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Chapter 1

Forests of Panama and Costa Rica

Tree Diversity in the Tropics of Central America

Southern Central America excels in tree species richness. On a world map, Costa Rica and Panama, along with western Colombia, Ecuador, and Peru, have the highest plant diversity (Barthlott et al. 1996). Understanding why begins with understanding the topographic and climatic diversity of the region. The Andes in South America and the central cordillera of Central America are a long, near-continuous spine of mountains, and the variation in elevation from lowland to mountain peaks creates variation in habitat. From the warm lowlands to the cool and windswept mountain tops, communities differ, whether of trees, birds, or butterflies. Particularly important in Central America is the contrast between the Pacific and Caribbean flanks of the mountains, which we will return to shortly.

But there is more to high diversity in Central America than a mountain range. Colorado and Switzerland have mountains, but nowhere near the number of tree species. Indeed, all of North America has about 1000 tree species, compared to 2300 in much smaller Panama. We don't know the total number of tree species in all of South America, but it is somewhere around 20,000. Scientists have debated this contrast in species richness since von Humboldt traveled the Amazon 200 years ago, and there are nearly as many theories as there are theoreticians. One obvious possibility is glaciation: during the past 200,000 years, while North America and Europe were under ice sheets, Central America maintained a moist, warm climate and dense vegetation. There is plenty of evidence that northern regions suffered extinction during the glacial epoch of the past few million years.

High species richness is one reason botanists find it difficult to learn, describe, and document plant richness of Latin America. There are far fewer botanists, more species, and less money available for environmental concerns than there are in North America. Indeed, there remain immense gaps in our knowledge of trees in Central America. We have carried out inventories for 20 years throughout Panama, yet we are still unable to identify every tree we see. In fact, in more remote areas that are difficult to visit, it is typical for tropical botanists to leave as unidentified 25% of the species encountered. There is nowhere in North America where an experienced botanist would have anywhere near this difficulty.

Those North American botanists have excellent field guides (e.g., Elias 1980; Petrides 1972). Comparable guides for trees anywhere in the tropics are scarce, though the number has been greatly expanding in the past decade (e.g., Zamora et al. 2000, 2004). Our hope here is to follow this trend and help other biologists expand their knowledge about the tropics. This guide covers 493 tree species, including 438 with color photos, and we offer descriptions of key features for identification and show where they are known in Panama and Costa Rica. We also offer brief notes about the tree species we do not cover, where they are known, and which of the illustrated species they resemble.

Geography, Climate, and Forest

Panama and Costa Rica are well inside the tropics, at 8–10°N latitude, where an atmospheric conveyor belt delivers storm systems out of the east—off the Caribbean—during the northern summer. During the winter, from December through April, this belt shifts southward and the region has its annual dry season.

The mountain axis of Central America is high enough to intercept storms off the Caribbean, and thus the wettest areas of Panama and Costa Rica are on the Caribbean flanks of the mountains. There, annual precipitation is greater than 3000 mm, with many sites

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getting 4000 or 5000 mm. The Pacific slope of the isthmus is generally drier, getting less than 3000 mm, and as low as 1500 or even 1000 mm at the driest locations. Though generally drier than the Caribbean slope, the Pacific slope is variable and has both wet and dry areas (Figs. 1.1 and 1.2). The central axis of mountains between the Caribbean and Pacific is nearly everywhere wet, often with clouds and fog.

To the tree species of Central America, the variation in rainfall is crucial. On the wettest Caribbean slopes, there is enough moisture even during the December–April dry season to keep the soil damp, and forests are wet and green all year. In contrast, much of the Pacific slope has hard, dry soil by April, and many species are deciduous then. By sitting on the cusp of this gradient from dry forest to wet forest, Panama and Costa Rica capture a great diversity of tree species, because the ability to tolerate a dry season is a crucial adaptation.

In the 1950s and 1960s, a pioneering ecologist named Leslie Holdridge worked for years in Costa Rica and Panama (Holdridge 1967). Holdridge noticed how the variable climate of the region has a conspicuous impact on the forests and developed a system for classifying vegetation to describe it. The Holdridge system has been widely used by tropical ecologists since, especially in Central America. There are a total of 17 categories in the Holdridge system, but a good basic understanding of forest communities in Central America can be gained by abstracting five broad units: dry, moist, wet, lower montane, and upper montane.

(1) Dry forest. In Panama and Costa Rica, dry forest is found in two regions where rainfall is less than 1500 mm annually, one in central Panama west of Panama City, the other in northwestern Costa Rica (Fig. 1.1). True dry forest in the tropics is short, seldom more than 20 m tall, and many trees lose their leaves during the dry season, quite different from the classic image of tropical rainforest. Fine-leaved trees of the legume family are common. In the driest areas of Central America, there are even columnar cacti and the mesquite tree (*Prosopis jubata*), both common sights in North American deserts. But it is not a desert in Panama and Costa Rica: trees would occupy the entire region, given the chance. We will return to human impacts later.

(2) Wet forest. The lowland forests of the Caribbean slope are wet forests of the Holdridge system. Here, the classic image of rainforest holds: trees are tall, the canopy is dense and continuous except for small gaps created by fallen trees, and epiphytes are conspicuous. Trees do not shed their leaves during the weak dry season. Much less conspicuous is what you can decipher only after learning tree species: wet forests have many more species than do dry forests. There are substantial blocks of wet forest throughout Central America, including extensive and unbroken stretches in San Blas, much of western Panama, and the national parks of Costa Rica's Caribbean slope as well as the Osa Peninsula (Fig. 1.1).

(3) Moist forest. For the forests between wet and dry, we use Holdridge's phrase "moist forest." This grows where more than 1500 but less than 3000 mm of rain falls, but where the dry season is pronounced and lasts 3–4 months. Trees are tall; indeed, the biggest trees in the area are characteristic of moist forest (e.g., the kapok [*Ceiba pentandra*] and the espavé [*Anacardium excelsum*]). On the other hand, there are deciduous species during the dry season. All the easy-to-see forest near the Panama Canal is moist forest (Fig. 1.2), as is a large block in Darien National Park in eastern Panama and much of the Pacific slope of Costa Rica (Fig. 1.1).

The remaining climatic zones in our abbreviated version of Holdridge are montane: forests above 800 m elevation. There is an important division at about 1500 m, so we consider two categories.

(4) Lower montane forest. From about 800 to 1500 m elevation, forests resemble lowland wet forests, with tall trees and dense canopy, and wet and lower montane zones share many species. Tropical cloud forests fall in this range, and are typical on the tops of lower mountains, where clouds often sit. There are high densities of epiphytes—orchids, bromeliads, ferns, and mosses—in cloud forests.

(5) Upper montane forest. Above 1500 and especially 2000 m elevation, forests are quite different, and are sometimes classified as temperate, like forests of North America. Indeed, oak (genus *Quercus*) and alder (*Alnus*) are conspicuous above 2000 m, along with many other temperate groups familiar in North America

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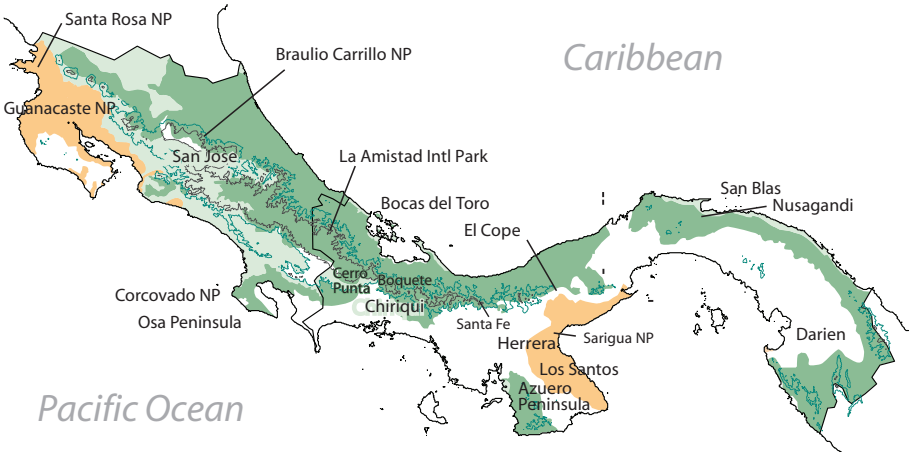

Figure 1.1. Place names and forest zones in Panama and Costa Rica. The dry zone is indicated by yellow, the moist zone by light green, and the wet zone by dark green. A light green topographic line demarcates the lower montane zone, at 800 m elevation, and a black line shows the upper montane zone, at 1500 m.

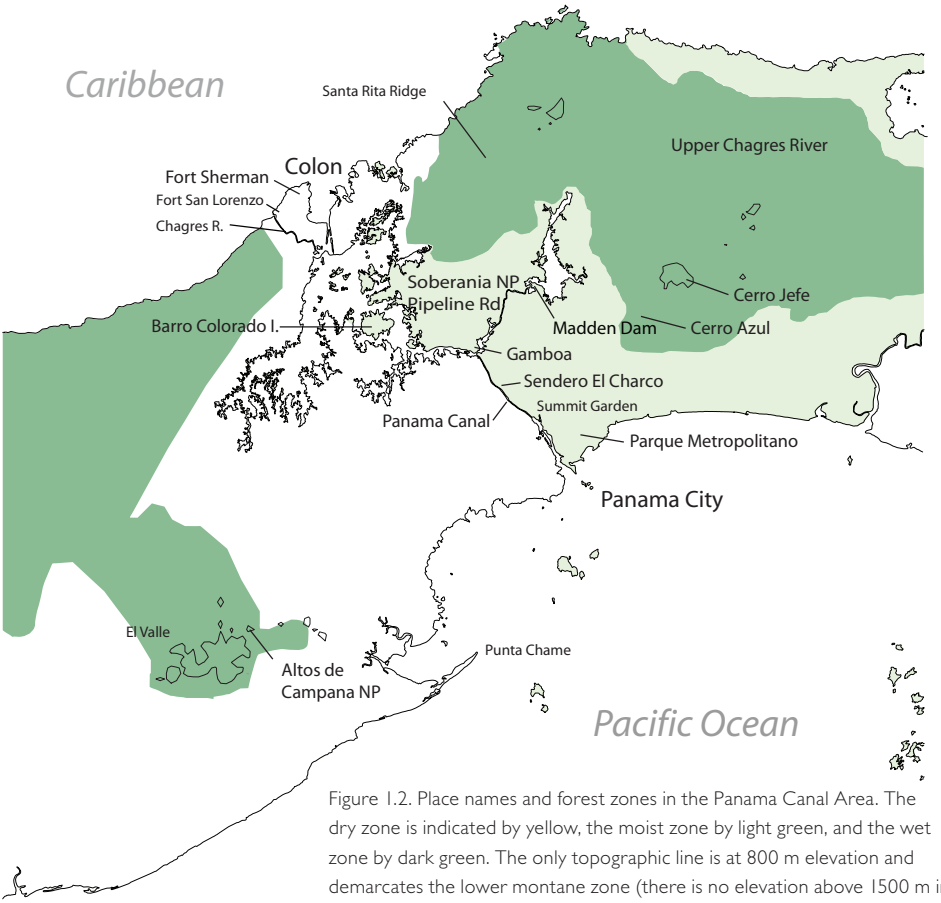

Figure 1.2. Place names and forest zones in the Panama Canal Area. The dry zone is indicated by yellow, the moist zone by light green, and the wet zone by dark green. The only topographic line is at 800 m elevation and demarcates the lower montane zone (there is no elevation above 1500 m in the canal area).

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and Europe. Among these temperate trees, though, is a high diversity of tropical taxa. Upper montane forests are not giant forests. Trees are generally less than 20 m tall, and on windswept mountain peaks, trees become sparse or even absent.

The boundaries between these zones are blurred, and the use of 5 (or even 17) categories is arbitrary. The transition between all types is gradual. There is no place one can stand and point to one forest type on the left and another on the right. Three of the five zones we describe are especially blurred: moist, wet, and lower montane. But categorization is how humans learn to understand variation, and this is why the Holdridge system became popular. To aid in understanding the climate zones, Figure 1.3 shows three distribution maps illustrating typical tree species ranges that are linked to forest zones.

Where forest remains, all five forest zones are rich in tree species by the standards of North America or Europe, though wet forest is richer than dry forest. Crucial to Central American diversity is another kind of diversity—the change in species between climatic divisions. The wet Caribbean slope is very different in tree species from the moist and dry forests of the Pacific half of the isthmus, and montane forests differ from either, though they are much closer to wet forests. Near the Canal in Panama, the wet forests of Santa Rita and the moist forests near Panama City (Fig. 1.2) are only 50 km apart but share almost no tree species. Much of our scientific research has been about this sharp change in tree species composition in central Panama and the rainfall patterns that cause it (Condit et al. 2001, 2002, 2004, 2005; Engelbrecht et al. 2007). In Costa Rica, very different species can be seen within 150 km in Santa Rosa National Park in the northwest to Braulio Carrillo in the northeast, crossing the mountains in between (Fig. 1.2).

Human Impact

As we all understand too well, forests are altered and often simply removed by humans, and the categories of Holdridge do not include human impacts. In fact, deforestation is closely linked to climatic zones (Condit et al. 2001). Humans prefer the tropical dry climate to the tropical wet climate, and tropical dry forests have largely been removed in Central America and indeed much of the world. In Panama and Costa Rica, the drier Pacific slope is mostly pasture interspersed with cities and towns, and we don't really know what mature dry forest would look like, because there is none. In contrast, the mountains and the Caribbean lowlands of Central America still retain much of their forest and have far fewer humans. Tellingly, there is substantial Pacific forest in wet areas, such as the west side of the Azuero Peninsula in Panama and the Osa Peninsula in Costa Rica (Fig. 1.2), as well as on mountains near the Pacific, where the climate is wet due to high elevation.

Visiting Forests in Panama and Costa Rica

Both countries have lovely and extensive forests readily accessible via good roads. In Panama, the easiest forests to reach—and the most familiar to us—are moist lowland forests near the Canal, from Panama City to Gamboa and Pipeline Road (Fig. 1.2). Parque Metropolitano near the city has hiking trails, and though the forest has been heavily disturbed, it is rich in tree species. Taller and more attractive forest can be found at Sendero El Charco, just past Summit Gardens, on the main highway toward Gamboa, and there is a short hiking trail there. Both Metropolitano and El Charco are in moist, secondary forest, with many species typical of the Pacific half of the isthmus.

The paved road ends at Gamboa, which is surrounded by moist secondary forest. Just beyond starts Pipeline Road, a long dirt road through unbroken forest in Soberania National Park. The first half of the road has a recent disturbance history, but beyond the Rio Limbo, the forests are mature and have been little impacted for at least a century. From a tree perspective, Pipeline Road provides a fascinating switch from the Pacific to the Caribbean: the first two kilometers have a Pacific coast element, with *Bursera simaruba* and *Castilla elastica*, but the stretch of road up the steep hill after the Rio Limbo has species of Caribbean coast wet forest (e.g., *Welfia regia* is easy to see). Permission and a four-wheel-drive vehicle are needed to reach the

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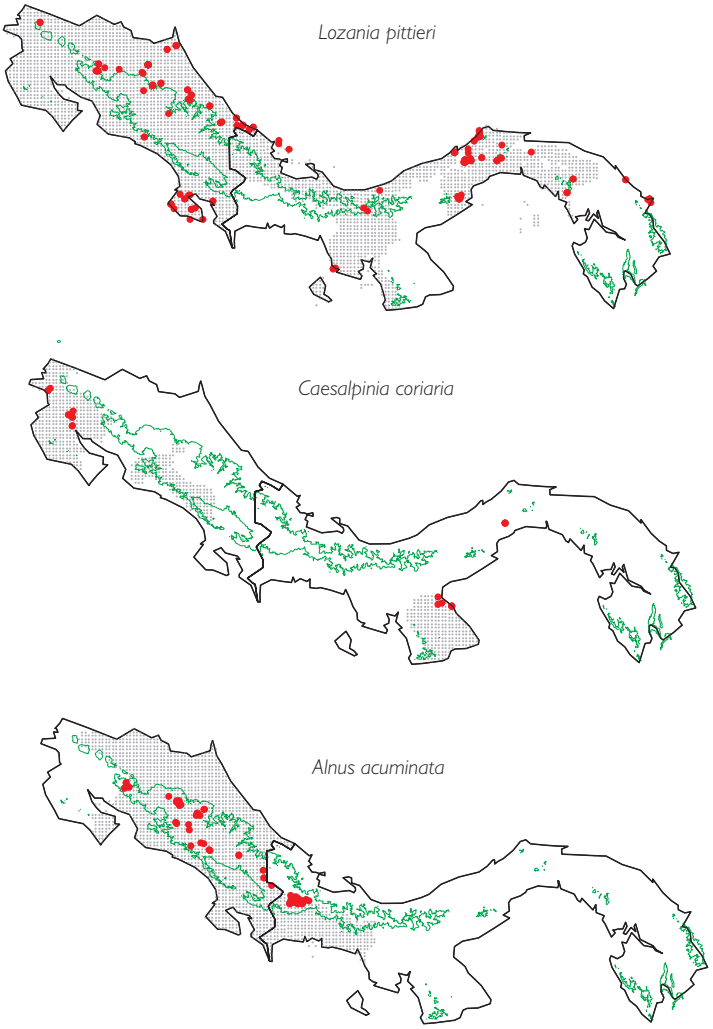

Figure 1.3. Sample species distribution maps illustrating major forest types. *Lozania pittieri* (Lacistemataceae) has a typical wet-forest distribution, mostly on the Caribbean half of the isthmus, but conspicuous at the Osa Peninsula and other Pacific sites where rainfall is higher. It also occurs at some lower montane sites. *Caesalpinia coriaria* (Fabaceae—Caesalpinioideae) is only found in the two dry zones of central Panama and northwestern Costa Rica. *Alnus acuminata* (Betulaceae) is confined to the highest mountains in far western Panama through Costa Rica. Red dots are locations from herbarium records or our own inventories, where precise coordinates were noted. All provinces where a species is known are also stippled; because there are records where the province was noted without coordinates, there may be stippling in areas with no dots. Moreover, provinces are political boundaries and not climatic zones, and stippling in a province does not necessarily mean the species occurs throughout the province. Notice that the map of *A. acuminata* shows stippling along the Caribbean coast in Costa Rica, even though the tree only occurs in the central mountains. This is because boundaries of several provinces straddle the mountains and reach the coast.

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wet-forest area, but it is an excellent area to visit for both flora and fauna.

The best example of undisturbed tropical moist forest in Panama is on Barro Colorado Island. It is intermediate between the coasts geographically and also floristically, and species of the Pacific slope (such as the cuipo [*Cavanillesia platanifolia*]) along with hints of wetter forests (*Virola surinamensis* as a large example) are common there. Barro Colorado Island also has the biggest trees in Panama, all either kapok (*Ceiba pentandra*), espavé (*Anacardium excelsum*), or the sandbox tree (*Hura crepitans*). The island can be visited with permission from the Smithsonian Tropical Research Institute.

Excellent Caribbean wet forest also can be visited in a 1-day trip from Panama City, though not as easily as Pipeline Road or forests near the city. A road runs up the Santa Rita Ridge from the Transisthmian Highway, and not far from the highway, near the radio towers, there are small stands of true Caribbean wet forest. Further up the road there are more extensive stands of forest, but it is difficult driving, requiring four-wheel drive and even then not recommendable after wet weather. Similar wet forest can be visited at Nusagandi, about 4 hours east of Panama City, where there are rustic accommodations for tourists. Both Santa Rita and Nusagandi are highly diverse and claim many wet-forest species impossible to see at Barro Colorado Island or Pipeline Road. Another site near the Caribbean that can be reached from Panama City in a few hours is San Lorenzo National Park, at the mouth of the Chagres River. There are accommodations at the former US military base called Fort Sherman.

Montane forest at 800–1000 m in elevation is also easy to visit near Panama City, at Cerro Campana about 1 hour west of Panama City, and Cerro Azul and Cerro Jefe, which are just north of the Tocumen (Panama City) airport. Cerro Campana has good trails through cloud forest, and there are various trails and cabins around Cerro Jefe. Both sites are much wetter than the nearby lowlands and have some cloud-forest specialists as well as a broad contingent of wet-forest species that otherwise occur only near the Caribbean coast.

There are several other areas to visit montane forest in Panama: El Valle not far from Cerro Campana, El Cope, and several sites in Chiriqui, including La Amistad International Park. There is a road from the Pan-American Highway over the mountains to Bocas del Toro that crosses through cloud forest near the Fortuna Dam. Further west, the popular sites for visitors are around the towns of Boquete and Cerro Punta, and this is the only area in Panama where forests above 2000 m in elevation can easily be visited. These harbor a temperate-like flora, with oaks, alder, dogwood, and elm, but also many tropical taxa.

Unfortunately, nearly all true dry forest in Panama has been cut down. Forested sites near Panama City are drier than the Caribbean coast but are really moist forest. Savanna-like remnants of dry forest can be seen along the Pan-American Highway west of Cerro Campana and at Sarigua National Park near the town of Chitre, but you need to visit Costa Rica to see extensive dry forest.

Costa Rica has excellent parks spanning the range of climates, indeed, Panama's parks aspire to match Costa Rica's system. Near San Jose, the capital city, Santa Rosa, Guanacaste, and Braulio Carrillo national parks offer easy access and excellent trails. Santa Rosa, in the far northwest, has been allowed to regenerate for 30 years, and is the only spot in either Panama or Costa Rica where true dry forest can be seen. From Santa Rosa eastward over the mountains and down through Braulio Carrillo offers a marvelous transect through all the climate zones.

In the far south, the Osa Peninsula is peculiar for having a wet-forest climate near the Pacific coast. The extensive forest there is protected in Corcovado National Park, and there are lodges around the park and remote camps and cabins within. Indeed, thanks at least partly to the popularity of ecotourism, visitors can easily reach all manner of forests in Costa Rica and Panama without much difficulty, from remote and undisturbed wildernesses to city parks. Whether by bus, rented automobile, or with tour groups, all forest zones of the two countries can be visited within a day of the major

ists learn something about the trees as excellent guides (Ridgely 1978) do for the birds.