Chapter 1

Many Tropical Rain Forests

It is easy to make generalizations about tropical rain forests. Travel posters, magazine articles, and television programs give the casual observer the impression that tropical rain forests from any spot in the world are one interchangeable mass of tall, wet trees – the canopy filled with brightly colored birds, chirping tree frogs, and acrobatic monkeys, the ground level home to silent predators, tangled vines, and exotic flowers. This popular perception has been useful because it creates a compellingly attractive image of an untamed, beautiful place that is, on the one hand, a source of infinite mystery and adventure, and on the other, a fragile natural treasury that must be protected. Both conservation and ecotourism rely on this generalized image to promote the idea of tropical rain forests as a "good thing" to be preserved and enjoyed. Yet, beneficial as this image may be in encouraging travel and conservation, it obscures the fact that the world's tropical rain forests have major differences from one another in addition to their obvious similarities.

A major drawback of this generalized image is that it encourages a belief that saving "the rain forest" is a single problem with a single, universally applicable, set of answers. Nothing could be further from the truth. There are many different rain forests, all of which need action for protection, but this action must be targeted at the specific threats present in each region and adapted to the specific ecological characteristics of each rain forest. Policies, tactics, and techniques that work in one region may prove ineffective in another. The major differences between the tropical rain forests in different regions also mean that successes in one region will not compensate for losses in another. The task we are faced with is not "saving *the* rain forest," but "saving the *many* rain forests."

Scientists also have usually emphasized the common appearance of rain forests on different continents and highlighted examples of similar-looking species in separate regions of the world. This emphasis on the common features of rain forests worldwide has had the unintended effect of discouraging research that makes comparisons between regions. The assumption that all rain forests are alike has also led to a tendency to fill gaps in the scientific understanding of one rain forest region by reference to studies in other regions. This tendency

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Tropical Rain Forests: An Ecological and Biogeographical Comparison, Second edition.

Fig. 1.1 The current global distribution of lowland tropical rain forests. (Courtesy of UNEP World Conservation Monitoring Centre, 2004.)

in turn gives the false impression that our understanding of rain forests is greater than it really is, so that scientific research that could fill the gaps is given a low priority. It also implies that differences between regions are minor, at least in comparison with the similarities.

Our principal reason for writing this book is that we do not believe that the differences between rain forests are minor. It is our contention that the various rain forest regions are sufficiently distinct from one another that they merit individual consideration. In this book, therefore, we will compare the major rain forest regions of the world. The three largest of these rain forest regions are in the Amazon basin of South America, in the Congo River basin of Central Africa, and on the everwet peninsula and islands of Southeast Asia (Fig. 1.1). There are also two smaller and very distinctive rain forest regions on the giant islands of Madagascar and New Guinea. We will show that the rain forests of these five regions are unique biogeographical and ecological entities, each with many distinctive plants, animals, and ecological interactions that are not found in the other regions.

Rain forests occur outside of these core areas as well, but they are less extensive in area and usually less diverse in species. There are rain forests in Central America and coastal Brazil that are basically similar in species composition to those found in the Amazon, but have fewer species and occupy a much smaller area. Similarly, the rain forests of Sri Lanka and the Western Ghats of India resemble those of Southeast Asia, and Australian rain forests have many similarities to the more extensive and diverse forests of New Guinea. Each of these many areas has numerous noteworthy features and unique species, which we will mention in this book, but the focus will be on the differences among the five main regions. In addition, there are also small but distinctive areas of rain forest on many tropical oceanic islands, which are the subject of a separate chapter.

Each rain forest region has different geographical, geological, and climatic features; each region supports plants and animals with separate evolutionary histories; and each region has experienced different past and present human impacts (Table 1.1). These differences have important implications for understanding how rain forests work and deciding how they should be exploited or conserved. Results from scientific research in one region may not apply in the others. At the end of each chapter, we suggest comparative investigations and experiments that could provide deeper insights into rain forest biology. Each rain forest area, and even local areas within each of these regions, must be viewed separately

Table 1.1
Some key characteristics of the main rain forest regions.

	Neotropics	Africa	Madagascar	Southeast Asia	New Guinea
Main geographical feature(s)	Amazon River basin and Andes Mountains	Congo River basin	Forests along eastern edge of island	Peninsula and islands on Sunda Shelf	Large, mountainous island
Distinctive biological features*	Bromeliad epiphytes, high bird diversity, small primates	Low plant richness, forest elephants, many forest browsers	Lemurs, low fruit abundance	Dipterocarp tree family, mast fruiting of trees, large primates	Marsupial mammals, birds of paradise
Annual rainfall (mm)†	2000–3000	1500–2500	2000–3000	2000–3000, often > 3000	2000–3000, often > 3000
Largest country	Brazil	Democratic Republic of Congo	Malagasy Republic	Indonesia	Papua New Guinea

* Unfamiliar terms are explained in the text.
† Rainfall is highly variable within each region. These are the ranges over most of the core rain forest area (1000 mm equals 40 inches).

when scientific investigation, conservation efforts, and responsible development are undertaken. The issues of human impacts, conservation, and development will be considered in detail in the final chapter.

What are tropical rain forests?

Tropical rain forests are the tall, dense, evergreen forests that form the natural vegetation cover of the wet tropics, where the climate is always hot and the dry season is short or absent. This broad definition allows for a considerable range of variation, as is necessary for any global comparison. One important variable is the proportion of deciduous trees in the forest canopy. We have excluded the predominantly deciduous tropical forests that occur in areas with a long dry season, but many forests that we and others call rain forest have some deciduous trees in the canopy. Where this proportion is large, the forests can be called semievergreen (or semideciduous) rain forest. Another important distinction is between lowland and montane rain forests. On high mountains in the wet tropics, forests extend from sea level to around 4000 m (13,000 feet), but the typical tall, lowland rain forest is confined below an altitude of 900–1200 m. Rain forests above this altitude are termed "montane" and have a distinctive ecology of their own.

Precise definitions are difficult in ecology, and there are large areas of forest in the tropics that some ecologists call rain forest while others do not. Definitions also differ between regions, with less strict, more inclusive, definitions in areas where rain forests are less extensive. Thus, on the very dry continent of Australia, almost any area of closed forest is called rain forest. Conversely, foresters familiar with the everwet rain forests of equatorial Southeast Asia might exclude much of what their African counterparts call rain forest. In this book, we focus on hot, wet, tall, and largely evergreen tropical rain forests and we have made it clear when we are referring to unusual or marginal types.

Where are the tropical rain forests?

On a simpler planet, tropical rain forests would form a broad belt around the equator, extending 5–10° to the north and south. On our untidy Earth, interactions between wind direction and mountain ranges, variations in sea surface temperature, and various other factors exclude rain forest from parts of this belt – notably most of East Africa – and, in other places, extend it for some distance outside (Fig. 1.1). At least, that was the situation until very recently. During the last few hundred years, and particularly in the last few decades, between one-third to one-half of this rain forest has been converted into other land uses, ranging from productive farmland or tree plantations to urban areas or unproductive grasslands. This book is mostly about the rain forests that still survive, but the devastating effects of human impacts are considered in the last chapter.

The Neotropics

Approximately half of the world's tropical rain forests are in tropical America, the region that biologists call the Neotropics (literally "new tropics" or New World tropics). The Neotropical rain forests form three main blocks. The single largest block of tropical rain forest in the world covers the adjoining basins of the Amazon and Orinoco Rivers (Fig. 1.2). The Amazon River basin is centered on northern and central Brazil. It stretches more than 3000 km (2000 miles) from the foothills of the Andes Mountains in western South America, across the entire South American continent, until the Amazon empties into the Atlantic Ocean. The Orinoco River basin drains eastern Colombia and Venezuela and adjoins the Amazon basin along the Brazilian border. This rain forest block also continues to the northeast of Brazil into the countries of Guyana, Surinam, and French Guiana.

In addition to this giant block of rain forest centered on the Amazon basin, there were two other major blocks of tropical rain forest in the Americas. The Brazilian Atlantic Forest ran along the southeast coast of Brazil from Recife south to São Paulo. This narrow band of forest was over 2000 km long and covered an area of 1.5 million square kilometers, although by no means all of that was rain forest. It was separated from the Amazon forest block by hundreds of kilometers of dry scrub and savanna. This forest has now been reduced to 11–16% of its original area, with most of what remains existing as small, widely separated, fragments (Ribeiro et al. 2009). A third block extended from the Pacific coast of northwest South America through Central America to southernmost Mexico. The rain forests of northwest South America became separated from the Amazon basin rain forest by the uplift of the Andes beginning around 25 million years ago, and then became continuous with those of Central America when the final marine barrier between them disappeared 3 million years ago (see below). Only fragments of this rain forest block survive today. There

Fig. 1.2 The estimated historical extent of tropical rain forest in South and Central America. (From multiple sources.)

were also smaller areas of rain forest on many of the Caribbean islands, where very little now remains.

Africa

The second largest block of tropical rain forest is in Africa, centered on the Congo River basin (Fig. 1.3). About half of this rain forest is in the Democratic Republic of the Congo (formerly Zaire), with most of the rest divided between the Republic of the Congo, Gabon, and Cameroon. This Central African rain forest block formerly extended northwest into southern Nigeria, but little of this now remains. Rain forest also extended until recently as a belt, up to 350 km (200 miles) wide, along the coast of West Africa, from Ghana through Côte D'Ivoire (Ivory Coast) and Liberia to the eastern margin of Sierra Leone. Most of this has now gone and the remaining fragments are under threat. The larger Central and smaller West African rain forest blocks were separated by 300 km of dry woodland and savanna at the Dahomey Gap, in Togo, Benin, and eastern Ghana. There are also outlying "islands" of rain forest in East Africa, mostly centered on mountains, and surrounded by a "sea" of dry woodland. Although the total area of these East African rain forest patches is small – approximately 3,500 km^2 – some of them, on older mountains, are apparently of great age and have been isolated from the forests of West and Central Africa for millions of years (Burgess et al. 2007). On a longer timescale, all the rain forests of modern Africa can be seen as remnants of the much more extensive rain forest that spanned the entire continent until around 30 million years ago (Plana 2004).

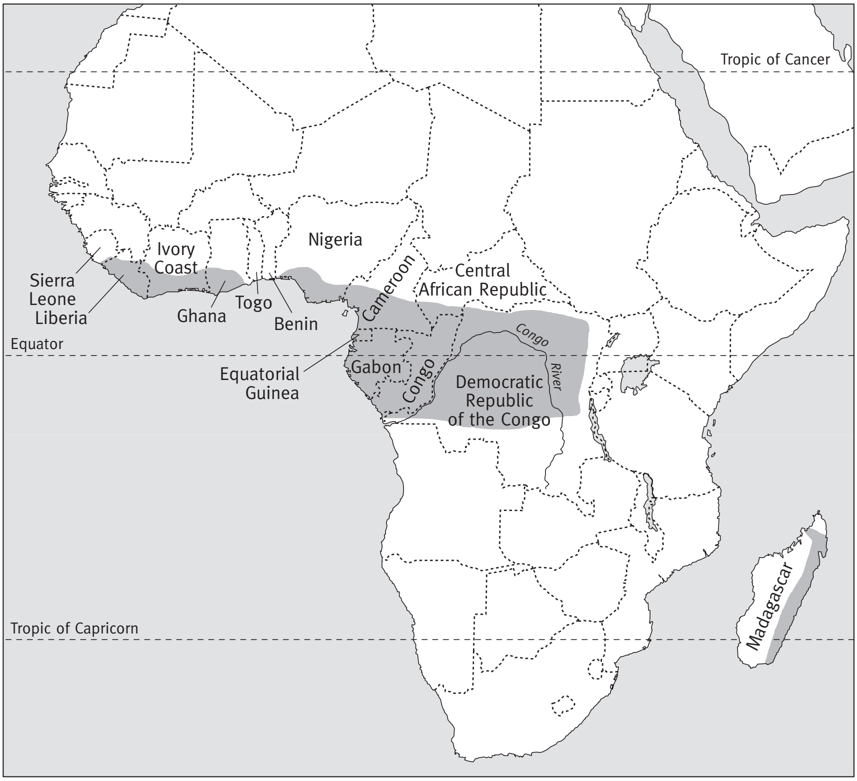


Fig. 1.3 The estimated historical extent of tropical rain forest in Africa and Madagascar. (From multiple sources.)

Asia

The third largest rain forest area until recently occupied most of the Malay Peninsula and the large islands of Borneo, Sumatra, and Java (Fig. 1.4). Ecologists call this region "Sundaland," after the surrounding Sunda continental shelf, and we will follow the convention in this book. Despite the large expanses of sea between the major islands, the Sundaland rain forests are surprisingly uniform and can be considered as a single block. Similar forests also covered much of the Philippines, as well as Sulawesi and many of the smaller Indonesian islands east of Borneo. Rain forest also extended north from Sundaland into the more seasonal climates of mainland Southeast Asia, including most of Cambodia, Laos, and Vietnam, and much of Thailand and Myanmar (formerly Burma). However, large areas in the interior of Myanmar and Thailand did not support rain forest as a result of rainshadows caused by several long north–south mountain chains. Rain forest also once covered much of tropical southern China, in a mosaic with drier forest types, east to the southern tip of Taiwan. To the north, this tropical rain forest merged gradually into the subtropical and warm temperate forests (Corlett 2009a). Today a billion people inhabit the East Asian tropics, so it is not

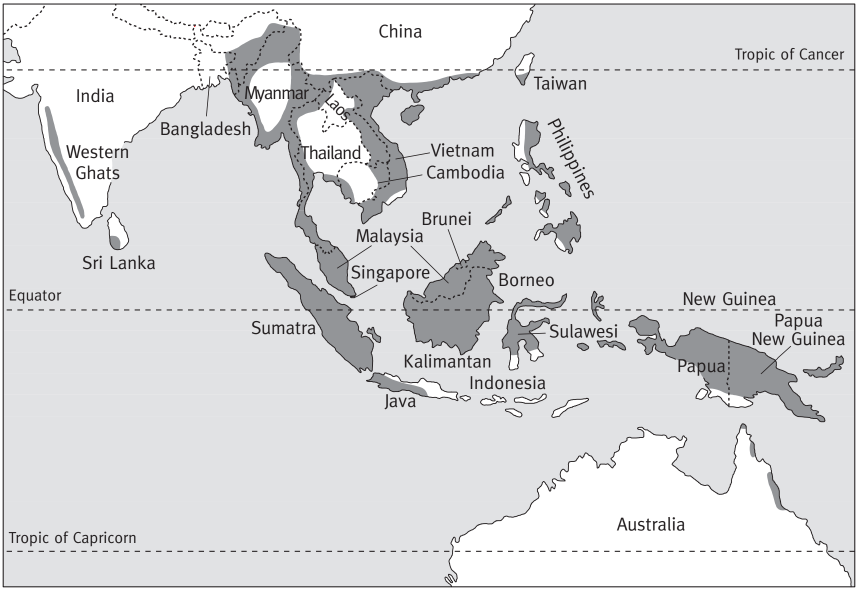


Fig. 1.4 The estimated historical extent of tropical rain forest in Asia, New Guinea, and Australia. (From multiple sources.)

surprising that rain forest has already been eliminated from much of the region and is under threat almost everywhere where it still survives.

The rain forests of Southeast Asia extend westward through Myanmar into northeastern India. India also had a completely separate rain forest area as a long narrow strip, 50–100 km wide, running parallel to the west coast for 1500 km along the crest of the Western Ghats. This now fragmented rain forest band occurs on the tops and sides of these hills, where sea mists can drench the plants even during the dry season. Apart from this isolated ridge, the remainder of India south of the Himalayas is too dry to support rain forest. Just across the Palk Strait lies the island of Sri Lanka. Formerly much of the southwest of the island supported rain forest, but now only small fragments remain.

New Guinea and Australia

The fourth largest block of rain forest covers most of the large island of New Guinea, except for the dry southern and eastern margins, and the highest mountain peaks (Fig. 1.4). Although biologically uniform, the island is divided politically into two halves: the western half forms the Indonesian province of Papua and the eastern half is the independent country of Papua New Guinea. The neighboring and largely dry continent of Australia also supports a small area of rain forest in the northeast. The largest block of rain forest occurs along the coast between Cooktown and Townsville, but there are also numerous smaller patches.

Fig. 1.5 Reconstruction of an early Miocene (~20 million years old) rain forest community from the Riversleigh World Heritage site in northwestern Queensland, Australia. (By artist Dorothy Dunphy from the book *Riversleigh* by Michael Archer, Suzanne J. Hand, and Henk Godthelp; Reed, Chatswood NSW, 1994.) The site supported a far wider range of marsupial forms than inhabit Australia's rain forests today, including marsupial lions, carnivorous kangaroos, and browsing cow-sized diprotodontids.

Australia's tiny rain forest area has many similarities to the much more extensive rain forests of New Guinea – similarities that were even greater in the recent past (Hocknull et al. 2007) – but also many differences, including several distinctive endemic plant genera. These differences reflect the very different histories of the two regions, despite their proximity and intermittent contacts. Rain forest covered much of northern Australia during the early to middle Miocene (23 to 15 million years ago) (Fig. 1.5), but has become restricted to the north-east because of the subsequent drying of the continent (Long et al. 2002). Most of the rain forest in New Guinea, by contrast, occupies land that was uplifted above sea level only in the last 10–15 million years, making this the youngest of the major rain forest blocks.

Madagascar

The final major area of rain forest is on the island of Madagascar (now the Malagasy Republic) (see Fig. 1.3). Although Madagascar has about two-thirds the land area of New Guinea, most of the island is very dry, and rain forest was confined to a 120 km (75 miles) wide band along the eastern edge. Humans first arrived in Madagascar around 2000–2500 years ago, resulting in mass extinctions among the larger and more vulnerable vertebrates (Burney et al. 2003). Rain forests seem to have been the last habitat to be settled by humans, but most of the rain forest band has now been cleared, and what remains is fragmented and in many places highly degraded.

Rain forest environments

Rainfall

The very name "tropical rain forest" suggests a steamy jungle that is unfailingly hot and wet, every day of the year. In reality, there is no place on Earth where it rains every day, and rain forests are found in a surprisingly wide range of climates. In the tropical lowlands, these forests grow on almost all soil types where the annual rainfall is well distributed and greater than about 1800 mm (70 inches). Mean annual rainfall can be as low as 1500 mm on sites with soils that can hold water well or where dry-season water stress is moderated by cloud or low temperatures. At the other extreme, the mean annual rainfall is greater than 10,000 mm (33 feet!) at Cherrapunji in northeast India, Ureka in Equatorial Guinea, and in parts of the Chocó region of western Colombia.

To a first approximation, the amount and timing of rainfall in the tropics is controlled by the seasonal movements of the Intertropical Convergence Zone (ITCZ) – a band of low pressure, cloudiness, and rainfall that migrates north and south a month or two behind the overhead sun. The ITCZ results from rising warm air masses over regions where the sun is most directly overhead at midday. In this simple model the equatorial region is continuously influenced by the proximity of the ITCZ, so it is wet all year, with two rainfall peaks, a month or so after the equinoxes. Away from the equator, rainfall is concentrated in the periods when the ITCZ is present and there are dry periods when it moves away. With increasing distance from the equator, the two rainfall peaks move together and the "winter" period of low rainfall becomes longer and drier. Near the margins of the tropics, there is only one, relatively short, wet season, and a long, rainless dry season.

This simple model works fairly well over the oceans, but many factors introduce complications over land. While all rainfall results from upward movements of moist air, surface heating by the overhead sun is by no means the only mechanism that can cause this. The most important disruptions to the general pattern described above occur when moist air is forced to rise over a mountain range, producing rainfall on the windward slopes. Where mountains face a sustained flow of moist air throughout the year, this effect can produce an everwet climate well away from the equator. This explains the presence of rain forest in eastern Madagascar, at latitudes where we might expect a seasonally dry climate. Other examples of high rainfall resulting from such “orographic” uplift include parts of the Caribbean coast of Central America, eastern Brazil, West Africa, the west coast of India, coastal Queensland, and many tropical islands. There are also anomalies in the opposite direction: dry climates at latitudes we expect to be wet. The most striking interruption to the equatorial belt of rain forest climates is in East Africa, where a combination of relatively dry monsoon air flows and large latitudinal movements of the ITCZ makes most of the region too dry for rain forest. Cold ocean currents produce anomalously dry climates in western Ecuador, while other dry areas are in the lee of mountain ranges. As a result of these and other factors, the overall patterns of rainfall and rainfall seasonality in the tropics can be very complex.

All the major rain forest regions have relatively dry and relatively wet areas, but the amount of rainfall in the most extensive forest type varies between regions (Fig. 1.6). In general, the wettest rain forests are those of equatorial Southeast Asia, centered on the core Sundaland region of western Indonesia and Malaysia, and those on the island of New Guinea. In both these regions, the mean annual rainfall exceeds 3000 mm over large areas. In contrast, most Madagascan and American rain forest receives 2000–3000 mm, although there are wetter areas receiving 3000 mm or more in the upper Amazon basin, western Colombia, and the eastern slopes of Central America. The Atlantic Coastal Forest of Brazil is mostly somewhat drier, with less than 2000 mm of rain. Most African rain forests are distinctly drier than rain forests elsewhere, with an annual rainfall of only 1500–2000 mm, except in narrow fringes along the coast where the rainfall can exceed 4000 mm. Within particular regions, there is often considerable variation in rainfall, determined by distance from the coast, elevation, land use patterns, and other climatic factors. For example, in the Amazon River basin, rainfall varies from less than 1200 mm per year to over 6400 mm, with higher rainfall along the coast and in the northwestern edge of the basin.

Even in regions with very high total rainfall, most rain forests experience some dry months, when the water lost by evaporation and transpiration – around 100 mm per month – is greater than the amount of rain that falls. In tropical Asia outside the everwet Sundaland core, in almost all African rain forests, and in most of those in tropical America, there is an annual dry season lasting 1–4 months. This dry season is harsher in tropical America and continental Asia, where it is usually accompanied by cloudless skies, than in much of the African rain forest, where the rainless months are often misty and overcast (McGregor & Nieuwolt 1998). The predictable rainfall seasonality in these forests is reflected in all aspects of their biology, with more or less regular annual peaks in leafing, flowering, fruiting, and animal reproduction.

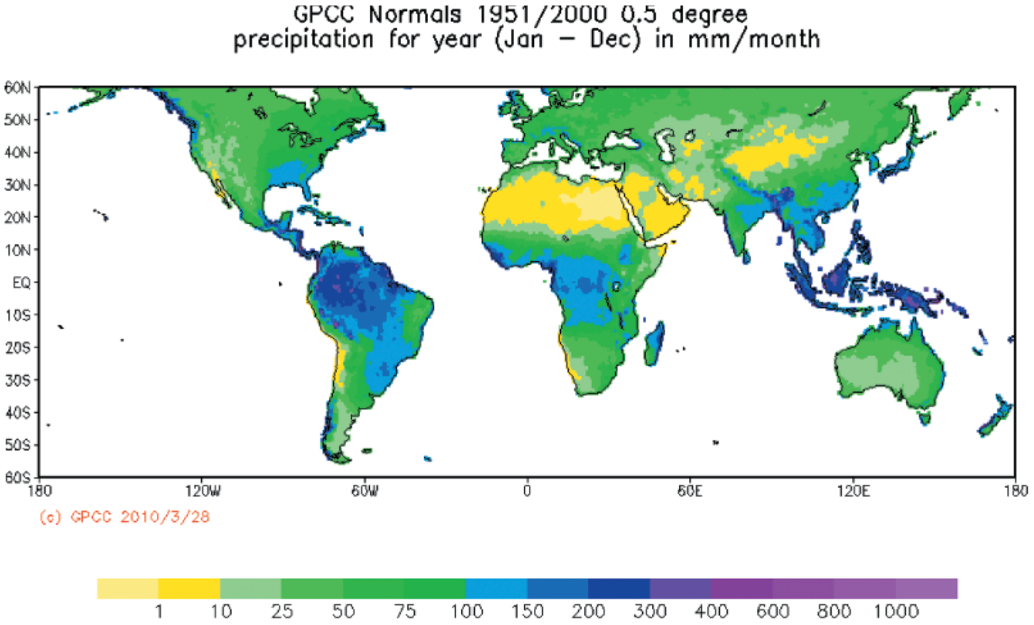


Fig. 1.6 Worldwide distribution of rainfall over land (1951–2000). The scale is in mm/month. (Global Precipitation Climatology Centre.)

In striking contrast to the typical African or American rain forest, there are large areas of Sundaland and on the island of New Guinea where there is no regular dry season, and the mean rainfall for every month is over 100 mm. In some places, dry months are very rare, and longer dry periods are unknown. In most Sundaland rain forests, however, dry periods occur every few years, with important consequences for their biology. These forests show what can only be described as "multiyear seasonality." Just as the fall in temperate zones brings on specific biological changes, such as leaf-dropping by deciduous trees and hibernation in some mammals, these less frequent events in Sundaland rain forests trigger dramatic biological changes, including mass flowering of many tree species, increased reproduction in many animal species, and large-scale migrations in others (see Chapters 2–7). The relative unpredictability of food availability in these forests has been used to explain many of their ecological characteristics.

In Borneo and the eastern side of the Malay Peninsula, these dry periods are associated with the El Niño–Southern Oscillation cycle (ENSO). The term El Niño means "Christ child" and was originally used by Peruvian fishermen to describe the warm current appearing off the western coast of Peru around Christmas time. Today, El Niño refers to the warm phase of a naturally occurring sea surface temperature oscillation in the tropical Pacific Ocean. The El Niño cycle is associated with the Southern Oscillation – a seesaw shift in surface air pressure between Darwin, Australia, and the Pacific island of Tahiti. Hence, the name El Niño–Southern Oscillation or ENSO cycle for this complex coupled cycle in the ocean–atmospheric system. There are three phases in the cycle: (i) a normal

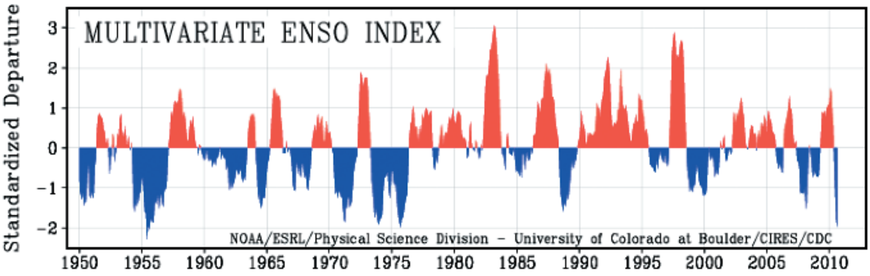


Fig. 1.7 Graph of the Multivariate ENSO Index (MEI) developed at NOAA: positive values represent El Niño events and negative values La Niña events. (From the NOAA MEI website.)

or neutral phase; (ii) the El Niño phase with unusually warm sea surface temperatures in the tropical Pacific; and (iii) the opposite La Niña ("little girl") phase with unusually cold sea surface temperatures. La Niña events occur after some, but not all, El Niños.

El Niño events generally occur at intervals of 2–8 years, although their intensity varies greatly (Fig. 1.7). The strongest recent events – and probably the strongest for the last century – were in 1982–3 and 1997–98, while there were weaker events in 1986–7, 1991–2, 1993, 1994, 2002–3, 2004–5, 2006–7, and 2009–10. A strong El Niño brings low rainfall to large areas of Indonesia and Malaysia, and coincides with mass flowering, then synchronized fruiting, by most individuals of the dominant tree family, the dipterocarps (Dipterocarpaceae), across huge areas (see Chapter 2 for more details). Many nondipterocarps flower and fruit at the same time so, for a few weeks only, the usually green and monotonous rain forest experiences a burst of colorful reproductive activity. The superabundance of flowers and fruits, in turn, leads to an inflow of nomadic animals, including giant honeybees, parakeets, and bearded pigs, and a burst of reproduction in the resident animal species.

Strong El Niño episodes lead to dry periods of increased severity in most other rain forests as well, including those of New Guinea, Africa, Central America, and Amazonia. However, the impact of these extreme events on the forest seems to be much greater in the Sundaland rain forests, which lack a regular dry season, than in forests that are adapted to an annual shortage of water. At Lambir in Sarawak, the long-term average rainfall of the driest month is 168 mm, which is not low enough to cause any water stress. During the exceptional El Niño-associated drought of 1998, in contrast, the total for the 3 months from January to March was only 139 mm, resulting in extensive leaf loss and a large increase in tree mortality (Potts 2003). The same El Niño episode in central Amazonia merely intensified the annual dry season, causing wilting and leaf fall but only a modest increase in tree mortality (Williamson et al. 2000).

El Niño episodes in the Neotropics also increase fruit production, but there is no equivalent of the mass, synchronized fruiting at multiyear intervals seen in the Sundaland rain forests. High fruit production during El Niño episodes on Barro Colorado Island, Panama, is followed by low fruit production in the wet, cloudy years that often follow, leading to increased mortality among primates and other fruit-eating animals (Wright et al. 1999). The same pattern occurs widely across Central and South America, leading to synchronous declines in the populations of frugivorous muriqui, spider and woolly monkeys in the year following El Niño events (Wiederholt & Post 2010). This Neotropical pattern of a regular fruit supply, with famines at multiyear intervals, is in striking contrast to the situation in the rain forests of Sundaland, where fruit famines are the normal situation and feasts occur at multiyear intervals. We will see in later chapters how these contrasting patterns of fruit (and flower) supply have apparently resulted in contrasting adaptations in the animals of these forests.

Before all differences between rain forests are attributed to the varying effects of the ENSO cycle, a note of caution is necessary. Reliable historical records of El Niño episodes go back only a century or so, but a variety of indirect sources of information suggest that both the frequency and intensity of El Niño events has varied considerably on timescales ranging from thousands to millions of years (Abram et al. 2007; Bush 2007). This raises the interesting possibility that the ENSO-associated patterns of plant and animal reproduction that can be observed today, particularly in the Sundaland rain forests, are not necessarily typical of even the last ten thousand years. Variability on longer timescales is likely to be even greater, so it is unlikely that plant and animal responses to the ENSO cycle are as finely tuned as they sometimes appear to be.

Temperature

Wetness is only half of the tropical rain forest equation: the other half is warmth. Typical equatorial lowland rain forests have a mean annual temperature of 25–26°C (77°F) and very little seasonal variation. At Danum in Sabah, Malaysia, for instance, the difference between the highest daytime temperature and the lowest nighttime temperature is 8–9°C (14–16°F), but the difference between the average temperature of the hottest and coolest months is less than 2°C (36°F) (Walsh & Newbery 1999). Even near the equator, however, brief incursions of cold air cause surprisingly low minimum temperatures in some rain forest areas. In the upper Amazon basin, cold air from temperate South America moves northwards along the Andes and can bring temperatures as low as 11°C to Iquitos, just north of the equator (Walsh 1996). Even lower minimum temperatures (8°C) have been recorded in the lowland rain forest at Cocha Cashu, in Manu National Park, Peru, 12° south of the equator. Annual temperature ranges increase with distance from the equator because of reduced solar radiation in winter, as well as an increased impact of these “cold waves,” known as “friagems” in Brazil. Near the southern margins of the tropical rain forest in South America and Australia, and the northern margins in Asia, frosts (i.e. subzero temperatures) can occur down to sea level, resulting in selective defoliation and shoot dieback in sensitive tropical plant species.

Nevertheless, the latitudinal limits of tropical rain forest are, in most places, set by drought rather than cold. Only in East Asia is there a continuous belt of lowland forest climates from the equator to the Arctic, without an intervening belt of climates too dry to support forest. Forests that closely resemble the typical tropical rain forests of Southeast Asia in terms of structure, floristics, and diversity extend north of the Tropic of Cancer in southwestern China, northern Myanmar, and northeast India (Corlett 2009a). The climate in southwest China is extreme for tropical rain forest, with a mean annual rainfall as low as 1500 mm and a long and very dry winter, with minimum temperatures regularly falling below 10°C (Zhu 1997). The low winter temperatures and the frequent thick fog reduce water stress, so the forest is still largely evergreen (Liu et al. 2008). An unforgettable experience for a tropical rain forest ecologist in China is to watch the fog clear on a wintry morning in Xishuangbanna, to reveal a rain forest with emergent dipterocarp trees rising to 60 m (200 feet). The dipterocarps all belong to one species – *Shorea wantianshuea* (*Parashorea chinensis*) – in contrast to the dozens of coexisting dipterocarp species in Bornean rain forests, but the whole appearance of the forest is distinctly tropical.

Temperatures also decline with increasing altitude above sea level, but in this case there is no associated increase in seasonality. On equatorial mountains, such as Mount Wilhelm in Papua New Guinea, the mean annual temperature at the altitudinal tree limit, at 4000 m (13,000 feet) above sea level, is only around 5°C (41°F), but there is very little seasonal variation (Hnatiuk et al. 1976). The temperature falls to near zero every night and rises above 10°C during the day: a climate that has been aptly termed "summer every day, winter every night." With increasing altitude above the lowlands, the rain forest becomes shorter, tree heights more even, the crowns and leaves smaller, rooting more shallow, and cold-intolerant plant families, such as dipterocarps and figs, progressively drop out. The direct effects of declining temperature may, however, be less important than changes in other factors, such as soil conditions, and a marked increase in soil organic matter is the most consistent environmental change at the upper limits of the lowland rain forest (Ashton 2003). The most dramatic vegetation changes often coincide with the zone of persistent cloud cover, where trunks and branches become gnarled and bryophytes – mosses and liverworts – cover all surfaces. This vegetation is often referred to as "cloud forest" or "mossy forest," although the bryophytes are mostly liverworts rather than mosses. In this book we focus our attention on lowland rain forests.

Wind

Another climatic factor with a major influence on the structure, if not the distribution, of tropical rain forest is wind. The combination of very tall trees and shallow root systems makes rain forests particularly vulnerable to strong winds. All rain forests are subject to occasional squalls of strong wind that may blow down single trees or, more rarely, fell large swathes of forest. Indeed, the ecological importance of these rare but widespread blowdown events may have been underestimated (Whitmore and Burslem 1998; Proctor et al. 2001). The most dramatic effects of wind, however, are in the rain forest areas subject to tropical cyclones (Fig. 1.8). Such cyclones are absent from the region approximately 10° either side of the equator that contains most tropical rain forest, but these storms affect with varying frequency the rain forests of the Caribbean, much of Central America, Madagascar, northern Southeast Asia (particularly the northern Philippines), northeastern Australia, and many oceanic islands. Sustained wind speeds during a major cyclone can exceed 70 m per second (150 mph), with brief gusts of much higher speeds.

The short-term impact of a single, severe, hurricane-strength cyclone is dramatic, with a large proportion of canopy trees uprooted or snapped off in the

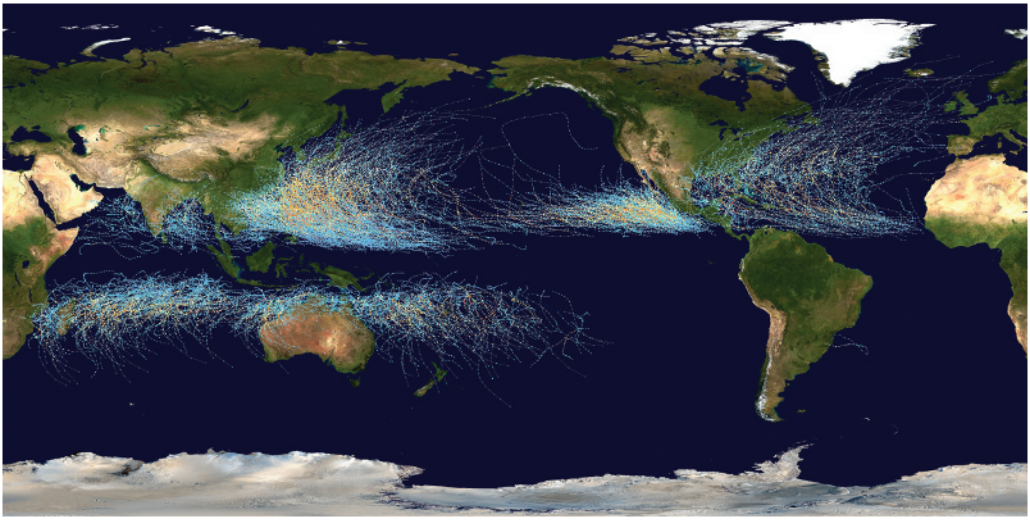


Fig 1.8 The tracks of all tropical cyclones from 1985 to 2005. Image created by Nilfanion, Wikimedia Commons (http://commons.wikimedia.org/wiki/File:Global_tropical_cyclone_tracks-edit2.jpg).

worst affected areas and almost complete defoliation in less damaged areas (Lugo 2008). Most of these damaged and defoliated trees will soon put out a new crop of leaves. However, "super cyclones" of extreme intensity occur at longer intervals in some regions, and may kill trees over a large area. In the longer term, repeated cyclone damage may allow an increased proportion of light-demanding tree species to persist in the forest. In areas with a very high frequency of cyclones, such as the islands of Mauritius and Fiji, and parts of Queensland, a distinct "cyclone forest" may develop. Such a forest is dominated by short-lived, rapidly reproducing, light-demanding species that are either less easily damaged by strong winds or able to complete their life cycle between successive hurricanes. Thus, the impact of a single cyclone will depend not only on its severity but also on the time since the previous one. Even rare cyclones eliminate the advantages for a tree of being taller than its neighbors, so rain forests in the cyclone belt tend to be relatively short (de Gouvenain & Silander 2003; Keppel et al. 2010).

Sunlight

In the equatorial region the sun is high in the sky throughout the year, but cloudiness and the high water vapor content of the air greatly reduce the amount of solar radiation reaching the forest canopy. A perhaps surprising consequence of this is that the availability of light – rather than water, temperature, or soil nutrients – can limit plant growth at certain times of the year. This was neatly demonstrated by installing high-intensity lamps above a canopy tree species, *Luehea seemannii*, in semievergreen rain forest in Panama (Graham et al. 2003). Trees given extra lighting during the cloudiest periods of the wet season grew more than those receiving only natural light. Light availability in the rain forest canopy is known to vary between sites, between seasons, and between phases of the ENSO cycle, but the potential consequences of this variation have not yet been investigated. It has been suggested, for instance, that above-average light intensities during El Niño events, as a result of reduced cloud cover, may be at least partly responsible for the enhanced fruit production observed in many rain forests (Wright and Calderón 2006).

Soils

There is an increasing amount of evidence that soil factors control plant distributions in tropical rain forests on both local and regional scales. Soil characteristics can also strongly influence plant biomass and, indirectly, animal biomass (Meiri et al. 2008). Exactly which soil factors are most important is still not certain, however, since soil texture, drainage, nutrients, and surface topography are all usually correlated and few studies in lowland rain forests have looked at the full range of possible factors.

Soil properties depend, in part, on the nature of the geological substrate from which they are formed. Over time, however, soil depth increases and the weatherable minerals in the soil are lost, leaving only quartz and clays. Those soil nutrients that were derived from weathering of the parent rock are either leached out of the soil (calcium, magnesium, potassium) or, in the case of phosphorus, form insoluble compounds that are unavailable to plants. High temperatures and rainfall in the humid tropics speed up these processes, but even then it can take several million years before the final stages are reached (Hedin et al. 2003). Soils this old are found only in geologically stable areas, such as the Amazon basin, Central Africa, and those parts of tropical Asia that are furthest from the margins of tectonic plates. Elsewhere, as in much of Central America, Southeast Asia, and New Guinea, tectonic movements or volcanic eruptions reset the clock at intervals, keeping the soils relatively young (Vitousek et al. 2010). The annual influx of river-borne sediments has the same effect in the floodplains of major rivers.

Deep, old, highly leached, and weathered soils are acid and infertile, with very low levels of plant-available phosphorus, calcium, potassium, and magnesium, and high levels of potentially toxic aluminum (Nortcliff 2010). Such soils are unsuitable for most forms of permanent agriculture, yet can support tall, dense, hyperdiverse rain forests. This apparent paradox reflects the ability of undisturbed rain forests on poor soils to recycle nutrients with very little loss. Most nutrients are withdrawn before leaves are dropped and the nutrients released in the litter layer are rapidly taken up by a dense mat of roots and their associated mycorrhizal fungi. If there is no unweathered parent material left within the root zone, the inevitable small losses of nutrients from the forest ecosystem must be replenished from the atmosphere, in dust and rain, and by biological nitrogen fixation.

Tropical rain forests occur on a wide range of soil types, by no means all of which are unsuitable for permanent agriculture. Relatively fertile soils occur in a variety of situations, such as in the volcanic areas of Java and on the floodplains of whitewater rivers in the Amazon region. Unsurprisingly, rain forests on these more fertile soils are particularly prone to clearance, while long-term protection is most likely for forests on the least fertile sites. Deforestation is thus concentrated in the areas that support the highest plant and animal biomass, so the impact on biodiversity and carbon storage is even greater than crude estimates of percentage area loss imply.

Variations in soil texture, drainage, and chemistry affect the botanical composition of the rain forest, but only the most extreme soil types support distinctly different vegetation types. Most distinctive are the heath forests, which are also known by a variety of different local names, such as *caatinga* in Amazonia and *kerangas* in Southeast Asia. Heath forests develop on infertile, drought-prone, sandy soils derived from coastal deposits or the weathering of sandstone. Compared with typical tropical lowland rain forests, they are lower in stature and the trees have smaller, harder leaves. The streams that drain these forests are blackish or dark brown as a result of the presence of particulate and colloidal organic matter. Heath forests are found in all the major rain forest regions but they are most extensive in the upper reaches of the appropriately named Rio Negro (Black River) in South America. Other distinctive, but more variable, forest types occur on soils derived from limestone, as well as those on ultramafic (iron- and nickel-rich) rocks. Forests on these soils are also typically low in stature, with many distinctive plant species.

Different forest types also develop on sites where peat, consisting largely of partly decomposed woody plant material, has built up to such a depth that the forest is isolated from the ground water. These peat swamp forests are totally dependent on nutrient input from the rainfall, which also saturates and preserves the peat, and both the height and species diversity of the vegetation decrease with increasing peat depth. Raised, deep peat beds are found only in areas with high rainfall and without a long dry season, and are particularly extensive on the islands of Borneo, Sumatra, and New Guinea. Deep peat also occurs in parts of the Amazon region, but its extent is currently unknown (Lähteenoja et al. 2009).

Flooding

Flooding by river water produces an array of different forest types depending on whether the floods are permanent or periodic, and whether the periodicity is daily, monthly, or annual. Freshwater swamp forests, known locally as várzea, are most extensive along the Amazon River, which has annual floods and is also influenced by tides up to 900 km (600 miles) from its mouth (Goulding 1989). Extensive, but little studied, swamp forests also occur in the Congo River basin, and there are smaller areas in New Guinea and Southeast Asia. Freshwater swamp forests generally support a lower diversity of plant species than dryland forests, presumably because of the problems of dispersal, germination, establishment, and growth in an environment that experiences such seasonal extremes (Lopez & Kursar 2007). Várzea swamp forests in Amazonia support a lower diversity of mammals than adjacent terra firme (unflooded) forests, but a higher density of arboreal primates (Haugaasen & Peres 2005) and the same is likely to be true in other rain forest regions. Near the mouths of major rivers, freshwater swamp forests are replaced by brackish-water swamp forests and then mangrove forest, which has a much simpler structure and lower plant diversity than other tropical forest types.

Rain forest histories

Plate tectonics and continental drift

To understand the similarities and differences between modern rain forests, it is necessary to learn about their pasts. Most of the land masses that currently support tropical rain forest have a common origin in the ancient southern supercontinent of Gondwana (Fig. 1.9) (Morley 2007). Gondwana means "land of the Gonds," and is named after a tribe from southern India whose land provided the first evidence that India had been part of the supercontinent. The core of modern Southeast Asia is made up of continental blocks that broke away

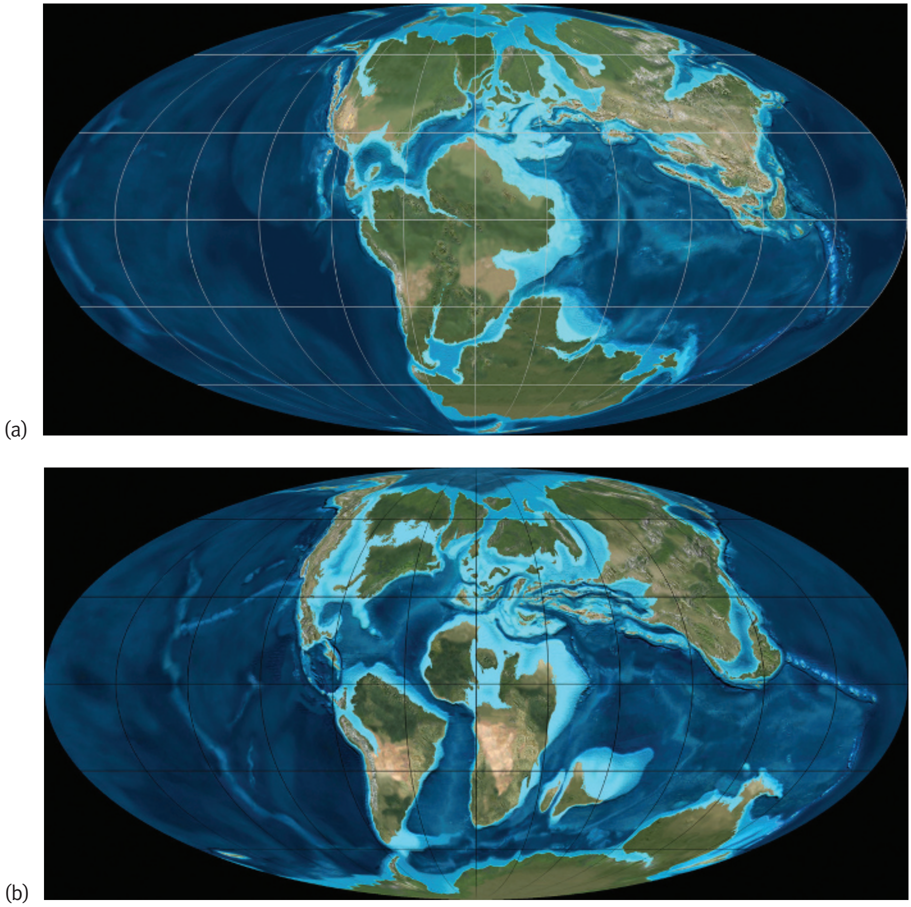
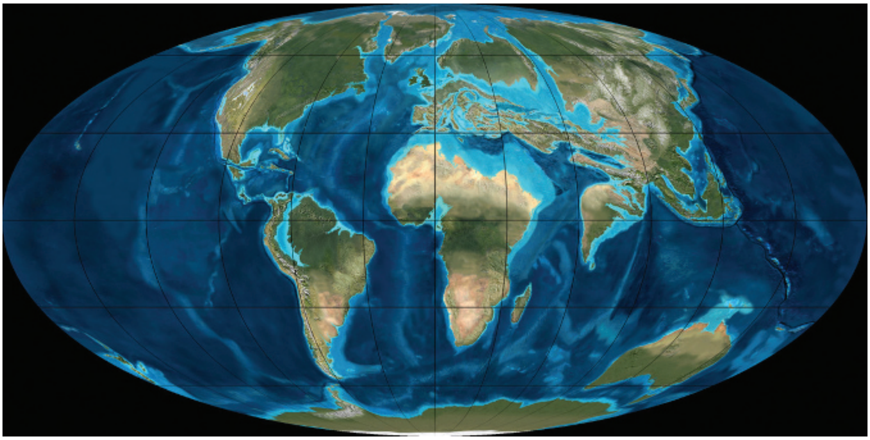


Fig. 1.9 Movements of the continents have had a big influence on the biogeography of the tropics. (a) In the later Jurassic (150 million years ago), the southern continents were connected into the supercontinent of Gondwana, and species could migrate among these areas. (b) By the late Cretaceous (90 million years ago), South America, Africa, India, and Australia had separated from one another, and connections with northern continents were severed.


(c)

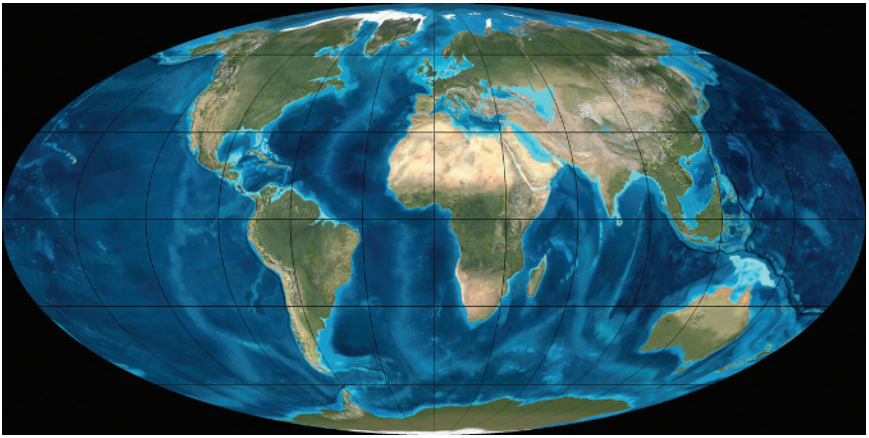

(d)

Fig. 1.9 (*cont'd*) (c) In the middle Eocene (50 million years ago), Madagascar had separated from Africa, India was moving toward Asia, and New Guinea had started to emerge. (d) By the early Miocene (20 million years ago), India had merged with Asia; Borneo, Sumatra, and neighboring islands had emerged; and Africa was connected to Asia.

from Gondwana between 400 and 160 million years ago, which is too early for them to have carried modern groups of plants and animals. Australia, India, Madagascar, Africa, and South America, in contrast, separated from each other and drifted north during the late Jurassic, Cretaceous, and early Tertiary (160 to 30 million years ago). This is the period during which many modern groups of plants and animals originated, so the sequence and timing of the break-up has had a significant influence on modern biogeographical patterns. New Caledonia, an island east of Australia, and the Seychelles, an archipelago east of Africa in the Indian Ocean, are also fragments of Gondwana.

India broke away early (130 million years ago) and, although the timing of India's collision with Eurasia is still uncertain (Rust et al. 2010), its modern flora and fauna are Asian. Africa's longer period of isolation in the late Cretaceous

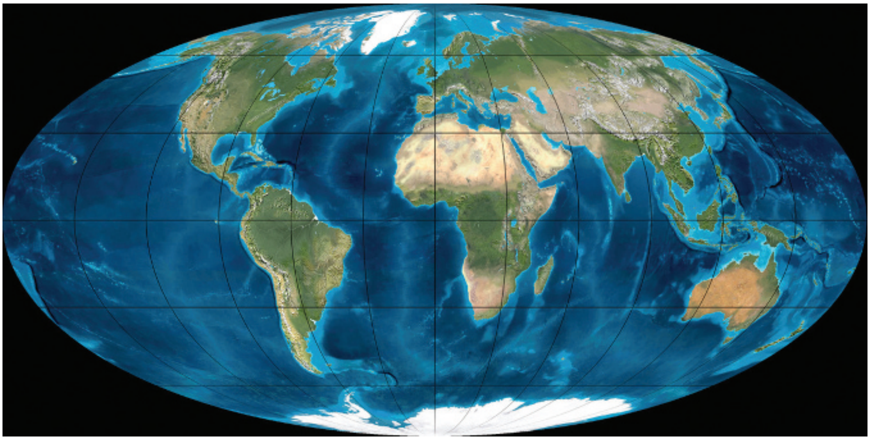


Fig. 1.9 (*cont'd*) (e) The modern world, showing the establishment of Central America and the broad contact of Africa and Asia. (Maps copyright Ron Blakey, Northern Arizona University, Geology.)

and early Tertiary produced a spectacular radiation of forms in an endemic clade of mammals, the Afrotheria, represented today by fewer than a hundred species in six orders: Proboscidea (elephants), Hyracoidea (hyraxes), Macroscelidea (elephant shrews or sengis), Tubulidentata (aardvark), Afrosoricida (golden moles and Madagascan tenrecs), and Sirenia (dugong and manatees). Although Africa has now been physically connected to Asia for at least 20 million years, climatic barriers such as large arid zones (represented today by the Sahara Desert) have allowed only limited exchange of rain forest taxa between the two continents for most of this period. Madagascar has remained isolated for 90 million years, and its relatively small rain forest area has developed on its own unique evolutionary path.

South America remained isolated from other continents for over 70 million years. This presented the opportunity for peculiar animal forms to evolve that are found nowhere else in the world, including the sloths, armadillos, and anteaters in the endemic order Xenarthra, the New World monkeys (see Chapter 3), and endemic radiations of marsupials, rodents, and ungulates (see Chapter 4). South America's long isolation finally ended when the Isthmus of Panama rose 3 million years ago, connecting the two American continents and allowing the intermingling of North American and South American faunas (Fig. 1.10). This dramatic event has become known as the Great American Interchange (Webb 1997). Some movement of animals between continents via rafting, long-distance dispersal, and island hopping appears to have begun as early as 8–10 million years ago and the formation of the land bridge seems to have been of less significance for plants (Cody et al. 2010). The North American invaders, which included such familiar mammalian groups as the cats, tapirs, deer, and squirrels, underwent explosive diversification in South America and, today, their descendents make up more than half the mammal fauna. Despite their ability to fly, bird exchanges increased greatly at the same time (Weir et al. 2009). This merging of previously separated faunas resulted in many extinctions, but may also have contributed to the exceptional diversity of the modern Neotropical biota.

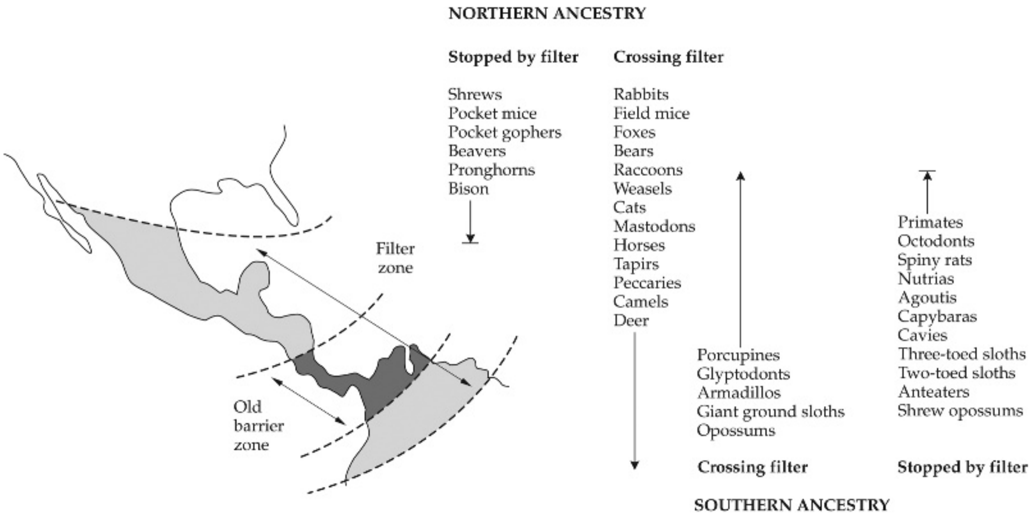


Fig. 1.10 The Central American land bridge, which was formed 3 million years ago, acted as a filter, preventing some North American animal families from crossing the barrier and allowing many others to pass on to South America. In contrast, many South American families did not disperse to North America. (From Lomolino et al. 2006.)

Central America is a composite of geological units of different ages and origins whose biota, before the Interchange, was dominated by North American organisms. The rain forests of Central America today, however, are overwhelmingly dominated by plants and animal groups that are shared with South America, and the effects of the deep-sea barrier that separated Central and South America until 3 million years ago have been almost totally erased.

Australia and New Guinea are still isolated from Southeast Asia by marine barriers, but the northward movement of Australia in the Miocene – continuing to this day – gave rise to the Indonesian archipelago, which has permitted an increasing interchange with Southeast Asia for organisms that can disperse from island to island, such as birds, bats, insects, and many plants. The modern rain forest biotas of Australia and New Guinea are thus a mixture of lineages from two very different origins: ancient Gondwana and post-Miocene Asia (Oliver & Sanders 2009). The distinctive differences in animal communities between Southeast Asia and New Guinea were first noted in the 19th century by the great naturalist Alfred Russel Wallace (Wallace 1859). In recognition of his discovery, the line of separation between these two biotic regions is now called "Wallace's line" and the region between Borneo and New Guinea, with its numerous islands, is known as Wallacea (Fig. 1.11). Geologists estimate that Australia and New Guinea will become connected to Asia in about 40 million years time, allowing their biotas to mix more completely in a "Great Australasian Interchange."

Changes in climate and sea level

Over the last few million years, rain forests expanded and contracted in area depending on the climate of the times (Morley 2007). Fossil evidence suggests

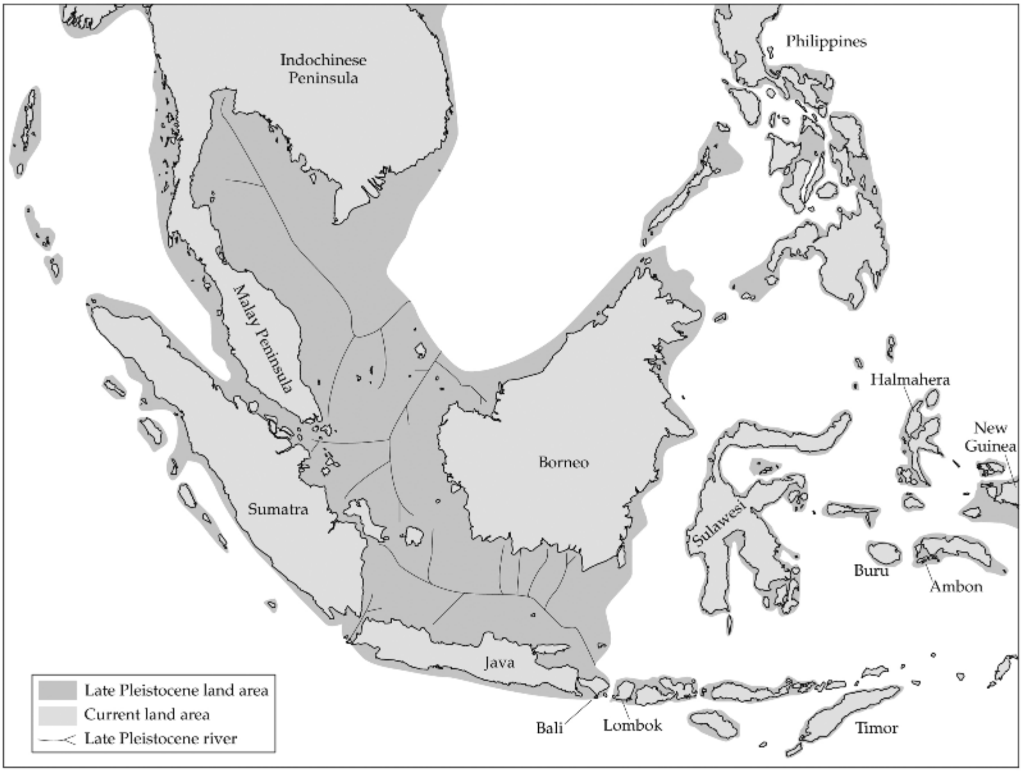


Fig. 1.11 The Sunda Shelf (shaded) was exposed during the last glacial maximum, allowing the movement of animals and plants between Borneo, Sumatra, Java, the Malay Peninsula, and many smaller islands. Note that the Philippines and Sulawesi were still separated from the Sunda Shelf. The area between the Sunda Shelf and the Sahul Shelf, which surrounds New Guinea and Australia, is known as Wallacea; the western boundary of Wallacea was described by Wallace as the eastern limit of distribution for many species of Asian animals, and is known today as Wallace's line. (From Lomolino et al. 2006; after Heaney 2004.)

that the tropical lowlands were both substantially cooler and, in large areas of the tropics, a lot drier during the glacial periods (ice ages) that occupied most of the last 2 million years. Lower atmospheric carbon dioxide levels during the glacial periods may also have been an important factor and may complicate the interpretation of the climatic records. These changes altered the composition of tropical rain forests and reduced their ranges. Pollen records from many sites show that montane or savanna plants were more widespread in glacial times and that rain forests disappeared from marginal areas. Rainfall remained high in many upland areas, but lower temperatures probably made these areas unsuitable as "refuges" for lowland rain forest organisms.

Australia and Africa show the strongest evidence for glacial drying and rain forest contraction. In Africa, rain forest was reduced to perhaps 10% of its area during the glacial maximum, persisting only in a few areas with high rainfall and as gallery forests along river margins (Morley 2000). This desiccation of African rain forests is a major reason for the far lower current diversity of palms, orchids, epiphytic species, and amphibians in African rain forests in comparison with rain forests in the Amazon and Asia (see Chapter 2). The impact of glacial changes was less severe in the Asian and American tropics, and on the islands of Madagascar and New Guinea, due to higher levels of rainfall associated with mountain ranges. Such upland areas are notably lacking in the Congo basin, and are found only as isolated mountains in East Africa.

Lower sea levels (up to 130 m (430 feet) below the present level) during glacial maxima linked the major land masses of insular Southeast Asia – Sumatra, Java, and Borneo – to the Malay Peninsula and Asian mainland, and greatly increased the exposed land area (Fig. 1.11). Although much of Southeast Asia seems to have been too dry to support rain forest during glacial times, both modeling studies and a limited amount of fossil evidence show that large areas of lowland rain forest persisted (Cannon et al. 2009). Much of this rain forest was on the exposed Sunda Shelf so, in striking contrast to the other rain forest regions, the total extent of rain forest in Southeast Asia was larger in glacial times than in the interglacials. Past land connections between the major modern land areas of Southeast Asia are reflected in the similarities of their modern forest biotas, although recent studies suggest that migration across these glacial land bridges was more limited than previously assumed, presumably because the lowest sea levels coincided with the driest climates and greatest fragmentation of the forest (e.g. den Tex et al. 2010). Connections among the islands could have occurred via migration along river valleys that extended from the coastal plains of northwestern Borneo, Sumatra, western Java, and the east coast of the Malay Peninsula onto the exposed Sunda Shelf. In contrast, most of the Philippines, Sulawesi, and the smaller islands between Sulawesi and New Guinea remained as islands, albeit often larger and connected among themselves, even at the lowest sea levels.

New Guinea had land connections to Australia during the glacial maxima, with the most recent connection being interrupted only 8000 years ago. However, the cooler, drier climate of those periods probably restricted interchange to those species that could migrate along the forested margins of waterways, and recent molecular studies suggest that most dispersal events pre-date the Pleistocene (e.g. Malekian et al. 2010). New Guinea and Australia share rain forest species of tree kangaroo, possums, birds, snakes, frogs, and even fishes – and shared more as recently as 300,000 years ago (Hocknull et al. 2007) – but New Guinea, with its larger rain forest area, has also developed its own unique biota, which is far richer than that now found in Australia.

A key point here is that the drier, cooler glacial episodes contracted African forests and divided them into smaller, isolated blocks, and probably had a similar effect on the Amazon basin as well. In contrast, glacial periods created land connections among the islands of Southeast Asia and the Asian mainland, and between New Guinea and Australia. As a result, the rain forests of Southeast Asia are more uniform, and those of Africa and South America less uniform, than might be expected from their present-day geography. Moreover, the cyclical changes in the total area of rain forest in response to the glacial cycles appear to have been in opposite phase in Africa (glacial minimum) and Asia (glacial maximum), with the other regions between these extremes.

Human occupation

One of the most important, but least understood, differences between rain forest regions is in their histories of human occupation. The popular idea that tropical rain forests were untouched, virgin ecosystems until the 20th century is a myth that has proved very hard to dispel, even among scientists. All rain forests have been modified by people and they cannot be understood if this fact is ignored. The broad picture of the evolution and spread of humans across the Earth's surface is now quite well documented (Fig. 1.12). Modern humans originated in Africa and spread overland to the warmer regions of Asia. New Guinea, Australia, and the Americas were colonized during the last glacial period, when low sea levels eliminated or reduced the water gaps. Larger water gaps remained a barrier until the development of improved boating technology within the last few thousand years. Madagascar was the last major tropical land mass to be reached by humans, a mere 2500–2000 years ago. Some smaller, more isolated tropical islands remained uninhabited until the last few hundred years.

The presence of people on a continent does not necessarily mean that they occupied the rain forest. Dense tropical forests are one of the least attractive environments for human occupation, since only a small proportion of the edible plant and animal material is accessible from ground level. Heavy rainfall washes away soil and mineral nutrients, requiring specialized techniques for agriculture, such as shifting cultivation and tree farming. Tropical rain forests may, however, have appeared more attractive before the first human hunters eliminated the most vulnerable ground animals, and recent archeological work

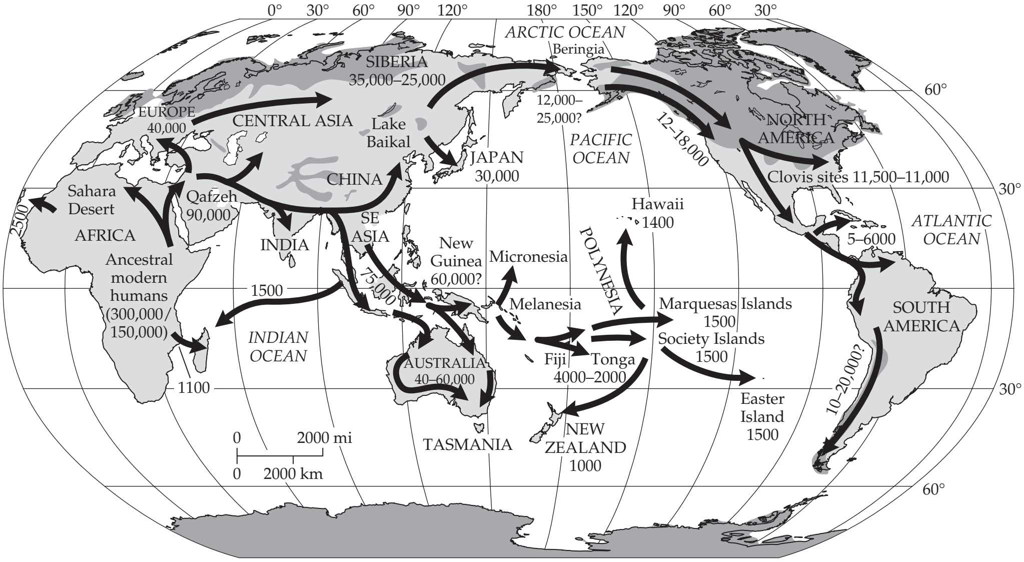


Fig. 1.12 The spread of modern humans over the world's surface. Values indicate the number of years that humans have been in a place; for example, humans arrived in Australia 40,000–60,000 years ago. (From Lomolino et al. 2006.)

has tended to push back the dates of first occupation (Mercader 2003). Some areas have been inhabited long enough for a distinct human body type to have evolved (Perry & Dominy 2009). "Pygmies", with average adult male heights < 155 cm (5 feet), occur in Africa, Southeast Asia, and South America, largely in populations that hunt and gather food in rain forest. And although hunters were the first humans to enter rain forests, evidence for cultivation, in the form of charcoal layers, broken pottery, crop remains, and modified soils, shows that most rain forest regions have also supported agricultural populations for millennia. In Amazonia, pre-Columbian agriculture left scattered patches of rich, black soil, known as *terra preta de Indio* (Indian dark earth), which are still prized by farmers for their fertility (Junqueira et al. 2010).

Origins of the similarities and differences among rain forests

The similarities and differences among the tropical rain forests in different regions can be explained in two major ways: "ecological" explanations relate the similarities and differences between rain forests to similarities and differences between their present-day environments, while "historical" explanations relate them to events that happened in the past. Each of these major types of explanation can, in turn, involve a huge range of possible factors; for example, soil nutrients and rainfall seasonality are ecological factors, while the movement of tectonic plates, changes in climate and sea level, and past human impacts are all historical factors. Further complications arise when ecological and historical factors interact as, for instance, when human impacts have been concentrated on the most fertile soils.

To distinguish between the many possible explanations for the distribution of a particular group of organisms, we need to know several things. First, we need to know the pattern of branching of lineages during evolution of the group – its phylogeny. The phylogeny for the primates, for instance, tells us that New World primates arose as a branch of the Old World primates (see Chapter 3), while that for army ants shows that the New and Old World species evolved from a common ancestor (see Chapter 7). Second, we need to know the timing of these branching events in relation to the availability of dispersal routes between rain forest regions. If, as current evidence suggests, the New World primates branched from their Old World ancestors around 30 million years ago, then they must have crossed the sea to reach the Americas, since no land route was available during this period. In contrast, the split between the two main army ant lineages may just be old enough for it to have occurred while there were still dryland connections between Africa and South America. Finally, we need to know the pattern of extinctions. Today, only Africa and Asia support really large (> 800 kg) species of mammals, but the fossil record shows that tropical America had a diverse "megafauna" when humans first arrived.

In the past, most discussions of these issues were largely speculation. In the last few decades, however, molecular techniques have greatly improved our understanding of the phylogenies of major plant and animal groups. These techniques can also provide approximate dates for branching events, by counting the number of mutations that have accumulated since, although this "molecular clock" must be calibrated from the very incomplete fossil record. The DNA evidence so far has provided a surprising result: most lowland rain forest species examined appear to have diverged from their nearest living relative prior to the Pleistocene glaciations of the last 2–3 million years, indicating that these biological communities are very old and speciation processes are slower than expected. This new understanding of phylogeny has coincided with the equally striking advances in our understanding of the Earth's history that have come from developments in plate tectonics and paleoclimatology (the study of past climates). Together, these developments have given us new insights into rain forest communities.

Similarities

Some similarities between rain forests in different parts of the world, such as the many shared families and genera of plants, may be inherited from ancient Gondwana. For a group of organisms to have reached all the major parts of Gondwana before it broke up, it would need to have originated at least 130–140 million years ago, but land connections persisted longer between some fragments than others, so such regions would be expected to have more similarities than areas that broke away completely at an earlier time. Moreover, dispersal between the fragments of Gondwana would have been relatively easy while they were still close together in the late Cretaceous and early Tertiary. A Gondwanan origin has therefore been suggested at one time or another for many groups of rain forest organisms, with a ride north on India providing a plausible route into tropical Asia. However, very few of these suggestions have been backed up by evidence – from fossils or molecular clocks – that the organisms involved existed early enough to take advantage of these opportunities. One exception is the worm-like scolecophidian snakes, where the timing of the initial diversification appears to match that of the break-up of Gondwana, but even in this ancient group several oceanic dispersal events are need to explain the current distribution (Vidal et al. 2010).

In the early Tertiary, the extension of frost-free climates to much higher latitudes than at present provided an alternative, northern, route between some of the rain forest regions. Around 50 million years ago, during the early Eocene, tropical forests grew at latitudes that today would be considered temperate, and a land bridge across the North Atlantic via southern Greenland provided a frost-free link between western Eurasia and North America (Milne 2006). Many rain forest plant genera are old enough to have used this "boreotropical connection." Cooling at the end of the Eocene broke this link forever by making the high latitudes too cold for tropical organisms.

Other similarities undoubtedly reflect later dispersal events as the Gondwanan fragments approached, and were eventually joined with, the northern continents: first India (34–55 million years ago), then Africa (20 million years ago), and finally South America (3 million years ago). Although there is still no dry-land connection between Australia/New Guinea and Southeast Asia, the largest water gap that an organism would have needed to cross during the last period of low sea level was less than 70 km (45 miles), making dispersal relatively easy for some types of organisms. Dispersal across much larger water gaps is rare, but not impossible, particularly for plants, and its significance in explaining current distribution patterns may have been underestimated (Givnish & Renner 2004).

Many other similarities between rain forest regions are not a result of shared ancestry at all, but of convergent evolution – the development of similar adaptations by unrelated organisms because they inhabit similar environments. Similarities resulting from convergent evolution have received a lot of attention in the past, but they are often superficial, as we shall see later in the book. Common ancestry and convergence are not mutually exclusive explanations for similarities, since the more closely related two organisms are, the more likely they are to evolve similar adaptations to similar environments.

Differences

The main theme of this book is not the similarities, but the many and important differences between rain forest regions. Such differences could have arisen for a variety of reasons, which are often impossible to disentangle. The simplest explanation for many of the biological differences is the ecological one: that they are a response to the differences in the physical environments of the various regions that have been outlined already. Even closely related organisms may evolve divergently in each region because the rain forest environments differ. For the same reason, some types of organisms may be able to invade and diversify in the rain forest in one region but not in another. The major differences among regions in the amount and seasonal distribution of rainfall have been called upon to explain many of the differences among rain forest regions. Rain forest organisms themselves also form an important part of the environment, and late arrivals may be unable to establish or diversify if their potential niches are already occupied. Thus the absence of specialist leaf-eaters among the New World primates may reflect their late arrival in a continent that already had leaf-eating sloths (see Chapter 3).

The different plate tectonic histories of the rain forest regions can also explain many of the differences in which groups of organisms are present or absent. Particular groups of plants and animals are shared between regions only if these regions were once connected or dispersal between them was once possible. Without the land bridge provided by the Isthmus of Panama, for instance, the rain forests of South America would be even more distinctive in comparison to rain forests elsewhere than they are now. Chance may play a major role here, particularly when dispersal on or over the open sea is involved. In many cases, the presence of a particular group of organisms in a region appears to be the result of a single, very unlikely event. The presence of primates in South American and Madagascan rain forests, and their absence in New Guinea, can perhaps be explained in this way.

Extinction is another cause of differences, and one that is often difficult to detect. The recent chance discovery of a single fossil honeybee (*Apis* sp.) in Middle Miocene rocks in Nevada, for example, has changed our understanding of honeybee biogeography, proving that their absence from the native bee fauna of the Americas reflects post-Miocene extinction, rather than a failure to get there (Engel et al. 2009). Changes in climate, as a result of plate movements, mountain uplift, or global climate change, may eliminate sensitive organisms from one region while they survive in another. Past human impacts are another, often overlooked, source of differences between regions. In the Neotropics, Madagascar, and New Guinea, the "megafauna" – the very large animals – were largely eliminated by

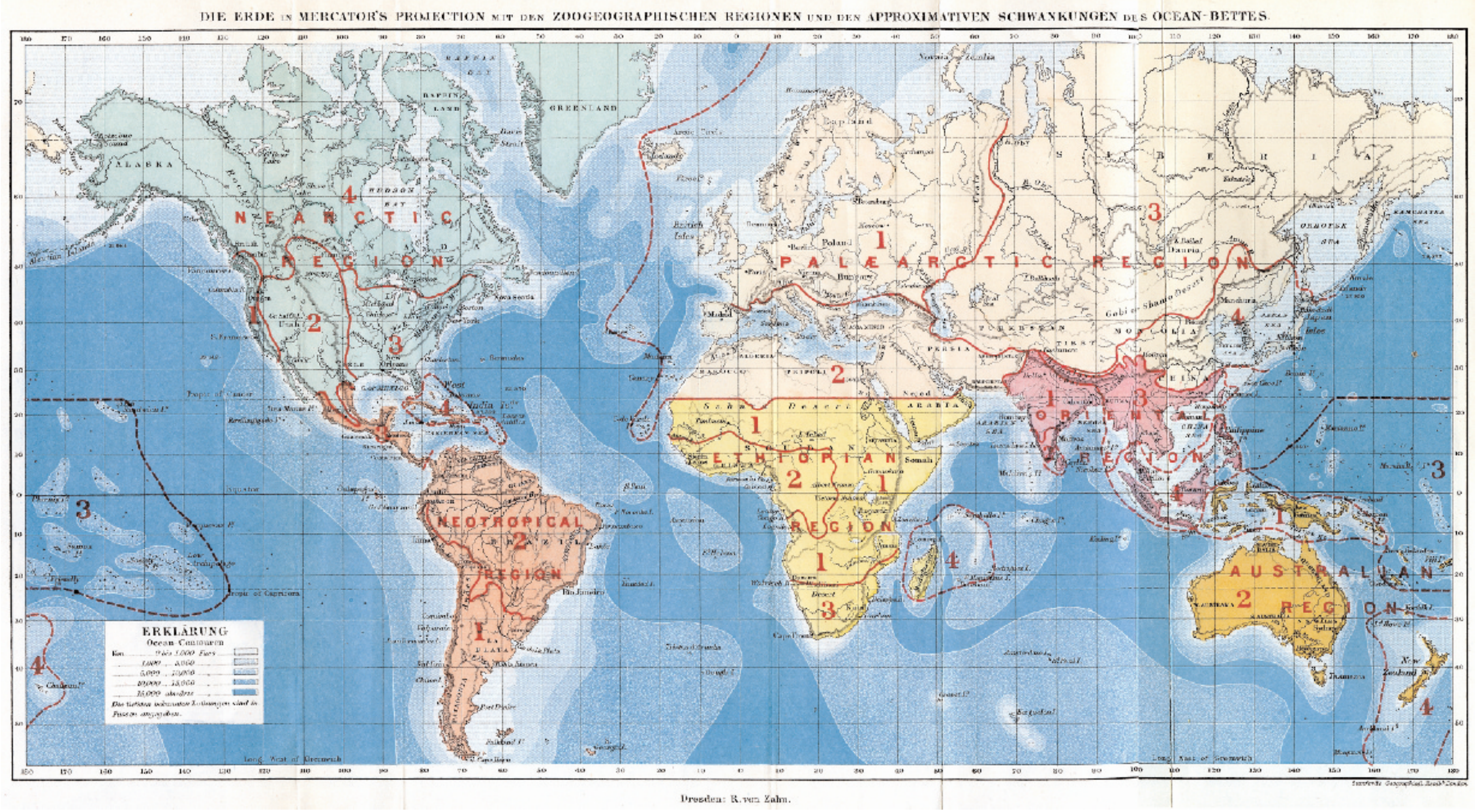


Fig. 1.13 Map of the world showing Wallace's zoogeographical regions, from the German edition of his book, *The Geographical Distribution of Animals*, published in 1876. This differs from the scheme used in this book only in the inclusion of Madagascar as a subregion in the Ethiopian (African) Region and the inclusion of Sulawesi in the Australian Region. Wallace later changed his mind on Sulawesi and transferred it to the Oriental (Asian) Region. (From Wikipedia.)

the first human arrivals, long before their ecological roles had been documented (Martin & Steadman 1999). In most cases, it is not even known if they inhabited rain forests.

Given time, evolution may fill the niches left vacant by the initial absence or subsequent extinction of a particular group of organisms. But evolution is a gradual process and can only act on the organisms that are present in the region. Particular niches may remain unfilled for a long time, or be filled in very different ways. When this happens, rain forests may differ not only in their biotas but also in the ways in which they function.

Functional consequences

The major question about tropical rain forests that we attempt to answer in this book is: why is what where? This is a very traditional approach to ecology, but one that has benefited greatly from the recent scientific advances outlined above. An alternative or complementary approach would be to look at the functioning of the whole rain forest ecosystem: such attributes as the production of biomass, the cycling of nutrients, and the rate at which these processes recover after natural and human disturbance. Combining the two approaches, we can ask what, if any, are the functional consequences of the observed differences between the biotas of the different rain forest regions? Does the presence of fungus-growing termites in Old World rain forests affect nutrient cycling? Does the absence of primates from New Guinea affect seed dispersal?

The answer to the great majority of such questions has to be that we do not know. We can and do speculate, but identifying functional differences requires comparisons between sites that have been carefully matched for the major environmental factors. These comparisons have not yet been made. Identifying which of the numerous biological differences between regions are responsible for particular differences in function will require the experimental removal or addition of the organisms in question. In some cases, such experiments could be done quite easily (e.g. the exclusion of browsing herbivores from an area of rain forest), in others they have already been done by accident (e.g. the introduction of honeybees to tropical America), while many more would be too dangerous to carry out in practice and should remain forever as “thought experiments” (e.g. the introduction of leaf-cutter ants to the Old World).

Many rain forests

For the reasons outlined above, the tropical rain forests of each region have distinctive characteristics and elements that give each a quality all its own. These differences were first formally recognized by Wallace 140 years ago (Fig. 1.13). The Neotropical rain forest is the most extensive, most diverse, and in many ways the most distinctive. The richest Neotropical rain forest sites have more tree species (see Chapter 2), more bird species (see Chapter 5), more bat species (see Chapter 6), and more butterfly species (see Chapter 7) living together than rain forests elsewhere, and the same pattern is found in many, but not all, other groups of organisms. The effects of South America’s long isolation have not been erased by the influx from the north after the formation of the Panama land bridge, and many characteristic groups of plants and mammals are found in no other rain forest region. The epiphytic plant family Bromeliaceae gives an unmistakable appearance to the forest and their water tanks provide a unique canopy resource that is exploited by numerous species (see Chapter 2). Hummingbirds (see Chapter 5) and the flowers that they pollinate (see Chapter 2) show a degree of evolutionary diversification that is unparalleled in other rain forests, while other New World endemic groups of birds dominate the insectivore, frugivore, and scavenging niches. Both primates (see Chapter 3) and rodents (see Chapter 4) diversified along very different lines in the Neotropics from their ancestors in the Old World, with giant, long-legged rodents partly filling niches occupied by ungulates in Africa and Asia. The fruit bats (see Chapter 6) in Neotropical rain forests are an entirely separate evolutionary radiation from the fruit bats in all other rain forests, with different flight, sensory, and fruit-processing capabilities. Long columns of leaf-cutter ants (see Chapter 7) bringing cut wedges of leaf back to their underground nests are another distinctive feature of Neotropical rain forests that has no equivalent elsewhere.

African rain forests could hardly be more different. They are mostly drier, lower, and more open than rain forests elsewhere and have a relatively less diverse flora (see Chapter 2), apparently as a result of both present and past climates. Diversity is high in some other groups, however, including the primates (see Chapter 3) and termites (see Chapter 7). Perhaps the most distinctive feature of the African rain forests is the abundance and diversity of large, ground-living mammals, including many species of primates (see Chapter 3) and terrestrial herbivores (see Chapter 4). The African elephant is the largest of all rain forest mammals and the gorilla by far the largest primate. The bird fauna shares most major groups with Asian rain forests, but there is an endemic group of frugivores, the turacos (see Chapter 5).

Most Asian rain forests can be characterized as "dipterocarp forests," because they are dominated by large trees in the family Dipterocarpaceae (see Chapter 2). Many dipterocarps are among the tallest trees in any rain forest. Probably because of this dominance by a single family, Southeast Asian dipterocarp forests show a unique pattern of mass flowering and fruiting at 2–7-year intervals, described in more detail in Chapter 2. The short periods of "feast" separated by long periods of "famine" for any animal that eats flowers, fruits, or seeds, appear to shape the whole ecology of the forest. Another peculiar feature of these forests – the abundance and diversity of gliding animals (see Chapter 6) – may be connected to this phenomenon.

The rain forests of New Guinea are a paradox, with a basically Asian flora (see Chapter 2), but a very un-Asian fauna (see Chapters 3 and 4). This is the only rain forest region without primates or placental carnivores. Indeed, bats and rodents are the only placental mammals, and marsupials occupy most other mammalian niches. New Guinea and Australia are also notable for several unique radiations of birds (see Chapter 5), including families such as the cassowaries, birds of paradise, and bowerbirds that could probably not have survived predation by placental carnivores.

The assembly of Madagascar's unique rain forests appears to owe a great deal to chance. The entire nonflying mammal fauna can be explained by four colonization events, involving, respectively, a single ancestral species of lemur (see Chapter 3), a mongoose-like carnivore (see Chapter 4), a rodent, and an insectivore. Most of the birds also represent endemic radiations from a very small number of initial colonizers (see Chapter 5) and the same pattern is shown whenever modern molecular techniques are brought to bear on other groups of organisms.

Conclusions

In this first chapter, the major rain forest regions of the world have been introduced. The rain forests differ in their biogeographical histories and in both their past and present environments. Most notably, the presence or absence of particular groups of animals and plants gives each region a distinctive character. However, the purpose of this book is not merely to list differences in biogeography, environment, and species, but to show how the differences impact on evolutionary and ecological relationships. And, in the end, the goal is to bring together the accumulated insights to examine how conservation strategies might use this information.

In the next chapter, plant communities are examined first, as plants represent the building blocks of the biological community. Subsequent chapters will consider animal communities.