2

Rainforest Structure and Diversity

TALL, green, complex-looking, and surprisingly dark inside. . . . Feeling just a little claustrophobic beneath the dense foliage above. . . . Strange bird sounds heard over a cacophony of calling insects. . . . A screeching parrot flock dashes overhead. . . . The tree crowns seem so far away, not easy to see what's in them. . . . Tree trunks propped up by tall, flaring roots. . . . No thick ground or shrub cover, actually rather easy to walk among the widely spaced trees. . . . Except worried about encountering snakes. . . . Lots of palms, some with thorny trunks. . . . Palm fronds russle in the slightest breeze. . . . Occasional openings in the canopy, sunny islands surrounded by a sea of deep shade. . . . Tangled growth in these sunny spots. . . . Lots of sunflecks. . . . Vines draped everywhere, some twisted, looking braided like rope, interconnecting trees. . . . Brilliant, almost neon-colored butterflies. . . . Lizards make thick leathery leaves crackle as they scamper over them. . . . Trails muddy, and mud sticks to boots. . . . Hot, even though shady; oppressively humid.

These are some typical notebook entries that might be made upon initial encounter with tropical rainforest. It doesn't matter whether you're standing in Peruvian, Brazilian, Ecuadorian, Belizean, Costa Rican, or Venezuelan rainforest, it all at first glance looks pretty much the same. It even sounds, smells, and feels generally the same. All over the equatorial regions of the planet where rainforest occurs, the forest tends to have a similar physical structure and appearance. Of course, on closer inspection, numerous differences exist among rainforests both within and among various geographical areas. On a global scale, one does not find orangutans or rattan palms in Venezuela, nor sloths or hummingbirds in Sumatra. And within the Neotropics, rainforests in Costa Rica are different in many significant ways from their counterparts in Brazil. And in Brazil, Amazonian forests show considerable differences from site to site, some sites hosting dense rainforest, some more open forest with palms, some open forest without palms, and some open forest with abundant lianas (Pires and Prance 1985). Rainforests on poor soils differ markedly from those on richer soils, just as rainforests on terra firma are distinct in some important ways from those on floodplains. However, the overall similarities, apparent as first impressions, are striking. Charles Darwin (1839) wrote of his initial impressions of tropical rainforest: “In tropical forests, when quietly walking along the shady pathways, and admiring each successive view, I wished to find language to express my ideas. Epithet after epithet was found too weak to convey to those who have not visited the intertropical regions the sensation of delight which the mind experiences."

Field Trip to a Peruvian Rainforest

Imagine we are standing at the edge of a tropical rainforest near Iquitos, Peru, along the westernmost part of the massive Amazon River in the very heart of equatorial South America. More kinds of plants and animals are to be found here than just about any other place on Earth. It's just after dawn, the hot sun has not yet risen high, and the air is so humid that the dampness makes it seem almost cool. Storm clouds are already gathering, but it's not yet raining. There is a well-marked trail leading us into the forest. We enter. It rained during the night and the trail is muddy and slippery.

Structural Complexity

Figures 13, 22, 46

Once inside a rainforest, structural complexity is obvious. How immense it seems, and how dark and enclosing as dense canopy foliage shades the forest interior, especially in the attenuated early morning light. Near a stream beside the forest edge, a pair of blue-and-yellow macaws (*Ara araraura*), their brilliant plumage muted, perch high on a moriche palm frond. With a pale sky overhead and shade inside the forest, highly colorful birds like these large macaw parrots often look subdued. Even at midday, when the sun is high overhead, only scattered flecks of sunlight dot the interior forest floor. Shade prevents a dense undergrowth from forming, and we certainly do not need our machete to move about. Plants we've seen only as potted houseplants grow here "in the wild." There's a clump of *Dieffenbachia* directly ahead on the forest floor. Large arum vines, philodendrons like *Monstera*, with its huge, sometimes deeply lobed leaves, are climbing up tree trunks. The biggest trees tend to be widely spaced, many with large, flaring buttressed roots, some with long, extended prop roots. All the trees are broad-leaved. There seem to be no equivalents of the needle-leaved trees of the temperate zone, the pines, spruces, and hemlocks. Palms abound, especially in the understory, and many have whorls of sharp spines around their trunks. Tree boles are straight and most rise a considerable height before spreading into crowns, which, themselves, are hard to discern clearly because so much other vegetation grows among them. Clumps of cacti, occasional orchids, many kinds of ferns, and an abundance of pineapple-like plants called bromeliads adorn the widely spreading branches. It's frustrating to try to see the delicate flowers of the orchids so high above us, but binoculars help. Vines, some nearly as thick as tree trunks back home, hang haphazardly, seemingly everywhere. Rounded, basketball-sized termite nests are easy to spot on the trees, and the dried tunnels made by their inhabitants vaguely suggest brown ski trails running along the tree trunks.

North American broadleaf forests are often neatly layered. There is a nearly uniform canopy, the height to which the tallest trees, such as the oaks and maples, grow, a subcanopy of understory trees such as sassafras and flowering dogwood, a shrub layer of viburnums or mountain laurel, and a herbaceous layer of ferns and wildflowers.

The tropical rainforest is not neatly layered (Richards 1952), and up to five poorly defined strata can be present (Klinge et al. 1975). The forest structure (called physiognomy) is complex (Hartshorn 1983a). Some trees, called emergents, erupt above the canopy to tower over the rest of the forest. Trees are of varying heights, including many palms, in both understory and canopy. Most trees are monotonously green, but a few may be bursting with colorful blossoms, while others may be essentially leafless, revealing the many epiphytes that have attached themselves to their main branches. Shrubs and other herbaceous plants share the heavily shaded forest floor with numerous seedling and sapling trees, ferns, and palms. It is difficult to perceive a simple pattern in the overall structure of a rainforest. Complexity is the rule.

Typical Tropical Trees

Figures 25, 34

A mild irony of nature in the tropics is that, though there are more different tree species than anywhere else (see below and chapter 3), many are sufficiently similar in appearance so that one can meaningfully describe a "typical tropical tree." Broad-leaved trees inside a rainforest tend, on first inspection, to look much alike, though an experienced observer can accurately identify many, if not most, at least to the level of family (and often genus). What follows is a general description of tropical tree characteristics, a description that will apply not only in the Neotropics but also to rainforests in tropical Africa and Southeast Asia.

STATURE

Figures 33, 34, 35

Tropical rainforests have a reputation for having huge trees. Old engravings depict trees of stunning size with up to a dozen people holding hands around the circumference of the trunk. No pun intended (well, truth be told, it is intended), but such accounts generally represent "tall tales." Tropical trees can, indeed, be both wide and lofty, but bear in mind that many look taller than they really are because their boles are slender (just as a thin person gives the appearance of being taller than a stocky person of equal height), and branches tend not to radiate from the trunk until canopy level, thus enhancing the tall look of the bole. The tallest tropical trees are found in lowland rainforests, and these range in height between 25 and 45 meters (roughly 80–150 ft), the majority around 25–30 m. Tropical trees occasionally exceed heights of 45 m (150 ft), and some emergents do top 61 m (200 ft) and may occasionally approach 90 m (300 ft), though such heights are uncommon. I have been in quite a few temperate-zone forests with equally tall or taller trees. In the United States, Sierra Nevada giant sequoia groves, coastal California redwood groves, and Pacific Northwest old-growth forests of sitka spruce, common Douglas fir, western red cedar, and western hemlock all routinely exceed the height of the trees comprising the majority of tropical forests. So do the temperate bluegum eucalyptus forests in southeastern Australia. Neither the

Profile diagram of primary mixed forest, Moraballi Creek, Guyana. The diagram represents a strip of forest 41 m (135 ft) long and 7.6 m (25 ft) wide. Only trees over 4.6 m (15 ft) high are shown. From Richards (1952). Reproduced with permission.

tallest, the broadest, nor the oldest trees on Earth occur in rainforest: the tallest is a California redwood, at 112 m (367 ft); the broadest is a Montezuma cypress in subtropical Mexico, with a circumference of almost 49 m (160 ft); and the oldest is a bristlecone pine in the White Mountains of eastern California, about 4,600 years old.

BUTTRESSES AND PROP ROOTS

Figures 57, 58, 59, 60

A buttress is a root flaring out from the trunk to form a flangelike base. Many, if not most, rainforest trees have buttressed roots, giving tropical rainforests a distinctive look in comparison with temperate forests (though old-growth temperate rainforest trees such as are found in the Pacific Northwest are sometimes weakly buttressed). Several buttresses radiate from a given tree, surrounding and seeming to support the bole, often making cozy retreats for snakes. Buttress shape is sometimes helpful in identifying specific trees. Buttresses can be large, often radiating from the bole six or more feet from the ground.

The function of buttressing has been a topic of active discussion among tropical botanists. Because buttressing is particularly common among trees of stream and river banks as well as among trees lacking a deep taproot, many believe that buttressing acts principally to support the tree (Richards 1952; Longman and Jenik 1974). I was once told of a team of botanists in Costa Rica who were discussing several esoteric theories for the existence of buttresses when their local guide offered the comment that buttresses hold up the tree. When the guide's opinion was dismissed lightly, he produced his machete and adeptly cut away each of the buttresses from a nearby small tree. He then casually pushed the tree over. Whether it is true or false that buttresses function principally for support, they may indeed serve other functions related to root growth patterns (page 54). Some trees lack buttresses but have stilt or prop roots that radiate from the tree's base, remaining above ground. Stilt roots are particularly common in areas such as floodplains and mangrove forests (page 240) that become periodically innundated with water. Some tropical trees, including the huge Brazilnut tree (*Bertholletia excelsa*), lack both buttresses and prop roots and have instead either horizontal surface roots or deeper underground roots. In a few cases, large taproots occur.

TRUNKS AND CROWNS

Figures 25, 26, 31

As we look around the Peruvian forest, we notice that many trees have tall, slender boles. The bark may be smooth or rough, light colored or dark, almost white in some cases, almost ebony in others. Bark is often splotchy, with pale and dark patches. There is much variability. Tropical tree bark may be thin, but on some trees it can be thick (and the wood inside may be very hard—remember that wood-eating termites abound in the tropics). Bark is not usually a good means of identifying the tree, as many different species may have similar-appearing bark. Some trees, however, such as the chicle tree (*Manilkara zapota*) of Central America (the original source of the latex base from which chewing gum is manufactured), have distinct bark. Chicle bark is black and vertically ridged into narrow strips, the inner bark red, with white resin. The color and taste of the underlying cambium layer is sometimes a good key to identifying the tree species (Richards 1952; Gentry 1993).

Many canopy trees have a spreading, flattened crown (Richards 1952). Main branches radiate out from one or a few points, somewhat resembling the spokes of an umbrella. Each of these main radiating branches contributes to the overall symmetrical crown, an architectural pattern called *sympodial* construction. Of course, the effect of crowding by neighboring trees can significantly modify crown shape. Single trees left standing after adjacent trees have been felled often have oddly shaped crowns, a result of earlier competition for light with neighboring trees. Many trees that grow both in the canopy and in the shaded understory have foliage that is *monolayered*, where a single, dense blanket of leaves covers the tree. Trees in the understory are often lollipop-shaped and monolayered. Because they have not yet reached the canopy, their crowns are composed of lateral branches from a single main trunk, a growth pattern termed *monopodial*. Lower branches will eventually drop off through self-shading as the tree grows and becomes a sympodial canopy tree. Trees growing in forest gaps where sunlight is much more abundant (see below and chapter 3) are *multilayered*, with many layers of leaves to intercept light (Horn 1971; Hartshorn 1980, 1983a). The architecture of tropical trees is discussed further in Halle et al. (1978).

Many tropical trees, not just in the Neotropics but globally, exhibit a unique characteristic termed *cauliflory*, meaning the flowers and subsequent fruits abruptly grow from the wooded trunk, rather than from the canopy branches. Cauliflory generally does not occur outside of the tropics. Cocoa (*Theobroma cacao*), from which chocolate is produced, is a cauliflorous understory tree (page 185). Some trees may be cauliflorous due to the large, heavy fruits that are produced, the weight of which could not be supported on outer branches (though it is equally arguable that the opposite may be the case—the fruits may have grown large and heavy *because* they were growing from the trunk, not the outer branches). The presence of cauliflorous flowers may facilitate pollination by large animals such as bats, or, equally likely, cauliflorous fruiting may facilitate dispersal of seeds from fruit consumption by large, terrestrial animals that could not reach canopy fruits. A similar phenomenon, ramiflory, is the bearing of flowers on older branches or occasionally underground.

LEAVES

Figure 37

Leaves of many tropical tree species are surprisingly similar in shape, making species identification difficult (but see below, *Identifying Neotropical Plants*). The distinctive lobing patterns of many North American maples and oaks are missing from most tropical trees. Instead, leaves are characteristically oval and unlobed, and they often possess sharply pointed ends, called *drip tips*, which help facilitate rapid runoff of rainwater (page 49). Leaves of most species have smooth margins rather than "teeth," though serrated leaves are found in some species. Both lowland and montane tropical forest trees produce heavy, thick, leathery, waxy leaves that can remain on the tree for well over a year. Many tropical species produce palmate leaves, where the leaflets radiate like spokes from a center, forming a shape similar to that of a parasol. Some leaves, particularly those on plants that are found in disturbed areas such as gaps, are very large, well in excess of temperate zone species. Though many trees have simple leaves, compound leaves are by no means uncommon, particularly due to the abundance of legumes, a highly species-rich plant family (page 70). Tropical leaves, with some exceptions, tend to show little obvious insect damage (see chapter 6).

FLOWERS

Many tropical trees have colorful, fragrant blossoms, often large in size. Typical examples include such species as coral tree (*Erythrina* spp.), pink poui (*Tabebuia pentaphylla*), cannonball tree (*Couroupita guanianensis*), frangipani (*Plumeria* spp.), and morning glory tree (*Ipomoena arborescens*). Many striking trees that are abundantly represented in the Neotropics are actually imported from other tropical regions. For instance, the gorgeous and widespread flamboyant tree (*Delonix regia*), the national tree of Puerto Rico, is actually native to Madagascar. The bottle brush tree (*Callistemom lanceolatus*) is from Australia, and the Norfolk Island pine (*Araucaria excelsa*) is from, well, you guessed it. (In case you didn't, it's from Norfolk Island in the southern Pacific Ocean.)

Red, orange, and yellow are associated with bird-pollinated plants such as *Heliconia*, while lavender flowers such as *Jacaranda* are more commonly insect-pollinated. Some trees, such as silk-cotton or kapok (*Ceiba pentandra*), flower mostly at night, producing conspicuous white flowers that, depending on species, attract bats or moths. Fragrant flowers are mostly pollinated by moths, bees, beetles, or other insects. Bat-pollinated flowers smell musty, kind of like the bats themselves (page 129). Because of the high incidence of animal pollination, especially by large animals such as birds, bats, and large lepidopterans, flowers tend not only to be large but also to be nectar-rich and borne on long stalks or branches away from leaves, or else on the trunk (cauliflory, above). Many flowers are tubular or brushlike in shape, though some, particularly those pollinated by small insects, are shaped as flattened bowls or plates. Though animal pollination is fairly general, wind pollination occurs in some species of canopy trees.

FRUITS AND SEEDS

Many tropical trees produce small to medium-sized fruits, but some produce large, conspicuous fruits and the seeds contained within are large as well. Indeed, another distinctive characteristic of tropical forests is the abundance of trees that make large fruits. Many palms, the coconut (*Cocos nucifera*) for example, produce large, hard fruits in which the seeds are encased. The monkey pot tree (*Lecythis costaricensis*) produces thick, 20-cm (8-inch)-diameter "cannon ball" fruits, each containing up to fifty elongated seeds. The seeds are reported to contain toxic quantities of the element selenium (Kerdal-Vargas in Hartshorn 1983b), perhaps serving to protect the tree from seed predators (see below). The milk tree (*Brosimum utile*) forms succulent, sweet-tasting, edible fruits, each with a single large seed inside. This tree, named for its white sap (which is drinkable), may have been planted extensively at places like Tikal by Mayan Indians (Flannery 1982 and page 183). The famous Brazil nut comes from the forest giant *Bertholletia excelsa*. The nuts are contained in large, woody, rounded pods that break open upon dropping to the forest floor. Many tree species in the huge legume family package seeds in long, flattened pods, and the seeds tend to contain toxic amino acids (page 147). Among the legumes, the stinking toe tree (*Hymenaea courbaril*) produces 12.7-cm (5-in) oval pods with five large seeds inside. The pods drop whole to the forest floor and often fall prey to agoutis and other forest mammals as well as various weevils.

Large fruits with large seeds are a major food source for the large animals of the forest. Among the mammals, monkeys, bats, various rodents, peccaries, and tapirs are common consumers of fruits and seeds, sometimes dispersing the seeds, sometimes destroying them. Agoutis, which are rodents, skillfully use their sharp incisors to gnaw away the tough, protective seed coat on the Brazil nut, thus enabling the animal to eat the seed contained within. Some extinct mammals, such as the giant ground sloths and bovinelike gomphotheres, may have been important in dispersing large seeds of various tropical plants. Birds such as tinamous, guans, curassows, doves and pigeons, trogons, toucans, and parrots are also attracted to large fruits and the seeds within them. Along flooded forests, some fish species are important fruit consumers and seed dispersers (page 204). Insects especially are frequent predators of small seeds.

Some trees have wind-dispersed seeds and thus the fruits are usually not consumed by animals. The huge silk cotton or kapok tree is so-named because its seeds are dispersed by parachute-like, silky fibers that give the tree one of its common names. Mahogany trees (*Swietenia macrophylla* and *S. humilis*), famous for their superb wood, develop 15-cm (6-in) oval, woody fruits, each containing about forty seeds. The seeds are wind-dispersed and would be vulnerable to predation were it not for the fact that they have an extremely pungent, irritating taste.

Palms — *Figures 16, 29*

Palms, which occur worldwide, are among the most distinctive Neotropical plants, frequenting interior rainforest, disturbed areas, and grassy savannas. They are particularly abundant components of swamp and riverine forest. There are 1,500 species of palms in the world and 550 in the Americas (Henderson et al. 1995). Alfred Russel Wallace (1853) made a detailed study of South American palms and published an important book on the subject. All palms are members of the family Palmae, and all are monocots, sharing characteristics of such plants as grasses, arums, lilies, and orchids. The most obvious monocot feature of palms is the parallel veins evident in the large leaves, which themselves are referred to as palm fronds. Palms are widely used by indigenous peoples of Amazonia for diverse purposes: thatch for houses, wood to support dwellings, ropes, strings, weavings, hunting bows, fishing line, hooks, utensils, musical instruments, and various kinds of food and drink. Indeed, many palm species have multiple uses and are thus among the most important plant species for humans.

Palms are often abundant in the forest understory and are frequently armed with sharp spines along the trunks and leaves. Be especially careful not to grab a palm sapling as the spines can create a wound and introduce bacteria.

Identifying Neotropical Plants — *Figure 41*

Palms are fairly easy to identify, at least to the level of genus, but what about all those other trees and shrubs in the rainforest? The bad news is that for the vast majority of students of Neotropical biology, it will not be possible to identify accurately most plants (including palms) to the level of species. There are just too many look-alike species, and the ranges of many species are not precisely known; thus species identification must be left to taxonomic experts. Also, there are essentially no field guides to Neotropical plants, at least not at the level of species. Lotschert and Beese (1981) is a useful but very general guide to many of the most widespread and conspicuous tropical plants, and Henderson et al. (1995) is a complete guide to palms of the Americas. Gentry (1993) is currently the most useful guide to Neotropical woody plants, but, though 895 pages in length and weighing in at about three pounds (softcover), it includes only the countries of Colombia, Ecuador, and Peru and deals with identifications only at the level of family and genera (a smaller-format version is now available). Croat (1978) is a large volume (943 pages) on the flora of Barro Colorado Island in Panama. Hopefully, as the Neotropics become better known, more guides to plants will be published for various regions.

The good news is that it is indeed possible to identify many, if not most, Neotropical plants to the level of family, and many of those to the level of genus (Gentry 1993). Using combinations of characteristics such as leaf shape (palmate, pinnate, bipinnate), compound versus simple leaves, opposite versus alternate leaves, presence or absence of tendrils, presence or absence of spines, smooth or serrate leaf edges, fruit and/or flower characteristics, and even, in many cases, odor and taste, you can, with a guide such as Gentry's, master the flora, no mean feat since Gentry describes 182 flowering plant families.

Climbers, Lianas, Stranglers, and Epiphytes

As we continue our perambulations through the Peruvian rainforest we cannot help but notice the plethora of vines and epiphytes. Trees are so laden with these hitchhikers that it is often a challenge to discern the actual crown from the myriad ancillary plants. With binoculars and practice, however, we can begin to make some sense of what is growing where and on what. In this lowland Peruvian forest epiphytes are abundant, but there is much variability from one forest site to another. Generally epiphytes and vines are most abundant where humidity is highest, declining in frequency in forests that experience a strong dry season.

VINES

Figures 22, 23, 50, 51, 52, 58

Vines are a conspicuous and important component of most tropical rainforests (though vine density is often quite variable from site to site), and they come in various forms. Vines are a distinct and important structural feature of rainforests, in a sense literally tying the forest together. They account for much of the biomass in some rainforests, they compete with trees for light, water, and nutrients, and many are essential foods for various animals. In the Neotropics, 133 plant families include at least some climbing species. Some, called *lianas*, entwine elaborately as they dangle from tree crowns. Others, the bole climbers, attach tightly to the tree trunk and ascend. Still others, the stranglers, encircle a tree and may eventually choke it. All told, there are nearly 600 species of climbers in the Neotropics (Gentry 1991). Tropical vines occur abundantly in disturbed sunlit areas as well as in forest interiors, at varying densities and on virtually all soil types. Humans make extensive use of vines for foods, medicines, hallucinogens, poisons, and construction materials (Phillips 1991). For a comprehensive account of vine biology, see Putz and Mooney (1991).

A liana usually gets its start when a forest opening called a gap is created (page 33), permitting abundant light penetration. Lianas typically begin life as shrubs rooted in the ground but eventually become vines, with woody stems as thick or thicker than the trunks of many temperate zone trees. Tendrils from the branches entwine neighboring trees, climbing upward, reaching the tree crown as both tree and liana grow. Lianas spread in the crown, and a single liana may eventually loop through several tree crowns. Lianas seem to drape limply, winding through tree crowns or hanging as loose ropes parallel to the main bole. Their stems remain rooted in the ground and are oddly shaped, often being flattened, lobed, coiled like a rope, or spiraled in a helixlike shape.

The thinnest have remarkable springiness and often will support a person's weight, at least for a short time. Some liana stems are hollow, containing potable water, attainable through the use of a machete.

Liana is a growth form, not a family of plants, and thus lianas are represented among many different plant families (Leguminosae, Sapindaceae, Cucurbitaceae, Vitaceae, Smilacaceae, and Polygonaceae, to name several). Lianas, like tropical trees, can be very difficult to identify, but some lianas can be identified to the level of genera by noting their distinctive cross-sectional shapes (Gentry 1993).

In Panama, a single hectare (10,000 square meters, or about 2.5 acres) hosted 1,597 climbing lianas, distributed among 43% of the canopy trees (Putz 1984). In the understory, 22% of the upright plants were lianas, and lianas were particularly common in forest gaps. A heavy liana burden reduced the survival rate of trees, making them more likely to be toppled by winds. Fallen lianas merely grew back onto other trees.

Other vines, such as the well-known ornamental arum *Monstera deliciosa* or various philodendrons, are bole climbers. They begin life on the ground. Their seed germinates and sends out a tendril toward shade cast by a nearby tree. The tendril soon grows up the tree trunk, attaching by aerial roots, and the vine thus moves from the forest floor to become anchored on a tree. There it continues to grow ever upward, often encircling the bole as it proliferates. In humid tropical forests it is quite common to see boles totally enshrouded by the wide, thick leaves of climbers. As it grows the plant ceases to be rooted in the ground and becomes a climbing epiphyte (technically referred to as a hemi-epiphyte), its entire root system invested on the tree bark.

The most aggressive vines are the stranglers (*Ficus* spp.). There are approximately 150 species of *Ficus* (figs) in the Neotropics, and an additional 600 or so in the Old World tropics. In the Neotropics, most species are strangers, begining as a seed dropped by a bird or monkey in the tree crown among the epiphytes. Tendrils grow toward the tree bole and downward around the bole, anastomosing or fusing together like a crude mesh. The strangler eventually touches ground and sends out its own root system. The host tree often dies and decomposes, leaving the strangler standing alone. The mortality of the host tree may be caused by constriction from the vine or the shading effect of the vine. It is a common sight in Neotropical forests to see a mature strangler, its host tree having died and decomposed. The strangler's trunk is now a dense fusion of what were once separate vines, now making a single, strong, woody labyrinth that successfully supports a wide canopy, itself now laden with vines.

Vines of many kinds frequent disturbed areas where light is abundant. Members of the family Passifloraceae, some 400 species of passion-flowers (page 155), most of which are native to the Neotropics, are among the most conspicuous vines in the tangles that characterize open areas and roadsides.

EPIPHYTES

Figures 38, 39, 55, 56

As the prefix *epi* implies, epiphytes (air plants) live *on* other plants. They are not internally parasitic, but they do claim space on a branch where they set out roots, trap soil and dust particles, and photosynthesize as canopy residents. Rainforests, both in the temperate zone (such as the Olympic rainforests of

Washington and Oregon) and in the tropics, abound with epiphytes of many different kinds. Cloud forests also host an abundance of air plants. In a lowland tropical rainforest nearly one quarter of the plant species are likely to be epiphytes (Richards 1952; Klinge et al. 1975), though the representation of epiphytes varies. As forests become drier, epiphytes decline radically in both abundance and diversity.

Many different kinds of plants grow epiphytically. In Central and South America alone, there are estimated to be 15,500 epiphyte species (Perry 1984). Looking at a single tropical tree can reveal an amazing diversity. Lichens, liverworts, and mosses, many of them tiny (see below), grow abundantly on trunk and branches, and often leaves. Cacti, ferns, and colorful orchids line the branches. Also abundant and conspicuous on both trunk and branch alike are the bromeliads, with their sharply pointed, daggerlike leaves. The density of epiphytes on a single branch is often high. I witnessed this under somewhat alarming circumstances when, following a heavy downpour in Belize, a tree limb fell from onto my (fortunately for me) unoccupied tent. Though the tent was ruined, I at least (sort of) enjoyed seeing the many delicate ferns and orchids growing among the dense mosses and lichens that completely covered the upper surface of the branch that could have killed me.

Epiphytes attach firmly to a branch and survive by trapping soil particles blown to the canopy and using the captured soil as a source of nutrients such as phosphorus, calcium, and potassium. As epiphytes develop root systems they accumulate organic matter, and thus a soil-organic litter base, termed an epiphyte mat, builds up on the tree branch. Many epiphytes have root systems containing fungi called mycorrhizae. These fungi greatly aid in the uptake of scarce minerals (see below). Mycorrhizae are also of major importance to many trees, especially in areas with poor soil (page 50). Epiphytes efficiently take up water and thrive in areas of heavy cloud cover and mist.

Though epiphytes do not directly harm the trees on which they reside, they may indirectly affect them through competition for water and minerals. Epiphytes get first crack at the water dripping down through the canopy. However, some temperate and tropical canopy trees develop aerial roots that grow into the soil mat accumulated by the epiphytes, tapping into that source of nutrients and water. Because of the epiphyte presence, the host tree benefits by obtaining nutrients from its own canopy (Nadkarni 1981). Perry (1978) suggests that monkeys traveling regular routes through the canopy may aid in keeping branches from being overburdened by epiphytes.

Bromeliads are abundant epiphytes in virtually all Neotropical moist forests. Leaves of many species are arranged in an overlapping rosette to form a cistern that holds water and detrital material. Some species have a dense covering of hairlike trichomes on the leaves that help to absorb water and minerals rapidly. The approximately 2,000 New World bromeliad species are members of the pineapple family, Bromeliaceae, and, like orchids (below), not all grow as epiphytes. There are many areas where terrestrial bromeliads make up a significant portion of the ground vegetation. Epiphytic bromeliads provide a source of moisture for many canopy dwellers. Tree frogs, mosquitos, flatworms, snails, salamanders, and even crabs complete their life cycles in the tiny aquatic habitats provided by the cuplike interiors of bromeliads (Zahl 1975;

Wilson 1991). One classic study found 250 animal species occurring in bromeliads (Picado 1913, cited in Utley and Burt-Utley 1983). Some species of small, colorful birds called euphonias (page 264) use bromeliads as nest sites. Bromeliad flowers grow on a central spike and are usually bright red, attracting many kinds of hummingbirds (page 260).

Orchids are a global family (Orchidaceaé) abundantly represented among Neotropical epiphytes (Dressler 1981). There are estimated to be approximately 25,000–35,000 species worldwide (World Conservation Monitoring Centre 1992), a huge plant family indeed. In Costa Rica, approximately 88% of the orchid species are epiphytes, while the rest are terrestrial (Walterm 1983). Many orchids grow as vines, and many have bulbous stems (called pseudobulbs) that store water. Indeed, the origin of the name "orchid" is the Greek word meaning "testicle," a reference to the appearance of the bulbs (Plotkin 1993). Some have succulent leaves filled with spongy tissue and covered by a waxy cuticle to reduce evaporative water loss. All orchids depend on mycorrhizae during some phase of their life cycles. These fungi grow partly within the orchid root and facilitate uptake of water and minerals. The fungi survive by ingesting some of the orchid photosynthate; thus, the association between orchid and fungus is mutualistic: both benefit. A close look at some orchids will reveal two types of roots: those growing on the substrate and those that form a basket, up and away from the plant. Basket roots aid in trapping leaf litter and other organic material that, when decomposed, can be used as a mineral source by the plant (Walterm 1983). Orchid flowers are among the most beautiful in the plant world. Some, like the familiar *Cattleya*, are large, while others are delicate and tiny. (Binoculars help the would-be orchid observer in the rainforest.) Cross-pollination is accomplished by insects, some quite specific for certain orchid species. Bees are primary pollinators of Neotropical orchids. These include long-distance fliers, like the euglossine bees that cross-pollinate orchids separated by substantial distances (Dressler 1968). Some orchid blossoms apparently mimic insects, facilitating visitation by insects intending (mistakenly) to copulate with the blossom (Darwin 1862). Aside from their value as ornamentals, one orchid genus is of particular importance to humans. There are 90 orchid species in the genus *Vanilla*, of which two are of economic importance, their use dating back to the Aztecs (Plotkin 1993). Dressler (1993) provides a field guide to orchids of Costa Rica and Panama.

In many tropical moist forests, even the epiphytes can have epiphytes. Tropical leaves often are colonized by tiny lichens, mosses, and liverworts, which grow only after the leaf has been tenanted by a diverse community of microbes: bacteria, fungi, algae, and various yeasts, as well as microbial animals such as slime molds, amoebas, and ciliates. This tiny community that lives upon leaves is termed the *epiphyllus* community (Jacobs 1988), and its existence adds yet another dimension to the vast species richness of tropical moist forests. Epiphylls also grow liberally on moist wood, including the spines on trunks of many understory palms and other tree species. This is a good reason to use disinfectant promptly if you are scratched by tropical thorns, as they may have innoculated you with bacteria that could result in an infection (see appendix).

The Understory and Forest Gaps — *Figures 24, 27, 36*

Much of the understory of a tropical forest will be so deprived of light that plant growth is limited. Low light intensity is a chronic feature of rainforest interior and is an important potential limiting factor for plant growth. This is why it is fairly easy to traverse a closed-canopy rainforest. Many of the seedlings and shoots that surround you are those of trees that may or may not eventually attain full canopy status, and a small, unpretentious sapling could be well over twenty years old.

Certain families of shrubs frequently dominate rainforest understory. These include members of the family Melasomataceae (e.g., *Miconia*), the Rubiaceae (e.g., *Psychotria*), and the Piperaceae (e.g., *Piper*). In addition there are often forest interior Heliconias (page 69) and terrestrial bromeliads. Many ferns and fern allies, including the ancient genus *Selaginella*, can carpet much of the forest herb layer.

The understory is frequently far from uniform. The deep shade is interrupted by areas of greater light intensity and denser plant growth. The careful observer inevitably notices the presence of many forest gaps of varying sizes, openings created by fallen trees or parts thereof (like the tree branch that fell on my tent in Belize). Gaps permit greater amounts of light to reach the forest interior, providing enhanced growing conditions for many species. Though understory plants and juvenile trees are adapted to grow very slowly (Bawa and McDade 1994), many are also adapted to respond with quickened growth in the presence of a newly created gap. Recent research at La Selva has revealed a surprisingly high disturbance frequency caused by treefalls and branchfalls, where estimates are that the average square meter of forest floor lies within a gap every hundred years or so (Bawa and McDade 1994). As described by Deborah Clark (1994),

> The primary forest at La Selva is a scene of constant change. Trees and large branches are falling to the ground, opening up new gaps and smashing smaller plants in the process. Smaller branches, bromeliads, and other epiphytes, 6-m-long palm fronds, smaller leaves, and fruits fall constantly as well. The lifetime risk of suffering physical damage is, therefore, high for plants at La Selva.

Gap dynamics has become an important consideration in the study of plant demographics in the rainforest (see chapter 3).

High Species Richness — *Figures 32, 116*

Looking around inside the Peruvian rainforest, we cannot help but wonder just how many things we are looking at and, for that matter, how many are looking back at us. Both animal and plant life are abundant and diverse. The terms *species richness* and *biodiversity* refer to how many different species of any given taxon inhabit a specified area; thus we speak of such things as the species richness of flowering plants in Amazonia, or ferns in Costa Rican montane forests, or birds in Belize, or mammals in Rio Negro igapo forest, or beetles in the canopy of a single ceiba tree, or whatever. High species richness among many different taxons is one of the most distinctive features of tropical forests worldwide and Neotropical lowland forests in particular. In a temperate zone forest it is often possible to count the number of tree species on the fingers of both hands (though a toe or two may be needed). Even in the most diverse North American forests, those of the lush southeastern Appalachian coves, only about 30 species of trees occur in a hectare (10,000 square meters, or about 2.5 acres). In the tropics, however, anywhere from 40 to 100 or more species of trees can occur per hectare. Indeed, one site in the Peruvian Amazon has been found to contain approximately 300 tree species per hectare (Gentry 1988). Brazil alone has been estimated to contain around 55,000 flowering plant species (World Conservation Monitoring Centre 1992). Altogether, about 85,000 species of flowering plants are estimated to occur in the Neotropics (Gentry 1982). This is roughly double the richness of tropical and subtropical Africa, about 1.7 times that of tropical and subtropical Asia, and 5 times that of North America.

British naturalist Alfred Russel Wallace (1895) commented upon the difficulty of finding two of the same species of tree nearby each other. He stated of tropical trees:

> If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colour are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct.

As Wallace implies, though richness is high, the number of individuals within a single species often tends to be low, which is another way of saying that rarity is usual among many species in the lowland tropics. Though some plant species are abundant and widespread (for example, kapok tree), the majority are not, existing in small numbers over extensive areas. The concept of identifying a forest type by its dominant species, which works well in the temperate zone (i.e., eastern white pine forest, redwood forest), is much less useful in the tropics, though not always. On the island of Trinidad one can visit a *Mora* forest where the canopy consists almost exclusively of but a single species, *Mora excelsa*, a tree that can reach the height of 46 m (150 ft). The understory is also dominated by *Mora* saplings, but examples of such low-diversity forests are extremely rare in the Neotropics. At La Selva Biological Station in Costa Rica, one leguminous tree, *Pentaclethra macroloba*, is disproportionately abundant compared with all other species (Hartshorn and Hammel 1994); nonetheless, many other species are present. Among animal taxa, high species richness and rarity also tend to correlate, especially at lowest latitudes (page 86).

Within the Neotropics, species richness, though generally high, shows clear variability. Knight (1975), working on Barro Colorado Island in Panama, found an average of 57 tree species per 1,000 square meters (10,764 sq ft) in mature forest and 58 species in young forest. Knight found that in the older forest, when he counted 500 trees randomly, he encountered an average of 151 species. In the younger forest, he encountered an average of 115 species in a survey of 500 trees. Hubbell and Foster (1986b) have established a 50-

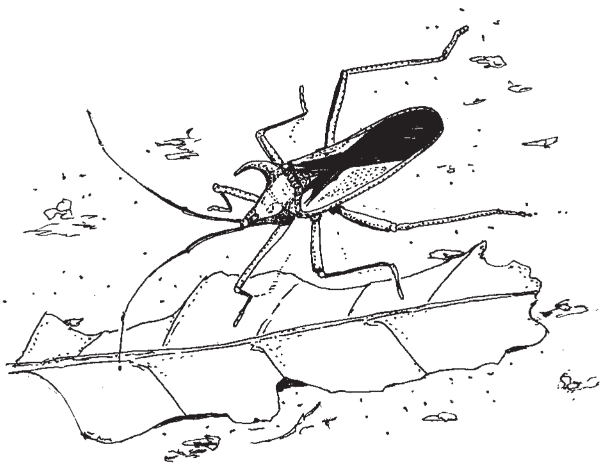
hectare (500,000 sq m) permanent study plot in old-growth forest at BCI. They surveyed approximately 238,000 woody plants with stem diameter of 1 cm (2.5 in) diameter breast height (dbh) or more and found 303 species. They classified 58 species as shrubs, 60 as understory treelets, 71 as midstory trees, and 114 as canopy and emergent trees. Gentry (1988), working in upper Amazonia and Choco, found between 155 and 283 species of trees greater than 10 cm (25.4 in) dbh in a single hectare. When he included lianas of greater than 10 cm dbh, he found that the total increased to between 165 and 300 species. Prance et al. (1976) found 179 species greater than 15 cm (38.1 in) dbh in a 1-ha plot near Manaus, Brazil, on a terra firme forest characterized by poor soil and a very strong dry season.

If all vascular flora are taken together (trees, shrubs, herbs, epiphytes, lianas, but excluding introduced weedy species), the inventory for BCI is 1,320 species from 118 families (Foster and Hubbell 1990; Gentry 1990b). By comparison, the total number of vascular plant species documented at La Selva Biological Station in nearby Costa Rica is 1,668 species from 121 families (Hammel 1990; Gentry 1990b). Let's compare these totals with those from Amazonian rainforests. A floodplain forest on rich soils at Cocha Cashu Biological Station along the Rio Manu, a whitewater tributary of the vast Rio Madeira in southeastern Peru, was found to contain 1,856 species (in 751 genera and 130 families) of higher plants (Foster 1990a). At Reserva Ducke, a forest reserve on poor soils near Manaus in central Amazonia, 825 species of vascular plants from 88 families were inventoried (Prance 1990a; Gentry 1990b).

When the two Central American sites described above (BCI and La Selva) are compared with the two Amazonian sites (Cocha Cashu and Reserva Ducke), there are several important differences. Tree species richness is far greater in Amazonia (Gentry 1986a, 1988, 1990a), but the richness of epiphytes, herbs, and shrubs is greater in Central America. At La Selva, 23% of all vascular plant species are epiphytes, the highest percentage recorded among the closely studied sites (Hartshorn and Hammel 1994). The most species-rich of any of the four sites is Cocha Cashu, located on fertile varzea soils in western Amazonia. A total of 29 plant families that are present at BCI, La Selva, and Cocha Cashu are absent from Reserva Ducke, presumably because of the poor soil conditions at that site. However, the similarities among these four geographically separated forest sites are perhaps more compelling than the differences. The dozen well best-represented plant families are essentially the same for each of the sites. Legumes (Leguminosae), for instance, are the most species-rich family at BCI, Cocha Cashu, and Ducke, and the fifth richest family at La Selva. Of the 153 vascular plant families represented in at least one of the four sites, 66 (43%) are represented at all four sites, a high overlap (Gentry 1990a).

Plants are not the only diverse groups. Insects, birds, amphibians, and most other major groups also exhibit high species richness. A guide to birds of Colombia lists 1,695 migrant and resident species occurring in that country (Hilty and Brown 1986). At Cocha Cashu Biological Station in Amazonian Peru, in an area of approximately 50 square km (19 sq mi), the total species list of birds is approximately 550 (Robinson and Terborgh 1990). At La Selva Biological Station in Costa Rica, an area of approximately 1,500 ha (3,705 acres), 410 species of birds have been found (Blake et al. 1990). In Amazonia, at the Explorer's Inn Reserve in southern Peru, about 575 bird species have been identified within an area of approximately 5,500 ha (13,585 acres) (Foster et al. 1994). By comparison, barely 700 bird species occur in all of North America. More species of birds exist in the Neotropics than in the temperate zone largely because of the unique characteristics of the rainforest (Tramer 1974, and page 95). Bird species richness drops dramatically as soon as you leave the rainforest.

At one site in the Ecuadorian Amazon, the species richness of frogs is 81, which is exactly how many species occur in all of the United States. Indeed, the researcher collected 56 different species on a single night of sampling and reports that it is routine to find 40 or more species in areas of rainforest as small as two square kilometers (Duellman 1992).



Assassin bug

Insect species richness can seem staggering. For the small Central American country of Costa Rica, Philip DeVries (1987) describes nearly 550 butterfly species. At La Selva alone, 204 butterfly species have been identified, and 136 species have been documented for BCI (DeVries 1994). At Explorer's Inn Reserve, 1,234 butterfly species have been identified from an area about 2.0 square km within the reserve (Foster et al. 1994). Edward O. Wilson (1987) reported collecting 40 genera and 135 species of ants from four forest types at Tambopata Reserve in the Peruvian Amazon. Wilson noted that 43 species of ants were found in one tree, a total approximately equal to all ant species occurring in the British Isles! Terry Erwin studied the insect species richness of Neotropical rainforest canopies (page 41) and found 163 beetle species occurring exclusively in but one Panamanian tree species, *Leuhea seemannii*. Erwin then multiplied this figure by the number of different tree species present in the global tropics and concluded that the potential species richness of beetles alone was over 8 million! Since beetles are estimated to represent approximately 40% of all tropical terrestrial arthropod species (including spiders, crustaceans, centipedes, millipedes, and insects), Erwin suggested that the total arthropod species richness of the tropical canopy might be as high as 20 million, and that figure climbs to 30 million when you add in the ground and understory arthropods (Erwin 1982, 1983, 1988; Wilson 1992). Such a species richness seems staggering given that only a total of 1.4 million species of plants, animals, and microbes have as yet been named and described, and it is by no means clear that Erwin's assumptions in making his calculations are accurate. It is nonetheless obvious that many, if not most, aspects of insect species richness remain poorly known, in much need of additional research. New species are virtually guaranteed from every collecting trip.

Species richness and biodiversity patterns of the Neotropics are discussed further in chapters 4 and 14.

A Rainforest Walk: Sights and Sounds of Animals *Figures 93, 112, 146*

The rainforest, unlike the African savanna, does not provide easy views of its abundant animal life. Erwin (1988) noted that most beetles and their six-legged and eight-legged colleagues are in the canopy, far from where you are standing on the forest floor. You really have to work at it to see rainforest animals well. Many are highly cryptic, a result of evolution in a predator-rich environment (page 79). Even the most gaudy birds may appear remarkably dull in the dense forest shade. To make matters worse, some tropical birds, such as trogons and motmots, tend to sit very still for long periods and can easily be missed even when close by. Monkeys noisily scamper through the canopy, but tree crowns are so dense that we can only catch a glimpse of the often hyperkinetic simians. Iguanas remain still, suggesting reptilian gargoyles stretched out on tree limbs high above the forest floor. The animals are there, but finding them is a different matter.

In searching for rainforest animals you should try to adhere to the following guidelines: First, dress in dark clothing. You don't need to wear military-type camouflage, but dark clothing is definitely preferable to light. A bright white T-shirt that says "Save the Rainforest" in scarlet Day-Glo letters is fine back at the field station, but it will give away your presence in the forest. Second, move slowly and quietly, keeping your body motions minimal. Take a few steps along a trail and then stop and look around, beginning with the understory and working your eyes up to the canopy. Third, look for movement and listen for sounds. Leaf movement suggests a bird or other animal in motion. Listen for the soft crackle of leaves on the forest floor. Secretive birds such as tinamous and wood-quail as well as mammals such as agoutis and coatis are often best located by hearing them as they walk.

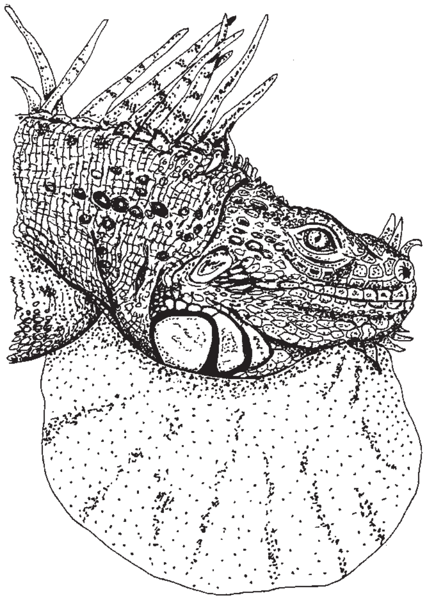
Sounds reveal some of the forest dwellers: there is often a dawn chorus of howler monkeys, the various troops proclaiming their territorial rights to one another, their tentative low grunts soon becoming loud, protracted roars, their combined voices creating one of the most exciting, memorable sounds of Neotropical forests. Cicadas provide a much different kind of background din, their monotonous stridulations reminding one of the oscillating (and irritating) high-low pitch of a French ambulance siren: "HHEeeee-ooooh, heeeee-ooooh, eeeee-ooooh." Parrots, hidden in the thick foliage of a fruiting fig tree, reveal themselves by an occasional harsh squeek, sounding like a door hinge in desperate need of oil. Scarlet macaws, flying serenely overhead with deep, dignified wing beats, so close to us that they fill our binocular field, suddenly emit a gutteral, high-decibel squawk, about as musical as screeching brakes. Macaws are a feast for the eyes but an assault on the ears. Peccaries, Neotropical relatives of wild pigs, grunt back and forth to one another in low tones as they root for dinner. A white-tailed trogon (*Trogon viridis*) calls softly, "cow, cow, cow, cow." Much louder, a sharp, ringing, highly demonstrative "PEA-HE-HAH," sounding vaguely like the crack of a whip, is the mating call of a common though drab understory bird, the screaming piha (*Lipaugus vociferans*).

We walk along the muddy forest trail, careful to listen and look. At several places we can't help but notice lines of leafcutter ants, their well-worn trails crossing ours. Leafcutters are abundant throughout the Neotropics and occur nowhere else. We notice that the ants come in various sizes, the largest bearing big leaf fragments, neatly clipped in a circular pattern. The leaves won't be eaten by the ants but will, instead, be taken to a vast underground colony, where they will be used to cultivate a fungus species that the ants farm. It is the fungus that is the real food of the ants (page 133). Rain begins, soft at first, soon heavy. We are surprised at how little of it seems to wet us. The rainforest canopy is, indeed, a fine umbrella. Soon the downpour ceases, though we are at first fooled by the steady dripping from the canopy, making it seem like it is still raining. A loud sound, not too distant, indicates that a big branch, or perhaps a tree, has fallen, a common event in rainforests.

A small blackish-brown animal resembling a cross between a tiny deer and an oversized, tailless mouse tentatively prances across the trail, pausing just long enough for us to get a binocular view of it. It's an agouti (*Dasyprocta fuliginosa*), a common fruit-eating rodent unknown outside of the Neotropics. We come to a stream and walk along it a short distance. Overhead, thin lianas hang limply downward, though one seems abnormally short and stiff. Binoculars reveal that it's not a vine at all, but a long, thin tail, belonging to an iguana (*Iguana iguana*). Before we have finished looking at the arboreal lizard, a bright green and rufous bird zooms purposefully by, an Amazon kingfisher (*Chloroceryle amazona*). Following in rapid, bouncing flight behind it is the large, brilliantly colored blue morpho butterfly (*Morpho didius*), a huge lepidopteran, dazzling electric blue in flight as its shimmering inner wing surfaces are illuminated among the sun flecks.

After rejoining the trail we begin to notice the quiet. Rainforests often seem all too serene, especially toward midday. Even bird song and insect cacophony cease, the seemingly tireless screaming piha being perhaps the one exception. Things don't really become active again until dusk.

Were we here as darkness fell we might catch sight of a great tinamou (*Tinamus major*), a chunky, ground-dwelling bird with a seemingly undersized, dove-like head, which greets vespers with a melancholy, whistled song known to move emotionally more than one Neotropical explorer. We might encounter a family group of South American coatis (*Nasua nasua*) resembling sleek, pointy-nosed raccoons. We might hear the odd treetop vocalizations of romping kinkajous (*Potos flavus*), arboreal members of the raccoon family. We might even encounter an ocelot (*Felis pardalis*) hunting stealthily in the cover



Common iguana

of darkness. And, of course, there is always the possibility of glimpsing a jaguar (*Panthera onca*). We probably won't, but we can always hope. There are cat tracks along the streambed, too small for a jaguar, but quite possibly left by an ocelot. Finally, were we here at night, there would be many species of bats flying about the canopy and understory. In the Neotropics, bats own the night skies. But none of these can we find, at least not easily, during the day.

The silence is suddenly broken by birdcalls. Incredibly, birds seem everywhere, when minutes ago there was none to be found. Soon we locate the reason for the flock. The trail is being crossed by several columns of a large troop of *Eciton*, army ants. Being careful not to step where the ants are, we don't want to miss the opportunity of seeing the ant-following bird flock. Antbirds, unique to the Neotropics, join with many other bird species to feed on the numerous arthropods, the insects, spiders, and their kindred, flushed by the marauding ant horde (page 326). A medium-sized brown bird with a black throat and face and bright, rusty head, a rufous-capped antthrush (*Folmicarius colma*), walks methodically beside the ants. From the lower branches we briefly glimpse a black-spotted bare-eye (*Phlegopsis nigromanulata*), an ebony bird with rusty markings on its wings and bright orangy bare skin surrounding each eye. The frenetic bare-eye skillfully snatches a katydid, launched from its hiding place by the oncoming ants. Birds are everywhere, or so it seems. Perched on an understory branch, three nunbirds (*Monasa nigrifrons*) are loudly calling, their whole bodies shaking as they sing in chorus, emphasizing their bright orangy-red bills adorning an otherwise black bird. Another antbird appears, this one utterly outrageous looking, deep rusty orange with gray wings and a tufted headdress of upright, white, shaggy feathers above its bill, nicely framed by a thick, white, feathery beard below it. This, the white-plumed

White-plumed antbird

antbird (*Pithys albifrons*), often the most abundant of the ant followers throughout much of Amazonia, is a constant follower of army ants. Indeed, we can hear two others responding to the loud calls of the bird we are watching. On a tree trunk we find a large, woodpecker-like bird, deeply rufous brown, a barred woodcreeper (*Dendrocolaptes certhia*). On a horizontal limb of a nearby small tree a large, rufous motmot (*Baryphthengus ruficapillus*) sits upright, swinging its long, pendulum-like tail methodically from side to side. Nearby a trogon flips off a branch in pursuit of a dragonfly. The trogon, seen only momentarily, has a yellow breast. Several species have yellow breasts, and we don't get a good enough look to identify it. That will happen more than once. Before we leave the ants, we've seen at least a dozen bird species, and possibly more are around.

The trail has brought us out to a clearing, a large forest gap (page 57), where it seems suddenly much hotter, especially with the accompanying high humidity. We encounter a dense clump of thin, spindly trees with huge, umbrella-like, lobed leaves. These distinctive trees, whose slender trunks are reminiscent of bamboo, seem to occur wherever an opening exists, and they are certainly common along roadsides. They are cecropias (*Cecropia* spp.), among the most abundant tree species on disturbed sites. We'll look at these in more detail later (page 71), but for now we pay little attention since, sitting idly in the midst of a large cecropia, is a serene-looking three-toed sloth (*Bradypus variegatus*). Sloths have such a slow metabolism that they barely move, and this one is no exception. Slowly it raises its left forearm, a parody of slow-motion photography. Like the Tin Man in the *Wizard of Oz* before he was oiled, the sloth's muscles seem to begrudge it the ability to move.

The sloth's cecropia is flowering, the slender, pendulous blossoms hanging down under the huge leaves. Soon a mixed-species flock of tanagers, honeycreepers, and euphonias fills its branches, gleaning both insects and nectar from the tree. Unlike the antbird flock, this group is brilliantly colored: metallic violets, greens, and reds.

Beneath the cecropia grows a clump of heliconias, with huge, elongate, paddlelike leaves quite similar to those of banana plants. A long-tailed hermit hummingbird (*Phaethornis superciliosus*) plunges its elongate, sickle-shaped bill into the small flowers that are highlighted by cuplike, bright orange bracts that surround them. A mild commotion along the forest edge is caused by a small troop of saddleback tamarins (*Saguinus fuscicollis*), miniature monkeys that frequent edges and areas of dense growth. The gnomelike simians seem to slide up and down the tree branches. They are active and wary, not easy to see well.

The sky begins to cloud up again. The high humidity has taken its toll, and we are feeling a bit tired. One more small trail leads back into the rainforest. Should we do just a little bit more exploring? It's going to rain again soon, that's obvious, but still, we take the trail. As we approach a large, buttressed tree alongside the trail, we hear an odd sound ahead of us, like dry leaves buzzing. It's better not to go on until we locate the sound. Soon we find the source of the buzzing, and, in spite of the heat, it inspires a few chills. Coiled alongside the trail, in the protection of a large buttress, is a 1.5-m-long (approx. 5 ft) *Bothrops atrox*, a pitviper similar to the well-known snake called fer-de-lance. It has seen us and is vibrating its tail rattlesnake-style in the leaves. Highly venomous, this animal is to be avoided, as its bite can be lethal. It's a beautiful and exciting animal, however, and its soft browns and black diamond-shaped pattern impressively camouflage it against the shady brown background of the litter. However, its large and distinctive triangular head and slitted, catlike eyes warn us of its potential for harm. We look at the serpent from a respectful distance, admire it, know we have been lucky to see it, and carefully retreat, leaving it very much alone and undisturbed.

The rain begins again in earnest, feeling cool, helping offset the high humidity. We put our binoculars in tightly sealed plastic bags and begin walking back to the field station, ever so alert, having already seen one pitviper. But when you really think about it, seeing a pitviper safely is cause for celebration. It's exciting to see a poisonous snake. And it's quite safe to walk in rainforest if you know how to keep alert for possible danger (now might be a good time to read the appendix). We did. It continues pouring rain. Obviously time for a beer. And, as the beer is consumed, our newly refreshed minds wander to the rainforest canopy itself. We had a great walk, but we were never really close to that vast layer of green, with all its varied inhabitants. What would it be like up there?

The Rainforest Canopy, Up Close and Personal

Figures 42, 43, 44, 45, 47, 48

Even with binoculars, seeing the tropical rainforest canopy from the forest floor is a real challenge. Imagine that you wish to take a close look at something, perhaps a bird, an insect, a flower. Or, from a scientific perspective, imagine that you wish to take data on it. Then imagine that you must do so from a hundred or more feet away. It's kind of like looking at a beetle walking across home plate when you are on second base or even in the outfield! That, of course, is exactly the situation when you are on the forest floor attempting to study something in the upper canopy. But, at least in a few places, it is now possible to access the rainforest canopy directly. And, to borrow a phrase from astronaut John Glenn when he lifted off on his *Friendship 7* orbital mission in 1962, "Oh, that view is tremendous."

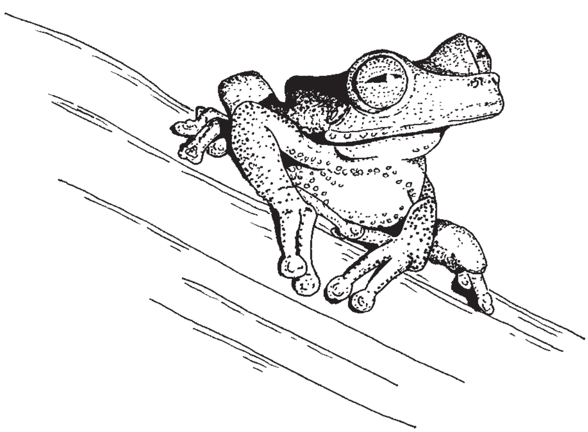
There is a tower not far from Manaus, Brazil, located within primary rainforest, a tower sufficiently tall that it just exceeds the canopy. From the gentle sway atop this structure one can enjoy miles of vista, seeing vast tracts of forest, while at the same time surrounded by the crowns of dozens of canopy trees. It is from such a vantage point that one might actually see a harpy eagle (*Harpia harpyia*) soar overhead, or catch a glimpse of the rare crimson fruitcrow (*Haematodevus militaris*). Colorful birds, such as the pompadour cotinga (*Xipholena punicea*), sit upright, perched on emergent branches from emergent trees. From the ground, you'd never know they were there. Mixed foraging flocks of canopy birds are now at eye level. Colorful butterflies, many of them strict canopy dwellers rarely or never seen in the understory, are easy to observe. Monkeys, squirrels, and other canopy-dwelling creatures can be seen from above, as you actually look down on them. But a tower, for all its advantages, is limited. It occupies a very restricted area. An even better way to see and study the canopy would be to walk within it, kind of like what howler monkeys do. And there is a place where that is possible.

The Amazon Center for Environmental Education and Research (ACEER) is located in one of the most species-rich areas in upper Amazonia, along the Napo River about 161 km (100 mi) east of Iquitos, Peru. The feature that makes ACEER unique among field stations is that the site includes a superbly engineered canopy walkway of over 0.4 km (0.25 mi) in length, an elaborate arboreal pathway interconnected with fourteen emergent trees, permitting one literally to walk through the rainforest canopy. Each of the trees used in the walkway is fitted with strong wooden platforms allowing several people to stand and look out at the canopy. The narrow spans between the platformed trees are built rather like suspension bridges, supported by strong metal cable and meshed at the sides to provide total security and safety (see figures). The spans vibrate a bit, especially when more than one person is walking across. One of the spans is nearly the length of a football field, affording a breathtaking, if shaky, look at the rainforest below. The first platform is about 17 m (55 ft) above the forest floor, but the spans eventually take you to a platform that is fully 36 m (118 ft) above the ground. From that privileged position, you gaze upon a panorama of unbroken rainforest for many, many miles. And yes, that view is tremendous.

From within the canopy you get an immediate, almost overwhelming impression of the richness of the rainforest. Trees are anything but uniform in height—and there are so many species, you wonder if, in the quarter mile of walkway, you pass two that are the same or if every tree you pass is different from every other. You notice the many different leaf sizes and shapes and see that some leaves are damaged by leafcutter ants, the insects having patiently walked 30 m (100 ft) up the tree bole to collect food for their subterranean fungus gardens. Now you can really look at the fine details of epiphytic plants such as orchids and bromeliads. You can see down into the cisternlike bromeliads and learn what kinds of tiny animals inhabit these microhabitats high above the forest floor. You note the uneven terrain below and realize that the canopy is by no means continuous, but is punctuated by frequent gaps, openings of various sizes. A male collared trogon (*Trogon collaris*) is perched 6 m (20 ft) below the walkway. How odd it is actually to look down on such a creature. A male spangled cotinga (*Cotinga cayana*) sits in display at eye level, a stunning turquoise bird whose plumage seems to shimmer with iridescence in the full sunlight.

A tree near one of the platforms is in heavy fruit, hundreds of small, orange, berrylike fruits peppering the branches. Fruit trees normally attract a crowd, and this one is no exception. Colorful tanagers of six different species fly in to feast on the fruits, at most 3 m (10 ft) away from us. Equally gaudy aracaris and toucanets join the tanagers. Two sedate, long-haired saki monkeys (*Pithecia monachus*), apparently a female and an adolescent, stop at the fruiting tree. The long, bushy tails of the monkeys hang limply below the branch on which they sit, as these simians do not have prehensile tails, like howlers, spiders, and woolly monkeys. The simians soon realize they are not alone. The female sees us and rubs her chin on the branch. She stands fully erect and emits a short, demonstrative hoot to warn us to come no closer. She needn't worry. We are not about to leave the security of the walkway. And we marvel at how monkeys have adapted the requisite skills to move effortlessly through such a tenuous three-dimensional world as rainforest canopy. A frenetic Amazon dwarf squirrel (*Microsciurus flaviventer*), a chipmunk-sized evolutionary relative of the northern acorn collectors, scurries with nonchalance on the underside of a branch over 30 m (100 ft) from the ground below. A thought reoccurs, and has occurred many times: from the ground, we'd never know this little animal was up here.

The canopy walkway affords a unique and broad window into the life above the forest understory. It is exciting to visit it, to be on it at dawn, when the forest below is still clothed in mist, or to watch the sun set over what seems like an endless vista of rainforest. But it also affords an opportunity for the kind of research that needs to be done to ascertain accurately an understanding of the rhythms of life in this essential habitat. We'll soon know more about rainforests because of the ACEER canopy walkway and others like it that are being or have been constructed in various other rainforest localities (Wilson 1991; Moffett 1993).



Tree frog