1

Tropical Climates and Ecosystems

NEVER does nature seem more bountiful than in the tropics. Anyone with a passion for natural history must try and visit the tropics and experience Earth's most diverse ecosystems firsthand. This is a book about the New World or *Neotropics.* Alexander von Humboldt, Henry Walter Bates, Charles Darwin, Alfred Russel Wallace, Louis Agassiz, Thomas Belt, Charles Waterton, William Beebe, Frank M. Chapman, and other eminent naturalists have each been profoundly influenced in their beliefs about natural history by visits to the Neotropics. Their spirits of adventure and investigation are no less fervent today. Thousands of tourists annually travel to Neotropical jungles and rainforests in hopes of seeing some of the myriad bird species, colorful butterflies and other diverse insects, noisy monkey troops, and numerous other attractions of these majestic ecosystems. Students and professional researchers by the dozens are patiently and painstakingly unraveling perhaps the most complex Gordian knot in ecology, the multitudes of interactions among plants, animals, and microbes resulting in the vast biodiversity of tropical forests.

There is an urgency about the science of tropical ecology: tropical forests, which occupy approximately 7% of Earth's surface but may harbor as much as 50% of the world's biodiversity (Myers 1988; Wilson 1988), are being cleared at alarming rates (Repetto 1990). Cattle ranches and soybean fields are replacing rainforests. Though tropical rainforests also exist in Africa and Asia, approximately 57% of all rainforests remaining on Earth are in the Neotropics, with 30% in Brazil alone. Many of these are being cut: already only 12% of Brazil's unique Atlantic coastal forest remains (Brown and Brown 1992), and in 1987 alone some 20 million acres of Brazilian rainforest were cut and burned (Miller and Tangley 1991). Other Neotropical areas in danger and judged to require immediate conservation attention include the Colombian Choco, forests of western Ecuador, and the uplands of western Amazonia (Wilson 1992). At the current rate of deforestation, within 177 years all tropical rainforests on Earth could be gone. Right now, less than 5% of the world's tropical forests are protected within national parks or reserves. Though some encouraging data suggest a slowing of Amazonian rainforest clearance (Bonalume 1991), concerns remain about the long-term future of these rainforests as well as other tropical ecosystems, not just in the Neotropics but globally. Obviously, the ecosystems comprising the main subject of this book are potentially endangered. These ecosystems deserve better. Alexander von Humboldt, one of the first of the great naturalists to learn from the tropics, captured the sense of wonder one receives upon seeing rainforest for the first time:

> An enormous wood spread out at our feet that reached down to the ocean; the tree-tops, hung about with lianas, and crowned with great bushes of flowers, spread out like a great carpet, the dark green of which seemed to gleam in contrast to the light. We were all the more impressed by this sight because it was the first time that we had come across a mass of tropical vegetation. . . . But more beautiful still than all the wonders individually is the impression conveyed by the whole of this vigorous, luxuriant and yet light, cheering and mild nature in its entirety. I can tell that I shall be very happy here and that such impressions will often cheer me in the future. (Quoted in Meyer-Abich 1969.)

Most people who have never been to equatorial regions assume them to be continuous rainforest, much as described by Humboldt. Tropical rainforest is, indeed, a principal ecosystem throughout much of the area and is the major focus of this book. Other kinds of ecosystems, however, also characterize the tropics (Beard 1944; Holdridge 1967; Walter 1971). Climate is generally warm and wet but is by no means uniform, and both seasonality and topography have marked effects on the characteristics of various tropical ecosystems. In this chapter I will present an overview of the tropical climate, seasonality, and major ecosystem types occurring in the Neotropics.

The Climate

Definition of the "Tropics"

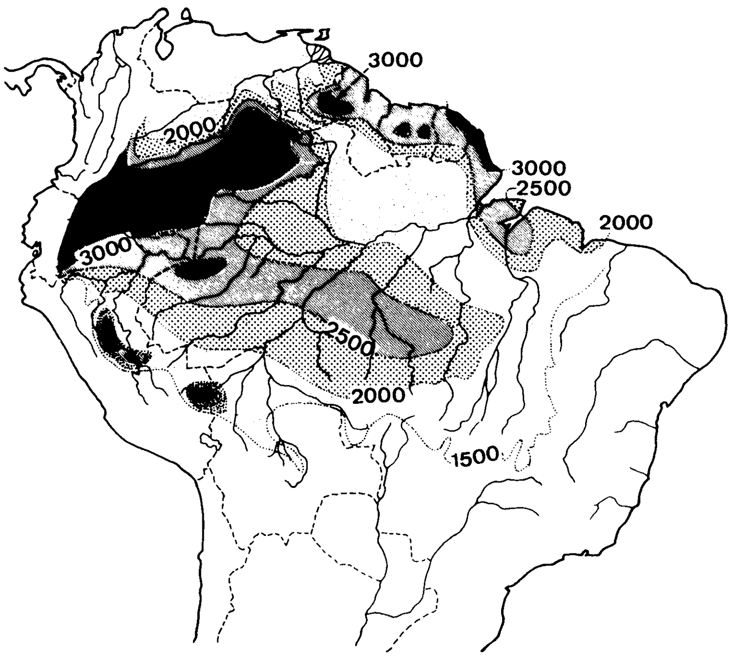
Should you decide to move to Manaus, Brazil, or perhaps to Iquitos, Peru, both well within the Amazon Basin, you should expect at least 130 days of rain per year, and in some places up to 250 days. Temperature will be consistently warm, often hot (highs of about 31°C [88°F], nighttime low of about 22°C [72°F]), and relative humidity will never be less than 80% (Meggars 1988). Though it can rain on any given day, rainfall, in most places, will be seasonal. That, in a nutshell, is what it's like in the tropics. In the Amazon Basin, the very heart of the Neotropics, climate is permanently hot and humid, with the temperature averaging 27.9°C (82°F) during dry season and 25.8°C (78.5°F) in rainy season. In the tropics, daily temperature fluctuation exceeds average annual seasonal fluctuation (see below) and air humidity is quite high, about 88% in rainy season and 77% in dry season (Junk and Furch 1985).

Geographically, the tropics is an equatorial region, the area between the Tropic of Cancer (23° 27′N) and the Tropic of Capricorn (23° 27′S), an approximately 50-degree band of latitude that, at either extreme, is subtropical rather than tropical. The Tropic of Cancer passes through central Mexico and just south of Florida. The Tropic of Capricorn passes through northern Chile, central Paraguay, and southeastern Brazil, almost directly through the Brazilian city of Sao Paulo. The Neotropics thus include extreme southern North America, all of Central America, and much of South America. You can visit the Neotropics by traveling to southern Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Guyana, Surinam, French Guiana, Ecuador, Peru, Brazil, and parts of Bolivia and Paraguay. In the Caribbean Sea, the Greater and Lesser Antilles are within the Neotropics.

The tropics are warm and generally wet because the sun's radiation falls most directly and most constantly upon the equator, thus warming Earth more in the tropics than at other latitudes. As one travels either north or south from the equator, Earth's axial tilt of 23° 27′ results in part of the year being such that the sun's rays fall quite obliquely and for much shorter periods of time, thus the well-known cycles of day length associated with the changing seasons of temperate and polar regions. At the equator, heat builds up and thus the air rises, carrying the warmth. Water is evaporated so water vapor rises as well. The warm, moist air is cooled as it rises, condensing the water, which then falls as precipitation, accounting for the rainy aspect of tropical climates. The normal flow of warm, moisture-laden air is from equatorial to more northern and southern latitudes. As the air cools it not only loses its moisture to precipitation, but also becomes more dense and falls, creating a backward flow toward the equator. At the equator, two major air masses, one from the north and one from the south, along with major ocean currents, form the Intertropical Convergence (ITC), the major climatic heat engine on the planet.

In the Amazon Basin, precipitation ranges between 1,500 (59 in) and 3,000 mm (118 in) annually, averaging around 2,000 mm (79 in) in central Amazonia (Salati and Vose 1984). About half of the total precipitation is brought to the basin by eastern trade winds blowing in from the Atlantic Ocean, while the other half is the result of evapotranspiration from the vast forest that covers the basin (Salati and Vose 1984; Junk and Furch 1985). Up to 75% of the rain falling within a central Amazonian rainforest may come directly from evapotranspiration (Junk and Furch 1985), an obviously tight recycling of water, and a recycling system that clearly demonstrates the importance of intact forest to the cycling of water. This vast precipitation and water-recycling system is essential in maintaining equilibrium, and large-scale deforestation could significantly upset the balance (Salati and Vose 1984; see also chapter 14).

Tropical areas fall within the trade-wind belts (so named because winds were favorable for sailing ships trading their goods) except near the equator, an area known as the intertropical convergence or doldrums, where winds are usually light, often becalming sailing ships. From the equator to 30°N, the eastern trade winds blow steadily from the northeast, a direction determined because of the constant rotation of Earth from west to east. South of the equator to 30°S, the eastern trades blow from the southeast, again due to the rotational motion of the planet. As Earth, tilted at about 23.5° on its axis, moves in its orbit around the sun, its direct angle to the sun's radiation varies with latitude, causing seasonal change, manifested in the tropics by changing heat



Annual rainfall (mm) in Amazonia. Black areas, near the base of the Andes, represent regions with more than 4,000 mm of rain per year. From Haffer and Fitzpatrick (1985). Reproduced with permission.

patterns of air masses around the intertropical convergence that result in seasonal rainfall. In the Western Hemisphere, from July throughout October, severe wind- and rainstorms called hurricanes can occur in parts of the Neotropics. Similar kinds of storms are referred to as monsoons in the Old World tropics.

Seasonal variations in day length are not nearly as dramatic in the tropics as in the temperate zone. At the equator, a day lasts exactly twelve hours throughout the year. North of the equator, days become a little longer in the northern summer and shorter in winter, but this only means that summer sunset is at 6:15 or 6:20 rather than 6:00 P.M. Temperature fluctuates relatively little in the tropics. Typically, daytime temperature is somewhere around 29°C (85°F), though in many areas it may be 32–37°C (in the 90s), with surprisingly little seasonal fluctuation. In general, there is no more than a 5°C difference between the mean temperatures of the warmest and coldest months. For example, at La Selva Biological Station in Costa Rica, August is the month with the highest mean temperature, 27.1°C (80.5°F), while January has the lowest mean temperature, 24.7°C (77°F) (Sanford et al. 1994). Relative humidity, as noted above, is generally high in the tropics, especially in lowland rainforests where humidities ranging from 90% to 95% at ground level are common. Humidity is less in the rainforest canopy, usually no higher than 70%.

El Niño—Southern Oscillatiion

South American and, indeed, global climates are periodically and sometimes dramatically affected by a still poorly understood climatic event called *El Niño* ("The Child"), or the Southern Oscillation. Originally named because it tends to begin around Christmas, El Niño causes sufficient short-term climate change to produce major disruptions to ecosystems, especially marine ecosystems (Glynn 1988). An El Niño event involves the unpredictable warming of eastern Pacific Ocean surface waters around the equator.

El Niño occurs periodically, approximately every two to seven years, when a high-pressure weather system that is normally stable over the eastern Pacific Ocean breaks down, destroying the pattern of the westward-blowing trade winds. Trade winds thus weaken severely, sometimes reversing from their normal westward direction. Warm water from the western Pacific flows eastward, enhancing the Equatorial Counter Current and causing an influx of abnormally warm water to the western coast of South America. Instead of winds pushing water from the west coast of South America, creating an upwelling of deeper, colder, nutrient-rich water (page 15), the trade winds quit. When that happens, warm waters flow along the normally cold South American coast, global heat patterns vary, and weather systems change, causing floods in some regions and droughts where there should be rainfall, effects that can be anywhere from mildly stressful to disastrous to plant and animal populations. For example, some parts of South America experience abnormally heavy downpours while other areas, particularly in Central America, become drought-stricken. Droughts can also occur in places such as Australia, Indonesia, and southern Africa.

There have been eight major El Niño events since 1945, and at least twenty during this century. In 1982–83 an El Niño considered up to then to be the most powerful of this century caused an estimated $8.65 billion worth of damage worldwide. An even more severe El Niño occurred in 1986–87. A comparable El Niño occurred in the winter of 1994–95. The California coast was inundated by rain, resulting in extensive flooding and mudslides from Los Angeles to the Russian River area north of San Francisco, while New England experienced far less winter precipitation than usual. Satellite data indicated that the northern Pacific Ocean was nearly eight inches higher than normal, due to the influx of warm surface waters. The causal factors responsible for the periodicity of El Niños are thus far unknown (Canby 1984; Graham and White 1988), but it is clear that the Intertropical Convergence, a complex system of oceanic and air currents, migrates to a lower latitude, raising sea surface temperatures and destroying the normal upwelling pattern along the west coast of South America. The cessation of an El Niño occurs then the ITC returns northward to its normal position (hence the alternate term for El Niño, the Southern Oscillation). Tropical ecosystems, already sensitive to seasonal variation (see next section), can be anywhere from moderately to severely affected by changes caused by El Niño (Glynn 1988; also see Foster 1982b, below). Indeed, El Niño of 1986–87 has been suggested to have contributed strongly to the apparent extinction of two amphibian species, the golden toad (*Bufo periglenes*) and the harlequin frog (*Atelopus varius*), from Monteverde Cloud Forest Preserve in Costa Rica (Pounds and Crump 1994).

The Importance of Seasonality

Rainfall in tropical latitudes varies seasonally, often dramatically. Because of warm air throughout the year, precipitation is in the form of rain (except atop high mountains such as the Andes, where snow occurs, even at the equator), but the amount of rain varies considerably from month to month and from one location to another. Overall, precipitation is highest in the central Amazon Basin and the eastern Andean slopes and lowlands, and less to the north or to the south, varying from about 6,000 mm (eastern Andean slopes) to 1,500 mm (236–59 in) (extreme north or south) (Junk and Furch 1985). Even within the central Amazon Basin, seasonal rainfall is variable from place to place. For example, Iquitos, Peru, along the Amazon River, receives an average of 2,623 mm (103 in) of rainfall annually, while Manaus, Brazil, also on the Amazon River, receives an average of 1,771 mm (70 in) and experiences a strong dry season. As a more extreme example, Andagoya, in western Colombia, receives 7,089 mm annually (approximately 280 in). (The area that receives the most rainfall on Earth is not in the Neotropics but in the United States! It is Mount Waialeale, Hawaii, averaging 11,981.18 mm [471.7 in] annually.)

Throughout most of the tropics, some rain falls each month, but there is usually a pronounced wet and dry season, and sometimes two wet and dry periods, each of which differs in magnitude. Where the dry season is pronounced, many, often most, trees are deciduous, shedding leaves during that season. Such tropical dry forests are often termed "monsoon forests," since they are in leaf only when the monsoon rains are present. Dry season is defined as less than 10 cm (3.9 in) of rainfall per month, and rainy season features anywhere from 2 to 100 cm (0.8–39 in) (occasionally more) of rainfall per month. A typical tropical rainforest receives a minimum of 150 to 200 cm of rainfall annually (60–80 in).

The rainy season varies in time of onset, duration, and severity from one area to another in the tropics. For example, at Belém, Brazil, virtually on the equator, dry season months are normally August 1 through November, and the wettest months are January through April. In Belize City, Belize, at 17°N, the rainy season begins moderately in early June but in earnest in mid-July and lasts through mid-December and sometimes into January. The dry months are normally mid-February through May. In general, when it is rainy season north of the equator, it is dry season to the south. Because the Amazon River flows in close proximity of the equator, parts of the huge river are experiencing wet season while other parts are in dry season.

The seasonal shift from rainy to dry season has direct effects on plants and animals inhabiting rainforests as well as other tropical ecosystems. One common misconception about the tropics is that seasonality can generally be ignored. Images of year-round sunny skies and soft trade winds are the stuff of myths. The truth is that seasonal shifts are normal and often pronounced, with many ecological patterns reflecting responses to seasonal changes. Some shifts are obvious, but others are subtle and vary considerably depending on the magnitude of the seasonality. During the rainy season, skies are typically cloudy for most of the day and heavy showers are intermittent, often becoming especially torrential during late afternoon and evening. Such cloud cover, blocking sunlight from reaching the forest, can be a strong limiting factor on total photosynthesis; thus plant growth is often greater during dry season, when skies are clear for up to ten hours during the day and showers, though sometimes heavy, are brief.

Seasonal differences are not trivial to organisms. Henry Walter Bates, in *The Naturalist on the River Amazons* (1863), wrote of seasonal patterns as they affect life along the Amazon. At the onset of rainy season, "All of the countless swarms of turtle of various species then leave the main river for the inland pools: sand banks go under water, and the flocks of wading birds then migrate northerly to the upper waters of the tributaries which flow from that direction, or to the Orinoco; which streams during the wet period when the Amazons are enjoying the cloudless skies of their dry season." More recent studies, particularly those carried out by researchers on Barro Colorado Island (BCI) in Panama (Leigh et al. 1982) and La Selva Biological Station in Costa Rica (McDade et al. 1994), have documented the compelling drama of the changing seasons of the tropical forest.

Trees flower more commonly during the dry season (Janzen 1967, 1975) when less frequent and less intense showers permit insect pollinators to be active for longer periods, thus enhancing cross-pollination. Some tree species synchronize their flowering after downpours (Augspurger 1982), which may increase pollination efficiency by concentrating the number of pollinators (Janzen 1975). Dry season pollination also enables more seedlings to survive because they sprout at the onset of rainy season, when there is adequate moisture available to ensure their initial growth. A study of 185 plant species on Barro Colorado Island determined that most seedlings emerged within the first two months of the eight-month rainy season (Garwood 1982). Forty-two percent of the plant species underwent seed dispersal during dry season and germination at the onset of rainy season. Forty percent of the species experienced seed dispersal at the beginning of rainy season, with germination occurring later in rainy season. Approximately 18% of the species produced seeds that were dispersed during one rainy season, were dormant during the next dry season, and germinated at the onset of the second rainy season. The species most sensitive to the onset of rainy season were "pioneer" tree species, lianas, canopy species, and wind- and animal-dispersed species. Understory and shade-tolerant species were less sensitive.

Fruiting patterns, not unexpectedly, are also under strong seasonal influence. In general, most fruiting roughly coincides with peak rainy season, with lowest fruit availability at the onset of dry season (Fleming et al. 1987), though there is much variability among species. Fruiting patterns on Barro Colorado Island are seasonally influenced (Foster 1982a). The timing of fruiting in many species appears to be a compromise between the desirability of seeds germinating at the onset of rainy season and the advantages of flowering early in the rainy season, when insects are most abundant (see below).

Pioneer tree species often germinate at the onset of rainy season, which is when tree falls tend to be most common, opening gaps in the forest where these shade-intolerant species can become established (see chapter 3). At BCI, one large gap per hectare occurs on average every 5.3 years, a frequency sufficient to support a high population of quick-growing pioneer tree species (Brokaw 1982).

Grazing rates on leaves are more than twice as high during the rainy season as during the dry season (Coley 1982, 1983). New leaves are more vulnerable to insect herbivores because they lack protective tissues and chemicals (see chapter 6). Most trees grow their new leaves during early rainy season. Some trees are deciduous during the dry season, dropping their leaves entirely.

As might be expected, arthropods, many of which are highly dependent on plants, also show seasonal changes in abundance. A study conducted among several habitats in southeastern Peru showed that forest floor arthropod biomass was most abundant during the wet season. Virtually all arthropod taxa showed clear seasonal patterns (Pearson and Derr 1986). Similar seasonal effects were noted for Panama (Levings and Windsor 1982) and Costa Rica (Lieberman and Dock 1982), where arthropod abundance peaks at the end of dry season and beginning of rainy season.

Rainforest birds are sensitive to seasonal rhythms. In Costa Rica, most nesting occurs from March through June, the end of the dry season and beginning of the rainy season, with little nesting occurring from October through December (end of rainy season and beginning of dry season), a pattern noted for much of Central America (Levey and Stiles 1994). Seasonal changes in distribution and abundance of nectar-eating, fruit-eating, and understory birds are well documented for Panama (Leck 1972; Karr 1976; Karr et al. 1982) and Costa Rica (Levey and Stiles 1994). Manakins, small birds that feed almost entirely on fruit (page 274), have been found not to breed during seasons of fruit shortage, and, at least at one location near BCI, the manakin population fluctuates with fruit availability (Worthington 1982). On Grenada, the bananaquit (*Coerba flaveola*), a small, nectar-feeding bird (page 265), synchronizes its breeding to coincide with the onset of the wet season (Wunderle 1982). A study conducted on Puerto Rico concluded that birds needed adequate rainfall to breed successfully during their normal season of April–July (Faaborg 1982).

The tamandua (*Tamandua mexicana*), a common forest anteater, shifts its diet from ants in rainy season to termites in dry season (Lubin and Montgomery 1981). Termites are juicier than ants and so afford a higher moisture content to the anteater. Termites (*Nasutitermes sp.*) are also attuned to the seasons, swarming during the onset of rainy season (Lubin 1983). The mass emergence may ensure that each swarming insect has a better chance of reproduction, because it is more likely to encounter another termite quickly. Also, potential termite predators cannot possibly eat all of the swarming masses. Thus some termites survive to initiate new colonies. Many animals, such as monkeys, cats, iguanas, and various lizards, abandon deciduous forests during dry season when leaves have dropped. These creatures move to riverine gallery forests, which remain in leaf.

White-throated (faced) capuchin

On Barro Colorado Island the shortage of fruits at the end of the wet season affects the ecology of two common rainforest rodents. The agouti (*Dasyprocta punctata*), a small, diurnal (daytime-active) rodent, depends on relocating seeds that it has buried to sustain itself through the months of the dry season. Another rodent, the nocturnal paca (*Cuniculis paca*), survives the dry season by browsing more intensively on leaves and living off its stored fat. Both agouti and paca forage for longer periods during dry season, and their populations are indirectly limited by the dry season food shortage. Because they must forage for longer periods and take greater risks to satisfy their hunger, they fall victim to predators more frequently (Smythe et al. 1982).

A most extreme case of seasonal stress was documented at Barro Colorado Island (Foster 1982b). Two fruiting peaks normally occur annually, one in early rainy season and one in mid–rainy season. During 1983, an El Niño year (see above), the second peak failed to occur. Between August 1970 and February 1971 only one-third the normal amount of fruit fell, thus creating a famine. Not all plant species failed to produce a second fruit crop, but enough did to severely affect the animal community. Researchers on BCI noted that normally wary collared peccaries (*Tayassu tajacu*), coatimundis (*Nasua ilarica*), agoutis, tapirs (*Tapirus bairdii*), and kinkajous (*Potos flavus*) made frequent visits to the laboratory area to get food that had been put out for them. Peccaries seemed emaciated, and a kinkajou looked to be starving when it first appeared. Most amazing were the monkeys. To quote Robin Foster, "The spider monkeys, which normally visit the laboratory clearing at least once every day, now launched an all-out assault on food resources inside the buildings, learning for the first time to open doors and make quick forays to the dining room table, where they sought bread and bananas, ignoring the meat, potatoes, and canned fruit cocktail, and brushing aside the startled biologists at their dinner." Foster noted that dead animals were encountered much more frequently than in previous years. "The most abundant carcasses were those of coatis, agoutis, peccaries, howler monkeys, opossums, armadillos, and porcupines; there were only occasional dead two-toed sloths, three-toed sloths, white-faced monkeys, and pacas. At times it was difficult to avoid the stench: neither the turkey vultures nor the black vultures seemed able to keep up with the abundance of carcasses." The reason why the two sloth species, the white-faced monkeys (*Cebus capucinus*), and the pacas were less affected is that they feed on foliage. Fruit, not foliage, was in short supply.

The severe dry season of 1983, due partly to El Niño and partly due to long-term oscillations in climate, also resulted in greatly increased mortality rates among the canopy trees of Barro Colorado (Condit et al. 1995).

Studies cited above contrast strongly with the naive view of the tropics expressed in the Humboldt quotation at the beginning of the chapter. The tropics may appear luxuriant at first glance, but in reality they impose significant seasonal stresses upon the plant and animal inhabitants. Furthermore, the tropics do not host stable, unchanging ecosystems. Tropical ecology, as you will learn, is more than a little dynamic. It's a real jungle out there.

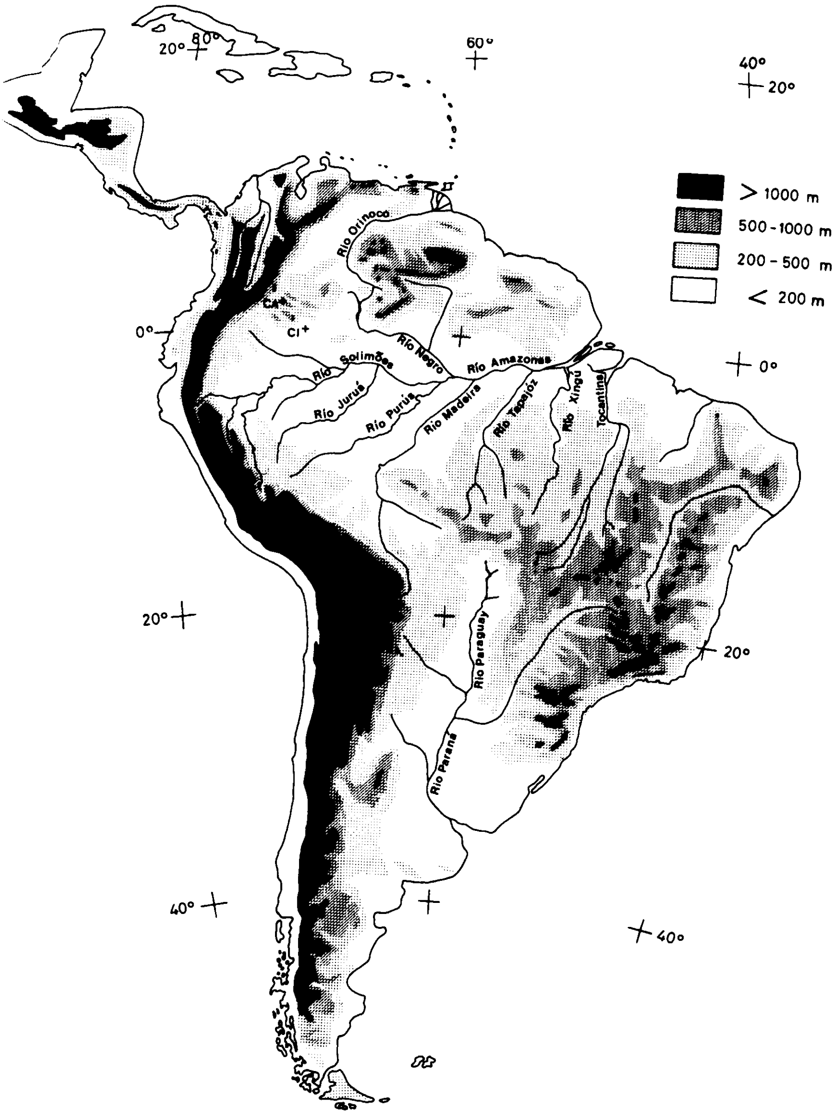
The Importance of Mountains

Figures 4, 5, 6, 7, 8, 9

The Andes Mountains began their rise approximately 20 million years ago (Zeil 1979). Orographic uplift has continued unabated to the present day with the Andes chain still one of the most active geological areas on the planet. As recently as a million years ago the northernmost part of the Andes was uplifted, and Charles Darwin (1906), on his voyage of the H.M.S. *Beagle*, bore witness to the awesome power of a major earthquake in Chile.

> A bad earthquake at once destroys our oldest associations: the earth, the very emblem of solidarity, has moved beneath our feet like a thin crust over a fluid; one second of time has created in the mind a strange idea of insecurity, which hours of reflection would not have produced.

Darwin's description of his perceptions while experiencing the quake were closer to reality than he probably realized. Geologists now generally agree that Earth's crust consists of huge basaltic plates that continually move, often in opposition to one another, a dynamic pattern termed plate tectonics. Granite continents sit atop these plates. The South American plate, containing the continent of South America, began its split from the African plate about 100 million years ago, creating the south Atlantic Ocean. Since then the South American plate has been moving westward. Eventually it met the eastward-



Surface relief of Central and South America, showing lowland nature of Amazonia. The 500 to 1,000 m level is indicated only in regions east of the Andes Mountains. From Haffer (1974). Reproduced with permission.

moving Nazca plate, containing the southeastern Pacific Ocean. When the two plates collided in earnest, the Nazca plate began sliding under the South American plate, creating the thrust that produced the Andes Mountains. This process, called subduction, continues today and is responsible for the geological activity evident in the volcanism and earthquakes that characterize the western part of South and Central America (Dietz and Holden 1972).

The chains of mountains stretching from southernmost Patagonia north through Mexico add to the climatic and, thus, biotic diversity of the Neotropics. Located in western South and Central America, the geologically youthful Andes and Mexican cordilleras host different altitudinal ecosystems and also serve as barriers that isolate populations, thus enhancing the speciation process (see page 109).

The north-south orientation of the Andes results in coastal Peru and Chile having some of the most arid deserts in the western hemisphere, places such as the Atacama Desert south of Lima at Paracas, Peru, and extending southward along the Chilean coast. As I walked across the dry, crusted, reddish soil, I could find no signs of plants or animals, the only time in my years as an ecologist that I've seen a place so devoid of obvious life (other than looking at the moon through a telescope). The Atacama-Sechura Desert extends along the Peruvian and Chilean coast for about 3,000 km (1,865 mi), some of it receiving only about one millimeter of precipitation annually. The driest place on Earth is considered to be Calama, Chile, in the Atacama Desert, where no rain has yet been recorded! Nonetheless, the desert is rather humid due to the fog and clouds produced by the proximity to the cool ocean currents. As with most deserts, temperature fluctuations are often dramatic. The Atacama can drop in temperature from 40°C (104°F) to 0°C (32°F) in little more than an hour.

The Andes Mountains act as a gigantic wall preventing moisture-laden air accumulating in the Amazon Basin from reaching the Peruvian and Chilean coasts. As the clouds are forced up by the tall mountains, the moisture in them condenses to snow or, at mid to low elevations, rain. Rain falls heavily on the eastern slopes of the Andes, creating conditions that support extremely lush montane and lowland rainforest. Snow melt from the Andes is one of the major sources of water for the Amazon Basin.

The Andes, in essence, keep precipitation recycling within the Amazon Basin (Salati and Vose 1984). The Amazon Basin is shaped like an immense horseshoe, with the ancient Guianan Shield bordering to the north, the Brazilian Shield to the south, and the Andes to the west. Because of this topography, all water exits the system to the east, at the huge mouth of the Amazon. This loss is replaced by input from rain and melting snow draining from the high Andes, keeping the Amazon Basin in a state of hydrographic equilibrium (Salati and Vose 1984).

The air that eventually passes over the tall mountains is fundamentally depleted of its moisture; thus, dry deserts occur on the western side. This is called a *rain shadow effect,* and consequently, ecosystems differ dramatically from one side of a mountain to the other, though their elevation may be the same. On a bus ride over a mountain in northern Peru between Jaén and Chiclayo I experienced the rain shadow effect. As our driver engineered his way up the steep mountain slope, we passed through cactus and shrubby desert. Approaching the crest, however, the clear air and blue skies gave way to misty overcast. Tall columnar cactus plants appeared, many heavily laden with bromeliads. At the crest, we were in a miniature cloud forest, bathed in permanent fog, whose ghostlike, stunted trees were adorned with all manner of orchids, bromeliads, and other air plants (epiphytes). As we descended the eastern side, the skies clouded and rain commenced. We left the elfin cloud forest, passing through rich coffee plantations and thick, cloud-enshrouded forests at the same altitudes where desert and dry grassland had occurred on the opposite side of the mountain.

Ironically, the oceanic ecosystem off the coast of southern Peru and Chile is perhaps the richest in the world, the very opposite of a desert. Steady, strong winds blow away surface water of the cold Humboldt current, creating a condition called *upwelling*, the rise to the surface of cold, subantarctic water rich with nutrients and oxygen. These winds are also partly responsible for the terrestrial desert, as they blow from the coast to the sea, and thus no oceanic, moisture-laden air is brought over land. In the sea, vast hordes of tiny plankton are supported by upwelling, and they become food for sardinelike anchovetas (*Engraulis ringens*), which, when they annually numbered well into the high millions, supported a very successful fishing industry until poor fishery management combined with effects of El Niños resulted in an anchoveta crash (Idyll 1973; Canby 1984).

Because of the effects of altitude as it relates to climate, ecosystems change, often dramatically, from the base to the top of a mountain. Working in the western United States in the late 1800s, C. Hart Merriam described what he termed *life zones*, distinct bands of vegetation, each encircling a mountain within a certain range of altitude. Creosote bush and cactus desert or *Lower Sonoran* life zone is replaced by a forest of pinyon pine and juniper or *Upper Sonoran* life zone, which is followed by ponderosa pine *Transition* zone, this giving way to spruce and fir of the *Canadian* and *Hudsonian* life zones. Zonation may appear to be sharp, but in reality one life zone gradually changes into another, often with much overlap. Life zones occur because altitude results in changing climatic conditions that favor different sets of species. It generally gets colder and wetter with altitude.

South American mountains also exhibit zonation patterns, noted in detail by Humboldt in the early nineteenth century. Though Merriam's life zone concept is well known, Humboldt actually preceded Merriam in describing the concept (Morrison 1976). He carefully documented how lowland rainforest gradually changes to montane rainforest, becoming cloud forest at higher altitudes. At its altitudinal extreme, cloud forest may be stunted, becoming a bizarre elfin forest of short, gnarled, epiphyte-laden trees (page 220). Higher still on some mountains is treeless paramo, an alpine shrubland, or puna, an alpine grassland. In general, temperature drops about 1.5°C (4°F) for every 305 m (1,000 ft) rise in elevation along a South American mountainside, an effect that is responsible in large part for the dramatic change in ecosystems. Tropical forest rarely occurs above 1,700 m (approximately 5,000 ft), with subtropical forest between 1,700 m and 2,600 m (5,000–8,500 ft). Above that, climatic conditions are sufficiently severe that only paramo or puna exists.

Zonation patterns are often complex. For example, in southern Peru, near Cuzco, I ascended to about 4,200 m (14,000 ft) and found wet puna, a heathland of orchids, heather, and sphagnum moss intermingled with paramo. Montane ecosystems, their ecology and natural history, are discussed in detail in chapter 9.

Major Neotropical Ecosystems

Hylaea—The Tropical Rainforest

Figures 13, 22, 32

> Here no one who has any feeling of the magnificent and the sublime can be disappointed; the sombre shade, scarce illuminated by a single direct ray even of the tropical sun, the enormous size and height of the trees, most of which rise like huge columns a hundred feet or more without throwing out a single branch, the strange buttresses around the base of some, the spiny or furrowed stems of others, the curious and even extraordinary creepers and climbers which wind around them, hanging in long festoons from branch to branch, sometimes curling and twisting on the ground like great serpents, then mounting to the very tops of the trees, thence throwing down roots and fibres which hang waving in the air, or twisting round each other form ropes and cables of every variety of size and often of the most perfect regularity. These, and many other novel features—the parasitic plants growing on the trunks and branches, the wonderful variety of the foliage, the strange fruits and seeds that lie rotting on the ground—taken altogether surpass description, and produce feelings in the beholder of admiration and awe. It is here, too, that the rarest birds, the most lovely insects, and the most interesting mammals and reptiles are to be found. Here lurk the jaguar and the boa-constrictor, and here amid the densest shade the bell-bird tolls his peal.

So wrote Alfred Russel Wallace (1895), who spent four years exploring along the Rio Negro and Amazon and is credited, along with Charles Darwin, for proposing the theory of natural selection (chapter 4). Though rainforest impressed both Wallace and Darwin favorably, it has been depicted in art and literature in ways that range widely, from hauntingly idyllic to the infamous "green hell" image that typified the writings of authors such as Joseph Conrad (Putz and Holbrook 1988). What, exactly, is rainforest?

The Neotropical rainforest was first described by Alexander von Humboldt, who called it *hylaea,* the Greek word for "forest" (Richards 1952). The rainforest is what much of this book is about, so I will merely define it here and save the details for later.

A rainforest, in its purest form, is essentially a nonseasonal forest dominated by broad-leaved evergreen trees, sometimes of great stature, where rainfall is both abundant and constant. Rainforests are lush, with many kinds of vines and epiphytes (air plants) growing on the trees. In general, a rainforest receives at least 200 cm (just under 80 in) of rainfall annually, though it can be much more, with precipitation spread relatively evenly from month to month. Most of the tropics consist, however, of forests where *seasonal* variation in rainfall is both typical and important. Technically, a tropical forest with abundant asonal rainfall is called a *moist forest*: an evergreen or partly evergreen e trees may be deciduous) forest receiving not less than 100 mm (4 in) of pitation in any month for two out of three years, frost-free, and with an al temperature of 24°C (75° F) or more (Myers 1980). Since the term *rest* is in such widespread and common usage, in this book I will continue efer to lush, moist, tropical forests, seasonal or not, as rainforests. I've been many, and, believe me, it rains a lot. Gets pretty muddy too.

The "Jungle"—Disturbed Forest Areas — *Figures 27, 36*

When rainforest is disturbed, such as by hurricane, lightning strike, isolated ee fall, or human activity, the disturbed area is opened, permitting the pene- ation of large amounts of light. Fast-growing plant species intolerant of shade e temporarily favored, and a tangle of thin-boled trees, shrubs, and vines sults. Soon a huge, dense, irregular mass of greenery, or "jungle," covers the ap created by the disturbance. Trees are thin boled and very close together. Palms and bamboos may abound along with various vines, creating thick tan- les. To penetrate a jungle requires the skilled use of that most important of all tropical tools, the machete. Jungles are *successional;* they will eventually re- urn to shaded forest as slower-growing species outcompete colonizing species. What has been realized in recent years is that tropical forests are far more subject to natural disturbance than had been previously thought. Disturbance may, in fact, be responsible for many of the ecological patterns evident in tropical forests, including the high diversity of species. I will discuss distur- bance patterns and ecological succession in the tropics in detail in chapter 3.

Tropical Riverine and Floodplain Ecosystems — *Figures 155, 156, 160, 162*

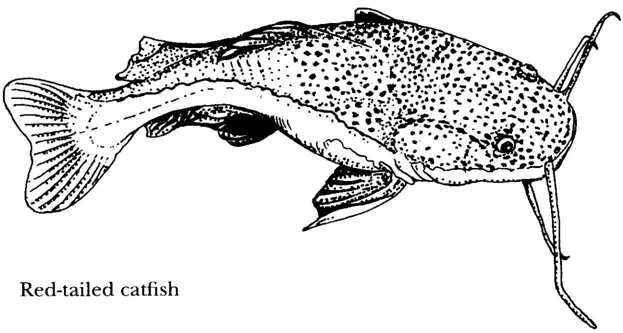
Two major river basins profoundly influence the ecology of South America: the Orinoco and the Amazon. These great rivers and their adjacent ecosystems form the subjects of chapter 8.

Forests that border rivers are termed *gallery forests,* and these forests are affected by often dramatic seasonal changes in riverine water level, which occur all along the Amazon, the Orinoco, and their various tributaries. The rainy season typically brings floods. Where rivers drain young mountain systems, such as the Andes, eroded mineral-rich soil from mountain areas is carried long distances, much of it eventually to be deposited along riverbank flood plains. In Amazonia, the term *varzea* is used for floodplain forests that line rivers rich in Andean sediment, and these forests make up only about 2% of the huge Amazon Basin area (Meggars 1988). The sediment-rich rivers tend to be cloudy from the sediment load and are called *whitewater rivers* (though "mocha" would seem a more apt term), as typified by much of the Amazon itself (especially the Solimoes or upper Amazon) as well as some of its major tributaries, such as the Madeira. Some rivers, such as the vast Rio Negro, drain geologically ancient soils that have undergone millions of years of erosion, becoming depleted of minerals. These waters carry almost no sediment, instead being clear but often dark, the so-called *blackwater rivers.* The dark coloration is caused by "humic matter," dissolved organics from vegetation decomposition (page 56). Forests along the floodplain of blackwater rivers are typically called *igapo.* Black- and whitewater rivers represent two opposites on a spectrum. There are also some rivers with low levels of sediment and intermediate concentrations of phenolics, organic compounds from decomposing leaves. These are termed "clearwater" rivers, as typified by the Rio Tapajos, the Rio Xingu, and the Rio Tocantins.

Of course, most forest (about 96–97%!) in Amazonia is found completely off the floodplain, and such forest is referred to as *terra firme.*

Only about 3–4% of the forest area in the Amazon Basin is floodplain. About half of these forests are *varzea* and receive rich sediment from the Andes during the time of flood, with a floodplain extending up to 80.5 km (50 miles) from the river bank. During wet season, the river depth may rise anywhere from 7.6 to 15 m (25–50 ft). Whole islands of vegetation are torn loose from the banks and drift downriver. Quiet pools may harbor groups of giant Victoria waterlilies (*Victoria amazonica*), a remarkable six-foot-wide lily pad with upright edges, the entire plant resembling a gargantuan green coaster.

Rivers and their banks support an exciting diversity of animals, including two species of freshwater dolphins, giant otter, capybara, anaconda, various alligator-like caimans, and many unique bird species. More than 2,400 species of fish, an astounding variety, inhabit the waters of the Amazon and its tributaries.



Red-tailed catfish

Savanna and Dry Forest

Figures 10, 11, 12

Part of the Neotropics consists of grasslands scattered with trees and shrubs, an ecosystem called a *savanna.* Savannas may be relatively wet, like the Florida Everglades, or dry and sandy. Neotropical seasonal savannas include the vast Llanos and Gran Sabana of southern Venezuela and the extensive Pantanal of southern Brazil and neighboring Bolivia, as well as much of the Chaco region of Paraguay. A combination of climatic and pronounced seasonal effects, occasional natural burning, and various soil characteristics produce savannas. Human influence also can contribute significantly to their formation. The African plains are an immense area of natural savanna, but savanna is considerably less extensive in the Neotropics, where rainforest dominates. Large expanses of savanna occur also in Central America. They are low-diversity

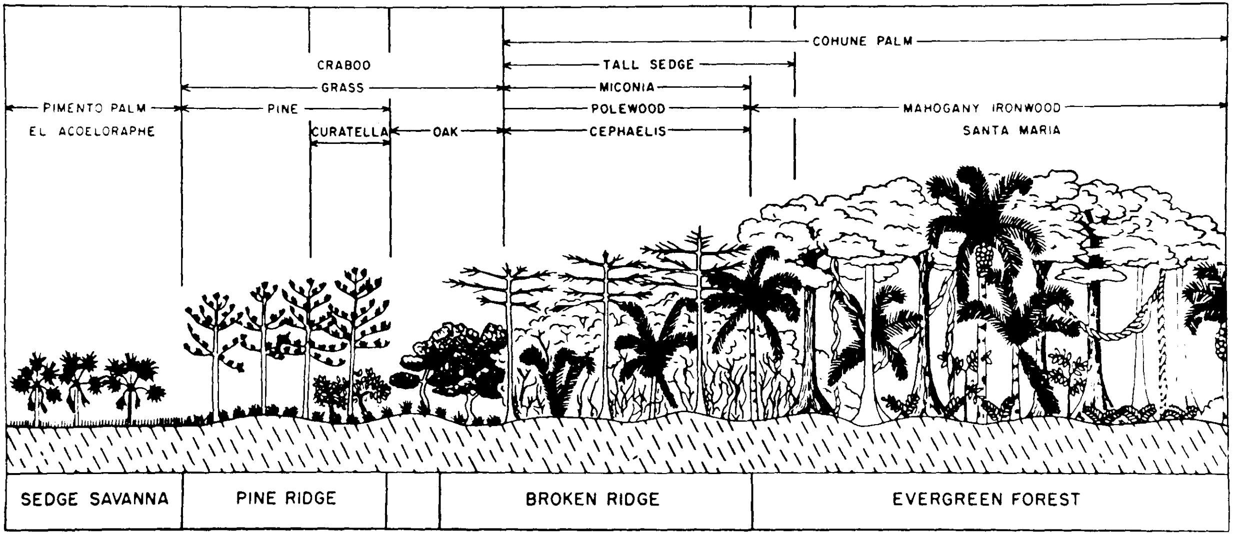


Diagram showing the range of ecosystem types present in parts of Belize.

eocsystems often numerically dominated by one tree species, Caribbean pine (*Pinus caribaea*).

Because they are open areas, savannas afford ideal habitats for seeing wildlife. Though Neotropical savannas lack the large game herds that characterize their African counterparts, there are numerous animal species that depend on savannas.

In addition to savannas, there are habitats of open woodlands, often with many decidous trees. These dry forests typically occur in areas where there is a pronounced dry season, and as such, dry forests often intermingle with savannas. Savanna and dry forest ecology and natural history are treated in chapter 10.

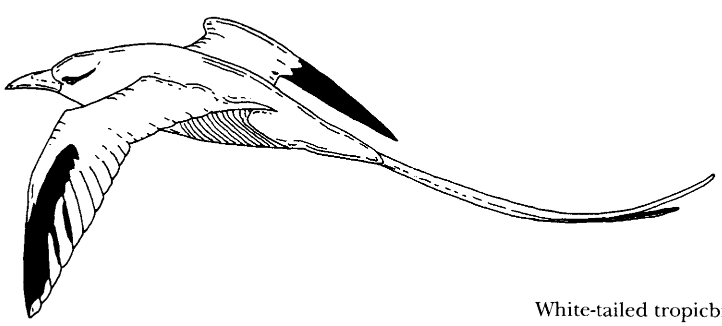
Coastal Ecosystems—Mangal and Seagrass *Figures 14, 15, 17, 18, 19*

Mangroves are a group of unrelated but highly salt-tolerant tree species forming the dominant vegetation along tropical coastlines, lagoons, deltas, estuaries, and cayes. The ecological community they form is termed *mangal.* Tangled forests of mangroves, some with long prop roots, others with short "air roots" protruding up from the thick sandy mud, are the nesting sites of colonies of magnificent frigatebirds (man-o-war birds) (*Fregata magnificens*), boobies (*Sula spp.*), and brown pelicans (*Pelicanus occidentalis*). Mangroves have an essential role in the ecology of coastal areas and contribute to the health of nearby coral reefs.

Protected by the mangrove cayes, beds of seagrass cover shallow, well-lit coral sand. Like the mangroves, seagrass contributes to the health of the diverse coral reef.

Coral Reef *Figures 20, 21*

To most visitors, the most exciting of all the coastal ecosystems is the coral reef. Approximately sixty species of coral occur in the Caribbean. Reefs of elkhorn, staghorn, finger, brain, and star corals provide habitats for myriad colorful fish, shrimps, lobsters, sea stars, brittle stars, and sea cucumbers. Mangrove, seagrass, and coral reef ecology is discussed in chapter 11.



White-tailed tropicbird