing importance in understanding

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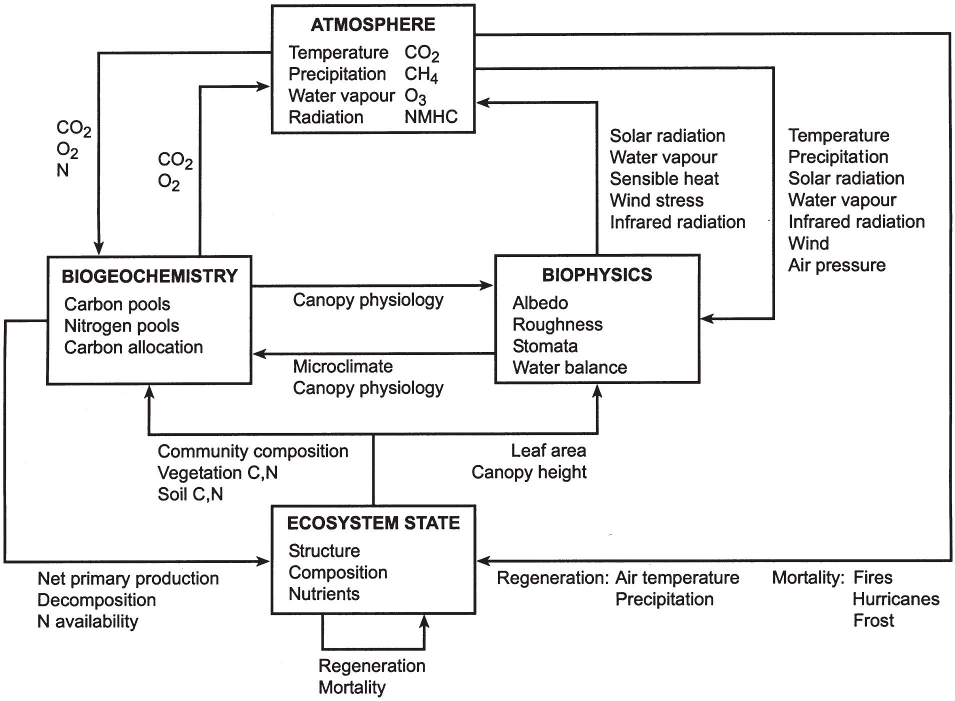

Figure 14.1. Biogeochemical and physical links between the Earth's atmosphere and ecosystems that need to be accounted for and parameterized within an earth system model.

global climates (Marchant and Hooghiemstra, 2004), biogeochemical cycles (Prentice *et al.*, 1996), developing biogeographical theory (Tuomisto and Ruokolainen, 1997), and understanding issues concerned with biodiversity and human–environment interactions (Rucina *et al.*, 2010). Modeling climate change impacts in tropical environments represents a special challenge for computer climate models, in part due to the sharp relief of the mountain areas, where a single one degree grid-cell will encompass a wide range of environmental and climate gradients. These difficulties are compounded by the poor availability of marine and terrestrial data important for accurate simulations (Valdes, 2000). However, as the complexity of the tropical environmental system, and its importance to contributing to Global Climate Models (GCMs) is being realised, models take an ever increasing number of parameters into account (Figure 14.1). However, there is a trade-off—these require significant computing power and can be relatively static in time (non-dynamic), though a compromise is available in models of intermediate complexity that can simulate climate evolution over thousands of years but use a relatively large grid-cell or a reduced number of inputs to attain a concomitant reduction in computational time.

This chapter will provide an overview of these different approaches, review the present understanding and identify future areas for research development by investigating two main areas of modeling; first, biosphere models focusing on vegetation change, and the links from these to biogeochemical fluxes; second, climate modeling. First we need to investigate the variety of modeling approaches; understanding model limitation is critical for future development and useful application (Peng, 2000). Such application may concern differences in the timing, intensity, and duration of the seasons that can have huge impacts on human prosperity, health, and the surrounding environment. For example, the winter of 1982/1983 was exceptional: the dry seasons in Peru and Chile were very wet and the rainy season in Indonesia was extremely dry. Similarly, 2009 was characterized by extensive drought throughout the Horn of Africa with the decimation of pastoral herds and grazing wildlife—the subsequent "dry" season in 2010 was exceptionally wet. Modeling can be focused to predict when a rainy season might fail, or when flooding or temperature extremes might be likely. However, if we cannot predict the weather next week, why should we trust climate predictions for next season, or 25 years time, or indeed 21,000 years ago! Moreover, some climatically important areas of the planet, such as the African Sahel, which appear to influence weather in other parts of the world, are notoriously difficult to model (Claussen *et al*., 2003). The situation is further complicated by abrupt changes in climate—the so-called "tipping-points" (Lenton *et al*., 2008) when the general patterns of climate undergo a fundamental change. We can however say something useful about the climate trends, how certain components of the Earth's system responds to such trends, and how these trends can influence our future climate associated environment and resources.

There are two basic modeling techniques: inverse and forward. In the former, comparisons rely on establishing empirical relations between modern and past environment observations through a transfer function (Kohfeld and Harrison, 2000); that is, geological data are translated into climatic (e.g., mean monthly temperature, precipitation) or bioclimatic (plant distribution) parameters that can then be compared with simulated results. In the forward modeling approach, models are used to produce a predicted response that can be compared with current observation. These two approaches should not be seen as independent but as complementary (Kageyama, 2001), such a hierarchy of models is useful to allow the move from large- to regional-scale investigation. This chapter will focus on modeling biosphere changes, although it should be noted that other components of the Earth's system are required to fully understand these. For example, geophysiological modeling can asses the feedback mechanisms acting between the geosphere and biosphere, the nature of the land surface, and impacts of changes on this, such as altering climate by albedo change influencing the reflectivity and absorption of incoming solar radiation, water vapour, convective precipitation, soil moisture, transpiration, hydrology, and latent heat flux (Figure 14.2).

14.2 BIOSPHERE MODELING

The analysis of species–environment relationships has always been a central issue in paleoecology. Species have shifted their ranges as climate has changed and these range shifts are often individualistic responses as opposed to wholesale migrations of

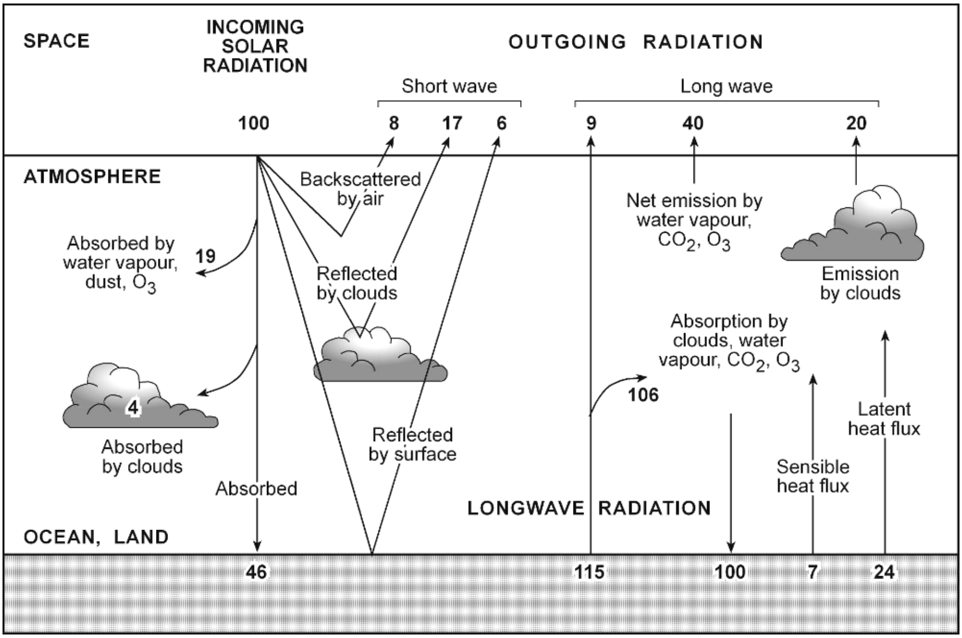

Figure 14.2. Indication of the amount of incoming and outgoing radiation and the percentage absorbed and reflected by the various atmospheric components.

ecosystems or biomes (Rucina *et al.*, 2009). Besides its prime importance as a research tool in ecology, predictive geographical modeling has gained importance as a tool to assess the impact of accelerated land use and other environmental change on the distribution of organisms (Guisan and Zimmermann, 2000). Vegetation is a major factor affecting land surface processes (Figure 14.3), and a good measure of ambient climate (and ambient climate change). Therefore, a central part of understanding climate change impact is to understand the correspondence between climate and the distribution of vegetation, both in terms of major vegetation formations, or biomes, and individual plants or species. Modeling the biosphere is not a new field of research. Initial attempts were carried out by Kostitzin (1935). Working on ideas about the interdependence between vegetation and climate he created the first mathematical model for the co-evolution of the atmosphere and biota. Individual-based models describe vegetation dynamics in terms of interactions between individual plants with little emphasis on ecophysiology and climate (Farquhar, 1997). A compromise between these schools are the popular forest gap models (van Tongeren and Prentice, 1986) that describe species-specific establishment, growth, death of trees, and interactions between them resulting in successional patterns. Species-based approaches create bioclimatic envelopes delimited by a combination of climate variables based on the correlation between the spatial distribution of individual species and climatic parameters. The bioclimatic envelopes can then be used to model potential species responses to climate change. Genetic algorithms are used

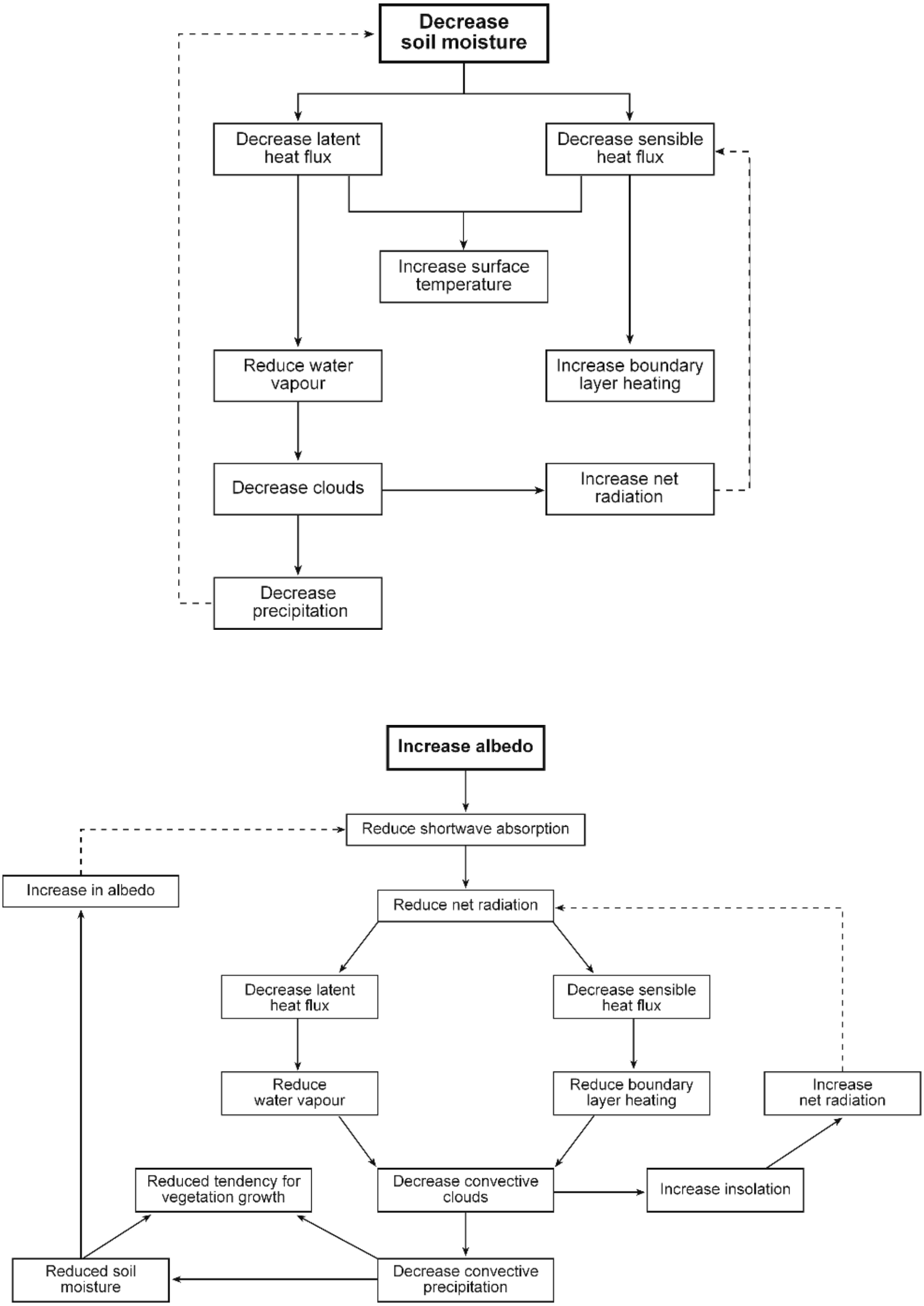

Figure 14.3. Impact on the biogeochemical components of the modeled ecosystem following a change in below-ground and above-ground biomass.

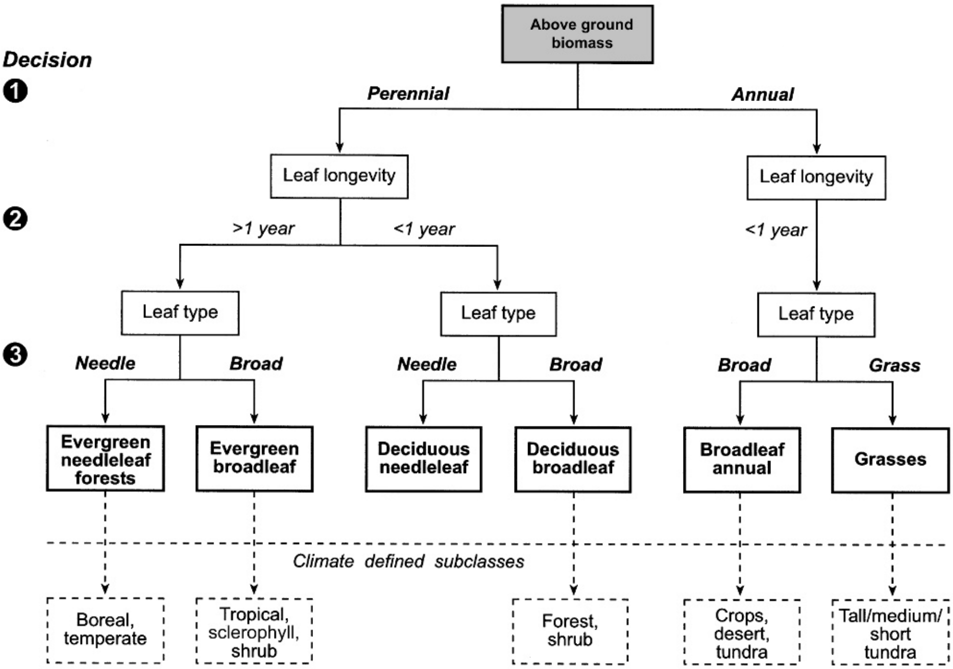

Figure 14.4. Schematic division to determine plant functional types based on a series of divisions, in this case on the growth form, tolerance to seasonal temperature and physiology of the parent plant.

to create the envelopes because of their ability to take into account a large number of climate variables (McClean *et al.*, 2005). The best-known approach for predicting the equilibrium response of broad-scale potential vegetation types to climate change is the climate–vegetation classification approach (Holdridge, 1947; Holdridge recognized some 37 "life zones"). Correlations between climatic parameters and species richness have also been used to model global patterns of changes in plant diversity in response to climate change (Sommer *et al.*, 2010). The disadvantage of such an approach is that the climatic variables may not be the factor to which vegetation responds (Peng, 2000). For example, in a study of plant responses to a warmer climate in European mountains two-thirds of 171 species studied increased their elevation, as would be expected in response to hotter temperatures, but one-third reduced their elevation (Lenoir *et al.*, 2008). Vegetation responds to a range of climatic influences, geomorphic substrates, and ecological disturbances (natural and human induced) with an incredible array of different species, growth, and competition habits and basic life forms (Figure 14.4). For example, simulations of vegetation patterns with and without fire show that large areas of C_4 grasslands in Africa and South America have the climate potential to support forests (Bond *et al.*, 2004). Functional groups work well, for example the FORMIND model was applied to lowland forest data from Indonesia. The analysis used 22 functional groups, comprising 436 species, based

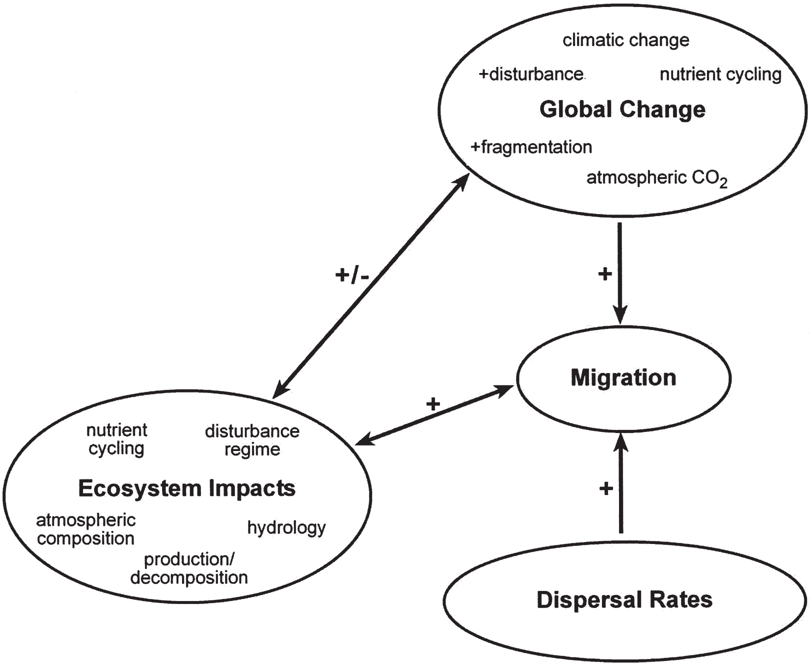

Figure 14.5. The increasing impacts of migration and dispersal being incorporated within dynamic vegetation models as feedbacks in conjunction with other ecosystem impacts such as disturbance type.

on diameter growth and light demand, with an additional criterion being based on height (Köhler and Huth, 1998). Plant functional types that group plant species by their physiognomic and morphological traits and responses to climate (e.g., tropical evergreen broad-leaf rainforest trees) are a very useful classification tool, particularly when dealing with the complexity of a tropical flora (Figure 14.4).

By including climate dependencies, biosphere models can account for climatic, immigration and competitional influences, thus providing a forecast of ecosystem impacts under various climate scenarios (Figure 14.5). In earlier studies, climate input data and timing of a species appearance were inferred from the pollen records to which the simulation results were compared. Such circular reasoning between cause and effect limits insights gleaned about factors controlling vegetation response, and has been easily broken by using climatic input from independent data sources. Additionally, there has been an increasing interest in paramatizing the role of dispersal (Figure 14.5), partly driven by the development of more appropriate (realistic) models and partly due to increased understanding of the dynamic nature of populations. These approaches are currently confined to the temperate realm but have interesting applications to tropical areas (Paradis *et al.*, 2002). This complexity has resulted in a number of approaches to studying biosphere responses to climate change that incorporate migration and adaptation (Kirilenko *et al.*, 2000), dispersal factors (seed production, fecundity, dispersal vector interaction), additional environmental factors (such as climate seasonality, edaphic factors, aspect), and ecological factors (such as association, parasite/disease, inertia) (Figure 14.5). In addition to changing areal extent and composition of the vegetation, changes in vertical structure are an important part of vegetation change (Cowling, 2004).

14.2.1 Biome modeling

A continental-scale study, the VEMAP project (VEMAP members, 1995), demonstrated the interdependence of biogeographical and biogeochemical aspects of the ecological response to climate change; assessing how global change will affect ecosystems and must therefore include both aspects. Such a combined approach is exemplified by the process-based equilibrium terrestrial biosphere model BIOME-3, that simulates vegetation distribution and biogeochemistry (Haxeltine and Prentice, 1996). BIOME-3 predicts plant functional type (PFT) dominance based on environmental conditions, ecophysiological constraints, and resource limitations. The model uses the inputs of temperature, precipitation, cloudiness (Leemans and Cramer, 1991), soil texture, atmospheric pressure, and $[CO_2]_{atm}$ (Figure 14.6). The level of $[CO_2]_{atm}$ prescribed to BIOME-3 has a direct influence on gross primary productivity via a photosynthetic algorithm and competitive balance between C_3 and C_4 plants (Haxeltine and Prentice, 1996). Combining these inputs, a coupled carbon and water flux model calculates leaf area index (LAI) and net primary productivity (NPP) for each PFT. The NPP is translated to a series of prescribed PFTs, which

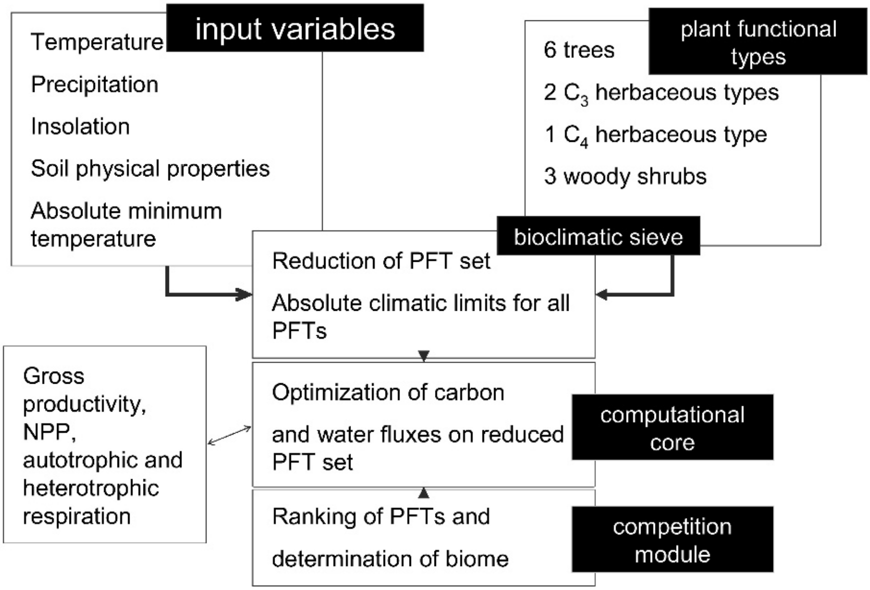

Figure 14.6. Biome model structure: a basic summary of the steps taken to calculate biomes on the basis of climatic input variables.

then combine to form biomes (Figure 14.6). Although developed as a global vegetation model, BIOME-3 allows simulation of changing environmental conditions on vegetation on a regional and local scale (Jolly and Haxeltine, 1997; Marchant *et al.*, 2002, 2004a). Biome-level modeling on a regional level has been used to show the Fynbos Biome (Southern Africa) stands to lose significant areas near its northerly (equatorward) limits, especially in the coastal forelands and inland plains along the west coast in response to projected climate change (Midgely *et al.*, 2003). These areas are therefore of special conservation concern, as it is unlikely that their vegetation and habitats have experienced this extent and rapidity of warming and desiccation in the recent geological past (Midgely *et al.*, 2003). BIOME-3 can also be used to represent vegetation change within a single pixel that can be used to isolate and manipulate environmental variables such as temperature, precipitation, seasonal variations of these, and changes in CO_2 concentration (Foley *et al.*, 1996; Haxeltine and Prentice, 1996). The BIOME-3 model output has been tested and compared against maps of potential vegetation on a global (Prentice *et al.*, 1992, 1993), continental (Jolly *et al.*, 1998; Williams *et al.*, 1998), and regional scale (Marchant *et al.*, 2001a, 2004b). Often, there are discrepancies between model-based reconstructions and potential vegetation; these result from numerous components, such as over-simplified soil hydrology (Marchant *et al.*, 2001b).

Of particular interest for understanding vegetation dynamics, is how climate system–biosphere interactions have developed since the Last Glacial Maximum (LGM) (Cowling and Sykes, 1999). With this LGM focus in mind, BIOME-3 is run to demonstrate the impact of reducing $[CO_2]_{atm}$ to levels (200 ppmV) ambient at the LGM (Petit *et al.*, 1999). Reduced cconcentrations of $[CO_2]_{atm}$ have a very significant impact on pan-tropical vegetation (Jolly and Haxeltine, 1997; Boom *et al.*, 2002) as we can see from the modeled output of vegetation (Figure 14.7). Under low $[CO_2]_{atm}$ (Figure 14.7, bottom) the amount of grassland (short and tall), xeric woodland, and scrub increase dramatically, particularly at the expense of tropical seasonal forest (Figure 14.7). Interestingly, the amount of tropical rainforest remains relatively constant as a consequence of largely being under control of changes in temperature and precipitation; the latter component needing to change significantly to effect notable changes in tropical rainforest distribution. There are likely to be major within-biome composition dynamics, both in terms of the importance of individual taxa and structure of the vegetation (not portrayed in the biome output). As gaseous exchange at the leaves involves both H_2O and CO_2 (Figure 14.8), changes in $[CO_2]_{atm}$ not only impact on the processes of photosynthesis and photo-respiration but also water-use efficiency (WUE) (Cowling and Sykes, 1999). Water-use efficiency is linearly related to the level of $[CO_2]_{atm}$, under low $[CO_2]_{atm}$ plants have to transpire more to achieve the same level of photosynthesis and hence NPP, in other words, halving the $[CO_2]_{atm}$ is comparable to halving the rainfall (Farquhar, 1997). Thus, it is likely to be the hydrological impact rather than physiological impacts of lowered CO_2 that causes the vegetation to change. Although it has been shown that some C_3 plants can respond to decreased $[CO_2]_{atm}$ by increasing the amount of stoma on the leaf lamella (Wagner *et al.*, 1999), this is difficult to apply to the late glacial as the main impact, rather the physiological response to low $[CO_2]_{atm}$ appears to be reduced WUE (Cowling and

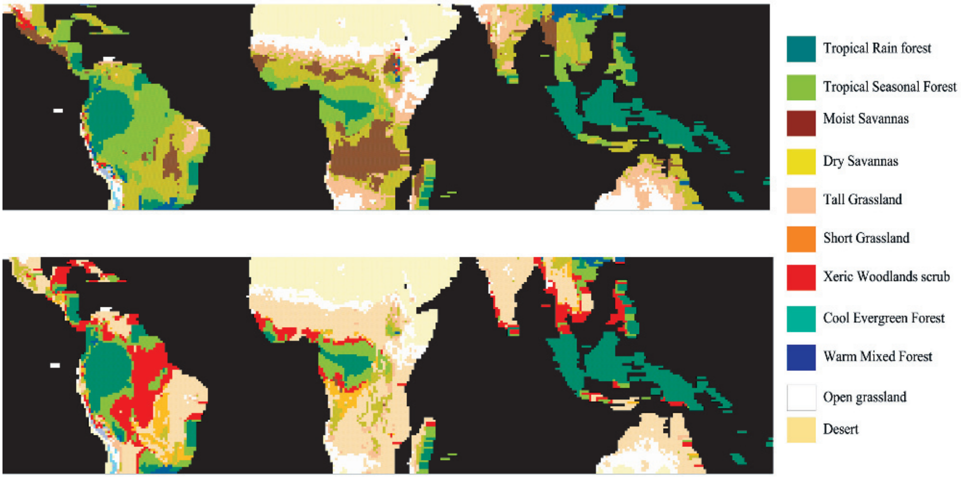

Figure 14.7. BIOME-3 run for the tropics with inputs of model climate, in the bottom output CO_2 has been reduced to glacial levels (200 ppmV) with no change in the other environmental inputs.

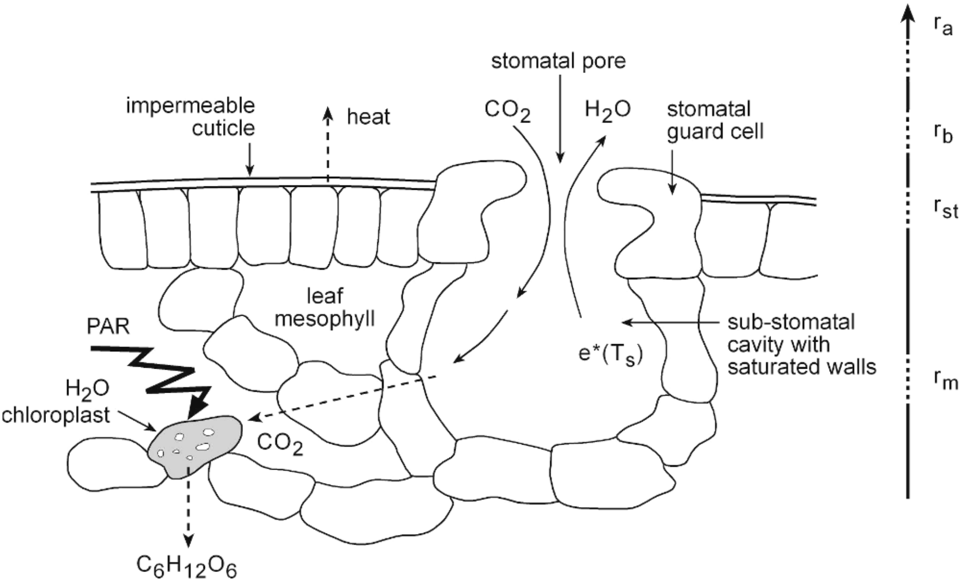

Figure 14.8. Leaf cross-section indicating the gaseous exchanges taking place—particularly CO_2 and H_2O.

Sykes, 1999); thus, if the stomata have a wider aperture, or are more frequent, this will result in more water being evaporated. Therefore, no matter how the stomata compensate for the variation in $[CO_2]_{atm}$, C_4 or CAM plants will always have a competitive advantage over C_3 plants in warm environments subject to water stress (Boom *et al.*, 2002; Ehleringer *et al.*, 1997).

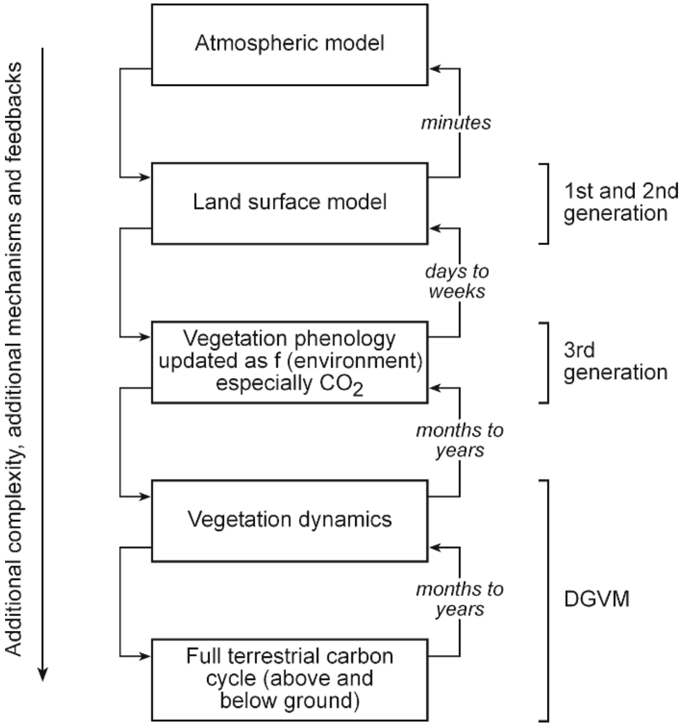

Figure 14.9. Schematic of the increasing level of detail being added to surface modeling approaches. In this case the requirements are additive (i.e., a fully coupled DGVM requires the traditional land surface model).

An interesting application of vegetation models is to use them as a vehicle to display output from climate (Claussen, 1994, 1997) and biogeochemical models (Peng *et al.*, 1998; Prentice *et al.*, 1993). This use allows model outputs to be translated into maps of potential natural vegetation (Claussen and Esh, 1994; Foley *et al.*, 1996; Prentice *et al.*, 1996; Williams *et al.*, 1998) used for the coupling of biosphere, atmosphere, and oceanic components (Claussen, 1994; Texier *et al.*, 1997) and the testing of biogeochemical dynamics (Peng *et al.*, 1998). Climate shifts are displayed as shifts in biome boundaries and areal extent; which can be used to investigate the feedback between atmosphere, biosphere, and oceanic systems under changing boundary conditions (Figure 14.9). However, it must be stressed that as there are a number of different scenarios available to drive the vegetation model, the results will vary depending on the model output used and the feedbacks to the climate system (Figure 14.1). Such differences, particularly when outputs are compared against independent data, can be used to assess model performance and determine the importance of model components such as the land–ocean feedback, or the use of dynamic rather than fixed ocean temperatures.

14.2.2 Dynamic global vegetation models

Extreme environmental events such as droughts and fires are important factors in global vegetation processes, yet data on them are sparse, unreliable, or completely lacking. Furthermore, how these extreme environmental events are parameterized within models is even worse! Techniques to estimate the rates, extents, and magnitudes of extreme events, and the ability to quantify uncertainty in results, need to be developed. The role of biogeophysical vegetation feedback is not considered but can be an important aspect of the tropical climate—by altering the wet season and thus amplifying the response to orbital forcing (Doherty *et al.*, 2000). These changes affect local, regional, and global climates which feedback to the biogeography and physiology of the vegetation (Cao and Woodward, 1998). The influence of such dynamics and impact on vegetation can be assessed within a vegetation model developed to run over time (Thonicke *et al.*, 2001). There are also internal feedbacks that need to be accounted for (Figures 14.3 and 14.9). Such feedbacks can be incorporated by developing dynamic global vegetation models (DGVMs); of course, this results in a more complex model with associated computing limitations. Potential applications of DGVMs can be summarized within three main areas, simulating the transient changes in global vegetation patterns under future climate change, investigating human disturbance scenarios, and estimating the transient behavior of carbon pools and fluxes to provide a fully interactive representation of the biosphere within GCMs to investigate potential vegetation–climate feedback mechanisms (Peng, 2000). To express these changes, the vegetation model needs to run to equilibrium; taking into account vegetation development and impacts of factors such as fire. Such an approach will have advantages over equilibrium models—driving our understanding of ecosystem dynamics and the impacts of a suite of forcing factors.

14.2.3 Models of biogeochemical cycles

With the premise that terrestrial ecosystems play a central role in regulating global biogeochemical and climate systems, a suite of models concerned with biogeochemical cycles, particularly carbon and nitrogen (Melillo *et al.*, 1993), have been developed. Such models commonly use a series of mass balance equations to obtain values for given biogeochemical components and rates of fluxes. The relationship between biosphere carbon stocks and $[CO_2]_{atm}$ during glacial to interglacial cycles may help us understand the mechanisms that drive change during the 21st century and beyond. How tropical vegetation contributes to the global carbon budget is an area of continued discrepancy and hence research activity (Lewis *et al.*, 2004; Lewis *et al.*, 2009). With rising atmospheric carbon derived from human activities there is a focus on investigating changes in the global carbon cycle that has resulted in dozens of models simulating atmosphere–biosphere CO_2 exchange processes. For example the terrestrial biosphere model "Carbon Assimilation in the Biosphere" (CARAIB), now in its fourth incarnation, records a slight increase in the extent of tropical rainforest linked to the colonization of exposed continental shelf, such as Sunda. Carbon stocks are commonly calculated from biosphere models that use standing stock and NPP. Efforts can be divided into models oriented toward global simulations and those orientated toward plot-scale simulations—that generally have a complex structure and require a large number of parameters. Indeed, there remain many challenges to scale-up the single leaf process, and to parameterize respiration, allocation, deposition, and sequestration (Ito and Oikawa, 2002).

14.3 CLIMATE MODELING

A detailed and comprehensive discussion on climate modeling is outside the scope of this chapter but can be found in the excellent review by McGuffie and Henderson-Sellers (2005). Climate models are used in a range of applications from investigating atmospheric processes to fluctuations of deep-ocean circulation and increasingly, the impact of perturbations caused by the world's human population (Pitman, 2003). Models of the global climate system have several uses; such as interpolating and explaining paleodata, studying climate processes, separating natural variability from anthropogenic impact in the climate record, and investigating the nature of the climatic response and influence of various components such as oceanic feedback. The ultimate aim of such approaches is to be able to forecast future climate where two factors are paramount; first, investigating impacts of higher $[CO_2]_{atm}$ levels (Houghton *et al.*, 2001), and second, the impacts and feedback of land-cover change on the climate system (Cao and Woodward, 1998).

Atmospheric general circulation models (AGCMs) are continually improving in their ability to simulate the major features of today's climate, and over time have proved useful for investigating mechanisms of past climate change (Joussaume, 1999). There is broad similarity in the reconstruction of different AGCMs as they are ultimately based on the laws of physics, constants, and particle motion, given only a small number of external boundary conditions such as the solar constant and atmospheric concentrations of radioactively active gases and aerosols. Models are often set with lower boundary conditions of sea surface temperatures (SSTs) and sea ice amounts—with a three-dimensional representation of atmosphere motions. Dynamic climate models exhibit a problem not evident in those with prescribed SSTs and sea ice; in particular fluxes of heat, momentum, and water across the ocean–atmosphere interface lead to *ad hoc* flux adjustments regarded as necessary to correct problems; these so called "flux adjustments" can be relatively large in models that use them, raising questions about the realism of the climate reconstructions and associated feedback processes (Gates *et al.*, 1998).

Despite their similar foundations, different models give somewhat contradictory results mainly due to subtle differences in assumptions about clouds and their role in absorption, reflectance, and moisture transport (Figure 14.2). To try and deal with such discrepancies, a series of working groups were established such as the Atmospheric Model Inter-comparison Program (AMIP) (Gates *et al.*, 1998) and the Palaeoclimate Model Inter-comparison Program (PMIP) (Joussaume and Taylor, 1995) to evaluate, test, and develop climate models, co-ordinate the systematic study of AGCMs, and to assess their ability to design experiments to simulate changes of climate such as those that occurred at the LGM. For example, in the AMIP simulations, sea ice and SST are prescribed to match recent observations, and the atmospheric response to boundary conditions; in CMIP, the complete physical climate system including the oceans and sea ice adjust to prescribed $[CO_2]_{atm}$. These projects also provide climate scientists with a database of coupled GCM simulations under standardized boundary conditions, and thus have enabled an assessment of why different models give different outputs in response to the same input.

Thus, there are a variety of climate models, just two are mentioned here; these latest Earth system models incorporating fully coupled ocean–atmosphere–biosphere components are thought to be the way forward to assess the impact of climate change on ecosystems. One such model, HadCM3LC, when run with a LGM climate, demonstrates structural, as well as purely distributional change, in tropical forest with leafe area index (LAI) reducing significantly as the tropical canopy becomes more open (Cowling, 2004). Another model, GENESIS-IBIS incorporates an assessment of the global ecosystem through the Integrated Biosphere Simulator (IBIS) and terrestrial hydrology through a model (HYDRA), as well as a fully coupled climate–vegetation model that incorporates new datasets of global climate systems. The IBIS is one of the few computer models to incorporate a range of ecosystem processes within a single framework that is then integrated within a climate model. The IBIS simulates:

- energy, water, and carbon dioxide exchange between plants, the atmosphere, and the soil;
- physiological processes of plants and soil organisms, including photosynthesis and respiration;
- seasonal changes of vegetation, including spring budburst, fall senescence, and winter dormancy;
- plant growth and plant competition; and
- nutrient cycling and soil processes.

To characterize potential impacts of precipitation and temperature change, both in terms of magnitude and seasonal distribution, models can calculate predicted monthly values for the future. These monthly precipitation and temperature predictions can be derived from a range of well established GCMs (such as ECHAM, HadCM3, MIROC, and NCAR) which have been used in the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (available from *https://esg.llnl.gov:8443/*) and cover a wide variety of different model types, projections, and sensitivities. For each model, climate change projections have been produced under forcing from contrasting emission scenarios, provided by the Special Report on Emission Scenarios of the Intergovernmental Panel on Climate Change (Solomon *et al*., 2007): such as the pessimistic A2, the balanced A1B, and the optimistic B1 emission scenarios. Regional-scale climate models do offer promise for reflecting localized complexity in the climate system; however, these remain in the exploratory phase and only in some regions has downscaling of climate change simulations to the regional level been achieved (Christensen *et al*., 2007). Many climate models thus display substantial uncertainty in regional climate change estimates, with uncertainties being much higher for precipitation than for temperature (Randall *et al*., 2007). As precipitation is the most important climatic factor (Funk *et al*., 2008) for determining ecosystem composition across the tropics the utility of many tropical climate change predictions, focusing on temperature shifts associated with global warming, come with a number of caveats.

14.4 MODELING THE LAST GLACIAL PERIOD

Part of the PMIP effort was focused on the LGM to understand the impacts of extreme cold conditions and to study the feedbacks associated with a decrease of $[CO_2]_{atm}$ and an ice sheet elevation of 2 to 3 km above North America and northern Europe. The LGM was simulated by 17 models through the PMIP that prescribed a series of set boundary conditions (Pinot *et al*., 1999); an update of the ice sheet extent and height was provided by Peltier (1994); the Laurentide and Fennoscandian ice sheets being 1,000 m lower than the previous reconstruction (CLIMAP, 1981); $[CO_2]_{atm}$ was prescribed to be 200 ppmV as inferred from Antarctic ice cores (Raynaud *et al*., 1993); and Earth's orbital parameters were changed according to their values at 21,000 years BP. Over the oceans, two sets of experiments were defined: one with SST changes prescribed from estimates (CLIMAP, 1981), the other with SSTs computed using coupled atmosphere–mixed layer ocean models and assuming no change in the ocean heat transport. Each approach has its advantages and problems:

(1) Computing SSTs permits an evaluation of models used for future climate prediction but does not account for any changes in the oceanic heat transport, despite evidence of thermohaline circulation changes.
(2) Prescribing SSTs should yield better results over land; however, SST estimates are subject to substantial uncertainty (Duplessy *et al*., 1988).

Indeed, a limitation of model simulations has been the role of ocean dynamics, which is crucial for understanding changes in tropical up-welling (Bush and Philander, 1998; Ruter *et al*., 2004) and resultant rainfall regimes (Marchant *et al*., 2007). Model simulations still under-represent tropical cooling at the LGM, apart from over Eastern Africa where most of the models indicate a similar cooling (relatively minor) to the observational data. Following the debate on the degree of tropical SST cooling raised by Rind and Peteet (1985), Farrera *et al*. (1999), and Pinot *et al*. (1999) it can be shown that:

(1) All PMIP simulations using the relatively warm tropical SSTs given by (CLIMAP, 1981) tend to be too warm over land, except over equatorial Africa.
(2) Computed SSTs are colder than CLIMAP, especially over the tropical Pacific

where the erroneous warm pools of CLIMAP are not reproduced (Pinot *et al.*, 1999).

(3) Models with computed SSTs show a range of terrestrial cooling strongly related to the intensity of tropical SST cooling.

Some models produce a strong terrestrial cooling consistent with the paleodata, but this is associated with SST cooling that is too large when compared against recent alkenone data on SST. However, one model gives reasonable results over both land and oceans, "CLIMBER", a model of intermediate complexity, reconstructs a tropical land cooling of 4.6°C with SST cooling of 3.3°C in the Atlantic, 2.4°C in the Pacific, and 1.3°C in the Indian Ocean (Ganopolski *et al.*, 1998). This is in broad agreement with the data that shows tropical SSTs were 5°C colder in Barbados corals (the coldest throughout the tropics) although 2–3°C is a more common value (Guilderson *et al.*, 1994). Terrestrial temperatures simulated by the 17 models within PMIP are relatively similar showing the temperature was reduced by 5–6°C about the LGM. For some models run for both fixed and computed SSTs (UGAMP and GEN2), the annual mean change in temperature remains very similar on global average, although regional differences can be substantial (Dong and Valdes, 1998)—albeit comparable with data-based reconstructions that also document considerable variation.

Vegetation change in the tropical realm is primarily driven by precipitation changes: according to PMIP simulations the LGM was relatively dry apart from in East Africa and throughout the high elevations of South America and Papua New Guinea (Pinot *et al.*, 1999). Reduced precipitation, particularly in mid-latitude western South America is likely to result from a reduction in the intensity of westerly climate systems. In a comparison of two of the models within the PMIP suite (CCM3 and CSM) differences are quite small in most measures of the atmospheric circulation, with one exception involving tropical precipitation (Joussaume and Taylor, 1995). Moisture changes tend to be associated with changes at the regional scale when model simulations are characterized by a number of common features, including a reduction in the strength of the African–Asian monsoon and increased inter-tropical aridity, corroborated by various paleo-indicators. Changes in insolation, such as those occurring about the LGM due to changes in Earth's orbital parameters, would cause changes in the monsoonal climate and the associated feedbacks (Joussaume *et al.*, 1999). For example, application of a coupled ocean–atmosphere model (FOAM) indicates that SST feedbacks produce a much larger enhancement of precipitation in Central America than would have occured from direct radiative forcing alone (Harrison *et al.*, 2003).

Discrepancies between the LGM model runs and comparison with paleo-environmental datasets are likely to result from missing feedbacks, for example, all simulations omit the possible influences of vegetation change due to climate-induced shifts, and CO_2-induced changes in vegetation and leaf conductance. Indeed, numerous factors are not included, for example, mineral aerosol (dust) concentrations were many times higher than today during the LGM, especially in the polar stratosphere—this could have provided an extra cooling effect. Taking into account climate- and CO_2-induced vegetation changes to infer the dust distribution (which was in fairly good agreement with proxy data), computations indicate a small positive change in radiative forcing at high latitudes, but a larger negative change at the tropics. Ocean dynamic changes are also likely to be important at the LGM as demonstrated by models of intermediate complexity (Ganopolski *et al.*, 1998; Weaver *et al.*, 1998). Indeed dramatic changes in the ocean circulation are likely to be responsible for abrupt climate change during the last ice age and transition to the Holocene (Stocker and Marchal, 2000).

14.5 TESTING MODELS WITH DATA

The accuracy of climate models is often compared to the only means of validation available: climate estimates derived from proxy data. Data–model comparisons are useful for assessing the relative influence of past climate changes over various spatial and temporal scales. To enable comparisons to be carried out in a systematic fashion, compiled datasets are required that have two fundamental contributions to make to Earth system modeling: as input boundary conditions and as datasets for model evaluation (Kohfeld and Harrison, 2000). For example, the LGM Tropical Data Synthesis (Farrera *et al.*, 1999) contains quantitative reconstructions of the mean temperature of the coldest month and mean annual temperature (MTCO and MAT) and qualitative reconstructions of plant available moisture and run-off. The dataset combines pollen, plant macrofossil, noble gas, and speleothem between 32°N and 33°S. Such datasets need to contain sufficient information and documentation to evaluate the assumptions involved, interpret the data, exercise quality control, and select data appropriate for a specific goal (Kohfeld and Harrison, 2000). These need to:

1. Classify and describe errors and uncertainties in Earth observation data.
2. Represent dependencies, and the associated uncertainty.
3. Develop computational techniques for synthesis of multiple factors, allowing for model and data uncertainty.

Numerous databases of proxy indicators on past climate are amassed within the world centre for paleoclimatology (*http://www.noaa.gov*), such as the BIOME-6000 dataset, the Global Lake Status Database, and the tropical terrestrial data synthesis. Central to the integration of Earth observation data with environmental models is the development of techniques for quantifying and manipulating uncertainties in both data and models. To establish links between the climatic modeling and paleoecological communities, the BIOME-6000 project developed techniques to portray changes in pollen data as changes in biome distribution across the tropics (Elenga *et al.*, 2000; Marchant *et al.*, 2009; Picket *et al.*, 2004; Prentice and Webb, 1998). This link allowed pollen data-based environmental reconstructions to provide a validation tool for climate model-based reconstructions (Prentice *et al.*, 1996; Jolly *et al.*, 1998; Weaver *et al.*, 1998). However, displaying pollen data as biomes has a greater utility than just providing a benchmark for climate model output validation. Transformed pollen data can be used in conjunction with other data to understand the causal factors driving vegetation change over the recent geological past. Additionally, methods need to be developed to encompass errors and uncertainties: errors in raw Earth observation data, errors in input data (e.g., meteorological data), and the inherent limitations of the models themselves (e.g., scale effects) all need to be assessed.

Farrera *et al.* (1999) and Pinot *et al.* (1999) provide a detailed discussion on the comparison between PMIP LGM simulations and the available data from the tropics. Model comparisons with this dataset show that models continue to under-estimate the pattern of cooling, which is significantly spatially different: varying from 5–6°C in South America to 3–2°C in East Africa and Indonesia. Most models in the PMIP suite provide a uniform cooling, however, the United Kingdom Meteorological Office (UKMO) model provides a meriodinal patterning in tropical temperature reduction that is comparable with observations. Palaeodata–model mismatches arise for numerous reasons because of (a) inappropriate comparisons, (b) errors or uncertainties in data, and (c) model failures (Kohfeld and Harrison, 2000). Certainly within the tropics, despite valiant efforts from a relatively few, and thankfully growing, number of paleoecologisits, the data coverage remains too low to make meaningful comparisons—increased data coverage will lead to a re-evaluation of the patterns observed.

14.6 PRACTICAL APPLICATION OF MODEL OUTPUT AND FUTURE DEVELOPMENTS

Predicted change in the extent of individual forest type shows a wide spectrum of possible responses with differing model structures. Environmental changes will clearly affect most strongly vegetation types that are found at the extremes of ranges (Hilbert and Ostendorf, 2001; Sommer *et al.*, 2010). The differential impact is further complicated because the drivers of land use and land cover change are a complex mix of environmental and climatic factors. These linkages make a fully integrated modeling perspective highly challenging and, as further research reveals increasingly complex ecosystem interconnections, anticipating the response of future ecosystems seems to be increasingly outside our reach at present. For example projected changes in bird species richness in Kenya strongly depend on woody plants and how they are included in forecast models (Kislling *et al.*, 2010). Moreover, strong variability in future precipitation patterns as predicted by GCMs at tropical latitudes can further introduce high levels of uncertainty in forecasting the impacts of future climates on biodiversity and ecosystem functioning. Overall, the appropriateness of making forecasts of climate change impacts on biodiversity without taking biotic interactions and uncertainties in regional climate models into account is questionable (Kissling *et al.*, 2010)—using such studies to base socio-economic policy on even more so (Marchant, 2010). Although modeling the full complexity of landscape processes and associated feedbacks is making remarkable progress, and structures are in place to combine research communities and develop new integrated approaches that will produce more valid outputs and hence develop their use in management, there is much work to be done. To engender such a process, the collection and generation of new environmental datasets on past variability is crucial. In addition to developing new datasets, there are a number of methodological developments, for example neural networks (Grieger, 2002) and Bayes theory applied to vegetation dynamics that can provide good results where the floristic diversity is high and the mechanistic understanding of the ecosystem relatively low (Hilbert and Ostendorf, 2001). Improved comparisons between model output and proxy data can be made by upscaling the resolution appropriate from proxy data (catchment scale) and/or through the downscaling of regional climate models (Sailor and Li, 1999). Unfortunately, the application of scale changes and regional modeling remains in its infancy (Sewalle *et al.*, 2000), particularly concerning the tropics, with most regional applications remaining a subset of larger investigations.

Fully coupled land–ocean–atmosphere models, currently under active development with increasingly detailed (realistic) models, combined with improved climate datasets, will be required to arrive at a robust quantitative understanding of climate changes and associated environmental impacts. There are a number of developments underway that fall into three main areas. First, increase the number of components taken into account: complex models that allow the whole Earth–atmosphere–ocean–climate system to be interconnected and permit the analysis of feedback between the elements. Second, increase the duration of the model runs to study climatic transitions rather than equilibrium, this approach offsets the development of more complex models suggested above with some elements of the climate system needing to be simplified—so models are affordable to run given present (and developing) computer limitations. Third, increased spatial scale of the simulations that will aid in the understanding of data in a local context. This approach, still in its infancy, will help us to improve our understating of small-scale phenomena that are important for the behavior of the proxies recorded in the paleoclimate (Kageyama, 2001). Distribution models can provide conservation planning with high-resolution estimates of richness in well-researched areas, and predictive estimates of conservation importance elsewhere (Platts *et al.*, 2010). If species range shifts are the likely dominant species response to future climate change, then spatially explicit species-specific planning will be required. If modeling is to help inform efforts to place land under effective conservation management the models must provide information at regional and even sub-regional scales where most practical conservation decisions are made (Midgely *et al.*, 2003).

The impacts of increasing water stress are predicted to become more acute in many tropical countries (Soloman *et al.*, 2007). Even in East Africa, where most climate change models predict increased rainfall, recent research suggests that local circulation effects will actually result in decreased precipitation (Funk *et al.*, 2008). Anticipated climate changes pose great threats to food and water security, public health, natural resources, and biodiversity (Soloman *et al.*, 2007). A variety of models to investigate species' responses to climate predictions are becoming available with multi-species and niche-based models commonly used to show how species' ranges might alter in response to climate changes (Guisan and Zimmermann, 2000). For the last two decades it has been recognized that species will move into, and out of, protected areas as climate changes (Araujo *et al.*, 2004). Targeted assessments examining the effect of climate change on species' representation within protected areas and the associated extinction risk (Hannah *et al.*, 2005). However, even though the dynamic response of species to climate change is well established, it is quite alarming to note that many of the most vulnerable species are found within a network of relatively static protected areas and game reserves. The robustness of the protected area network is not just a matter of forest conservation; there is great wealth stored in natural capital held within savanna protected areas. Although the degree to which ecosystem readjustments can be compensated for by occupation of newly suitable ranges is highly uncertain (Hannah *et al.*, 2005). The present degree of protection that many species enjoy within protected areas is likely to erode as a result of predicted climate change. Current and future modeled ranges can be used to calculate the area of a species' range under protection, although it is important to keep in mind that a species' modeled potential range does not always precisely match its actual range (Pearson and Dawson, 2003).

Ecology, ecosystem modeling, archeology, and paleoclimate research strands need to be woven together in a cross-disciplinary effort to assess the range of natural environmental variability and associated response of tropical ecosystems to environmental shifts in the past, present, and future (Marchant, 2010). A good example of this has been the recent work on fire which is an under-appreciated control on tropical ecosystem composition, distribution, and structure. Dry forest ecosystems have been influenced by fire for millennia with the reduction of tree cover by burning resulting in the evolution of highly biodiverse ecosystems—facilitating the rise of C_4 grass-dominated floras and associated faunas (Bond *et al.*, 2004). Fire, not surprisingly, limits tree growth, as has been clearly shown by fire exclusion experiments (Bowman *et al.*, 2007). To understand the changing nature of the impact of fire there is a need for better information on the temporal and spatial character of fire activity and land cover impacts at the landscape level (Eva and Lambin, 2000). For example, there has been growing interest in the effects of changing atmospheric CO_2 as an additional and interacting factor with fire and grazing activity that influences vegetation composition and structure (Jolly and Haxeltine, 1997). Recently, it has become possible to disentangle correlation from causality using DGVMs designed to simulate vegetation responses to changing environments (Sitch *et al.*, 2003). For example, application of DGVMs has allowed an integrated assessment of the extent of fire-dependent ecosystems and an evaluation of the mismatch between climate potential and actual world distribution (Sitch *et al.*, 2003). Biome-type vegetation models have also demonstrated the important interacting influence by increasing CO_2 on African ecosystems (Sitch *et al.*, 2003). Increased tree growth and woody thickening allows trees to grow above a threshold where fire will maintain an open structure (Bond *et al.*, 2004). The resulting more densely forested landscape, while beneficial for biomass and carbon storage, is deleterious to wildlife and tourism—preventing the open savanna structure ideal for game viewing. Ecosystem modeling is a crucial tool for evaluating such impacts and enabling people to predict and hence manage such change. Although there are a variety of approaches that can be applied, each of these has its own drawbacks, and hence users—who favor one approach over another. While it is clear that future ecosystem composition, structure, and functioning will be dramatically different it is imperative to understand the full range of environmental variability, and how this will impact ecosystems. Such an understanding may be considered by conservation biologists to impart effective long-term management strategies that promote research capacity and the ability for communities to contribute to, and benefit from, their conservation. Tropical ecosystems deliver goods and services to humankind such as food, materials, energy, pollinators, and less tangible commodities such as carbon storage, the regulation of the carbon cycle, and the moderating flows of energy and water. Hence, they can influence local weather and moderate atmospheric composition. Maintaining the flow of these goods and services requires healthy ecosystems—a challenge in the face of increasing human-induced global environmental changes (Fisher *et al*., 2008).

14.7 CONCLUSIONS

Models have evolved from a very simple, implicit approach representing surface energy balance and hydrology to complex models that represent many of the key processes through which land surface and climate interact (Pitman, 2003). Model development has tended to focus on GCMs, that often perform relatively poorly in tropical regions, or have been developed in temperate areas where there is better input data in terms of climate and environmental parameters, the ecology of the taxa is generally better known, and as the total number of taxa are relatively few the system is relatively simple. Many additional unknowns remain in forecasting future patterns of biodiversity (Davis *et al*., 1998; Araujo and Rahbek, 2006). There are improvements required in the understanding of climate species relationships (Kisling *et al*., 2010; Platts *et al*., 2010) before we even start to consider the important potential effects of dispersal under future climates (Svenning and Skov, 2007). This is particularly critical as ecological communities are unlikely to respond to future climate change in a similar way to how they did past climate change and hence be predictable (La Sorte *et al*., 2009). For example, we lack information on adaptable ecosystems, how individuals adapt to changing environmental conditions, and how the emergence of novel climatic conditions might promote the formation of novel species associations, or changes in current biotic interactions (Williams *et al*., 2007). Land use changes and interactions resulting from ecosystem changes also need to be incorporated into global change analyses (Ellis and Ramankutty, 2008). However, with the pressing questions that climate and land use change are asking (Marchant, 2010), the time is right to combine expertise from chemical, biological, geosciences, and remote sensing communities to work with climate modelers to build an integrated framework that is mutually beneficial—indeed the breadth of knowledge required to develop such a fully integrated approach is intimidating but can be developed through umbrella organisations such as the International Geosphere–Biosphere Programme Past Global Changes (IGBP-PAGES; *http://www.pages-igbp.org*) project. Although there are numerous improvements, it is apparent that the current generation of coupled ocean–atmosphere models still has relatively poor simulations of tropical climate change, possibly due to the spatial and temporal variable nature of tropical environments (Ruter *et al.*, 2004). Environmental change is rarely spatially uniform and as such necessitates an even greater wealth of data on present and past environmental states to determine the complexity and patterns behind this. New sites, located in key areas, combined with the application of a range of proxies of environmental change, are required to refine our understanding of tropical ecosystem responses to Late Quaternary climatic variations. There also needs to be a realization that the tropics must be not treated with the same assumptions applied to Europe and North America. Accurate representation of tropical areas in Earth system models is a continuing challenge, particularly due to incredible environmental and ecological diversity. To unravel this complexity there needs to be a combined approach, for example biome modeling may be a useful first-cut assessment in the regional modeling portion of a climate change study (Midgley *et al.*, 2003); however, species-level modeling is essential for practical applications like detailed conservation planning under future environments.

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15

Modeling future effects of climate change on tropical forests

L. Hannah, R. A. Betts, and H. H. Shugart

15.1 INTRODUCTION

Alterations in climate (or even the natural variation within the current climate) can affect forest communities by altering the internal processes or by altering the proportions of different species in the forests. Experience in assessing the consequences of major climate change is based mostly on paleo-reconstructions for northern hemisphere forests responding to the climate warming that followed the last ice age. These reconstructions demonstrate that climate change also can alter forests by tearing them apart and re-assembling them in novel combinations of species. This process is dramatic in temperate zones and less well-documented but no less certain in the tropics. While the evidence from the past is clear on these points, it is not abundant worldwide. Forming a complete picture of the past is elusive in many tropical regions, even those as prominent as the Amazon, and future climate change may lack past analogs. Our ability to understand the future based on our understanding of what has happened so far in tropical forests therefore faces serious limitations.

Computer modeling of forests can bridge some parts of this gap in understanding. It can be used to explore sets of future climatic conditions that do not currently exist or which have never existed in the history of the Earth. Currently, a wide range of models have been applied to predicting changes in vegetation in response to climate. These models have different data demands and are likely to have rather different domains of applicability. Some have been tested under novel conditions; others draw their credibility by their synthesis of the current best knowledge of ecosystem processes. The models are all flavored by the intended applications and the interests of their developers.

The most frequently applied modeling techniques have their theoretical underpinnings in ecology and ecophysiology. Ecological niche theory provides a framework for understanding two important types of models: species distribution

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models (SDMs) and gap models. Ecophysiology is relevant to understanding dynamic vegetation models, including the recently developed Earth System Models.

Through an evolving ecological literature, two concepts of niche have emerged. The first involves the factors that control the geographic distributions of species. This concept originated with Joseph Grinnell (1917) and finds substantial application among management-oriented ecologists today (see Shugart, 1998 for a review). It refers to the environmental requirements of species—for example, the range of temperatures a species can withstand—and may be termed *environmental niche* (Guisan and Thuiller, 2005). An alternate concept of the niche was introduced by Charles Elton (1927) and defined species niches based on feeding relations. This *trophic niche* concept refers to the way a species obtains and uses resources, especially with respect to other species—for example, a species role within a food web. Over the years, the initial "who eats whom" trophic niche concept was developed to emphasize competition (as opposed to the predator/prey relations implied by Elton's trophic definition). Hutchinson (1957) attempted a synthesis of the Eltonian and Grinellian niche concepts relating the overlap in environmental requirements (Grinnellian niche) with the likelihood of strong competitive interactions (a post-Eltonian niche concept). In retrospect, this latter development was very important in motivating theory but somewhat less successful at reconciling two rather different concepts of the niche.

Environmental niche theory provides a framework for models that aim to describe species distributions with respect to current and future climate. These models are therefore sometimes referred to as "niche models" (e.g., Peterson *et al.*, 2002) but are also widely known as "climate envelope", "bioclimatic", or "species distribution" models (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). In these models, a direct or statistical relationship is established between a species known distribution and current climate, and rules to describe this relationship are developed and applied to future climates. Theory would suggest that each species has a total range of environmental tolerance, or *fundamental niche*, that is greater than the range it actually occupies, or *realized niche*, due to competition, dispersal history, and other factors—but this distinction is little formalized in models of environmental niche.

Trophic niche theory suggests that species compete for resources and evolve specific resource competition strategies relative to other species. An analogy is sometimes given that the trophic niche is a species' "job" while the environmental niche is its "address". Forest gap models have been developed to simulate resource competition at a small site approximately the size of a tree-fall gap in the forest, using quantitative information about species growth rates and other parameters. Qualitative models including trophic niche interactions have also been developed (e.g., the FATE model; Moore and Noble, 1990). If resource competition determines species survival at a site, it then also influences its distribution at a landscape scale, and these models have begun to be applied on broader scales as computing power has improved.

Ecophysiology theory allows construction of models that describe how plants fix and partition carbon, including the cycling of carbon in soil pools. For some well-studied crop plants, it allows building models of how individual species will respond to specific growth conditions. Tropical forest species are not sufficiently well-studied to be amenable to species-based ecophysiological modeling. However, broad models of carbon partitioning are built from first principles and can be applied in all regions of the world. These models provide information on plant growth forms (or "plant-functional type") that may dominate at a particular site under specified climatic conditions and disturbance regimes. These models are known as "dynamic global vegetation models" (DGVMs). They can be important in simulating distributions of tropical biomes—such as savanna, dry forest, and wet forest. Simplified versions of these models may be integrated into models of global climate. The resulting Earth System Models provide important insight into the interactions of global vegetation changes on climate. Changes in tropical forests have proven to be especially important in this regard.

There are at least two outstanding challenges in modeling tropical forest ecosystems under changing conditions. One challenge involves best including what we know about the photosynthesis process at a cellular level or leaf level in a model. Models constructed to be tested against micrometeorological "flux tower" measurements are likely to include fairly detailed scaled-up leaf processes and attempt to simulate the carbon dioxide, heat, and water fluxes of a forest canopy at a fine temporal resolution. Typically, models that represent the interactions of the planet's surface with global models of climate (DGVMs and Earth System Models) are strongly oriented toward this first challenge.

The second challenge involves predicting the change in structure and composition of vegetation in response to climate changes. In models oriented toward this challenge, the life history attributes of species expressed as parameters for birth, death, and success of species is a central focus. There is also an explicit recognition of the differences in structure of the forest as an overall feature influencing the long-term dynamics of vegetation. Because these models seek to represent the structure of the forest, they better estimate longer-term processes including decomposition and death aspects of forests than models emphasizing the first challenge.

At this time, the problem of simultaneously meeting both of the challenges to model under altered conditions is far from solved—at least with a universally accepted solution (Shugart, 1998). This may stem from the rather large differences between the fine temporal and spatial scales over which photosynthesis is studied compared with the much coarser scale of understanding compositional and structural forest dynamics (Woodward, 1987). A prudent way to proceed is to better understand how different models of forest systems are composed, tested, and applied. Such knowledge is key to interpreting the results from any of the different modeling approaches. Promotion of this understanding is the objective of the review that we present here.

15.2 BIOCLIMATIC MODELS

Bioclimatic or niche models of individual species provide insight into possible range shifts due to climate change. Examples of this modeling approach include BIOCLIM

(DOMAIN), generalized additive modeling (GAM), generalized linear modeling (GLM), artificial neural networks (ANNs), genetic algorithms, genetic algorithm for rule-set prediction (GARP), and several others (Guisan and Thuiller, 2005). Each of these techniques uses information about a species' present range and present climate to simulate its present or future range.

For climate change studies a model constructed of the present relationship between a species' distribution and climate may be projected into the future by coupling it with a global climate model (e.g., general circulation model, GCM). Such model projections may be useful in assessing the impact of climate change on individual species, or in designing conservation strategies for suites of species (Hannah *et al.*, 2002).

In its simplest form, a bioclimatic model of a species' range can be constructed by measuring the range of variation in a number of environmental variables from points at which a species has been observed. For each grid-cell, the model calculates whether each environmental variable is within the range observed for the species (Box, 1981). If it is within the observed range for every variable, the species is modeled as present in that grid-cell. If any variable is outside the observed range for the species, the species is modeled as absent in that grid cell. This type of model was proposed by Box (1981) and is sometimes referred to as a "Box model". Box models have limitations. Box's original formulation was for what he termed "life forms", based on combinations of whole plant form and morphology, size, and features of the leaves. A Box (1981) life form might be a"tropical evergreen sclerophyll tree", a "xeric tuft-treelet", or a "leaf-succulent evergreen shrub". Each of Box's 100 or so life forms was taken to have a distribution in a seven-dimensional climate statistical space. Box tested his model in predicting the life forms expected at several hundred locations with wildly contrasting climatic conditions.

More complex models build on this concept, using statistical or other measures to improve the sophistication of prediction. BIOCLIM (Nix, 1986) creates one-tailed percentile distributions for each variable, while DOMAIN calculates a distance statistic between the environmental values in a cell and the environmental values in occurrence points from the observational record. GAM and GLM are statistical modeling techniques that can be used to construct a model of species presence/absence, based on known occurrences (Hastie and Tibshirani, 1990). Other approaches—ANNs and genetic algorithms—may be applied to get a similar result. The MAXENT algorithm is noteworthy in that it was designed specifically for simulating species responses to climate change, and has scored well in comparative evaluations of model performance (Phillips and Dudík, 2008; Elith *et al.*, 2006).

One test of models using these methods has been geographic applications involving the estimation of species' current ranges. For example, a bioclimatic model may be used to estimate a climatically suitable range for a species that is currently only known from a handful of observations. To test such an application one obvious approach is to determine whether the modeling predictions match known locations of the species that have been omitted from the model calibration step. One such test was developed by Webb (1988), who calibrated the modern climatic niche occupied by tree species using current distributions and then predicted prehistoric spatial distributions of spruce (*Picea* sp.) and other major tree taxa across North America in response to climate changes and evidenced in pollen samples from lake cores. This reconstruction was developed at three millennial intervals over the past 18,000 years.

Others have used essentially the same approach to describe the niches of individual plant species and then used these data to simulate ranges under altered climate. An important example of this approach is by Iverson and Prasad (1998, 2001) who mapped the distributions of 80 tree speces over eastern North America. This application was based on data from millions of trees sampled systematically in the National Forest Inventory overlain with spatial climatic data sets. Such massive systematic data collections do not exist for most tropical countries (a notable exception is Malaysia) and tropical applications are likely to have several data limitations. Since many species have limited (<100) numbers of observational records, the range of any one variable from the observations is unlikely to capture the full range of variation the species is actually able to tolerate. Conversely, for variables which have no role in controlling the limits of a species' distribution, the range of the variable within the observational records is actually irrelevant (unless those variables become limiting under altered climate regimes).

The strength of bioclimatic models is that they yield results for individual species, and thus are directly relevant to measuring impacts on biodiversity at the community level of ecological integration. However, the complexity of bioclimatic models varies greatly and they have numerous assumptions that may not be relevant in the real world (Pearson and Dawson, 2003). The most often cited is the assumption that current species' ranges are in equilibrium with present climate or that at least the current range of the species expresses the full environmental range of the species. Many species may in fact be responding to minor climatic cycles (e.g., the Little Ice Age), in some cases still coming into equilibrium with the transition from the last glacial period, or for records gathered over the last 30–50 years responding to anthropogenic climate change.

A second important assumption is that a species' range is limited by climate, rather than other factors—such as competition or dispersal. This is not a trivial assumption. Many species may have distributions limited by biogeographic accident or other factors not related to climate. A prominent cautionary example is the Monterey pine (*Pinus radiata*) which has a very limited range in California but has become one of the most widely planted plantation–forestry species in the international subtropics.

Competition, which is assumed to be unimportant in correlational models, in fact probably plays a significant role in the distribution of most species. Whether or not this factor is important enough to badly distort statistical (correlational) models is problematic. Box's original formulation of bioclimatic models included an algorithm (based on an environmentally calculated potential canopy cover) that accounted for competition among life forms (Box, 1981). However, most subsequent models do not directly address questions of competitive interaction. They may also lack a direct mechanistic link between species' physiology and the climatic limits suggested in the modeling. While this may not be a problem for certain applications, one issue involves whether or not the bioclimatic approach takes into account the complicating factor of the highly elevated carbon dioxide levels in the atmosphere. If, for example, the direct effect of elevated CO_2 is increased water-use efficiency, then how should one recalibrate the bioclimatic indices for futuristic applications (see Körner, 1993). Future projections vary substantially depending on the model type (Thuiller, 2004). Other types of models are useful alternatives for addressing competition, physiological limits, and carbon-cycle interactions.

Bioclimatic modeling has been applied to relatively few tropical tree species. Hughes *et al.* (1996) used the climatology of BIOCLIM to examine the climatic range of species in the *Eucalyptus* L'Herit genus in Australia. Over 31 tropical species in the genus had mean annual temperature ranges of less than 1°C, spanning both wet and dry habitats across Australia. Ferreira de Siquiera and Peterson (2003) examined the Cerrado tree species of tropical Brazil, finding major range shifts and consequent changes in patterns of species richness. More recently, Miles *et al.* (2004) assessed the effects of future climate change on 69 Amazonian tree species using GLM and life history simulations to 2095 under Hadley Centre climate projections. In this simulation 43% of all species became non-viable by 2095 (Miles *et al.*, 2004). These studies suggest a relatively high vulnerability of tropical tree species to climate change, but these early results must be viewed with caution. Tropical trees may occupy the upper limits of current temperatures, and thus bioclimatic models are not presented with the full range of conditions under which the species can exist. There may be warmer climates with no current analog, in which tropical species are perfectly capable of surviving but which models project as unsuitable.

Bioclimatic modeling has been conducted for more vertebrate species than tree species, but the number of independent studies is still small. Williams *et al.* (2003) modeled range changes of mammals, reptiles, amphibians, and birds in the Queensland tropical rainforests of Australia. These primarily montane species showed strong range reductions with temperature increases as species' ranges migrated upslope (Williams *et al.*, 2003). Peterson *et al.* (2002) used GARP to model the climate change response of large numbers of Mexican vertebrates, many of which were tropical. Range reduction was pronounced in some of these species, but large reductions were less widespread than in the species examined in the Australian study, perhaps due to the more varied topography of Mexico (Peterson *et al.*, 2002).

The issue of no-analog climates is of strong relevance for the interpretation of bioclimatic models for the tropics. Saxon *et al.* (2005) have projected that over 60% of the United States will be occupied by no-analog climates by 2100. Temperature increases in the tropics may result in even higher proportions of no-analog climate space, but the physiological implications of these no-analog situations are not clear. Many tropical species may be well able to withstand higher temperature than those in which they currently exist. On the other hand, no-analog conditions in moisture balance or moisture balance combined with elevated CO_2 may be much more difficult for tropical trees to withstand. Bioclimatic models probably poorly reflect both positive and negative effects of no-analog climates on species' ranges.

15.3 PROCESS-BASED MODELS

More recently, a group of process-based or ‘‘eco-physiological’’ models are emerging for species distribution modeling (Morin and Lechowicz, 2008). These models use known responses to climate to estimate a species fitness under future climate change (Morin and Thuiller, 2009). For instance, the length of growing season might be used to determine a species’ ability to complete development and reproduce under future climatic conditions. Other phenological and physiological factors can be used to assess species survival and reproductive ability in novel climates.

Process-based models have now been applied to numerous temperate tree species (Morin and Chuine, 2005). These applications demonstrate that when tree ecology is sufficiently well known, the correlative approach central to most species distribution models can be abandoned in favor of a more mechanistic or process-based approach. The results yielded by the process-based models is qualitatively similar to those offered by correlational SDMs. Species ranges move poleward and upslope in process-based simulations, often with patterns similar to those in correlational SDMs. However, these patterns also show significant differences that may be important in ecological interpretation or conservation planning. The process-based approach is potentially applicable to any species, though it has been most applied in trees.

However, the understanding of phenology and physiology required for process-based models is unavailable for most tropical species. In the tropics, many species remain un-named and un-studied, making process-based models inapplicable. In this respect, process-based and gap models face similar limitations in the tropics. For individual well-studied tropical species process-based models may nonetheless yield important results.

Perhaps the most noteworthy process-based result for tropical species stems from work on population-level extinctions in lizards (Sinervo *et al.*, 2010). Population extinctions in Mexico due to thermal stress were used to build a eco-physiological model of lizard population extinction. This model was used to predict lizard population extinctions in other parts of the world and to estimate lizard global extinction risk. The model successfully predicted known population extinctions in regions outside of Mexico. It predicted global lizard extinctions approaching 20% by 2080, confirming early SDM estimates of extinction risk from climate change (Sinervo *et al.*, 2010; Thomas *et al.*, 2004). Additional process-based modeling in the tropics may provide other critical insights into the climate change response of tropical systems.

15.4 PHYSICAL INDICES

An alternative approach to biological modeling is to use physical indices of climate that are believed to relate to biological properties. The most important of these approaches is the assessment of novel and disappearing climates (Williams *et al.*, 2007). This global analysis showed that the tropics hosted a high proportion of novel and disappearing climates.

The index used in the global assessment built upon earlier work that showed that climates that had not existed in a region in the past correlated with novel plant assemblages (Williams *et al.*, 2001). This North American index was adapted to global analysis by substituting existing climatic variability in a location for regional climatic similarity. This was necessary for the global analysis because no single regional index would be applicable in all parts of the world.

However, because current climatic variability is low in the tropics, the global index using current variability would be expected to highlight the tropics. The prediction of high proportions of novel and disappearing climates for the tropics is therefore consistent with expectations, given the index employed. The more important question is whether current variability is limiting. For vegetation, paleo-ecological evidence suggests that much warmer conditions have not lead to large-scale extinction in the past (Morley, Chapter 1 of this book). So novel may not equate to fatal for tropical trees. Yet the process-based modeling of lizards described in the previous section suggests that at least some species in the tropics may be highly vulnerable to warmer, novel climates. The sensitivity of tropical forest species in relation to climate variability on contemporary and evolutionary time scales therefore remains an area of intense research importance.

15.5 GAP MODELS

In the late 1960s, several forestry schools in the United States developed a forest modeling approach based on simulating a forest by computing the birth (or planting), growth, and death (thinning or harvest) of plantation forest. Applications of these models included determining plant strategies for genetically improved tree crops and ascertaining the appropriate spacings for growing trees to produce metric-dimensioned lumber (see Shugart, 1998 for review). This emphasis on tracking individual trees was soon taken up by forest ecologists interested in the simulation of forest-structural and forest-compositional changes in forest succession and in response to environmental gradients (see Shugart, 1998, ch. 8, for a review of several of these applications and model tests).

One of the features of these early individual-based forest simulators (Huston *et al.*, 1988) was geometrically elaborate computation of the effect of each tree on the others through shading or the use of nutrient and/or water resources. One simplification of the rather laborious calculations was to assume the competitive interactions were primarily occurring on a plot of land that was roughly the size of a very large canopy tree. This is the space scale of a gap in a forest canopy associated with a large tree's death. Hence, this class of models was termed "gap models" (Shugart and West, 1980). Modern computers have lifted the computational limitations that caused gap model competition simplification. Nowadays, "gap model" refers to individual-based models of naturally regenerating multi-species forests.

A variety of gap models now exist—for example, the FORET model of Tennessee forests (Shugart, 1984) and of European mountain forests, and FORCLIM (Bugmann and Solomon, 1995). Gap models utilize the demography and natural history of plant species, including physiological trade-offs, plant growth, and reproductive processes, to simulate the compositional dynamics at the scale of a tree-fall gap. These parameters are used to simulate the response of individual plants of differing species within the gap, as well as the way the environment is modified by those individuals. Each individual tree is modeled both in spatial extent and in vertical structure and its consequent effects (such as shading of trees below). Gap modeling is therefore more suitable for assessing competitive interactions and small-scale impacts on biodiversity than is bioclimatic modeling.

One of the earliest modes of testing gap models was to simulate the altitudinal zonation of forests along montane climate gradients. This leads naturally to an interest in their ability to construct expected forests under altered climates. Consequently, there has been a proliferation of this class of models with reviews of their application in assessing climate change (Shugart *et al.*, 1992; along with two special issues of *Climatic Change*, with introductory papers: Bugmann *et al.*, 2001 and Shugart and Smith, 1996). The initial entry of gap models into the task of assessing the effects of climate change on forest ecosystems sprang from applications to understand expected forest responses to past climates. These paleo-reconstructions (Overpeck *et al.*, 1990; Solomon *et al.*, 1980; Solomon and Webb, 1985) lead naturally to the assessment of expected forest composition under future climate scenarios.

Because gap models require knowledge of the growth rates of trees along with the fundamental silvicultural features of trees—such as regeneration habit, size, growth rates, and heights—the lack of such information across the diverse array of species composing many tropical forests have made applications to tropical systems difficult. The lack of growth rate information from tropical forests has been a particularly limiting constraint. There is an associated difficulty in knowing how tree growth might change with climate. Nevertheless, there are several tropical forest gap models. The Kiambram model simulates 125 species in Australian montane rainforest (Shugart *et al.*, 1980). The Outenqua model (van Daalen and Shugart, 1989) similarly projects forest dynamics for African subtropical rainforests. Because of the lack of information on the climate response of tropical forest species, there have been relatively few climate-related applications. Doyle (1981) simulated the effects of altered hurricane disturbance frequencies for Puerto Rican montane rainforest with a gap model and O'Brien *et al.* (1992) explored landscape-scale interactions with hurricanes for the same site.

There have been applications of gap models in tropical settings using a gap model framework to produce the dynamics of forest structures over time. Bossell and Krieger (1994) have implemented a functional type (rather than species-based) model of tropical forests, basically on a gap model framework. Another important tropical application of gap models to tropical rainforests is the approach of Moorcroft *et al.* (2001), who parameterized a gap model for Amazonian rainforest using a postulated relationship between growth rate, photosynthesis, and wood density. This model was used to parameterize a statistical model of the size distribution of trees across the Amazon Basin using an approach pioneered by Kohyama (1993). This was then driven by a photosynthesis/production model to incorporate the effects of temperature and moisture.

15.6 DYNAMIC GLOBAL VEGETATION MODELS

It has long been recognized that climate exerts a general control on the vegetation zones of the Earth (Woodward and Williams, 1987). An early approach to modeling this effect was analogous to bioclimatic modeling of individual species. Models that correlated vegetation types with certain climatic conditions were shown to reproduce global vegetation zonation with reasonable accuracy. Such correlative models could also be used to project future vegetation types using projections of future climates from GCMs.

More recently, correlative models have been largely replaced by mechanistic models using plant physiology to simulate vegetation patterns. These models are known as ''dynamic global vegetation models'' (DGVMs). These models use equations describing basic plant physiological processes—such as photosynthesis and respiration—to determine net amounts of carbon available for plant growth and the allocation of that carbon (Prentice *et al.*, 1992; Woodward and Beerling, 1997). The results of these calculations are expressed as ''plant-functional types''—for example, ''evergreen needleleaf forest'', ''grass savanna'', or ''deciduous broadleaf forest''. Plant-functional types in these applications are direct analogs to Box's (1981) ''life forms''.

Numerous authors have contributed to the development of over half a dozen DGVMs that are being actively tested and refined. SDGVM (Woodward and Lomas, 2004), TRIFFID (Cox 2001), IBIS (Foley *et al.*, 1996), LPJ (Sitch *et al.*, 2003), VECODE (Brovkin *et al.*, 1997), MC1 (Bachelet *et al.*, 2001), and HYBRID (Friend *et al.*, 1997) are examples. DGVMs have great utility in assessing the impacts of climate change, fire, and other environmental drivers on gross vegetation structure and physiognomy, especially at large scales. They are less useful for studies on individual species or biodiversity assessments at small scale. DGVMs may also be integrated into climate models to assess influences of vegetation on carbon cycles and global climatic change.

Responses to climate change and elevated CO_2 modeled by DGVMs show broad similarities but also substantial inter-model variation. Cramer *et al.* (2001) used an ensemble of six DGVMs to make projections of global vegetation responses to transient climate change simulated with the HadCM2 GCM under the IS92a greenhouse gas and sulphate aerosol concentration scenario. The DGVMs generally overestimated the amount of tropical forest for current climates, especially in Africa but also in South America and Southeast Asia (Cramer *et al.*, 2001). Tropical dry forest tends to be over-predicted in Southeast Asia and under-predicted in Africa. TRIFFID and HYBRID particularly over-predict tropical wet forest, while results from VECODE and SDGVM more closely approximate tropical moist and dry deciduous vegetation classifications derived from satellite images.

A particular feature of this study was projection for a major reduction in forest cover in the eastern half of Amazonia, due to significantly reduced precipitation and increased temperature. A drying of the Amazonian climate emerges in a number of GCMs, generally associated with an El Niño like pattern of global climate warming, but it is important to note that not all GCMs show this response. All six DGVMs showed a tendency toward reduction in forest cover due to drier conditions, and a drop in Amazonian biomass by 2100 (Figure 15.1; Cox *et al*., 2004). Variability in outcomes is influenced by assumptions about photosynthetic response and more efficient water use by the vegatation due to increased CO_2 concentrations. While all models project a reduction in forest cover in northeastern Amazonia, considerable variability is evident in the models for other Amazonian outcomes.

DGVMs are rather difficult to test against independent data, in no small part due to their scales in time and space. The Foley *et al*. (1996) IBIS model has been tested globally against the flows of the major rivers of the world and regionally for the flows of the Amazon and its tributaries. The rationale is that the model computes evapotranspiration as one of its dynamic variables and water flow of a basin can be taken as the difference between rainfall and evapotranspiration when corrected for soil and ground-water storage. This regional- and global-scale DGVM testing is a healthy development particularly in that it uses data that are independent of model development and parameterization. Most DVGM model testing has been for consistency with overall patterns in the parameterization data or in the form of model comparisons (as opposed to independent data comparisons).

15.7 EARTH SYSTEM MODELS

Tropical ecosystems respond to climate changes, but the ecosystems themselves also exert influences on climate. For example, a number of studies have suggested that removal of the Amazonian forests may cause a warming of surface temperature and reduction in precipitation, due to a reduced level of transpiration from the deforested landscape (see, e.g., Lean and Rowntree, 1997 for summary). Such effects may be crucial in maintaining local climates in a state amenable to the forests themselves (Betts, 1999). Changes in forest cover may also influence the climate through changes in the production of aerosol particles, which affect cloud formation and rainfall production. As well as influencing local climate, tropical ecosystem changes may also exert more far-reaching effects. For example, changes in carbon stocks affecting the rate of CO_2 rise and changes in the near-surface energy balance and cloud processes may modify atmospheric circulatory (Hadley) cells near the equator. Gedney and Valdes (2000) have used robust atmospheric models to show that such changes in atmospheric circulation may have influences felt across the globe.

Given the potential for major feedbacks from ecosystems, it is clear that predictions of future climate change should consider ecosystem responses and their effect on climate. This has led to the development of "Earth System models" which couple models of the atmosphere and oceans (GCMs) to models of the terrestrial and marine biosphere (e.g., DGVMs) (Foley *et al*., 1996; Cox *et al*., 2000; Ganapolski *et al*., 2001). Physical and biological models interact via biogeochemical cycles and through the impact of life on the physical properties of

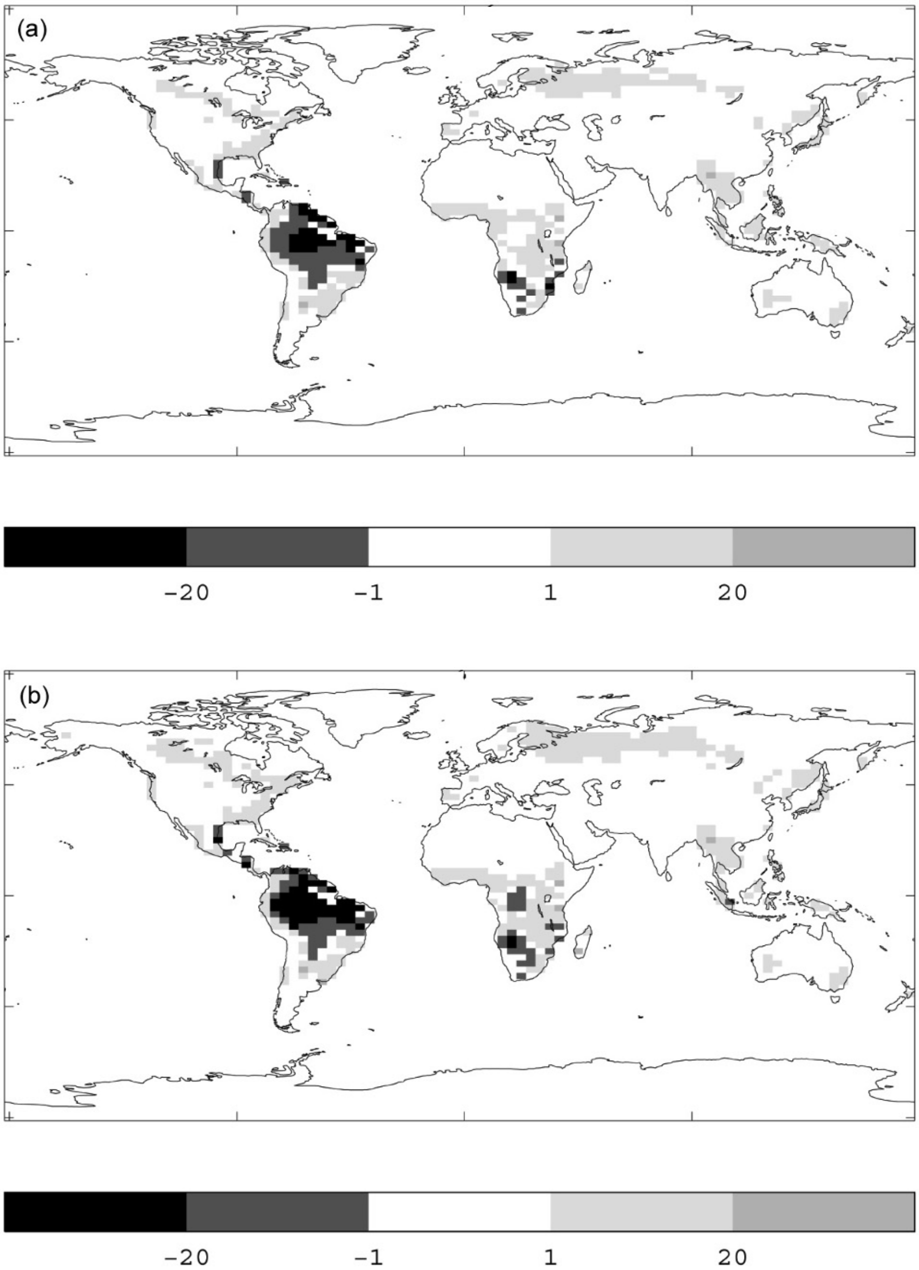

Figure 15.1. Global changes in broadleaf tree cover illustrating importance of tropical forests in CO_2 feedback effects. (a) Change in cover simulated by the HadCM3LC coupled climate–carbon cycle model (Cox *et al.*, 2000) from 1860 to 2100 without CO_2 climate feedbacks. (b) Additional changes with inclusion of CO_2 climate feedbacks (© British Crown Copyright 2003, by kind permission of the Met Office).

the Earth's surface. A number of such models have been developed with a wide range of spatial and temporal resolutions, attempting to trade off model complexity and detail against computational efficiency. The models used to study the interactions between climate change and tropical forests typically feature a DGVM and/or an interactive carbon cycle included within a GCM (Cox *et al*., 2000; Betts *et al*., 2004).

The inclusion of DGVMs in GCMs allows climate prediction simulations to include feedbacks from ecosystems responding to climatic changes at global and regional scales (Cox *et al*., 2000). Coupled GCM–DGVMs are therefore potentially valuable for understanding and predicting synergistic responses of ecosystems to climate change over time scales of centuries and spatial scales of hundreds of kilometers (Betts *et al*., 2004).

Early applications of Earth System models show that widespread increases or decreases in forest cover projected in response to CO_2 rise and climate change may indirectly contribute to regional and global climate changes through alterations to land surface properties. Furthermore, net changes in terrestrial carbon stocks in the tropics and elsewhere may influence the rise in CO_2 itself. Ecosystems may therefore exert a number of feedbacks on climate change, both at the regional and global scale.

In simulations using the Hadley Centre coupled climate–ecosystem model—HadCM3LC—the forests of Amazonia showed a very large reduction in tree cover as a result of decreased rainfall (Betts *et al*., 2004; Cox *et al*., 2004). Some signs of the beginning of this process were already simulated by 2000, with broadleaf tree cover reducing in the northeast of Amazonia in response to a drier climate than that simulated for 1860 (Figure 15.2). The reduction in rainfall spreads towards the southwest through the 21st century, and the tree cover reduces until it is less than 1% in the northeast quarter of Amazonia by 2100. Almost all of the Amazon Basin loses at least 50% of its tree cover by the end of the simulation, to be replaced mainly by C_4 grass but also with large areas of bare soil. The general character of the region fundamentally changes from dense evergreen broadleaf forest to savanna, grassland, or even semi-desert.

The changes in tropical forest ecosystems in these simulations had significant impacts on regional climates through changes in the physical properties of the land surface. Although the drying climate in Amazonia emerged even when vegetation was fixed at the present day state, regional climate changes were significantly affected by vegetation feedbacks. In particular, precipitation reduction over Amazonia was found to be enhanced by 25% by feedbacks from the loss of forest cover. In the western part of the basin, the feedback was greater still because of the greater dependency of rainfall on recycling through evapotranspiration in the continental interior. Here precipitation reduction was increased by over 30% as a result of drought-induced dieback of the forests, particularly to the east. Forest loss also increased surface albedo which reduced convection and moisture convergence, providing a further positive feedback on rainfall reduction (Charney *et al*., 1975).

The model simulations of Friedlingstein *et al*. (2001) also found a reduction in precipitation to be simulated in Amazonia, but the model did not include dynamic

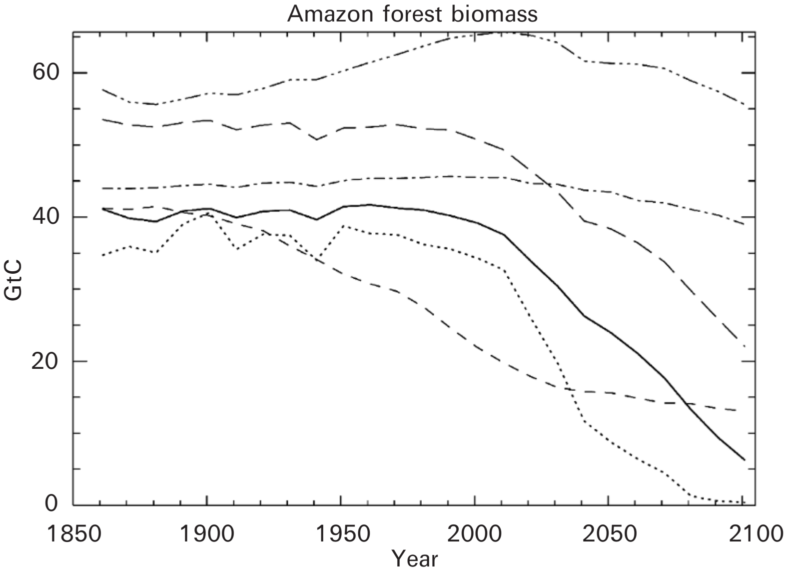

Figure 15.2. Decline of Amazon forest biomass in six different DGVMs, under a climate projection from the HadCM2 climate model (Cox *et al.*, 2004). These simulations do not account for the direct effect of rising atmospheric CO_2 in fertilization; other simulations including CO_2 fertilization using the same models showed smaller losses of biomass or small increases (© British Crown Copyright 2003, by kind permission of the Met Office).

vegetation so there was no feedback on climate through biogeophysical effects. The model used by Thompson *et al.* (submitted) included the IBIS2 dynamic vegetation model (Foley *et al.*, 1996; Kucharik *et al.*, 2000), but this model did *not* produce a drying in Amazonia.

In order to estimate some constraints on sustainable conditions for the Amazonian forests with reference to changes that have occurred in the past, Cowling *et al.* (2003) used HadCM3LC to simulate the coupled paleoclimate–vegetation state in Amazonia at the last glacial maximum (LGM) 25,000 years ago. At the LGM, forest cover was maintained but was less productive, consistent with proxy data from the paleorecord. This was despite a drier climate and lower CO_2 concentrations, both of which are less favorable for forest cover. Cowling *et al.* suggested that the variation in forest structure (leaf area index) at the LGM might have acted to drive speciation and diversity in Amazonian forests, through mechanisms somewhat analogous to those that have been proposed for forest refugia, without loss of continuous forest cover. The critical aspect of the climate at the LGM was cooler temperatures, which helped to reduce both photorespiration and evapotranspiration, leading to decreased loss of carbon and water from the vegetation. Cowling *et al.* noted that—for the future state—warmer conditions are likely to amplify the effects of any drying of the regional climate that may occur despite the likely effects of elevated CO_2.

15.8 CONCLUSION

Bioclimatic models suggest major impacts of climate change on tropical forests. However, several biases, not the least of which being the unknown physical tolerances of many tropical species to warmer climates, suggest that these results are in need of replication and confirmation. Gap models have seen relatively limited application to tropical forests, and still less use in assessing impacts of climate change on these forests. The difficulties of obtaining gap model parameters for tropical forests will probably continue to constrain their use, but ecosystem demography–type models (Moorcroft *et al.*, 2001) allow these results to be applied regionally (notably for the Amazon Basin). DGVM results indicate possible losses in tropical forest cover in some regions, which may support the findings of bioclimatic models. The Amazon is of particular concern, as many—but not all—DGVMs indicate loss of forest cover in the Amazon under future climate projections. This effect has been further explored in coupled GCM–DGVM simulations, and the enhanced forest loss observed in these coupled simulations provides one of the most remarkable modeling results for tropical forests under climate change.

The extreme 21st century precipitation decrease and forest dieback simulated in Amazonia by HadCM3LC is the result of a complex, coupled process emerging from interactions between the atmosphere, the oceans, and the land ecosystems of the Amazon and elsewhere. The outcome is a major change in forest cover which has significant implications for both the ecosystem itself and for global climate change. These model results are still subject to considerable uncertainties. Nevertheless, while these results should not be viewed as a prediction, the analysis to date suggests that under increasing concentrations of CO_2 and other greenhouse gases, a transition to a drier, less forested Amazon cannot be ruled out. Given our rudimentary understanding of climate change impacts in the tropics, these results for the Amazon provide reason for concern for impacts on other tropical forests.

The key role of feedbacks from forest loss has major implications for the importance of the sensitivity of Amazonian forests to climate change. While the true sensitivity of the forests is still uncertain, the results presented here show that, in principle, forests could be a significant component of the sensitivity of regional and global climates to radiative forcing. This has implications for the long-term effects of human activity in Amazonia. Activities such as road-building, partial deforestation and selective logging have been shown to increase the climatic sensitivity of parts of the forest not directly affected by the activity. The exposure of a new forest ‘‘edge’’ can increase susceptibility to fire, and may therefore increase the sensitivity of the forest to climate change. If forest sensitivity is increased in this way, this could enhance the feedback on both regional and global climates.

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16

Conservation, climate change, and tropical forests

L. Hannah and T. Lovejoy

16.1 INTRODUCTION

Conservation of tropical forests in the face of climate change is a major challenge, because of the huge losses already suffered to habitat loss and because of our still rudimentary knowledge of the biology of these systems. For example, in Southeast Asia, most moist tropical forest has already been lost, resulting in the severe imperilment of hundreds of well-known species, as well as the probable extinction of thousands of species before they are described by science (Brooks *et al*., 1997). In this setting, climate change will alter the abundance and distribution of many species whose continued existence is already precarious, in a landscape that permits little, if any scope for range dynamics.

While conservationists struggle against habitat loss, we seemingly lack even a strategy for coping with climate change. But that strategy is not completely elusive. It is clear that a two-pronged response is needed to effectively cope with climate change (Hannah *et al*., 2002a). First, on-the-ground conservation strategies must begin to consider climate change. Expanding planning horizons, modeling and assessing possible climate change effects, and monitoring potentially sensitive species are all elements of climate change integrated conservation strategies that are within easy reach (Hannah *et al*., 2002b). The second, and more difficult, element of conservation response is that of constraining greenhouse gas levels in the atmosphere (Hannah *et al*., 2002a). It is clear that no conservation strategy can be successful on the ground in the face of ever mounting climate change. Greenhouse gas levels must be stabilized in the atmosphere to limit climate change, implying a huge transition in the energy economy away from fossil fuels (Lackner, 2003).

In this chapter we will describe the challenges climate change poses to tropical forest conservation, followed by an analysis of the appropriate responses and their potential scope. We will then explore greenhouse gas stabilization in the atmosphere. Taking into account the possible scope of coping with climate change in conservation

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strategies, what level of atmospheric greenhouse gases is "safe" and what would be required to reach those targets?

16.2 CONSERVATION CHALLENGES

Several distinctive characteristics of tropical forest response to climate change pose significant challenges for conservation. Among these are the climate-making role of tropical forests, uncertainties about past responses, the introduction of warmth on an already warm inter-glacial climate, the critical role of precipitation in tropical forest eco-physiology and the synergies of climate change with ongoing habitat loss. This section will describe each of these challenges briefly.

Tropical moist forests have interactions with regional and global climate that have profound implications for their conservation. The Amazon Basin in particular plays meso- and global-scale climatic roles (Cox *et al.*, 2000, 2004; Betts *et al.*, 2004; Marengo, 2004; Hannah *et al.*, Chapter 15 of this book). The basis of this effect is the influence tropical forests have on moisture-cycling and the regional water balance. At a plot level, removing forest changes the radiative properties of the surface and reduces moisture release by evapotranspiration (Pitman *et al.*, 2000; Bush *et al.*, Chapter 2 of this book). These effects result in increased convection over the cleared parcel and may result in increased precipitation if the clearing is small and isolated. As the amount of clearing increases, the effect changes to one of reduced precipitation as convection has increasingly less surrounding moisture from evapotranspiration on which to draw.

At the scale of large forested areas—such as the Amazon Basin—the net effect of forest moisture turnover is to cycle moisture entering the system from the tropical Atlantic, making the western parts of the basin significantly moister than would be the case in the absence of forest (Bush, 1996; Bush *et al.*, Chapter 2 of this book). Clearing of a substantial fraction of the basin may therefore lead to additional forest loss due to loss of moisture-cycling and regional drying. This positive feedback appears to have repercussions at a global scale as well (Cox *et al.*, 2002). When carbon and surface vegetation models are incorporated into GCMs, climate change drying in eastern Amazonia leads to forest loss, progressive drying in western Amazonia, and accelerated global warming due to massive releases of CO_2 from the Amazon. Avoiding these effects may require maintaining a substantial fraction of the tropical forest cover of the basin as a whole.

A second feature complicating the conservation of tropical forests in the face of climate change is the limited knowledge of these systems' responses to past change (Flenley, 1998). This can be a key limitation is assessing the possible natural precedents for response to rapid climate change. Paleoecological evidence from the flank of the Andes suggests that forests responded to glacial–interglacial cycles, but not to the rapid climate "flickers" that appear to characterize North Atlantic climate and vegetation responses (Bush *et al.*, 2004). The very rapid millennial or shorter timespan climate "flickers" observed in Greenland ice cores are not reflected in the pollen record obtained from lakes on the flanks of the Andes. This could indicate either that these climate flickers did not occur in the tropics or that vegetation did not respond to them.

Other aspects of past response are still debated. While it is clear that tropical forests around the world have responded to climate change in the past (Flenley, 1998), the exact pattern is not well worked out for areas as significant as the Amazon (Bush, 1994). The retreat of Amazonian forests into "Pleistocene refugia" has been discounted based on a number of lines of evidence (Willis and Whittaker, 2000). However, deeper time refugia have been proposed (Haffer, 1997). It has also been suggested, based on modeling, that Amazonian forest cover may have been maintained in glacial–interglacial cycles, but that forest structure (as indicated by leaf area index in the models) may have shifted significantly, driving speciation in the absence of "refugia" (Cowling *et al.*, 2001). This suggests that direct CO_2 effects might impact evolutionary processes in ways that would be very difficult to control or modify through conservation actions.

The relative lack of evidence about past biotic change is aggravated by the lack of climatic precedents for the speed and nature of expected future change (Overpeck *et al.*, 2003). Warming is projected to be rapid and will occur in the context of a warm interglacial climate (IPCC, 2001). Most rapid warming over the past 2 million years has occurred in transitions out of glacial conditions. While some interglacials were warmer than the current climate, they then cycled into cooling towards a glacial period. Physical and biotic analogs to the expected warming on a warm climate are largely absent.

While lack of information is an obstacle, we have abundant data that demonstrate that all ecosystems, including tropical forests, experience climate change on a species-by-species basis. This individualistic response to climate change is reflected in numerous temperate records and in the limited tropical record. A Gleasonian view of communities as ephemeral collections of species with like climatic and biophysical tolerances is supported by this evidence. The challenge posed to conservation is how to deal with transitory communities. If climate change is to tear contemporary communities apart, as component species respond individualistically, there is no absolute baseline reference. Pre-European contact or pre-disturbance ecosystem conditions are peculiar to one point in history. Trying to replicate these conditions under future climates that have no exact past analog has no precise scientific foundation.

As no-analog communities emerge under climate change, another conservation problem surfaces. We have no precedent for managing these communities. So, just as their composition poses problems for the definition of conservation goals and end-points, the processes of these communities pose problems for the definition of appropriate management practices. Without objective goals or management points of reference, conservation becomes relative at best and subjective at worst. Responding to the challenge faced by loss of reference points is common to all ecosystems facing climate change, but may be particularly acute in the poorly understood and mega-complex tropical forests.

Finally, the imposition of dynamics on an already severely depleted and fragmented natural system is one of the great challenges faced by tropical forest conservationists confronting climate change (Peters and Darling, 1985; Hannah *et al.* 2002a). Plant communities have responded in step with remarkably rapid climate changes in the past (Markgraf and Kenny, 1995). But these responses have taken place in fully natural landscapes, in which mechanisms such as micropockets of vegetation change could persist and serve as expansion fronts for subsequent change (McGlone, 1995; McGlone and Clark, 2005). Current patterns of human land disturbance indicate that most areas of the planet are now fragmented (Hannah *et al.*, 1994; Sanderson *et al.*, 2002), obscuring or obliterating many of the mechanisms for rapid response to climate change.

Tropical forests are certainly not immune to heavy fragmentation. Most of the global biodiversity hotspots fall in tropical forests, and the hotspots by definition have lost 70% or more of their primary habitat (in addition to the more widely appreciated criterion of high endemism) (Myers *et al.*, 2000). And even large forested areas such as the Amazon have undergone highly publicized fragmentation.

Yet, the amplitude of dynamics relative to fragmentation in the tropics remains poorly understood. In one of the best studies of tropical dynamics, Bush *et al.* (2004) have demonstrated that vegetation responses on the Andean flank are quite different from the records described for more temperate forests. In these Andean forests, directional change, though present, is indistinguishable from background change at any particular point in time. Does this mean that climate "flickers" were less pronounced or absent in the tropics, that vegetation response to flickers was muted, or that the records obtained to date cannot resolve the response (e.g., taxonomically)? There will be no hard answer to these questions until new data are literally dredged up from the lakes of the tropics. For now, ecologists can only be concerned that fragmentation may be a serious constraint relative to amplitudes of even background change in these complex systems.

Addressing all of the challenges discussed here will be complicated by the massive uncertainty in climate models about the magnitude and even sign of possible precipitation changes (IPCC, 2001). While there is much greater agreement about warming, consensus on precipitation change, which is critical in determining water balance, remains elusive. Water balance may be a more critical limiting factor than temperature for both tropical moist and tropical dry forests (Pacheco, 2001). Until the uncertainties associated with precipitation projections are reduced, it may be difficult to assess possible impacts on tropical forest and appropriate conservation responses.

16.3 CONSERVATION RESPONSES

The regional feedback between tropical forests and climate is one of the conservation challenges most specific to tropical forests. The effect is expected to be greater for tropical moist forest than for tropical dry forest (Pitman *et al.*, 2000) and greater for the tropics in general than for temperate areas (Woodwell *et al.*, 1998), although the effect can play very important roles in higher latitudes as well (Pielke, 2001).

The spatial dependence of the forest–rainfall effect has been tested in the Atlantic Forest of Brazil (Webb *et al.*, 2005). In that study the relationship between forest cover and rainfall was found to be greatest at large spatial scales. The authors compared the scale of the forest–rainfall effect with areas needed to conserve mammals with large-range sizes, concluding that both area-demanding species and the forest–rainfall relationship required large reserves.

Perhaps the ultimate forest–rainfall system is the Amazon Basin. Here rainfall in the east is recycled many times through the forests of the basin, and, in fact, much of western Amazonia might not be moist forest without the rainfall generated (Betts *et al.*, 2004). Bush (1996) has suggested that preserving this moisture-recycling is probably more critical in setting conservation goals for the Amazon than are species-based concerns. Bush's suggestion is supported by the results of Webb *et al.* (2005) in the Atlantic Forest, a system with much less pronounced moisture-recycling than the Amazon. If the Amazon has a stronger forest–rainfall effect, it seems likely that the correlation between rainfall effect and scale will be even stronger, requiring even larger reserves.

The type of reserve needed to maintain forest cover may be very different from that needed for conservation of biodiversity, however. It is forest cover and physical properties that are important in the forest–rainfall effect, rather than functioning native ecosystems, so multiple-purpose reserves or even some types of plantation tree cover may be effective in maintaining moisture-recycling. At the same time, native ecosystems provide many other benefits to human society and biodiversity conservation, so the moisture-recycling properties of forest cover provide an additional strong reason for large protected areas in the Amazon. Indigenous reserves, multiple-use forest reserves and nature reserves may all depend one on the other for sufficient forest cover to maintain moisture-recycling in the basin and the future of the region's forests.

Our limited knowledge of the paleoecology of the tropics suggests that research is a critical component of conservation of tropical forest systems. Paleoecological pictures of Asian, African, and South American forests have emerged over the past 30 years (Maley, 1996; Flenley, 1998; Colinvaux and De, 2001). Yet many chapters remain to be written. Quantum improvements in spatial, taxonomic, and temporal resolution are all possible for most regions of the tropics. Some of the most celebrated of tropical forests, such as the Amazon, are among those about which the least is understood concerning past responses to climate change. The lesson for conservation is to recognize, and be open to, major research advances that will require rethinking and readjustment of conservation strategies.

The unprecedented speed and magnitude of coming change is an issue that is not unique to the tropics. Indeed, dramatic changes in the high latitudes in the early part of this century may overshadow or obscure huge tropical changes. The complexity of tropical forests and lower magnitude of change (at least in warming) will serve to make the tropical changes less obvious and slower to be documented, yet the sum impact on biodiversity as measured by species extinction may in the long run be much greater.

The recently documented amphibian extinctions in tropical forests of South America belie the idea that tropical extinctions will be slower or less dramatic. In these extinctions, synergy between climate change and chytrid fungal disease has resulted in a dramatic spate of extinctions that would not be predicted based on models of range shifts with warming. If such synergistic, threshold-linked extinctions turn out to be common, the tropical impacts of rapid large climate change may outshadow high-latitude change. It is difficult to suggest conservation responses to such unexpected effects. However, now that one such wave of extinctions has been documented, it is clear that two priorities are monitoring for rapid population crashes and capacity for rapid institution of captive breeding programs where such crashes are observed.

Individualistic species response and no-analog communities present parallel challenges to conservation. Each implies lack of historic or paleoecological precedents for acquisition and management, respectively. Resilience has been suggested as a principle to guide both acquisition and management, and for coral reef communities there is emerging evidence that properties associated with resilience can be defined (Salm *et al.*, 2001). However, in the more physically and biologically complex tropical forest systems, properties that may convey resilience may prove more elusive. It is far from clear that resilient forests would be the most diverse, suggesting a possible loss of biodiversity to attain resilience. Nonetheless, one principle that is clear is that removing current stressors is good for forests now and maintains biodiversity, at the same time that it makes forests more resilient to climate change (Hansen *et al.*, 2005). The resources for even this first step are far from secured, as will be discussed below.

Responding to dynamics in fragmented landscapes depends heavily on regional context and the relative scale of the two phenomena. The scale of the minimum dynamic unit in the Amazon may be nearly the entire basin owing to moisture-recycling, while in Central African forests—where moisture-recycling is less pronounced—the minimum dynamic unit may be much smaller and defined by the area demands of large species, rather than by the forest–rainfall effect. The only answer from a conservation viewpoint is to be aware of these effects and craft conservation strategies which incorporate careful consideration of scale and process. There is no substitute for intelligent design.

Uncertainty will continue to be high in impact assessments of climate change on biodiversity, yet we have done so little in our conservation strategies to get ready for climate change that there are many steps that can be taken with certainty. The following section describes some of the conservation strategies that can be employed to take these early steps.

16.4 CONSERVATION STRATEGIES

Conservation responses to climate change are drawn from the existing mainstays of conservation strategies—protected areas, conservation in multiple-use lands, connectivity between conservation areas—with new emphases and drawing on new elements necessary to respond to the challenges of a dynamic climate. In this section we will discuss these new and existing tools, and outline their application to the conservation challenges identified above.

Perhaps the greatest impediment to sound conservation in the face of climate change is the fact that present conservation systems are incomplete. The current global network of protected areas does not represent all species and is vastly underfunded, particularly in the tropics (James and Green, 1999; Rodrigues *et al.*, 2004). Responding to climate change would be a great challenge even in the presence of a comprehensive and well-funded system of parks and conservation measures. The problem of dealing with climate change is magnified when species range dynamics, alterations in phenology, and other changes must be addressed at the same time as completing species representation and meeting basic conservation management needs. Worse, the actions needed to confront the climate change challenge must compete for resources with these other, fundamental and often more urgent needs.

Therefore, completing representation of protected areas and adequate funding for basic management of parks and other conservation measures is the number one priority for addressing climate change. The representation and funding deficiencies are greatest in tropical forests. Over 1,400 species are under-represented in current protected areas considering vertebrates alone, virtually all of which are in the tropics (Rodrigues *et al.*, 2004). The global shortfall in protected area funding alone is estimated at $1.5 billion annually, with the majority of the shortfall occurring in the tropics (James and Green, 1999).

Connectivity between conservation areas is much less well-developed than the protected areas network, and is often presumed to be crucial in responses to climate change (Hannah *et al.*, 2002b). In principle, connectivity is an advantage as climate change dynamics become more pronounced. Not all connectivity is equally good for climate change response, however. Connecting forests along spines of mountain chains or ridgetops may not be as effective as connecting lowlands and uplands. Species will move upslope with warming, so connecting ridgetop forests has relatively less benefit than connecting lowlands and uplands. Similarly, a unit of connectivity in lowlands may be less relevant in climate change strategies than a unit of connectivity in uplands. This is because lowland species experience range shifts over relatively great distances as climate changes, while montane species are more numerous and experience range adjustments on smaller scales. Montane connectivity may therefore be more effective in species conservation on a per-unit basis. Thus, not all connectivity is equal from the perspective of climate change, and large investments in connectivity in the name of climate change should be qualitatively and quantitatively weighed against other conservation options.

For example, perhaps the most cost-effective action in a climate change conservation strategy is to invest in protected areas that harbor both species present range and their projected future ranges. Such investments offer the opportunity to improve both species current representation in protected areas and their potential future representation. In contrast to strategies to connect disjunct present and future ranges through connectivity, this approach is relatively robust to model uncertainty and it is a "no regrets" action (Williams *et al.*, 2005).

Beyond protected areas and connectivity, several new or modified conservation mechanisms will be important in dealing with climate change. These include most prominently vertical and lateral coordination of conservation planning and action. Vertical coordination is needed to ensure that national, regional, and local strategies work in concert in response to climate dynamics. Lateral coordination is needed between agencies to ensure that sectoral strategies are similarly aligned. This coordination currently exists, but will require conscious and systematic development as climate change intensifies. For example, strategies to promote transitions to new vegetation types must be coordinated across regions and between management agencies to ensure consistent management strategies and outcomes.

Creatively applied, these tools can make a substantial contribution to meeting the challenges posed by climate change (Hannah *et al.*, 2002b). Protected area systems can be expanded to compensate for range shifts resulting from climate change. Corridors can be designed specifically for climate change where range translocations for multiple species are anticipated. Conservation planning can adopt longer timeframes and emphasize vertical and lateral coordination to help improve the resilience of management strategies to climate change. Each of these tools can be fit to the climate change biology of individual regions.

For instance, for Amazonian tropical forests, protected area strategies must be sized and located with both species conservation and climate maintenance in mind (Bush, 1996). The forest area required for maintaining the internal moisture-recycling of the basin may be larger than that required for representing all species. The location of the conserved forest is important for both biodiversity conservation and climate maintenance, but the optimal geographic configurations of the two may not exactly overlap. Simultaneous consideration of both biodiversity representation and climate maintenance may be important for other moist tropical forests as well. This is a politically sensitive issue. For instance, the Brazilian government has been implementing conservations units in some parts of Amazonia, that have generated reactions among soybean producers and the timber industry.

Management in the face of the uncertainties surrounding tropical forest response to climate change will require patience and adaptability. If tropical forests have not faced rapid climate flickers in the past, they may be poorly adapted to cope with rapid future change (Bush *et al.*, 2004). Yet, their physiology may be relatively robust to warming, in comparison with temperate and boreal species. By the time climate change provides a practical demonstration of which of these factors may prevail, it will be far too late to address the source cause of that change. It is therefore prudent to consider how, and at what levels, atmospheric greenhouse gases (GHGs) could be constrained.

16.5 GREENHOUSE GAS STABILIZATION

The global instrument for dealing with climate change—United Nations Framework Convention on Climate Change (UNFCCC)—is designed to avoid dangerous interference in agriculture, economies, and ecosystems (Schneider, 2001). Since coming into existence at the time of the 1992 Earth Summit, it is becoming increasingly apparent that ecosystems are the most sensitive of the three (O'Neill and Oppenheimer, 2002).

There is statistically sound evidence of responses in nature to the climate change that has already taken place: changes in flowering and nesting times, changes in distribution of birds, butterflies, and some marine organisms (Parmesan and Yohe, 2003; Root *et al.*, 2003). More disturbing is the first extinction associated with climate change (in conservation-conscious Costa Rica) and the widespread and massive bleaching of coral reefs from warmer seas added to other stresses (Walther *et al.*, 2002). Ecosystem failures—like those of corals and the 3.5 million acres of Alaskan spruce weakened by over 15 years of above-average temperature and dying from insect attack—can be considered a preview of more such events to come.

As scientists look ahead at the impacts of additional climate change on biodiversity, a consistent pattern is emerging, no matter how imperfect, of serious biological degradation and species loss. Compounding the problem of climate change *per se* are the ubiquitous human-modified landscapes that create an obstacle course to the movement of organisms and survival of species: the normal response in past climatic changes—such as the glacial–interglacial swings dominant in the recent geological past of the northern hemisphere.

The convention specifically addresses rapidity of climate change, citing the need not to exceed rates at which species can adapt naturally. Ignoring the distinct possibility that it is a mistake to assume climate change will only be gradual and never have abrupt episodes, it is nonetheless clear that some species and ecosystems will not be able to adapt above certain levels of climate change no matter how leisurely the rate of change. Ecosystems of low-lying islands will succumb to sea level rise and those on mountain tops will simply have nowhere to go at higher altitudes as it becomes too warm for them to survive where they are. Safe levels of climate change would avoid such ecosystem disruption and the associated wave of extinctions.

So what might constitute safe levels? Where we are right now is probably safe even with 0.8°C of average global warming plus whatever additional warming would take place because of the lag between increase in gases and temperature rise. But, it is impossible to stop at this level because of rates of emissions from current energy use (IPCC, 2001).

There seems to be a growing consensus that a safe level would be at carbon dioxide concentration of 450 parts per million or less (the pre-industrial level was 280 ppm; today we are at 379 ppm). That roughly translates into an average global warming of 2°C. While hard to achieve, and complicated by the need to take other greenhouse gases into account, the sooner such a target is agreed upon, the easier it is to achieve. So, somewhere between 379 and 450 ppm may well be the safe zone.

This may mean more than a 2°C change for tropical forests, since change over land is higher than the global mean (because change over ocean is considerably less), and is regionally variable. Even 2°C is a very ambitious goal given the social/energy restructuring implied (Lackner, 2003). Hitting a greenhouse gas target of 450 ppm implies a total transition from fossil fuels to renewable energy in the next several decades. Given that renewables currently account for about 13% of energy consumption (and 80% of that is fuelwood use that may not be sustainable as currently practiced) and increase in renewables is rising less quickly than rise in overall demand, the change required is far from incremental.

Yet, it is a change that may be of critical importance to tropical forests. Early modeling results indicate major range changes in tropical species due to future climate change (Ferreira de Siqueira and Peterson, 2003; Miles *et al.*, 2004). Other studies indicate that changes in the past may have been muted (Bush *et al.*, 2004), and there is great uncertainty about past change and no analog from the past for future magnitude and speed of changes expected in the future.

16.6 REDUCING DEFORESTATION TO HELP STABILIZE EMISSIONS

The post-Kyoto implementing mechanism for the UNFCCC is now moving towards inclusion of reduced deforestation as an important mechanism for helping reduce GHG emissions. In the Kyoto protocol, reducing deforestation was not included because it was felt that industrialized nations that had caused most of the problem should take the first steps towards emissions cuts. However, as carbon markets were established with the entering into force of Kyoto, it became clear that tropical countries were left out of potentially billions of dollars in abatement funding. A movement started under the leadership of the Papua New Guinea delegation to introduce reduced deforestation into post-Kyoto implementation.

This reduced deforestation protocol is known as Reducing Emissions from Deforestation and forest Degradation (REDD). This would allow countries that make major reductions in deforestation to qualify to sell the CO_2 equivalent of that reduction in emissions reductions carbon markets. This represents a major potential source of finance for reduction in deforestation.

Deforestation accounts of about one-fifth of current global carbon emissions. For comparison, emissions from deforestation are similar in magnitude to those for the entire transportation sector in industrialized countries.

Reducing deforestation is a large political task, but the technical requirements are well understood. It is unlikely that deforestation can be brought to zero, but large reductions at reasonable cost are highly likely and can be achieved with concomitant major benefits to biodiversity. Schemes to assess biodiversity and deforestation of alternative UNFCCC implementation rules have emerged. One such system, OSIRIS, allows the calculation of both emissions reduction and biodiversity benefit of alternative rules for calculating reduced deforestation. Rule variants include means of calculating deforestation baselines against which change is judged, and how to treat countries with historically low levels of deforestation (da Fonseca *et al*., 2007).

REDD is a major advance in funding for conservation efforts to reduce tropical deforestation. The exact rules of its implementation will have repurcussions for biodiversity and environmental justice in tropical countries. Properly designed, country-level REDD initiatives have the potential to complement and strengthen efforts to ensure conservation strategies are well-adapted to climate change. REDD also makes a critical contribution to reducing emissions, and hence the damage from climate change to tropical forest systems.

16.7 CONCLUSION

International agreements have the right targets in place to take the first, most important steps towards protecting tropical forests from climate change. The Convention on Biological Diversity (CBD) has targeted a measurable reduction in global biodiversity loss, which implies completion of the global protected areas network, its adequate funding, and significant reduction of destructive practices outside of protected areas. The Kyoto Protocol of the UNFCCC is now in place, which sets a framework for international cooperation in emission reduction. The UNFCCC itself targets avoiding climate change that would impair ecosystems' ability to adapt naturally. Even though this formulation is technically awkward, its intent is clear.

But, reality clashes very strongly with these goals—in tropical forests and many other systems: habitat loss continues; evidence is mounting that climate change is compounding the damage of habitat loss; and some systems may already be past natural ability to adapt (corals). What can biologists do? In tropical forests we can work to understand critical clues to the possible future effects of climate change. These include better understanding of past responses, better understanding of current species distributions and ecology, and analysis and modeling of responses to future climate change. Above all, we can work to rapidly incorporate the results of that research into improved conservation strategies, and to advocate the lowest possible atmospheric greenhouse gas stabilization levels.

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