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Guide to the Ecological Systems of Puerto Rico

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Abstract

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This guide is an introduction to the ecological systems of Puerto Rico. It covers the diversity of ecological systems in the island, their most common plant and animal species, and salient aspects of their structure and functioning. Terrestrial, wetland, coastal, and marine ecosystems are included, as well as agroforest and urban systems. The discussion of the ecological systems of Puerto Rico is presented in the historical, cultural, and natural disturbance regime of the Island. In addition, we discuss the environmental infrastructure and organizations responsible for the conservation of Puerto Rico's natural resources, and provide useful information to facilitate field visits to representative examples of the Island's ecological systems.

Keywords: Ecological systems, rain forests, dry forests, tropical forests, coral reefs, estuaries, mangroves, seagrasses, Puerto Rico.

Preface

This publication arose as a result of a series of field trips conducted in Puerto Rico by Gary L. Miller and Ariel E. Lugo with students on courses in tropical ecology at various Puerto Rican and U.S. colleges and universities. The field trips in many cases were preceded by semester-long lecture courses with field courses varying in length from a few days to 4 weeks. Through the years, a variety of handouts have been prepared describing many of the topics covered in this publication. The amount of literature centered on Puerto Rico and the Caribbean has grown tremendously in the last two decades. Because these courses were geared toward undergraduates, however, much of the technical literature was too voluminous and, in some cases, too technical for a lay audience. In response, this book was written to include a mixture of technical and applied information that a diverse reading audience might find ecologically informative and generally interesting. It covers most of the important ecological systems, a selected group of species, and some of the important environmental issues confronting Puerto Rico and the Caribbean today. Although most of the technical publications and data sets cited were derived from studies conducted in Puerto Rico, much of what is generally described in terms of ecosystems and species is typical of most islands in the Caribbean. Clearly there is much variation from island to island in regard to size, soils, topography, altitude, rainfall, and accessibility. There is, however, considerable overlap in species and ecosystem presence. In addition, all of the Caribbean islands are experiencing similar problems related to expanding human populations, providing environmentally based amenities, protecting species and habitats; environmental catastrophies such as hurricanes, landslides, and floods; and loss of their fisheries owing to overfishing. For these reasons, this guide is relevant throughout the Caribbean region.

In addition, useful and practical information, such as the location of habitats for field trips, references to environmental agencies, field trip checklists, videotapes, maps, and guides to Puerto Rico has been provided in appendix 2. For those wanting more technical information, many citations to recent technical literature are provided in each section. The material is meant to be used according to areas of interest, and for this reason, we allow some redundancy among sections. We hope this publication will provide a better fundamental knowledge of the environmental conditions of Puerto Rico and the Caribbean.

Contents

1 **Chapter 1: Overview of Puerto Rico**
1 **Introduction**
4 **Puerto Rico—Its History, Politics, and Economy**
4 Early History
7 The Colonial Period
8 Steps Toward Autonomy
8 The American Period
12 Contemporary Puerto Rico
18 **Physical and Climatic Zones of Puerto Rico**
18 Geography
20 Climate
21 Hurricanes
23 Geology
25 Soils
27 **Chapter 2: Flora and Fauna of Puerto Rico and the Caribbean**
27 **General Review of the Flora**
33 Trees
36 **General Review of the Fauna**
52 Tree Frogs
55 Birds
58 Neotropical Migrants
63 Bats
67 Termites
70 Endangered Species
79 **Chapter 3: Terrestrial Ecosystems**
79 **Subtropical Forest Life Zones of Puerto Rico**
83 The Subtropical Dry Forest
94 The Subtropical Moist Forest
105 The Subtropical Wet Forest
113 The Subtropical Rain Forest
125 The Subtropical Lower Montane Wet Forest
132 The Subtropical Lower Montane Rain Forest
135 **Agroecosystems**
137 Typical Crops of the Tropics

157 **Chapter 4: Freshwater Wetlands and Coastal Ecosystems**
157 **Wetlands Ecosystems**
170 Wetlands Regulation
174 Coastal Ecosystems
174 Sandy Beach Habitat
188 Rocky Shoreline Habitat
195 **Chapter 5: Estuarine Ecosystems**
195 **Mangrove Forests**
200 Ecological Functions of Mangroves
205 Zonation of Mangrove Communities
207 Extent of Puerto Rico's Mangroves
209 Stressors
212 Values of Mangroves
213 Riverine Estuaries
219 **Chapter 6: Marine Ecosystems**
219 **Submerged Seagrasses**
233 **Coral Reefs**
248 Keeping Your Keel Off Coral
264 Symbiosis
267 Coral Dieback
273 **Chapter 7: Disturbances in Puerto Rico and the Caribbean**
273 **Hurricane Effects on Ecosystems**
274 Terrestrial Effects
278 Marine Effects
282 **High Rainfall, Drought, Landslides, and Fire Events**
285 **The Urban Forest Interface**
291 **Chapter 8: Environmental Organizations and Environmental Infrastructure**
291 **The El Yunque National Forest and the International Institute of Tropical Forestry**
298 **Puerto Rico's Commonwealth Forests and Nature Reserves**
304 **Caribbean Islands National Wildlife Refuge**
308 **Other Environmental Organizations**
310 **Acknowledgments**
310 **Metric and English Conversion**

311 **Literature Cited**
322 **Further Reading**
345 **Appendix 1: Common and Scientific Names of Plant and Animal Species**
363 **Appendix 2: Visiting Puerto Rico**
383 **Appendix 3: Ecotourism**
387 **Appendix 4: Tools**
404 **Glossary**
425 **Index**

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Chapter 1: Overview of Puerto Rico

Introduction

Puerto Rico offers a rich tapestry of environments in which to conduct field studies in tropical ecology. It has a mountain range oriented east-west with peaks as high as 1000 meters (4,000 feet). Its boundary on the north is the Atlantic Ocean and to the south, the Caribbean Sea. The island is bathed by the westerly **trade winds**,[1] which interact with the sea and mountains to produce an array of rainfall patterns and orographically induced **habitat** variation. Some areas in the mountains receive more than 5000 millimeters (200 inches) of rain annually. Other areas on the Caribbean **rain shadow** side receive as little as 254 millimeters (10 inches) in some years.

In addition, the rainfall produces considerable runoff that results in many rivers on the island in all directions. The south side has fewer perennial rivers and is a lower energy coast line, thus affording greater stability to **marine ecosystems** such as **coral reefs**, **mangrove swamps**, and **submerged seagrass beds**.

Because of its geographic position, half the year Puerto Rico is also exposed to major tropical storms. **Hurricanes** are one of the main ecological disturbances in Puerto Rico and all adjacent areas of the Caribbean, and have the potential of producing enormous instantaneous and long-term change in all ecosystems, terrestrial and marine.

Pre-Columbian Puerto Rico had no coconut palms,[2] no grapefruit or orange **trees**, no coffee groves, no mangoes, no flamboyán or African tulip trees with their beautiful flowers, and no sugarcane fields. The mangroves that hugged the coasts were larger and much more widely distributed. The **Taíno** people that lived on the island mostly fished and grew corn, yuca, yams, and cotton to supply their needs. In the 500-plus years since Columbus discovered Puerto Rico (1493, second voyage of discovery), the introduction and growth of nonindigenous European and African human **populations** has resulted in enormous habitat alteration throughout the island. In addition, thousands of **alien** species of plants and animals have been introduced, both intentionally and accidentally. Populations of some **native species** have undergone dramatic declines, whereas many **introduced species** have become naturalized. Destruction of native habitats occurred throughout the island as species such as sugarcane (*Saccharum officinarum* L.), tobacco (*Nicotiana tabacum* L.),

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[1] Bold terms are defined in the glossary.
[2] See appendix 1 for Common and Latin names.

citrus (*Citrus* spp.), coffee (*Coffea arabica* L.), and bananas (*Musa* x *paradisiaca* L.)—to name just a few—were introduced. Many native habitats and populations were destroyed without any written description of their presence having been recorded. Today, large expanses of agricultural lands are "returning to nature" as much of the sugar plantation land is being abandoned, as sugar is no longer the dominant crop that it was in the 18th, 19th, and first half of the 20th centuries. Consequently, Puerto Rico is an interesting case study in that it is an island undergoing significant natural reforestation. Many former agricultural sites will not return to forest as a result of rapid urban development, growth of tourism centers, golf courses, light industry, and transportation corridors for the rapidly increasing use of private automobiles. Human activity has also reduced and, in some cases, endangered many types of ecosystems, for example, the loss of coral reefs on the north coast, magnificent lowland forests of the **alluvial** coastal plains, coastal dune communities, and the **elfin forests** on the mountain tops, and the damming of numerous rivers.

Puerto Rico is neither a sleepy little Caribbean Island, nor is it a lush tropical paradise, as is sometimes depicted in tourism advertisements. There are places in Puerto Rico where both can be found, but, in fact, Puerto Rico today is the commercial engine of the Caribbean, and in many ways it has most of the contemporary problems and concerns that fully developed economies exhibit: air and water pollution, protection of **endangered species** and their habitats, forest management, regulation of all forms of waste and their disposal, pesticide regulation, marine protection, and others. Puerto Rico has over 2 million automobiles, trucks, and buses constituting one of the highest vehicle densities in the world. At times, its metropolitan traffic jams rival those of California freeways. It is currently building a 17.2-kilometer (10.3-mile) elevated train/subway at a cost of nearly $2 billion to alleviate traffic congestion in metropolitan San Juan. Old infrastructure is also a big problem for the island's water supply in that almost 50 percent—about 950 liters (250 million gallons) per day—of all potable water processed by the Water Authority is lost prior to delivery because of leaks, broken hydrants, and unmetered connections to the system. Puerto Rico's sewerage system is still developing. Fifty percent of the island lacks sanitary sewer lines, and some communities still have difficulty meeting secondary sewerage treatment standards, which is of concern to beach communities and the tourism industry. Sixty-eight treatment plants discharge into the ocean.

Given Puerto Rico's many wonderful terrestrial and marine species and ecosystems, there is need for a strong **conservation** ethic and commitment to a

sustainable future. Many of these species and ecosystems are interrelated and connected in complex ways and are the result of long-term geologic and biologic evolution. As Puerto Rico's population and associated necessary development increases, the demands and pressures on these ecosystems and species increase accordingly. Human activity in Puerto Rico is again changing Puerto Rico's complex landscape, but instead of being largely restricted to agricultural simplification of the landscape (for which there is an opportunity of recovery), much more destructive and permanent changes are occurring on the island. These include loss of large areas to **urbanization**; serious water pollution associated with improper disposal of sewage, including hazardous and other solid wastes (industrial and municipal); overpumping of critically important ground-water supplies; and the destruction of large numbers of **limestone** hills, sandy beaches, mangroves, freshwater swamps, and other **wetlands**. Development in Puerto Rico is growing at a rate that is surpassing regional carrying capacity in terms of public water supply in many areas, and at the expense of species and habitats. Puerto Rico is at a critical crossroads in its environmental history. Many systems are no longer able to perform their functions, and their restoration will be highly unlikely owing to both cost and complexity. Puerto Rico's complex environmental issues will need to be addressed based on needs assessments for future generations. Puerto Rico is heavily subsidized and depends on the importation of huge quantities of food, fossil fuels, and a vast array of other goods and services (worth $29 billion in 2002). **Sustainability** must become the island's watchword; and all important decisions must address the three "E's": equity, economics, and the environment.

Although Puerto Rico has undergone rapid development in the last five decades, it still has many special tropical terrestrial and marine habitats and species, and therefore represents an island with a tremendous mix of opportunities for pursuing a study of tropical ecosystems. Additionally, there is an excellent published technical information base for the island. Many current studies sponsored by a variety of federal and commonwealth agencies, universities, and nongovernment agencies are in progress.

In addition, with growing interest in the tropics, many secondary schools, universities, and teacher training institutes now offer experiential education classes centered on various aspects of tropical marine and terrestrial ecology. Less formal experiential education is also available through dozens of ecotourism companies that specialize in guided trips to the tropics. Tourism in general is now the largest industry in the world, and **ecotourism** is the fastest area of growth within this diverse industry. In 2002, Puerto Rico had 2 million hotel guests. Puerto Rico has

seen a substantial increase in ecotourism in the past decade and there is a list of specialty companies in appendix 3. This field guide is designed as an aid in educating these groups.

This publication was written to help guide a diverse audience—the teacher, student, class, or individual reader—in gaining the background needed to understand a select group of tropical ecosystems and species and where to find them while in Puerto Rico. This is by no means a comprehensive list, but a good representation of the main systems that are relatively easy to access.

A selected series of tropical terrestrial and marine ecosystems has been chosen for general description, and some of the species typical of those ecosystems will be highlighted. For more indepth reviews of these species and ecosystems, each section contains references for further reading that provides a broader review of the more technical literature on the topic.

Puerto Rico—Its History, Politics, and Economy

Early History

No one knows with certainty how long Puerto Rico has been inhabited, but it is likely that humans have been present on the island for 2,000 years. The earliest indigenous population is thought to be from a primitive group called the Siboney who hunted and gathered. Somewhat later the Igneri established farms and made pottery. About 700 A.D., the more advanced Taíno were developing population centers in many areas of the **West Indies**. By 1270 A.D., they controlled the island they called Borikén, which is present day Puerto Rico. As you travel throughout Puerto Rico today, you will see many references to Borinquen, which is commonly used as a business name. A form of the word—boricua—is used to designate (with pride) a person born on the island. The Taínos spread throughout the West Indies, probably from their origin in mainland Venezuela of South America. When the Spanish arrived, they called the Taínos the Arawaks. The Taínos were a peaceful agrarian society that grew corn, yams, and a variety of field crops. They made bread from yuca, wove cloth from native cotton, and were skilled potters. They lived in wood frame huts with thatched roofs and played soccer-like ball games on courts called bateyes (see app. 2, p. 368). It is estimated that approximately 30,000 Taínos inhabited Borinquen in 1493.

By the time Columbus discovered the New World, the Taínos had been under heavy attack by a very hostile Indian invader, the **Caribs**. The Caribs burned villages, slaughtered the villagers, took prisoners, and may have practiced cannibalism.

G. Miller

Figure 1—View of ceremonial areas in the Caguana Indígena Park.

It is from their tribal name that the word Caribbean was derived. The Caribs had more advanced technology than the Taínos with which to conduct battles: the bow and arrow. The Taínos only had spears. When the Spanish came to Puerto Rico, the Taíno culture went into rapid decline. Not much remains of the Taíno culture. There are a few words from their language that survive in modern English: barbecue, canoe, hammock, hurricane, and tobacco. In recent years, numerous excavations have been conducted in various places in Puerto Rico, and as a result, we have a better understanding of their society (fig. 1).

The Isle of Borinquen changed forever on November 18, 1493. It was during Columbus's second voyage to the New World that the island was discovered. Columbus's 17-vessel fleet anchored on the west coast on November 20. The ships sent landing parties and took on food and water. They found a Taíno village, but the people had fled to the mountains. Columbus named this new island San Juan Bautista (St. John the Baptist), and it was later renamed Puerto Rico (rich port) in 1521.

As seen in figure 2, Puerto Rico occupies a strategic point at the entrance to the Caribbean. It is the smallest and most eastern of the **Greater Antilles** and sits at the top end of the **Lesser Antilles**, which arc up from South America. Because of its position, it was of military importance and used as a stopover to and from Spain (for groups on their way to and from) and other colonization points in the New World.

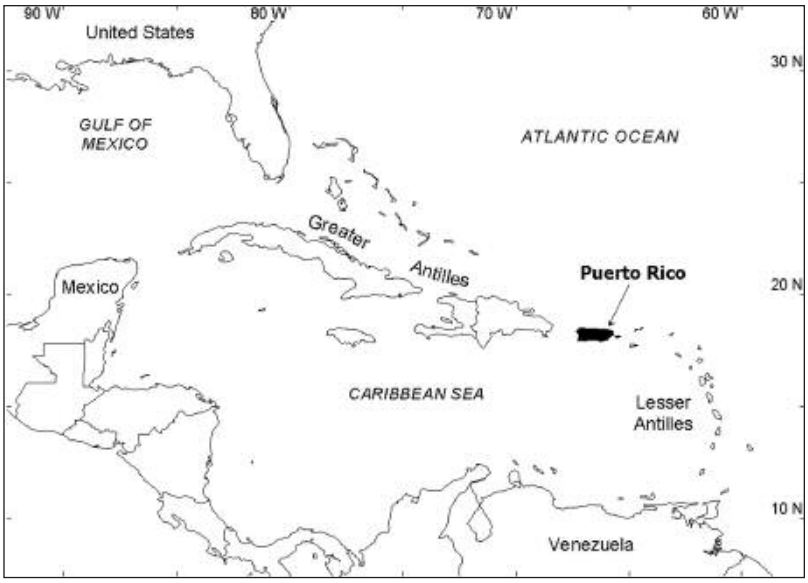


Figure 2—Islands of the West Indies and Caribbean Sea.

The earliest Spanish settlers were conquistadores (conquerors), and one of them aboard the 1493 (second discovery) voyage was Juan Ponce who was from the province of León in Spain. Juan Ponce, now known as Ponce de León, was named governor in 1508 and given royal permission to occupy and explore San Juan Bautista. Initially he searched for gold. In addition to gaining wealth, he was also interested in converting the indigenous population to Christianity and increasing the glory and wealth of Spain. He and his men landed in a well-protected bay on the north coast, which he called Puerto Rico. The bay was later renamed San Juan Bay. The first settlement started by Ponce de León at Caparra proved too distant and unhealthy to be maintained, and so a second settlement was developed on the island that protected the entrance to the bay. This was the start of present-day Viejo San Juan (Old San Juan) and it became the capital in 1521. San Juan is the second oldest city established by Europeans in the New World.

Ponce de León did discover gold and sent tens of thousands of pesos back to Spain annually from 1511 to 1520. In a 30-year period (1509–1539), almost 300,000 pesos were sent to Spain. Puerto Rico never achieved the high colonial status of Cuba, the Dominican Republic, or mainland areas such as Perú or México, because of its small size, lack of large amounts of precious metals, and relatively small areas of easily accessed fertile soil for agriculture.

By the 1570s, most mines were closed down, the Taínos were decimated, and their culture was being assimilated by the dominant European culture through intermarriage.

The Colonial Period

By the mid to late 1500s, it was not certain that the Spanish colonists could support themselves in Puerto Rico. As the mines failed and no other sources of wealth were easily accessible, new sources of cashflow had to be established. By this time, the demand by Europeans for sugar and its various related products was growing. It was therefore very timely that this lush tropical island, ideal for growing sugarcane, was in search of a new and sustainable way to pay its bills. There were, however, big problems associated with sugarcane. The two main problems were that the land had to be cleared of its native forests, and cane plantations required lots of labor. Initially, the Taínos were forced into performing these tasks, but they were rapidly dying out, and later became extinct. However, recent DNA analysis indicates that many Puerto Ricans have an ancestral link to the Taínos.

So where would the labor force come from? The conquistadores? No, conquerors rarely performed manual labor. Early in Puerto Rico's history (1518), 500 African slaves had been brought to Puerto Rico to work in the mines. The need for slaves was transferred to the agricultural sector; thus thousands of slaves were imported, both legally and illegally, beyond the Spanish quotas. As a result of the increased labor, sugar production grew and mills were constructed in various places on the island. Later, production of coffee, tobacco, and ginger also became profitable. Puerto Rico now had a land-based economy and landowners, with many workers. As the mines petered out, San Juan no longer shipped its own gold and silver, but served as a collection center and safe harbor on the perilous sea routes to and from Spain. Spain's treasure fleets were often attacked by pirates, freebooters, or other nation's vessels, so Spain decided to fortify San Juan.

In 1539, the construction of El Morro (app. 2), a classic 16th-century fortress, was initiated. It was not completed for almost 200 years and included moats, ramps, and tunnels all interlinked with the main fortress with its kitchens, troop quarters, powder magazines, and dungeons. As a result of the construction of El Morro and two nearby forts, Puerto Rico became the most fortified colony in the West Indies. El Morro was attacked many times by various countries, pirates, and freebooters, but the Spanish flag did not fall until 1898 when the United States took over the island by attacking the unfortified south coast.

Puerto Rico remained pretty much a Spanish defensive outpost protecting its New World colonies and an agrarian society for the next 300 years. As the sugar industry continued to prosper, by the latter part of the 19th century, Puerto Rico the Spanish heritage of the island were being built in Old San Juan. By the time of the American Revolution, Puerto Rico's population was nearing 100,000. Large

homes reflecting the Spanish heritage of the island were being built in Old San Juan. They were brick and stucco, with ornate arches, many with interior courtyards and balconies. By 1800, the population had grown to nearly 150,000. Spain had opened Puerto Rico to greater colonization and in the early 1800s, many Spanish loyalists sought refuge there from wars for freedom in other Latin American colonies. By the 1830s, Puerto Rico had a plantation economy with sugar, coffee, tobacco, and molasses the main exports.

Steps Toward Autonomy

In 1812, Spain elevated Puerto Rico's status to that of a province, which included representation in the Spanish Parliament. This status was short-lived, and within a couple of years it reverted to colonial status with a series of military governors appointed by the Spanish Crown. This led to resentment and hostility on the part of a growing body of Puerto Rican intellectuals. In 1868, an intellectual-led rebellion occurred in the mountain town of Lares where they proclaimed the free Republic of Puerto Rico. The revolt was put down by Spanish troops. Prior to the revolt, political parties had been outlawed, but shortly after the revolt, the first legal political party was allowed to organize (Liberal Reform Party). Under its influence, the Spanish government outlawed slavery in Puerto Rico in 1873. At that time only 5 percent of the population was African. Puerto Rico, since its colonial period, was pretty much culturally and racially homogenous. The Liberal Reform Party changed its name to the Autonomist Party in 1887 in order to seek autonomy rather than absolute independence from Spain. Autonomy was achieved in 1897 under the leadership of Luis Muñoz Rivera. Once again, Puerto Rico could elect voting delegates to the Spanish Parliament. The newly granted autonomy also permitted the election of Puerto Rico's first legislature in March 1898.

The American Period

These reforms and newly won freedoms were abruptly ended. In April 1898, the Spanish-American War started as a result of the blowing up of the U.S.S. Maine, a battleship at anchor in the harbor of Havana, Cuba. The war was very short, and by August 13, it was over in Puerto Rico. An American military force of 16,000 landed on the south coast at Guánica and marched overland to San Juan, but the war ended before they crossed the Cordillera Central Mountains. On October 18, the Spanish flag was lowered over the governor's residence at La Fortaleza. Under agreements signed at the Treaty of Paris, Puerto Rico was officially ceded to the United States on December 19, 1898.

At the start of the 20th century, Puerto Rico had a population of nearly 1 million that was mostly poor, agrarian, and illiterate with little or no opportunity for education. Most of the island's land was in the hands of a few wealthy families and absentee owners. Coffee was the dominant export product, but it waned owing to new tariffs imposed by the United States and catastrophic hurricane damage.

Almost overnight Puerto Rico's newly won opportunities for self-rule were gone and all local political power was turned over to the U.S. military government. It abolished the newly formed parliament, local governments were reorganized, and new judicial and tax systems were put in place based on American forms of government.

Many Puerto Ricans identified with American principles of democracy and the hard-won freedoms brought about by the U.S. revolution. They were hopeful that the United States would willingly grant Puerto Rico many new political freedoms. This did not occur. Instead, the U.S. Congress passed the Foraker Act (Organic Act) in 1900. It was more restrictive than the freedoms Puerto Rico had won under the autonomy agreements with Spain. Under U.S. rule, the governor would be appointed by the President, as were all other major office holders, including the justices of the Puerto Rico Supreme Court. Local laws passed by the newly established Puerto Rico House of Delegates were subject to veto by U.S. Congress. Puerto Rico could only send a nonvoting resident commissioner to Congress. The Foraker Act also prohibited Puerto Rico from negotiating trade treaties with foreign nations and retired the Puerto Rican peso at 60 cents to the dollar. This caused a breach in international trade relations and a 40-percent rise in the cost of living. It also caused the price of land to fall and allowed the big wealthy U.S. sugar corporations to come to Puerto Rico and acquire vast areas of land, even though no corporation was allowed to own over 202 hectares (500 acres). This then prompted the rapid rise of sugar as the main exportable crop. Because of the foreign trade restrictions, by 1930 more than 90 percent of the island's sugar trade was with the United States and resulted in a **monoculture** economy for Puerto Rico. The big four U.S. sugar companies were able to show huge profits (22.5 percent return on capital) in the 1920s and 1930s. Much of the profit was due to the extremely low wages paid by the companies to the Puerto Rican workers (63 cents for a 10-hour day in 1917).

The Foraker Act was restrictive politically and economically, but did provide for new and expanded economic activities such as free trade with the United States. It also exempted Puerto Rico and its inhabitants from U.S. taxes. Federal excise taxes on rum and tobacco produced in Puerto Rico were returned to the island's

treasury. Although the Foraker Act was economically good for Puerto Rico, it was despised politically and thus resulted in continued local interest in Puerto Rican independence. This undercurrent, coupled with World War I, caused the United States to review Puerto Rico's status resulting in the Jones Act in 1917. This act granted collective naturalized citizenship to all Puerto Ricans on a voluntary basis. There were 1.2 million Puerto Rico residents at the time and all but 288 accepted citizenship. The Jones Act also allowed Puerto Ricans to enter the United States without travel restrictions, and established a Puerto Rico Bill of Rights, which created a new two-house legislature. Popular elections would decide a 19-member Senate and a 37-member House of Representatives. The Jones Act also required Puerto Ricans to serve in the U.S. military, and 18,000 Puerto Ricans served in World War I. After the war, more attempts at autonomy were proposed but were rejected by the U.S. Congress.

Free trade with the United States greatly enhanced sugar trade, and by the 1920s, 75 percent of the employed people in Puerto Rico were involved in the sugar industry controlled by U.S. corporations. When the world's economy collapsed in the late 1920s, the period of the Great Depression was particularly hard on Puerto Rico. By the 1930s, Puerto Rico's population had grown to 1.5 million, and the effects of the depression increased unemployment, which made living conditions worse. Per capita net income dropped from $122 in 1930, to $85 in 1933. The U.S. Congress had its hands full at home and basically ignored the plight of Puerto Rico. As a result, for the first time, hostility and resentment fueled a strong independence movement in the 1930s; however, it was not strong enough to defeat the other pro-statehood parties. In 1936, a new political party and leader emerged who was to dominate Puerto Rican politics for three decades. Luis Muñoz Marín founded the Popular Democratic Party (PDP) or Populares. In combination with an enlightened New Deal Governor, Rexford Tugwell, who was appointed by President Roosevelt, they began to reorganize the economic and social structure of Puerto Rico. Unfortunately, the 202 hectares (500-acre) land provision of the Organic Act was never enforced, and by the end of the 1930s, 51 corporations owned more than 100 000 hectares (250,000 acres), much of it not used for food production. This forced Puerto Rico to import (by design) vast quantities of food from the United States at high prices because of U.S. tariffs. The result was to turn farmers into virtual serfs. One of Muñoz Marín's great initiatives was to press Governor Tugwell to help in the passage of a Land Reform Act. This was finally accomplished in 1941 after the U.S. Supreme Court in 1940 said that Puerto Rico had the right to enforce its land reform laws and limit land ownership to 202

hectares (500 acres) or less. True land reform was the result, with many rura l residents now able to buy 10-hectare (25-acre) parcels. This allowed them to grow crops for profit for both export and internal use, thereby breaking up the land monopoly of the large sugar companies. Many see this as the seminal event instrumental in the real socioeconomic gains that would come in the late 1940s with the advent of Operation Bootstrap, a massive effort to raise the standard of living for the island's inhabitants and make the island more self-sufficient. Little attention was paid to gaining Puerto Rico's independence for 10 years, and out of frustration, a schism occurred in the PDP and the modern Puerto Rican Independence Party (PIP) formed in 1946.

Upon Roosevelt's death, Harry Truman appointed a new governor, Jesús T. Piñero, the first Puerto Rican to be named to the post. This created better relations with the United States. The U.S.-Puerto Rico relations were also strengthened as a result of the 65,000 Puerto Ricans who served in World War II. In 1947, Congress amended the Jones Act allowing all future governors to be popularly elected and with power to appoint Puerto Rico Supreme Court Justices. In 1948, the first popularly elected governor was Luis Muñoz Marín.

From 1948 to 1960, Puerto Rico and the U.S. government formulated and implemented Operation Bootstrap. The result was 450 new factories and businesses being started and the beginning of a major transition for Puerto Rico from a largely rural agrarian society, to the modern industrial economy it is today. By 1956, industrial development had surpassed agriculture as the principal source of income. New initiatives in public education and vocational training were part of this program. There was a second phase in Operation Bootstrap in the 1970s that was stimulated by ***Fomento***, Puerto Rico's Development Bank and Economic Development Administration. This program attracted capital-intensive industries such as petrochemical and pharmaceutical companies. The Operation Bootstrap Program also made it possible to develop a thriving professional class of lawyers, engineers, business managers, and financial executives needed to make these businesses run. It worked, and Puerto Rico became a showcase for other less developed economies in the Caribbean to emulate.

In 1950, following Governor Muñoz Marín's request, the U.S. Congress declared Puerto Rico a Free Associated State (Estado Libre Asociado), or Commonwealth. As a commonwealth, all existing ties to the United States would remain, but Puerto Rico could now write its own constitution. In the watershed election of 1952, the PDP won 67 percent of the vote, PIP 19 percent, and the pro-Statehood Republican Party (SRP) 13 percent. By 1964, when Muñoz Marín retired from the

governorship, the SRP had grown to 36 percent of the vote, and the PIP had slipped to 3 percent. In 1967, there was a plebiscite over Puerto Rico's political status with the options being commonwealth, statehood, or full independence. In that instance, independence was soundly defeated, with statehood coming in second (39 percent) to the island's current commonwealth status (60 percent). Congress in 1979 passed a resolution supporting Puerto Rico's right to self-determination. Under new leadership the pro-statehood party was renamed Partido Nuevo Progresista (PNP) and, to date, has elected three governors. However, even with a PNP governor, in the last political status vote of 1998 the commonwealth received 49 percent, statehood 46 percent, and independence 4 percent. Once again in 1998, Puerto Ricans demonstrated their preference for the status quo. In November 2000, Puerto Rico elected the first female governor, Sila María Calderón, who ran as an anti-statehood candidate for the PDP. The current governor of Puerto Rico, Aníbal Acevedo Vilá, is from the PDP party.

Puerto Rico elects a new legislature and governor every 4 years. Governors can serve a maximum of two consecutive terms. The Governor appoints a cabinet consisting of his or her department heads. The bicameral legislature is made up of two houses; the House of Representatives has 54 members and the Senate 28. Both houses are popularly elected. The government operates on a model similar to that of the United States, and Puerto Rico is set up like 1 of the 50 states. The island has 78 political districts (municipalities; fig. 3) and each has its own local political machine and locally elected officials such as city mayors and town councils.

Puerto Rico now participates in U.S. presidential primaries and sends delegates to the national political conventions, but it still does not have any voting representation in U.S. Congress, nor do Puerto Ricans vote for the President unless they reside in one of the 50 states. Puerto Rico cannot enter into treaties, issue money or passports, maintain armed forces, or exchange diplomats with foreign countries. They still do not pay any federal taxes, but as it turns out, commonwealth taxes are usually as high as U.S. taxes. Should Puerto Rico strongly indicate by vote and formal request its desire to become the 51st state, all that Congress would have to do is pass an enabling act by simple majority of both houses and have it signed by the President. There are three standards for statehood consideration: (1) that the new citizens abide by the American form of government, (2) that the majority of the commonwealth's electorate wants statehood, and (3) that they be able to meet their state and federal obligations.

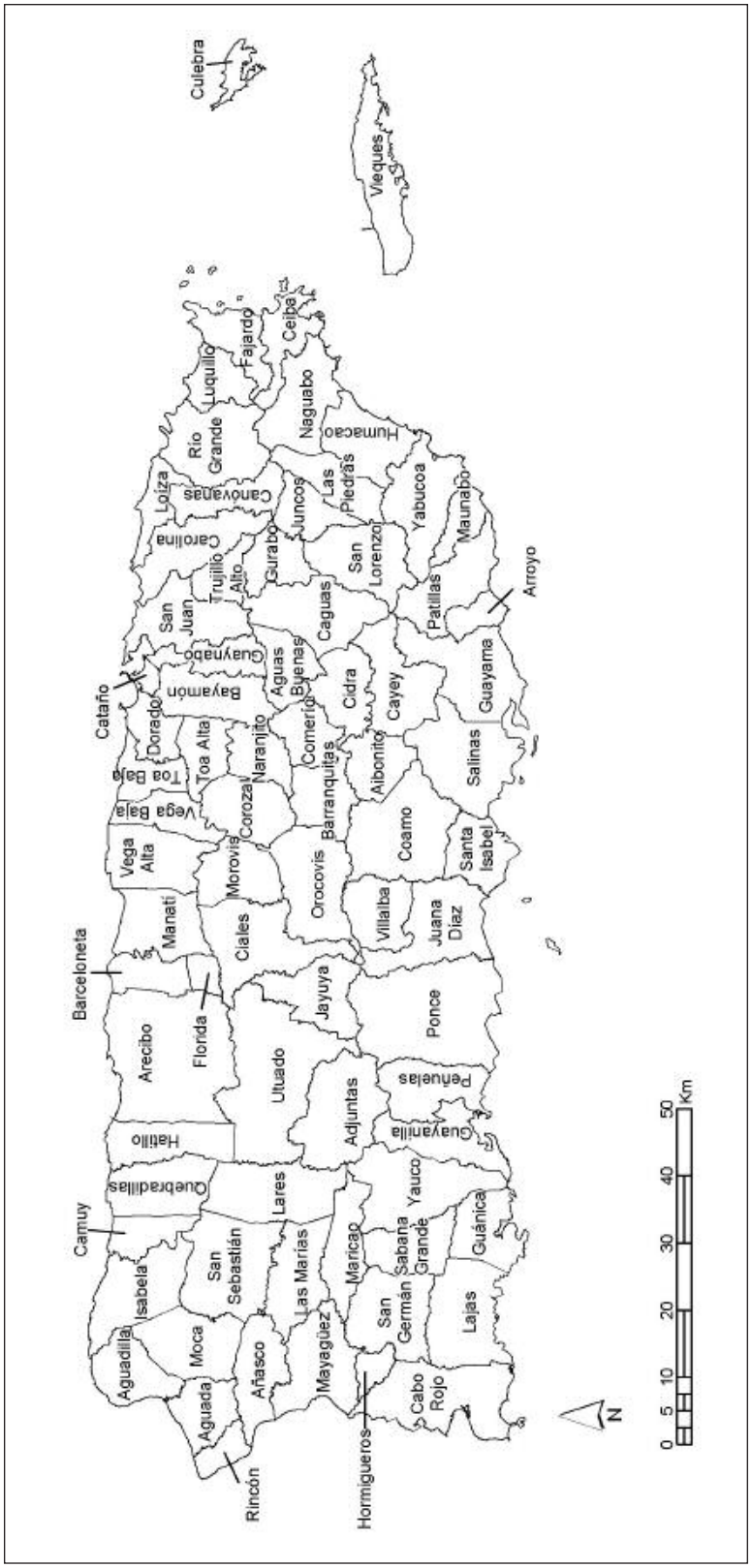


Figure 3—Municipalities of Puerto Rico.

Contemporary Puerto Rico

Population—

According to the 2000 U.S. census, the island of Puerto Rico has a population of slightly over 3.8 million compared to 3.15 million in 1990. There are also another 3.4 million Puerto Ricans residing in the United States, largely in metropolitan areas such as New York, Philadelphia, Chicago, and Orlando. More Puerto Ricans now live in Florida than in the capital of San Juan. These mainland residents are an outgrowth of a migratory shift in the Puerto Rican population that began in the 1950s and 1960s largely as a result of rapid population growth and poor economic opportunities on the island. Migration had an "Alice in Wonderland" effect, that is, the economy had to run very fast just to stand still because, during that period, Puerto Rico's birthrate was 35 per 1,000, while its death rate had dropped to only 7 per 1,000, so the population was growing rapidly. This migration trend was still occurring in the 1990s when on average 6,500 people per year left the island. Although Puerto Rico's population is still growing, its rate of increase is declining and may not be sufficient to replace itself (0.6 percent/year) in the long term.

The island's population is primarily urban (72 percent), with greater San Juan having a metropolitan population in excess of 1 million. The remaining 28 percent is spread throughout the rural areas except for restricted commonwealth or federal lands. Puerto Rico has one of the highest population densities in the world, in excess of 450 per square kilometer (1,100 people per square mile). Population density in metropolitan San Juan is about 4000 per square kilometer (10,000 per square mile). Life expectancy is slightly lower than in the United States at 80 years for females and 71 years for males. Infant mortality is somewhat higher than in the United States with 13.4 deaths per 1,000 live births.

Puerto Rico has a growing elderly population; people 60 years or older account for over 15 percent of the population. Those under 19 years account for about 33 percent of the population. According to the 2000 census, over 80 percent is white, 8 percent is black, and approximately 12 percent are members of other ethnic groups.

Puerto Rico is Spanish in atmosphere and culture. The island's population is 99.9 percent Hispanic and the first language is Spanish, with English as its second language. Most Puerto Ricans know some English, as it is a compulsory subject in the school system. Many older people use it sparingly, and school dropouts often do not attain fluency; thus English fluency is estimated to be less than 50 percent. The island's government is officially bilingual. The language and culture issues are quite contentious, as most Puerto Ricans do not want to give up their Spanish

heritage. Many still identify closely with Spain and Spanish-speaking South and Central American countries and do not want to give up Spanish as their official language. Historically, the religion of the island's people has been mostly Roman Catholic. Many non-Catholic denominations actively came to Puerto Rico looking for converts, especially the Adventists and Mormons. Today the people are 40 percent Roman Catholic, 40 percent Protestant, and 20 percent other religions. Puerto Rico is also North American in status and progress because of its unique commonwealth status with the United States. High standards of health, food preparation, water treatment, education, and the presence of organizations such as the Rotary Club, the Masons, the Lions Club, the Elks, and the Boy Scouts and Girl Scouts of America all provide a North American flavor to the island.

Puerto Rico has a 90 percent literacy rate. There are over 600,000 public school students, making it the third largest school district in the United States. Education is compulsory from ages 5 to 21. About 42 percent of Puerto Rican young people graduate from high school and many pursue advanced education. The University of Puerto Rico was founded in 1903 as a U.S. land grant institution (fig. 4). Its main campus in Río Piedras is a fully comprehensive Ph.D.-granting, teaching/research liberal arts university, with a law and medical school. Its land grant counterpart at Mayagüez offers a full array of degrees, and houses the engineering, agriculture, and marine sciences programs. The university also has a designated liberal arts campus at Cayey and eight other campuses. Total enrollment today is more than 71,000. The university's combined budget is more than $1 billion per year. There are 30 campuses of higher learning in Puerto Rico, and they graduate nearly 45,000 students per year.

Economics—

Puerto Rico is still very economically dependent on the United States. The U.S. presence affects Puerto Ricans' economic lives every day, from the U.S. currency in their pockets, to the many products sold on their store shelves. The U.S. government subsidizes Puerto Rico with about $15.48 billion in federal assistance payments yearly, which covers everything from education to food stamps. It is estimated that in 1999, federal subsidies for unemployment compensation and housing for a family of four cost the U.S. government over $19,000 per year. Should Puerto Rico become the 51st state, it would be eligible for another $3.5 billion in federal assistance (estimated). Approximately 40 percent of Puerto Rico's economy has been based on special tax exemption legislation that allows U.S. manufacturers to avoid paying federal tax on profits made in Puerto Rico. This is estimated to be in excess of $4 billion per year. The U.S. industries benefit from operations in Puerto

G. Miller

Figure 4—View of the main campus of the University of Puerto Rico, Río Piedras with the bell tower and royal palms lining the entrance.

Rico and generate billions of dollars in annual revenue. Puerto Ricans also benefit from the federal guarantee on bank savings, and from the millions of dollars received in disaster relief after a hurricane. Per capita income for the island is $7,600 a year, which is half that of the poorest state, Mississippi, but considerably higher than its nearest Greater Antilles neighbor, the Dominican Republic, where average per capita income is only $1,600 per year. More than 37 percent of households earn less than $10,000 per year. Official unemployment fluctuates between 11 and 20 percent, although there is considerable employment in various activities not included in the official statistics. Actual unemployment is probably higher, and may in fact be close to 20 percent. In 2000, 1.15 million people were employed. Nearly 60 percent of the population falls within the U.S. government's poverty definition, and over 30 percent of the population receives some form of public assistance. This includes some 425,000 families (1.1 million people) who received an average of $220 a month in the nutritional assistance program. It is estimated that

as much as 50 percent of this money ($650 million) goes to purchase nonfood items. According to the 2000 census, approximately 73 percent of homes are family-owned, and 64 percent of families own one or two automobiles.

The U.S./Puerto Rico association is also beneficial to the United States. The U.S. economy benefits on the order of $720 billion as a result of commerce with the island and the many U.S. companies located in Puerto Rico. Puerto Rico must use the U.S. Merchant Marine to transfer its products and cannot engage in international commercial activity without the consent of the United States. The United States has used Puerto Rico as a strategic military base since the turn of the 20th century, and it remained the U.S. Navy's primary training facility for amphibious warfare and carrier-based tactical bombing practice until 2003.

As cited earlier, numerous U.S. manufacturers have built manufacturing plants in Puerto Rico and account for 42 percent of the gross domestic product (**GDP**) employing about 24 percent of the workforce (160,000). Industry is the main source of income for Puerto Rico. The services sector accounts for 37 percent of GDP and employs 291,000 people. Various government agencies produce 11 percent of GDP and have 245,000 employees. The utilities sector also produces 11 percent of GDP, with 32,000 employees. Agriculture today accounts for only 1 percent of GDP and employs 26,000. Construction employs 85,000 people. Puerto Rico now has 70 pharmaceutical firms whose products are viewed as recession-proof. Puerto Rico exports more than $25 billion in products ranging from medicine, refined petroleum products, scientific equipment and machinery, to rum, clothing, and shoes. Unfortunately, the island's high-value mineral resource base is quite limited. It has a large population on a small land base, and island food production is now low. This results in the need for islanders to spend billions on food imports. In spite of this, Puerto Ricans enjoy the highest standard of living and per capita income in Latin America.

In August 1996, the U.S. government began the phasing out of federal tax benefits that had positioned Puerto Rico as the preferred site for stateside manufacturers. This resulted from the fact that not enough new jobs were being created for the large amounts of tax writeoffs the multinational corporations were receiving. This came at a time when the federal government was also trimming budgets and eligibility for social welfare program spending and preferential treatment for Puerto Rican products. As a result, from 1996 to 2000, Puerto Rico lost 16,500 manufacturing jobs. By early 2002, the total had risen to 27,000 jobs lost. In light of these changes, Puerto Rico's government is developing a new economic development program called the "New Economic Model," which has tax incentives, increased

foreign trade and investment, and greater-self reliance as major themes that will lead Puerto Rico's economy into the new millennium. The Puerto Rico government is also trying to convince Washington to amend Section 956 of the federal tax code, which again would provide favored tax status for controlled foreign corporations operating in U.S. territories. This would permit up to 90 percent of their earnings to be returned to the United States without taxation. There is also discussion about trying to have Puerto Rico included in the Earned Income Tax Credit system of the U.S. tax code, as it would subsidize minimum-wage employees, bringing wages up to $14,000 or $15,000 per year.

Another aspect of Puerto Rico's economy, of which little is known, is the informal, unregulated, and illegal underground economy. This is mostly a cash and service economy. The illegal trade of drugs, for example, has an estimated gross cashflow of $20 billion per year according to the Drug Enforcement Agency. An estimated 20 percent of all cocaine imported into the U.S. enters via Puerto Rico and the U.S. Virgin Islands. Four billion dollars remain in Puerto Rico and surface in the economy. For example, the largest Puerto Rican bank (Banco Popular) was fined $21 million for not reporting hundreds of millions of dollars in questionable cash transactions in one of its banks in Old San Juan. Some Puerto Ricans take the view that it does not pay to work in the official economy and that they are better off getting welfare payments, food coupons, and taking part in the underground economy. The underground economy may be as high as one third (or more) of the total island economy. All of which is untaxed and unregulated.

For more information on Puerto Rico's history, see Aliotta 1994, Cockburn 2003, Dietz 1986, Fernández 1996, Golding 1973, Haslip-Viera 2001, Lewis 1963, López 1981, Morris 1995, Rouse 1993, U.S. Department of Commerce 2001, and U.S. Department of the Interior 1996.

Physical and Climatic Zones of Puerto Rico

Geography

Puerto Rico is the smallest of the Greater Antilles chain, which also includes Cuba, Jamaica, and Hispaniola (Haiti and the Dominican Republic). Puerto Rico is 145 kilometers (90 miles) from the Dominican Republic to the west and 67 kilometers (40 miles) from the U.S. Virgin Islands to the east. It is 1665 kilometers (1,000 miles) southeast of Miami and 2840 kilometers (1,700 miles) south of New York City. On the north and east side is the Atlantic Ocean, and on the south and west is the Caribbean Sea. It is positioned at the north end of a group of lesser islands that

form an arc running down to Venezuela 847 kilometers (525 miles) to the south. They are called the Lesser Antilles and include the U.S. and British Virgin Islands, French Guadeloupe, Martinique, and numerous other islands down to Grenada, Barbados, and Trinidad. All totaled, in the Greater and Lesser Antilles, there are approximately 7,000 islands that make up what are called the West Indies (fig. 2).

The land area of Puerto Rico and adjacent islands is 8897 square kilometers (3,435 square miles). It is 56 kilometers (35 miles) north to south, 176 kilometers (110 miles) east to west, and is rectangular in shape. Puerto Rico is somewhat smaller than the state of Connecticut. Its coastline is 500 kilometers (311 miles) with numerous harbors and beaches. Its land cover is variable, with much of the center of the island consumed by high mountains (40 percent), surrounded by foothills (35 percent), and a narrow coastal plain (25 percent). Virtually all of the coastal plain is in intensive agriculture, roads, or under urbanization. In a recent study by Helmer et al. (2002), they found that 41.6 percent of the island is now covered by closed forest, 36.7 percent is in pasture and grassland, 5.9 percent is in agriculture, 2.4 percent is in coffee plantations, 10.5 percent is urban/developed, and 3.9 percent is in various other categories including mines, rock/sand areas, salt and mudflats, emergent wetlands, and water bodies. Approximately 5 percent of Puerto Rico's forest area is under protection.

There are a variety of ecosystems distributed laterally and vertically according to **topography**, altitude, soils, rainfall, and a variety of other factors. The island lies directly in the path of the trade winds that blow from the Atlantic Ocean to the east. This assures a fairly reliable source of rain and occasionally a hurricane or two. The presence of high mountains creates a very interesting rainfall pattern resulting in the creation of an **orographic rain shadow** on the Caribbean side of the central mountain ranges, and some rain shadow valleys in the interior sections of the mountains.

The highest altitude on the island is 1338 meters (4,389 feet) in the Cordillera Central range at Cerro de Punta, and there are numerous peaks over 915 meters (3,000 feet). Cerro de Punta is just north of Ponce within the Toro Negro Commonwealth Forest and can be accessed by Route 143 (Luis Muñoz Marín Panoramic Highway). Mountains can be seen from anywhere on the island. The entire center of the island is a continuous series of mountains that basically cuts the island in half as they run east to west from Humacao to Mayagüez. Approximately 25 percent of the island is above 305 meters (1,000 feet) altitude. The high mountains exhibit high degrees of slope to the south and east, and the north slopes are heavily eroded with numerous river valleys. The south slopes tend to be dry much

of the year owing to the orographic rain shadow. During tropical storms and hurricanes, rivers on the south coast may become rapid torrents that flood extensive areas and often kill domestic grazing animals or human squatters living in the dry riverbeds or flood plains. The Cordillera Central has a break in the area of Caguas, and the mountain range located northeast is the Sierra de Luquillo. This range also has a series of peaks in excess of 915 meters (3,000 feet), and these peaks experience the highest amounts of rainfall on the island. The Luquillo range includes the El Yunque National Forest, also designated as the Luquillo Experimental Forest and known as the world-famous Luquillo Rain Forest or El Yunque. This 11 200-hectare (28,000-acre) forest is a biosphere reserve site and attracts about three quarters of a million visitors per year.

The soils of the coastal plain are conducive to agriculture, and much of it was cleared in the 17th and 18th centuries for sugarcane. Adjacent to the coast, the land is fairly level and has been converted to agriculture, urban development, and transportation corridors. Periodically, there are rocky promontories and karst foothills such as those near Arecibo, Fajardo, Cabo Rojo, and Guánica. Sand dune areas and beaches such as at Isabela, Piñones, Luquillo, and Boquerón dot the coastline.

Climate

Puerto Rico is in that large area north and south of the equator called the tropics (25° N and S). Its maritime climate is very pleasant because it is bathed by warm sea breezes throughout the year. This prevents major fluctuations in temperature. Rainfall is distributed throughout the year, with May through November considered the rainy period. January to March is a bit dryer, but may have cold fronts coming in from the temperate zone to the north that can produce 1 to 2 days of rain. Extremes in temperature are rare, with high temperatures rarely going into the mid 30s °C (90 °F) except on the south coast and lows rarely below 25 °C (60 °F) in the mountains. Smallest daily temperature fluctuations occur in the coastal plain 5 to 8 °C (10 to 15 °F), whereas the mountains experience the largest daily fluctuations 8 to 12 °C (15 to 20 °F). There is not much variation seasonally like there is in the temperate zone, in fact there is greater night to day temperature variation than there is seasonally. However, there is considerable variation in temperature and precipitation resulting from variable topography and prevailing winds. The east-west mountain chain intercepts the easterly trade winds; thus it provides the north side with an abundance of rain. The Cordillera Central and Luquillo ranges cause the warm moisture-laden air masses to cool and lose much of their moisture

as they pass over the north and eastern sides. As they pass over the mountains, the amount of rain decreases resulting in the south coast being much dryer (fig. 5).

Areas in the Luquillo Rain Forest often receive more than 5000 millimeters (200 inches) of rain, whereas areas in the Guánica Forest 42 kilometers (50 miles) away may only receive 900 millimeters (36 inches). The capital city of San Juan annually receives 1700 millimeters (68 inches) of rain on the north coast, whereas the second largest city, Ponce on the south coast, receives only 950 millimeters (38 inches). Some areas on the south coast may receive only 254 millimeters (10 inches) in dry years. The island's average rainfall is 1800 millimeters (71 inches) per year.

The mountainous topography produces temperature variation. In general, for every 300-meter (1,000-foot) increase in altitude, temperature decreases 2 to 3 °C (3 to 4 °F). On average, San Juan's coastal temperature will be 4 °C (7 °F) warmer than a town in the mountains such as Barranquitas. Many mountain communities experience almost idyllic climate, with temperature regimes that require neither air conditioning nor heating. People in the warmer, more humid coastal areas may use air conditioning throughout the year. Puerto Rico does not experience freezing temperatures, even in the highest mountains where temperatures rarely fall below 18 °C (65 °F). Much of the island experiences high humidity year round.

Many streams are formed as a result of the mountainous terrain. There are hundreds of mapped streams on the island, 50 of these are classed as rivers. Most rivers on the north side are larger in volume and length. Six major rivers originate in the Luquillo chain. Most of the rivers are dammed and used for regional or community water supplies, irrigation, and power production. The majority of the reservoirs have problems with **sedimentation**, water quality, and introduced exotic aquatic plants such as *Eichornia crassipes* (Mart.) Solms (water hyacinth) and *Pistia stratiotes* L. (water lettuce).

Hurricanes

The island is in the hurricane belt of the western Atlantic and Caribbean. Most hurricanes form as tropical lows off the coast of Africa from June through October and intensify as they proceed west over the warm waters of the Atlantic. Hurricanes are Puerto Rico's number one weather problem because of the catastrophic high winds and waves, large volumes of rain, and the enormous structural change they can produce on natural ecosystems, and on human populations and their infrastructure. Most hurricanes are peripheral and produce minor effects, but those termed killer hurricanes owing to their intensity and direct hits, have the potential to produce

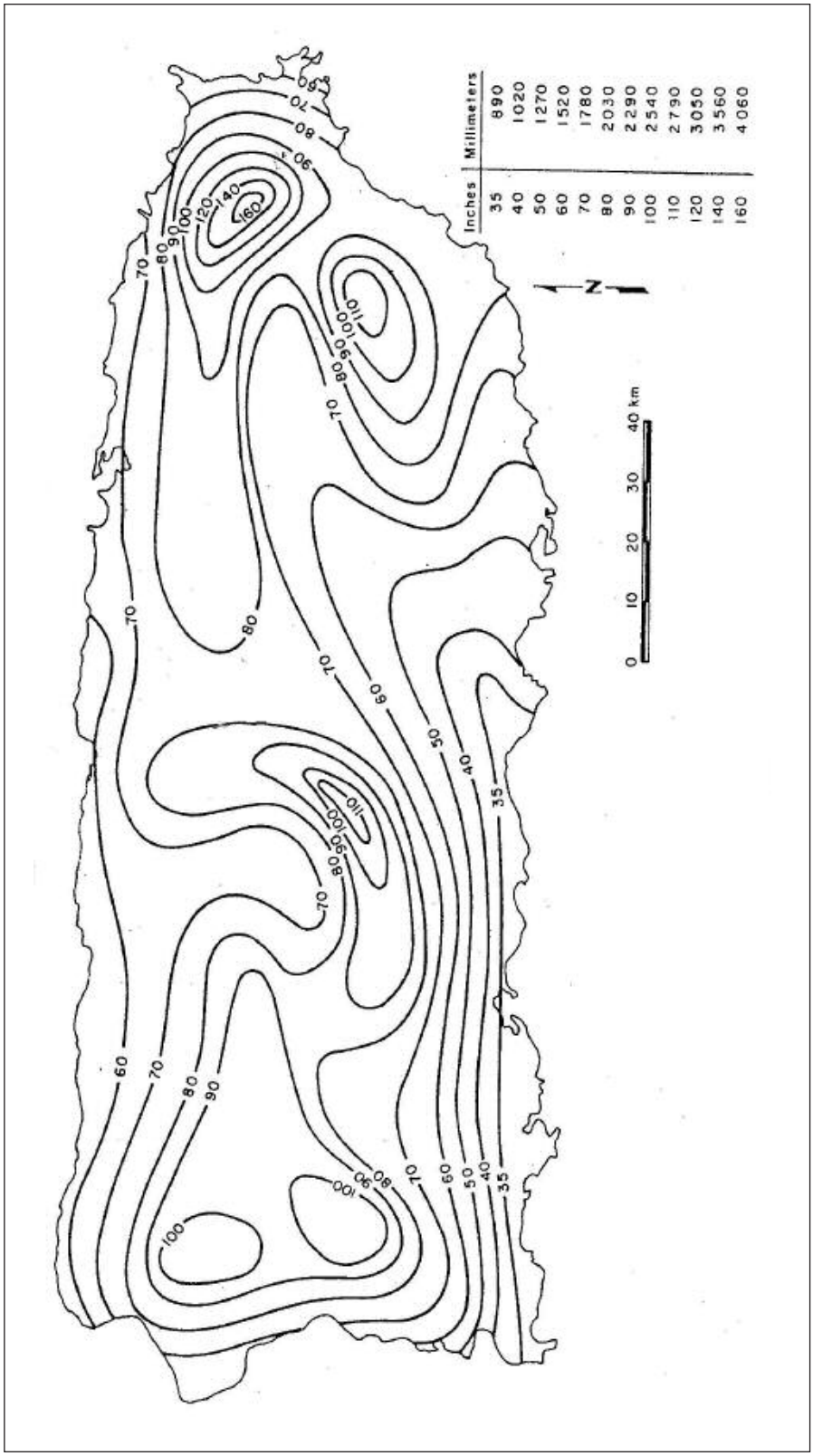


Figure 5—Annual mean precipitation for Puerto Rico.

enormous damage and hardship. Typically, 6 to 10 hurricanes develop yearly in the western North Atlantic region. Hurricanes have impacted Puerto Rico recently, with Hortense, Hugo, and George classed as major hurricanes. A separate section on hurricanes and other disturbances follows, and hurricane effects are discussed in the sections on forest zones and coral reefs.

Geology

Geologically, Puerto Rico is complex. Its origin is volcanic, and it initially arose as a result of seismic activity associated with the Caribbean-North American plate boundary zone. The initial formation was believed to have been 140 to 200 million years ago in the Triassic era. These **volcanic** deposits were then folded, faulted, and uplifted to produce the Cordillera Central Mountains province (fig. 6). Puerto Rico is relatively young, only about 100 million years old. Evidence of its volcanic period can be seen in weathered pillow lavas observable in road cuts south of Cayey on Route 52. Secondary **metamorphic** and **igneous** activities resulted in **gneisses** and **serpentinite** formations. Large outcrops of serpentinite occur on the western end of the Cordillera Central in the Maricao district west to Mayagüez (app. 2). This is a beautiful blue-green rock that produces a soil typically low in calcium and high in chromium or other metals. Some plants in western Puerto Rico show hyper-accumulations of nickel (Brooks 1987).

Younger sedimentary rocks and sediments are present throughout the coastal plain province. The carbonate province is located on the flanks of the central mountain core and is composed of marl, dolomite, and calcareous sandstones. On the north coast there is a spectacular display of karst topography that ranges back to 30 million years. A large area of limestone is located along the south coast and underlays the Guánica subtropical dry forest. In the karst district that runs from Loíza to just east of Aguadilla, many haystack-shaped hills dot the landscape by the thousands. They are locally called mogotes or **haystack hills**.

The rivers that run north from the Cordillera Central in the karst area produce deep cuts in the landscape owing to differential rates of erosion in the limestone. Some of the rivers periodically run underground in association with caves. There are thousands of caves and **sinkholes** in the region (see app. 2). A more detailed description of karst will be presented in the forest zone section.

Puerto Rico's geological formations have yielded very few mineable mineral resources. In the early 1500s, gold was mined, but gold was basically gone by the 1570s. Some commercial gypsum, dolomite, and phosphate have been mined (app. 2). Today, extensive areas of **aggregate** and road metal are being consumed. Most

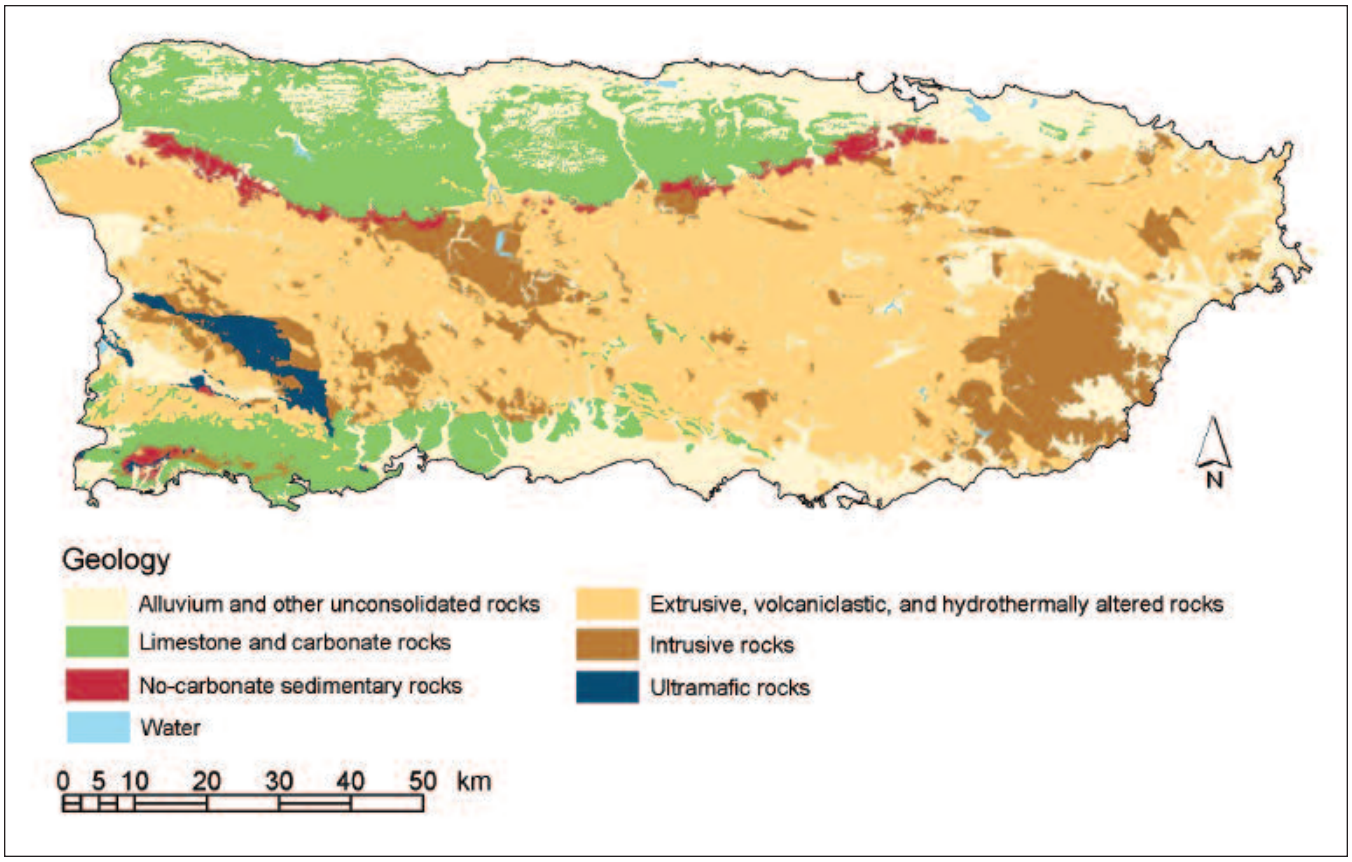


Figure 6—Geology of Puerto Rico.

houses today are constructed from cement. Large quantities of beach sand are mined, but at great expense to commercial grade beaches and resulting in areas of extensive coastal erosion such as at Isabela on the north coast. The most productive aspects of mining are nonmetals such as clays, marble, stone, sand, gravel, limestone, and salt. There are deposits of nickel and copper on the island. There is a large deposit of low-grade copper in the Cordillera Central near Lares. It has not been mined owing to cost, low metal concentration, and environmental concerns. There are peat deposits on the north coast, but probably not extensive enough for commercial mining. Roughly 10,000 workers are employed in mineral-related industries concentrated in the San Juan and Ponce areas. Puerto Rico has no coal, oil, or natural gas deposits. Fossil fuels, mainly oil, supply 90 percent of its power, and they must be imported. About 10 percent of its power is derived from dammed rivers. Many homes and businesses use **passive solar heating** for hot water.

Soils

Soil is the product of the weathering of rocks. When water runs across or through parent geologic strata, erosion and **leaching** occurs. Various other physical, chemical, and biological conditions of the environment further aid in the weakening and disintegration of these strata promoting the accumulation of released particles in the formation of soil. Many conditions are responsible for the characteristics exhibited by each soil type such as composition of the original substrate, slope, temperature, **aspect**, rainfall, acid rain, biological activities, and gaseous content to name a few. These conditions lead to the specific colors, structure, and nutrient availability of each soil. Because of its complex geology and climate, Puerto Rico shows a variety of soils, with 9 of the 11 possible soil orders present. The most extensive soil group is the Inceptisols, which cover 37 percent of the island. Inceptisols are found on steep slopes of 20 to 60 percent in eastern Puerto Rico. Many of these soils are eroded owing to cultivation on steep slopes. Inceptisols are typical of mountainous areas, are only slightly weathered, and their horizons are still developing. Landslides frequently occur on these soils.

Ultisols cover nearly 27 percent of the landscape and are found in uplands of the western sections of the Cordillera Central. These are typical of humid environments, usually nutrient poor, and mostly found on ancient strata or highly weathered alluvial sites. Mollisols constitute 21 percent of the island's soils and are found over limestone in the rain shadow foothills on the south side of the Cordillera Central, on limestone sediments on the north coast, and in various flood plains and alluvial fans in river systems. They have a dark, thick A-horizon; are soft and crumbly; and are high in organic matter. Six other soil orders cover the remaining 15 percent of the landscape (fig. 7).

Puerto Rico has 29 suborders and 164 classified soil series. About 28 percent of the island has soils suitable for agriculture. Much of this was historically used for sugarcane production. Today, some of the best soils are disappearing in areas undergoing rapid urbanization. This is critical because Puerto Rico is heavily dependent on food imports and the loss of the best agricultural soils only increases that dependence. For additional descriptions of the soils of the Caribbean and Puerto Rico, see the recent review by Lugo et al. 2000.

The physical features just described have a direct effect on the distribution of plant species and communities. Plant communities are distributed over the landscape based on elevation, soils, geology, rainfall, temperatures, aspect, and numerous interactions among other plants and animals; the distribution of communities

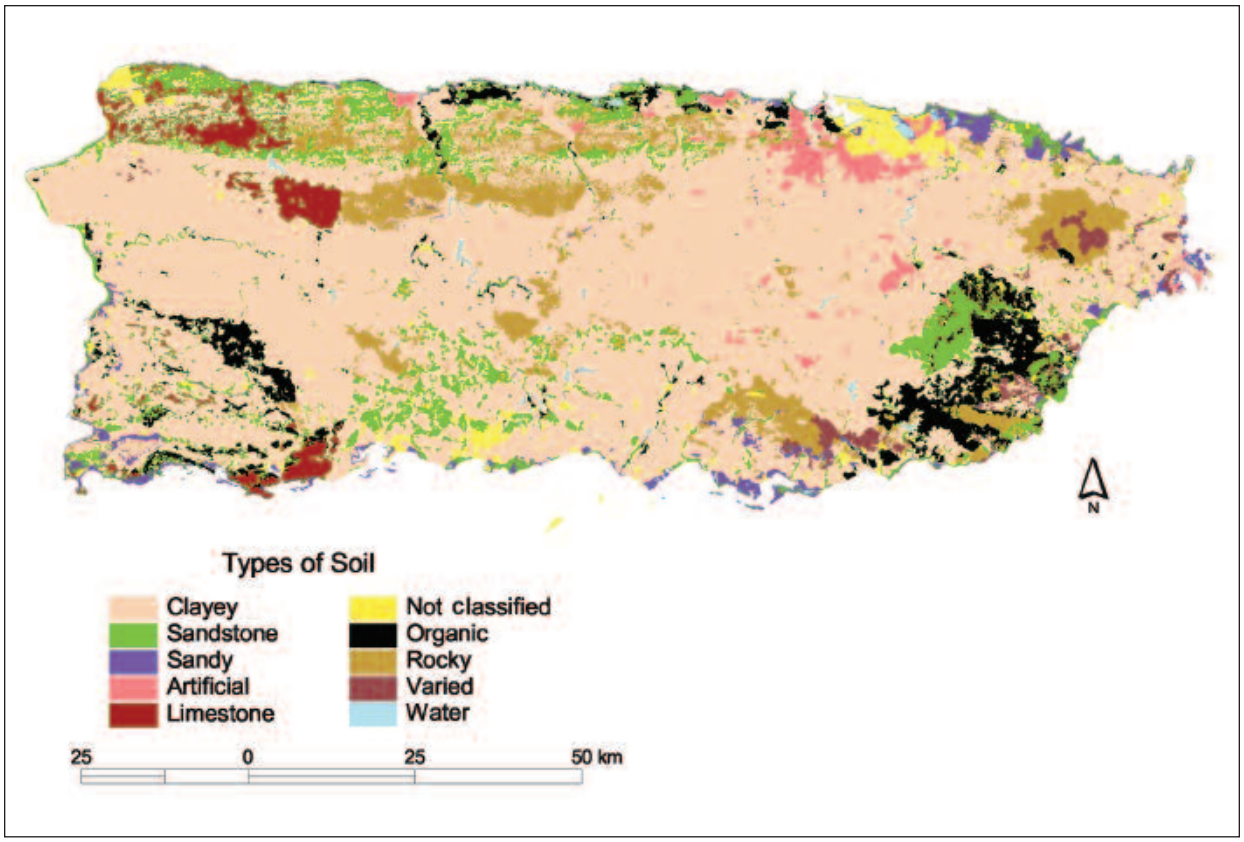


Figure 7—General soils of Puerto Rico.

Table 1—Forest type and distribution of parent material

	Forest type based on climate			
Parent material	**Dry forest**	**Moist forest**	**Wet forest**	**Rain forest**
Alluvial	X	X		
Limestone	X	X	X	
Ultramaphic	X	X	X	
Volcanic		X	X	X

that results spatially are referred to as plant geography or **phytogeography**. Later in this document is a description of the major forest types of Puerto Rico that will relate to these factors. However, for now, note that the major forest type distributions are related closely to parent materials as seen in table 1.

For more information on the physical and climatic zones of Puerto Rico, see Beinroth 1969, 1971; Birdsey and Weaver 1982; Bush et al. 1995; Calvesbert 1970; Giusti 1980; Lugo-López and Rivera 1977; Malfait and Dinkelman 1972; Monroe 1980; Picó 1974; and Weaver 1992.

Chapter 2: Flora and Fauna of Puerto Rico and the Caribbean

General Review of the Flora

Puerto Rico has a diverse native **flora**. More than 180 higher vascular plant families and 3,100 species are present. The vast majority are native species. Up to 300 species are naturalized aliens. There are more than 250 **endemics**. Currently, there are no known families or genera endemic to Puerto Rico. The flora is composed of 143 dicot families, 33 monocot families, and five families of **gymnosperms**. In addition, there are 15 families of lower vascular plants, including members of the Psilotaceae (wiskfern), Selaginellaceae (spikemosses), Isoetaceae (quillworts), and various fern families. Much of the plant diversity relates to the island's diverse set of habitats, which range from dry rocky coastlines, to very wet montane elfin forests. The presence of a high central mountain corridor with deep valleys, highly variable rainfall patterns, orographic rain shadows, and a variety of soil types all lend themselves to supporting a complex flora. In addition, an estimated 3,000 alien species have been introduced from various areas of the New and Old World tropics; thus, there are well over 200 plant families in Puerto Rico and the adjacent islands.

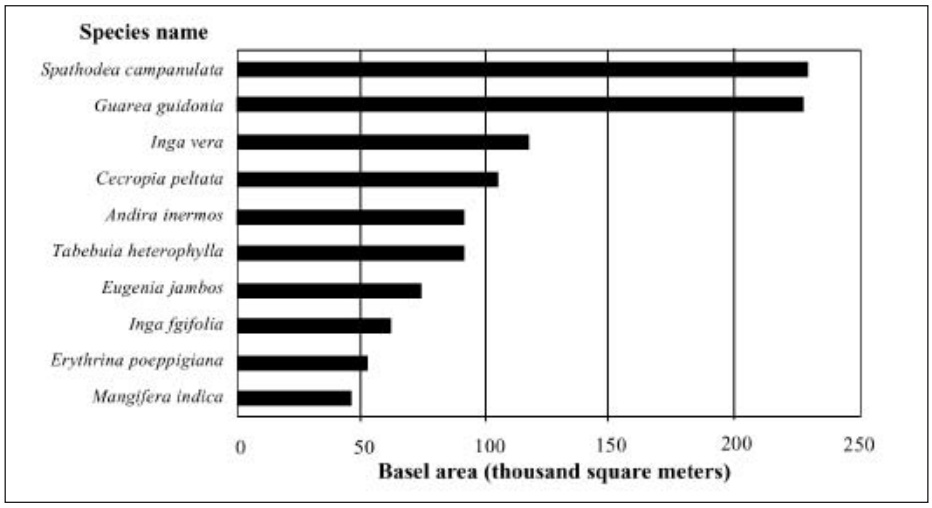
Puerto Rico's native flora has a high affinity with the flora of the Greater Antilles to the west (Hispaniola, Cuba, and Jamaica). It also has much in common with the flora of the Lesser Antilles and South America. Many of the plants are found throughout the Caribbean, such as the sandy beach plants, weedy grasses, **legumes**, asters, and lawn weeds such as the common plantain. A small number of plants also have an affinity with Florida and the Gulf Coast region of North America, some of which may have arrived via **Neotropical migratory** birds (feathers, feet, digestive tract **vectoring**). A few species probably rode the currents and the hurricane-force winds from Africa.

Of the alien species, probably 1,000 were introduced because of their beauty, such as *Spathodea campanulata* Beauv. (African tulip tree) (box 1).[1] Another 1,000 were probably brought because they afforded food, clothing, shelter, construction, or medicinal possibilities. For example, *Persea americana* Mill. (avocado) seeds do not float and are too large to be vectored by birds. It was probably brought to the island by indigenous people.

[1] See appendix 1 for Common and Latin Names.

Box 1. *Spathodea campanulata* Beauv. (African tulip tree)

It seems that no matter where you are in Puerto Rico, if you look out into the distance, you are likely to see a tree that looks like a red fountain. If you examine the flowers you will see brilliant orange-red petals much like the shape and color of tulips. Its origin is west central equatorial Africa, thus the name "African tulip tree." It belongs to the family Bignoniaceae, known worldwide for its large colorful flowers. It is a fast-growing tree, as are many introduced aliens, but its wood is light and has little commercial value. Owing to its beautiful flowers appearing from October to April (some plants bloom year round), it is widely planted in many tropical areas as an ornamental. In Puerto Rico, it has become naturalized and is the most common tree in the island's secondary forests (see graph). It is not a forest dominant and usually



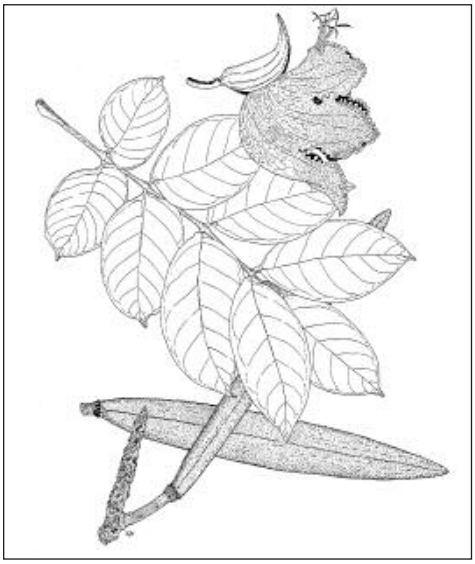
Relative species importance by basal area in Puerto Rico timberland in 1960.

fades as the stand matures because it is shade intolerant. Recently, almost pure stands of *Spathodea campanulata* have been found in Puerto Rico and are currently under investigation.

Its leaves are pinnately compound and oppositely arranged and may be over 30 centimeters (1 foot) long. They can grow in fairly dry areas where average moisture is about 1000 millimeters (40 inches), but grow best where mean annual precipitation is 1600 millimeters (64 inches) or more. When growing in dryer climates, they may become deciduous. Many people use them as shade trees in their yards where they can achieve heights in excess

Box 1. continued

30 meters (100 feet) in 30 to 40 years. Older trees may develop a flared trunk base, referred to as buttressing. The largest tree of this species is in the city of Arecibo and exhibits a height of 35 meters (115 feet), a crown diameter of 15 meters (49 feet) and a circumference of 5.49 meters (18 feet).



Leaves, flowers, and fruit of the African tulip tree.

African tulip trees are fairly resistant to infection, but their branches are subject to wind damage because of their light wood. This may lead to secondary heart-wood rot, which makes the tree susceptible to snapping during severe storms. As with many successional species, their life expectancy is short. They produce large volumes of small wind-dispersed seeds, thus they can be carried long distances. They are invaders of open sunny landscapes where they grow rapidly and help stabilize the soil.

In Africa the seeds have some food and folk medicine value. Although its wood has only low-grade commercial value, this plant is one of the true beauties of the Puerto Rican forest, and its true value is the pleasure it brings to people as its showy flowers light up the landscape.

For more details on the African tulip tree, see Francis 1990, Little and Wadsworth 1964, and Franco et al. 1997.

African tulip trees are found all throughout Puerto Rico commen.

Table 2—Floristic analysis of the Greater Antilles

Island	Area	Number of species[a]	Density of species[b]	Endemism
	km²			*Percent*
Puerto Rico	8 897	3,126	0.350	8
Jamaica	10 991	2,888	.262	27
Hispaniola	77 914	5,000	.064	36
Cuba	114 524	6,000	.052	49

[a] Number of species includes native and naturalized.
[b] Density of species is total species divided by square kilometer.
Source: Modified from Liogier and Martorell 2000.

Most of Puerto Rico's endemic species are associated with the mountain province. Mountains, with their variable growth conditions and deep valleys, can foster genetic variation and isolation that may lead to ecotypic variation, and over time, evolution of a new species. A higher percentage of endemics are found in the mountains than in the coastal province. The lowland species are more cosmopolitan in their distribution throughout much of the Caribbean. Puerto Rico is third in number and fourth in percentage of endemics in the Greater Antilles (table 2). Cuba has the highest number. On the other hand, Puerto Rico has the highest density of species, whereas Cuba is fourth. Liogier and Martorell (2000) indicated that the smaller the island, the higher the species density, and the larger the island, the higher the percentage of endemism.

Myrtaceae (myrtles) is the **family** with highest endemism in Puerto Rico (31 species), Asteraceae (asters) has 19 endemics present, and the Polypodiaceae (ferns) 16 species. Puerto Rico has only two endemic palms, whereas Cuba has 60 palm species that are endemic.

The Caribbean region is floristically rich. According to Lugo et al. (2000), the region harbors an estimated 12,000 to 15,000 vascular plant species, one endemic family, 200 endemic genera in 49 families, and 7,500 endemic species. The regional flora is highly endemic or Caribbean in distribution, rather than of mainland affinity. The flora exhibits numerous species per unit area as evidenced by species-area curves that exhibit steep slopes. It appears that species **extinction** in the region has been minimal. Again, according to Lugo et al. (2000), it appears that the forces that shaped Caribbean vegetation may have also provided resilience to the flora that would prove of benefit during the onslaught of human activity.

The three biggest plant families in the world are the Asteraceae (asters), Orchidaceae (orchids), and Fabaceae (legumes). Orchids and legumes are much more common in the tropics than the asters. Puerto Rico's four largest **angiosperm**

Table 3—Puerto Rico's largest plant families

Plant group	Family	Species present
Monocots	Poaceae	257
	Orchidaceae	144
	Cyperaceae	135
Dicots	Fabaceae	244
	Asteraceae	140
	Euphorbiaceae	109
	Rubiaceae	107
	Myrtaceae[a]	77
Ferns	Polypodiaceae	287

[a] Family with largest number of endemics.

Table 4—Partial list of plant families found in Puerto Rico with only one genus and one species

Plant group	Family	Plant names
Monocots	Ruppiaceae	*Ruppia maritima* L. (widgeon grass)
Dicots	Avicenniaceae	*Avicennia germinans* L. (black mangrove)
	Bataceae	*Batis maritima* L. (saltwort)
	Bixaceae	*Bixa orellana* L. (lipstick tree)
	Cannabaceae	*Cannabis sativa* L. (marijuana)
	Caricaceae	*Carica papaya* L. (papaya)
	Ceratophyllaceae	*Ceratophyllum demersum* L. (coontail)
	Cyrillaceae	*Cyrilla racemiflora* L. (palo colorado)
	Droseraceae	*Drosera capillaris* Poir. (sundew)
	Juglandaceae	*Juglans jaimaicensis* C. DC. (Jamaican walnut)
	Myristicaceae	*Myristica fragrans* Houtt. (nutmeg)
Lower plants	Psilotaceae	*Psilotum nudum* (L.) Beauv. (wiskfern)
	Azollaceae	*Azolla caroliniana* Wild. (water fern)
	Osmundaceae	*Osmunda cinnamomea* L. (cinnamon fern)

families are the Poaceae (grasses), Fabaceae (legumes), Orchidaceae (orchids), and the Asteraceae (asters). The largest family is the Polypodiaceae, which is one of the fern families. It has 287 species present. Twenty-eight ferns are limited to calcareous areas, five to serpentine, and five to salty habitats. Puerto Rico's largest plant families are presented in table 3.

Puerto Rico's flora has 37 plant families that are **monogeneric** and **monospecific** (table 4). Two families are monocots, 32 are dicot families, and 3 are lower vascular plant families.

In table 5 you will find a representative group of tropical plant families with some of their interesting genera and species that many people not from the tropics may be able to recognize because of products that are derived from them. Some

Table 5—Representative list of tropical plant families

Family	Species	Common name/notes
Agavaceae	*Agave* L. spp.	Century plant–tequila and rope sisal
Anacardiaceae	*Mangifera indica* L.	Mango–fruits
Annonaceae	*Annona reticulata* L.	Custard apple–tropical fruit
Apocynaceae	*Plumeria rubra* L. and *P. alba* L.	Frangipani–perfume and floral arrangements
Araceae	*Monstera* spp.	*Philodendron* group–**epiphytes**–2,000 species worldwide, 92 percent tropical–houseplants
Bixaceae	*Bixa orellana* L.	Lipstick tree, food coloring
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	Kapok–life vests and pillows
Bromeliaceae	*Ananas comosus* (L.) Merrill; *Guzmania* spp.	Air or well plants–epiphytes Piña or pineapple
Cactaceae	*Opuntia* spp.	**Succulent** desert and dry coastal forest plants
Caricaceae	*Carica papaya* L.	Papaya fruit
Clusiaceae	*Clusia rosea* Jacq.	Autograph tree, strangler epiphyte
Fabaceae (Leguminosae)	*Delonix regia* (Bojer) Raf.; *Mimosa pudica* L.	Flamboyán and sensitive plants–legumes are very important nitrogen fixers in the soil, attractive flowers
Flacourticeae	*Banara vanderbiltii* Urban.	Palo de ramón–rarest tree in Puerto Rico
Lecythidaceae	*Couroupita guianensis* Aubl.	Cannonball tree–**cauliflory**
Liliaceae	*Sansevieria* spp.; *Aloe vera*	Snake plant; mother-in-law's tongue–houseplants and lotions
Malvaceae	*Hibiscus rosa-sinensis* L.	Red hibiscus **shrub**.
Moraceae	*Artocarpus altilis* (Parkinson) Fosberg	Breadfruit;
Musaceae	*Musa* spp.	Bananas and plantains
Nyctaginaceae	*Bougainvillea spectabilis* Willd.	Brilliant flowering shrub–many colors
Orchidaceae	*Vanilla planifolia* G. Jackson	Vanilla for food additive; 20,000 species of orchid worldwide, second largest family of plants in the world
Palmaceae	*Roystonea regia* (H.B.K.) O.F. Cook- (royal palm); *Cocos nucifera* L.	Royal palm and coconut palm–the beautiful palms of the tropics
Pandanaceae	*Pandanus odoratissimus*	Screw pine, large **prop roots**
Piperaceae	*Piper* spp.	Pepper family
Poaceae (Gramineae)	*Saccharum officinarum* L.; *Bambusa vulgaris* Schrad ex. Wendl.	Sugarcane; bambo
Polygonaceae	*Coccoloba uvifera*	Sea grapes
Rhizophoraceae and Avicenniaceae	*Rhizophora mangle* L.	Red mangroves
	Avicennia germinans L.	Black mangroves **Vivipary**, specialized prop and pneumatophore roots
Rubiaceae	*Coffea arabica* L.	Coffee
Sapotaceae	*Manilkara zapota* (L.) V. Royen	Gum tree–Chicklets chewing gum
Sterculiaceae	*Theobroma cacao* L.	Chocolate tree
Strelitziaceae	*Strelitzia reginae* Banks ex Dryand	Bird-of-paradise
Zingiberaceae	*Alpinia purpurata* (Veill.) Schum.	Ginger for foods

people may have them as houseplants, or they may eat or drink them with some regularity.

For more information on the flora of Puerto Rico, visit the University of Puerto Rico, Botanical Gardens (app. 2) and see Liogier 1997, Liogier and Martorell 2000, Little and Wadsworth 1964, Little et al. 1974, and Proctor 1989.

Trees

Today, forests cover approximately 40 percent of Puerto Rico. At one point, more than 90 percent of the forests of the island had been cleared, and those forested areas that remained were heavily disturbed. Since the 1960s, forest cover has been steadily increasing owing to industrialization and urbanization. Many formerly cleared areas that were on steep slopes or that became unproductive owing to poor agricultural practices are undergoing natural reforestation. The island is greener today than at any time in the 20th century.

Over the past 60 years, the landscapes of the island have been transformed from agricultural to a mixture of urban and rural landscapes. The long-term trend in land use is for Puerto Rico to become an urban island. This transformation—powered by economic and social changes—has also transformed the ecosystems of the island. The forests of today are not the same as those of yesterday, and they will certainly be different in the future. For example, more than 200 species of trees have been introduced by humans and some are now naturalized and enrich the new forests of Puerto Rico. *Spathodea campanulata* Beauv. (African tulip tree), an alien species, is now the most common tree in the new landscape, a landscape dominated by humans. This new landscape has more species than the landscapes of the past, resulting from the introduction of alien species, a low rate of extinctions, and the creation of new habitats by people.

Most trees in Puerto Rico are tropical evergreen hardwoods, unlike fast-growing evergreen pine forests of the Southeastern United States. Many are slow growers, with high wood density and good commercial value such as *Manilkara bidentata* (A. DC.) Chev. (ausubo)—for use in cathedral and house beams—or have high specific gravity (>1) such as *Guaiacum officinale* L. (lignum vitae). Those species that grow fast have light woods like *Ochroma pyramidale* (Cav.) Urban (balsa), *Cecropia schreberiana* Miq. (trumpet tree), and *Bursera simaruba* (L.) Sarg. (Gumbo limbo).

Although there has been massive disturbance of forest habitat throughout the island, there has been no recorded extinction of tree species. Little et al. (1974) indicated that the island has 547 native tree species (table 6). Today, Puerto Rico

Table 6—Taxonomic groupings of Puerto Rico's trees

	Number
Native species	547
Introduced species	203
Total	750
Native genera	272
Introduced genera	104
Total	376
Native families	85
Introduced families	14
Total	99

Source: Little et al. 1974.

has an additional 120 species of naturalized alien tree species. **Naturalized species** are those that are growing and reproducing in the landscape and that appear "natural," even though there is an historical estimate of their approximate date of introduction. The total number of tree species in Puerto Rico is 667 when naturalized species are considered. Numerous other introduced trees are present (83 species on the island), but are not considered naturalized. Thus, the total number of trees rises to 750 when the alien species are included. This number is surprisingly higher than the total number of tree species found in the lower 48 continental United States (679 species). Most of the alien trees were introduced for utilitarian reasons such as ornamentals, food, drink, wood, and agricultural testing. More than 75 trees native to Puerto Rico are found in the Southern United States (Florida and adjacent Gulf States).

Table 7, modified from *Trees of Puerto Rico and the Virgin Islands* (second volume; Little et al. 1974) tabulates important families with large numbers of species. Thirteen plant families contain 387 tree species, which is more than 50 percent of the total. All of these families contain 15 or more species.

Because Puerto Rico developed as a submarine volcanic island from the ocean floor, it was never attached to a continent. As a result, all species present, both plant and animal, had to migrate great distances over open ocean or were of recent human introduction. An analysis of tree species' ranges and centers of distribution (table 8) illustrates the geographic affinities and important areas of origin of the woody flora of Puerto Rico.

The largest source of species appears to be from the Neotropical continental mainland. In addition, **speciation** was involved in migration of species via the Antillean chain of islands. It appears that endemism was important in the Puerto Rican flora whereby an original immigrant diverged genetically owing to physical and climatic isolation. Today, 21 percent of the trees in Puerto Rico and adjacent

Table 7—Important families with many tree species in Puerto Rico

Family	Total species	Native	Introduced
Fabaceae	70	29	41
Myrtaceae	54	45	9
Rubiaceae	48	42	6
Euphorbiaceae	36	27	9
Melastomataceae	35	34	1
Rutaceae	23	13	10
Sapotaceae	22	20	2
Moraceae	20	9	11
Lauraceae	17	13	4
Bignoniaceae	17	9	8
Solanaceae	15	13	2
Flacourtiaceae	15	12	3
Palmaceae	15	10	5

Source: Little et al. 1974.

Table 8—Probable origin of Puerto Rico's trees

Origin	Percent
Continental	41.9
South and Central America	22.1
South America only	10.1
Central America only	9.7
West Indies	32.4
Greater and Lesser Antilles	14.6
Greater Antilles only	14.1
Lesser Antilles only	3.7
Endemic to Puerto Rico	21.0
Puerto Rico only	19.9
Puerto Rico and adjacent islands	1.1

Source: Little et al. 1974.

islands are found nowhere else. This figure is higher than that cited for the entire vascular flora, which is 8 percent. Of the total 232 plant species endemic to Puerto Rico, 61 percent are trees (Figueroa Colón 1996).

Isolated oceanic islands are often areas that express high endemism. Little (1970) cited 61 trees endemic to Puerto Rico, with 25 species found only in the Luquillo Mountains. This number was expanded to 115 in the second volume of *Trees of Puerto Rico and the Virgin Islands* (Little et al. 1974). Of these, 29 endemics are considered rare or endangered and worthy of protection. Fortunately, most of these species benefit from de facto protection, as they are found in the public forests of Puerto Rico. Nineteen are not present in protected areas, but are found on private lands. The rarest tree in Puerto Rico is *Banara vanderbiltii* Urban

(Flacourtiaceae). There are only two known individuals found near the city of Bayamón. The highest degree of endemism is found in the mountain province, with the Luquillo Experimental Forest having 48 percent of all endemic trees in Puerto Rico. Most endemics are not widespread. Forty-seven percent of all Puerto Rico endemics are known to occur in three locations or fewer (Figueroa Colón 1996). The dry forest at Guánica has 16 endemics.

Alien species of plants and animals are of great concern throughout the world because of their potential competition with native species. A naturalized species is an alien that has been able to adapt to the new habitat and is able to successfully reproduce. *Swietenia mahagoni* (L.) Jacq. (West Indian mahogany) is now successfully reproducing in the dry zone forest of Puerto Rico. Other species are able to grow as **successional** species, that is, fast growing in well-lighted conditions. *Spathodea campanulata* is doing this throughout much of the island, especially in successional pasture lands and roadsides. Other aliens are naturalizing at the sites of human introduction such as parks, yards, and businesses. *Delonix regia* (Bojer) Raf. (flamboyán tree) with its brilliant red blooms and prolific seed production is very successful in these situations. Most species in this category of alien naturalization are rarely studied unless they become a pest. Then a plant-related agency is consulted to see what can be done. By then it may be too late and elimination impossible. Other alien trees invade pastures and reduce **herbaceous productivity** including *Albizia procera* (Roxb.) Benth (white albizia) and *Acacia farnesiana* (L.) Willd. (sweet acacia).

Boxes 2 to 6 are profiles of six woody plants likely to be seen throughout Puerto Rico. Some are native and others introduced. A couple cause dermatitis.

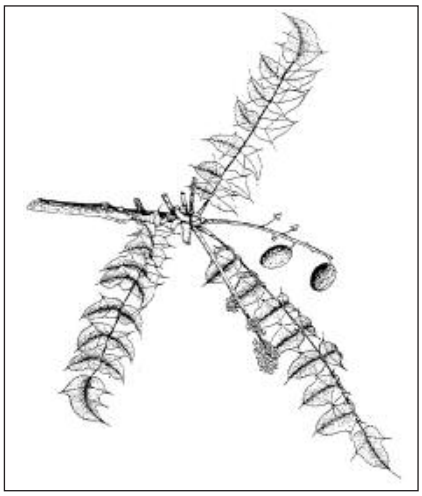
For review of the growth, reproduction, and ecology of tropical trees see Vozzo (2002), and for further reading see Birdsey and Weaver 1982; Chinea-Rivera 1990; Francis 1990, 1998; Francis and Alemañy 1996; Francis and Liogier 1991; Franco et al. 1997; Hargreaves and Hargreaves 1965; Little and Wadsworth 1964; Schubert 1979; and Wadsworth 1997.

General Review of the Fauna

Puerto Rico has a diverse **fauna**. Animals present on the island represent 30 of the 34 phyla and 72 of 84 classes of animals. There are over 275 orders present that contain 1,500 of 6,200 animal families. Three of the animal families present are endemic to the Antilles. At least 10,335 species have been identified for the

Continued on page 42.

Box 2. *Comocladia dodonaea* (L.) Urban (poison chicharrón)



Leaves, twigs, flower, and fruit of *Commocladia dodonea* (L.) Urban.

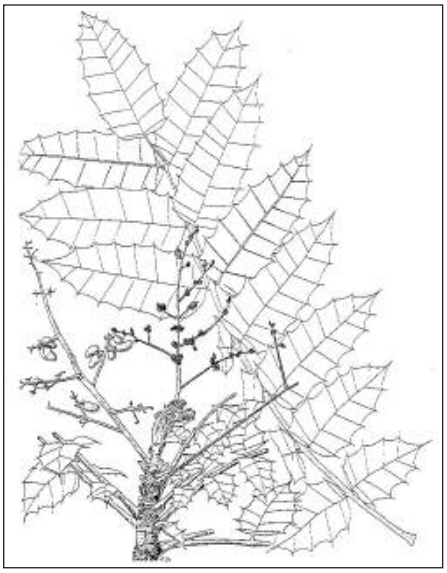
Puerto Rico has three plant species that are members of the Anacardiaceae (cashew family), which produce skin reactions in humans like those produced by *Rhus radicans* L. (poison ivy, also a member of the cashew family) in the United States. One of Puerto Rico's species is not as widespread as the others, so *Metopium toxiferum* (L.) Kang & Urban (Florida poison tree) will only be mentioned here. It is a small evergreen tree with alternate, pinnately compound leaves, with three to seven leaflets, orange fruits (drupe), and which produces a poisonous sap. It is present in the Guánica area on the south coast. It is very abundant on Mona Island off the west coast.

Two other shrubs/small trees that can produce serious cases of dermatitis belong to the genus *Comocladia* and are much more common. Fortunately, none of the species are as common as is poison ivy in the United States.

Comocladia dodonaea occurs mostly as a shrub (< 4.5 meters [15 feet], but on occasion it will be treelike in size (> 4.5 meters [15 feet]. It is easily recognized because of its prominent, spiny, odd, pinnately compound leaves. The plant does not produce an obvious crown; instead clusters of evergreen, alternately arranged leaves form around the ends of a few branches. The pinnately compound leaves range from 7.5 to 17.5 centimeters (3 to 7 inches) in length and may have 11 to 21 ovate leaflets that are sessile and appear curved. The leaflets are usually tinged red-orange and possess three to five sharp spines. It produces a nondescript panicle inflorescence with many small red flowers that produce a red fleshy fruit (drupe). Flowering is typically from December to March and fruiting, April to July. This species is very common in open areas of the dry southwestern coast, and in forest thickets throughout the dryer sections of the coastal plain and adjacent foothills up to 304 meters (1,000 feet) elevation. It is also common in the dryer upper elevation of haystack hills in the north coast karst region.

This species has no economic value other than its effects on humans because of its potentially serious skin irritation. All parts of the plant should be avoided.

Box 3. *Comocladia glabra* L. (J.A. Shultes) Spreng. (Poison *carrasco*)



Leaves, twigs, flower, and fruit of *Commocladia glabra* (J.A. Shultes).

Comocladia glabra L. (J.A. Shultes) Spreng. also grows both as a shrub or small tree up to 6 meters (20 feet). Occasionally it will also produce a vine-like habit. It grows as a slender understory species and is unusual in that it tends to grow unbranched with a terminal cluster of large odd pinnately compound leaves. The leaves are alternately arranged, can be 30.5 to 61 centimeters (1 to 2 feet) long, and can have 11 to 31 lance-shaped leaflets. The leaflets can be 5 to 17.5 centimeters (2 to 7 inches) long. Each main leaf vein extends through the margin in the form of a prominent spine. Both male and female flowers are on the same plant, with very small red petals densely crowded on a panicle-like inflorescence. The fruits are red-black fleshy drupes. Flowering and fruiting are intermittent throughout the year. Its bark is light gray and rough. This species is common in moist forest types of Puerto Rico up to 304 meters (1,000 feet) altitude. It is found in the lower elevations of the karst region on the north coast. This species is absent from the dry habitats of the southwest and from elevations over 304 meters (1,000 feet) in the mountains.

Like *C. dodonaea* it has no economic value. All parts of the plant should be avoided, especially its milky sap.

For more information on poisonous woody plants in Puerto Rico, see Little et al. 1974.

Box 4. *Ceiba pentandra* (L.) Gaertn. (kapok) (Known locally, as Ceiba)

The leaf, stem, and flower structure of *Ceiba pentandra* (l.) Gaertn. (Kapok).

As you travel around Puerto Rico, be sure to be on the lookout for large trees with big flared trunks called buttresses, and light gray bark and spines when young. On occasion you may see them preserved in highway medians such as on Route 2 west of Arecibo or in a special park developed to honor the largest tree in Ponce. This species can achieve great size and is probably one of the tree world's best examples of plank buttressing. These buttresses appear as flat triangular woody growths that form in the angle between the base of the trunk and a lateral root running radially at the surface of the soil. The "plank-like" buttress is secondary growth that develops from the upper side of the root. The buttress operates much like an engineered bridge buttress whereby the great weight of the tree is spread by the flared base. The root systems of kapok (also called ceiba or silk cotton tree) lack a well-defined tap root and consist of laterals with very shallow sinker roots. Size and number of buttresses differ with the mass and spread of the crown. Some buttresses can grow in excess of 6 meters (20 feet) in height and length (see photo below). The size and length of the roots and buttresses can crack roads, walls, and foundations. The adaptive value of buttress growth to the tree is the increased resistance to blowdown owing to storms or gravity. They also reduce stem rocking in storms, which would heavily damage the fine roots necessary for absorption. In windy areas, kapoks have a tendency to develop buttresses predominantly on the windward side. They grow well in both dry and wet areas and will be found from the coastal plain to the mountains in Puerto Rico.

Ceibas are native to South America and one of the largest trees in the Neotropics. They were probably introduced to Puerto Rico in prehistory. They require great amounts of light and are typical of open habitats, such as abandoned farm land and deforested slopes. Their leaves are **palmately compound**, with 5 to 8 leaflets. They normally flower December to February after they

Box 4. continued

reach 5 years of age. The flowers are white-pink and clustered at ends of branches. Inside the fruit pods (capsules), the seeds produced by kapok have long silky hairs, thus the name "silk cotton tree." This silk aids in wind dispersal. The silk is called kapok and has good commercial value. It is used as filler in life vests, pillows, mattresses, and as a cloth fiber.

G. Miller

Typical buttress development of *Ceiba pentandra* (L.) (kapok).

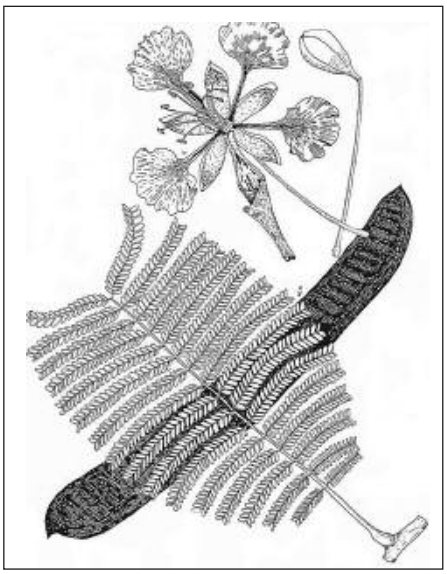
This tree is a plantation species. The kapok fiber makes it more valuable than its wood and will produce silk for half a century. The wood is good for paper production and a variety of low-end products like packaging or fuel. The plank buttresses can be used for table tops. In some cultures, kapok trees are sacred and various parts of the plant are used in herbal medicines. The seeds contain oil used as a lubricant and in soaps and paint. Its leaves can be used for animal fodder. Indigenous peoples carved sea-going canoes out of the kapok tree's main stem. One such canoe was reported to carry 150 passengers and was used to meet Columbus on his second voyage.

The largest kapok tree in Puerto Rico is in the village of Villalba. It is 38.7 meters (127 feet) tall, with a crown spread of 44.5 meters (146 feet) and a circumference of 19.8 meters (65 feet). Many cities in the tropics have kapok trees planted in the center of their town's plaza.

In Ponce on the south coast, there is a small public park dedicated to the protection of a giant 400-year-old *Ceiba pentandra* within the city limits. It is located just past the intersection of Routes 133 and 14 at the edge of the Portugués River. For years, groups wanted to cut it down to expand a bus park and an adjacent street. Each time, citizens fought for it until it received its current protected status. Unfortunately, storms over the years have greatly reduced its crown, and its buttresses have been severely cut back to accommodate city growth. In the 1970s, this tree was much larger than it is today, especially its buttresses.

For additional information on kapok, see Chinea-Rivera 1990 and Little and Wadsworth 1964.

Box 5. *Delonix regia* (Bojer) Raf. (flamboyant) (Locally known as *flamboyán*)



The leaf, flower, and fruit structures of *Delonix regia* (Bojer) Ref.

By most accounts this may be the most beautiful tree in the tropics (see photo). It is native to Madagascar, where it is an endangered species. It has been widely introduced throughout the tropical world, including Puerto Rico. It is often used as backdrop in commercial photography such as the production of postcards, calendars, and tourist brochures because of its brilliant orange-red flowers.

Flamboyán is a medium-sized tree with a broad umbrella-like crown that can achieve a height of 15 meters (50 feet). Their broad crowns often produce a tunnel effect when they are grown close together along roads. It is a deciduous species during the dry season. It produces even, **twice pinnately compound** leaves that are alternately arranged. The leaves are 20 to 50 centimeters (8 to 20 inches) long with numerous subdivisions bearing up to 40 pairs of very small, oblong sessile leaflets.

The persistent red-orange flowers cover the entire crown and are produced in profusion from May through August. Flowers are produced in racemes at the ends of branches. Each flower is 15 to 25 centimeters (6 to 10 inches) across and is composed of five unequally-sized petals, one of which has white streaks. The fruits are long, hard, black legumes (like string beans), which grow to 50 centimeters (20 inches) in length and contain many bean-like seeds. The pendulous legumes are persistent throughout much of the year and very evident when the trees are leafless.

Older trees will likely exhibit buttressed trunks, with gray-brown smooth bark and large lenticels. Long horizontal branches produce a crown that may be wider than the tree is tall. The tree's wood is heavy, coarse-grained, weak, and brittle, thus it is of low commercial wood value. It is easily broken during storms. The wood and the large machete-shaped fruits are often used for fuel.

Box 5. continued

Closeup of flowers of *Delonix regia* found all over Puerto Rico.

The largest *flamboyán* is located in Utuado. It is 32 meters (104 feet) tall, has a crown spread of 25 meters (83 feet), and has a circumference of 2.7 meters (8.8 feet).

Flamboyán is a widely planted tree throughout the island as a horticultural species around homes, in plazas, and along streets and highways for its shade and flowers. It grows well in both dry and moist areas of the island. It does best in full sunlight and in areas with a short dry period. It is common to see large brown termite mounds located on the trunk or axils of main branches.

For more information about this species, see Little and Wadsworth 1964 and Schubert 1979.

island[2] Table 9 provides an approximate number of species found in the principal animal groups.

According to Vélez, about 50 percent of Puerto Rico's animals are terrestrial (more than 5,100 species), marine species comprise 38 percent of the fauna (approximately 3,900 species), freshwater species make up nearly 8 percent (almost 800 species), and **symbiotic** species comprise 5 percent of the fauna (over 500 species).

Puerto Rico has no large terrestrial **charismatic** animal species and probably never did. Those animals that might be considered charismatic are the Puerto Rican parrot (*Amazona vittata*), the Antillean manatee (*Trichechus manatus*) and the

[2] Lecture delivered at the University of Puerto Rico by M. Vélez in 2001 on the taxonomic families and species represented in Puerto Rico.

Box 6. *Clusia rosea* Jacq. (postcard tree) (Locally called *Cupey*)

The leaf, flower, and fruit structures of *Clusia rosa* Jacq. (Postcard tree).

Clusia rosea is an unusual tree species because it can start out as an epiphyte and may become a strangler as it develops. It is also unusual in that its thick leathery leaves can be written upon, thus the common name postcard or autograph tree. In fact, early *conquistadores* are known to have made playing cards from the leaves, scratching figures and numbers on their surfaces.

The tree has a broad dense evergreen crown and may grow to heights of 18 meters (60 feet). The leaves are oppositely arranged, very thick, deep green, and with a shiny top surface. The leathery leaves are obovate in shape, the margins are turned under, and the apex is rounded or notched. It produces large showy white-pink flowers composed of 6 to 8 petals at the ends of branches. The species is dioecious (separate male and female trees). The yellow-brown fruits are capsules with 7 to 9 chambers that produce numerous yellow sticky seeds that are eaten and vectored by bats and birds. They are poisonous to humans. Cupey trees flower and fruit throughout the year. Its bark is gray, smooth to warty, with a pink inner bark; when cut it will exude a yellow latex.

In the wild, *cupey* often begins life as an epiphyte (air plant), much like figs, with its seeds germinating in the canopy and sending long aerial roots to the ground. The roots gradually coalesce and eventually encircle the structural host tree. The trunk of *Clusia* encases the host, which may die a few years later. A more complete description of epiphytes is included in the forest zones section. Very often at the base of the tree, prop roots will be present as the original root system does not start as a primary root. Prop roots may also grow from the main branches, producing the visual effect often associated with banyan trees. The largest *cupey* is located in San Juan and is 20.4 meters (67 feet) tall, has a crown spread of 24.4 meters (80 feet), and is 98 centimeters (39 inches) in circumference.

Cupey is native to Puerto Rico and most of the West Indies. It is frequently propagated by seed harvest or cuttings. It has a variety of low economic uses

Box 6. continued

including use of the fruits in dry floral arrangements and use of the wood for cheap furniture, fuel, fence posts, and rural construction. Its latex can be harvested and used to caulk wood structures or fill cracks. *Cupey* can grow in a variety of habitats, from the highest mountains to the beach. The tree is most typically found in shallow, rocky, moist soils. It is salt-spray resistant, thus can be used as a species to retain sand near beaches and as a seaside ornamental. It is common to riverine habitats and is most common in the moist forest karst areas of northern Puerto Rico, where it grows vine-like on cliff faces of the haystack hills and in sinkholes. *Cupey* is often considered a pest species because of its ability to strangle and kill more valuable trees, but this appears uncommon. Very often termites will build mounds in their branches. It is frequently damaged by hurricanes because it does not defoliate easily and thus its foliage acts like a sail, which causes the tree to topple or suffer crown damage.

For more information about this species, see Francis 1993, Little and Wadsworth 1979, and Schubert 1979.

Table 9—Number of species present in the principal animal phyla of Puerto Rico[a]

Phylum	Animal groups	Species present
Porifera	Sponges	151
Cnidaria	Hydra, jellyfish, anemones, corals	202
Platyhelminthes	Flatworms	226
Nematoda	Roundworms	250
Annelida	Segmented worms	262
Arthropoda	Insects, spiders, crustaceans	5,377
Mollusca	Snails, clams, squids, octopus, chitons	1,359
Echinodermata	Sea stars, sea urchins, sea cucumbers	110
Chordata	Tunicates, birds, reptiles, amphibians, fish, mammals	1,427

[a] Approximately 9,364 species are found in the nine largest phyla listed.

Coquí (*Eleutherodactylus coqui*) tree frog. Large native **mammal** species were historically extremely rare in Puerto Rico. Animals typical of Neotropical mainland lowland forests such as tapirs, jaguars, coatis, and monkeys were never found in Puerto Rico. The lack of large mammals can be accounted for because of the island's physical isolation, that is, no natural land bridge afforded migration from North or Central America and its physical location so far east in the Antillean

chain. Physically, these animals could not swim the distances involved, and likewise, large mammals are absent in all of the easterly Lesser Antillean islands.

Since discovery in 1493, animal extinctions have been recorded throughout the Caribbean islands. Waide (1987) cited 11 recent bird extinctions for the Caribbean, with two of those from Puerto Rico. There are currently a number of species on the U.S. and Puerto Rico **threatened** and endangered species list (see the section on endangered species that follows). According to the natural history record of Puerto Rico, there were ground sloths and large rodents called *hutías* on the island. There were also native rats, moles, shrews, and hedgehogs in the fossil record. All were apparently extinct by the beginning of colonization. All native terrestrial mammals are now extinct except for bats. Also, large populations of **reptiles** are reduced, with the rock iguana now confined to offshore islands. It is assumed that human disturbance activities associated with habitat destruction, the introduction of alien species, and possibly hunting pressures accounted for most of the problems encountered by the native fauna in the West Indies (see Puerto Rican parrot section that follows). According to Brooks and Smith (2001), species extinctions resulting from human pressures have struck the West Indies on a large scale. Of the 197 endemic mammals and birds found across the islands, at least 43 have become extinct over the last 500 years, three orders of magnitude higher than expected given species lifetimes in the fossil record. Worse yet, 84 more Caribbean endemic mammals and birds are classified on the Red List as threatened, with a high probability of extinction in the medium-term future.

Marine animal **biodiversity** is also declining in the Caribbean region. The native manatees, monk seals, and crocodiles once present, are largely extinct throughout most of their natural ranges. In addition, the populations of the large sea turtles (Green [*Chelonia mydas*], Hawksbill [*Eretmochelys imbricata*], and Leatherback [*Dermochelys coriacea*]) are all depressed and are all listed as endangered species throughout their ranges in the United States and Puerto Rico, as are all species of sea turtles.

At the time of Spain's ceding of Puerto Rico to the United States, little was known about Puerto Rico's animal life, but in 1916 a major expedition was organized to study all aspects of Puerto Rico's natural history by the New York Academy of Science. For a review of the history of various zoological studies conducted in Puerto Rico, see Wadsworth (1970) and Figueroa Colón (1996). The New York Academy expedition resulted in a long list of publications describing most of the main animal groups in the *Annals of the New York Academy of Science* through the 1940s. An updated 80-year reassessment of the island's natural history was recently published (Figueroa Colón 1996).

In terms of past and recent studies, the **insect** fauna, as would be expected, has the largest group of identified species. There are 5,066 species catalogued from 25 insect orders (Capriles 1996). The insect fauna of Puerto Rico is much better known than that of any other Antillean island. Although Puerto Rico has been explored and extensively studied for its insects, it appears that insect diversity should be twice as large as it is, compared to other West Indian land areas (Capriles 1996). Martorell (1945) explained the low **species diversity** on the basis of geography. It appears likely that Puerto Rico's geography, in terms of its eastern position in the Greater Antilles and northern position of the Lesser Antilles, restricts access to new insects. The trade winds that come from the open Atlantic in the east or northeast, where there are few land masses, do not promote the distribution of insects to Puerto Rico. However, hurricanes transport insects from Africa to Puerto Rico and the Caribbean. The heavy destruction of forested lands prior to extensive and intensive animal surveys may have caused species extinctions prior to their discovery. Another possibility for the undercount could relate to the fact that more research still needs to be conducted. A current example of this possible undercount of species is illustrated by the All Taxa Biodiversity Inventory currently taking place for the first time in the Great Smoky Mountain National Park in Tennessee. This will require an estimated 15 years of full-scale work in an area of only 202 429 hectares (500,000 acres). That study is only at its developmental stage and has already produced numerous new species (76) and new species records (557) for the park. A similar program is being conducted on Navassa, an uninhabited forested island 60 kilometers (36 miles) west of Haiti, by the Caribbean Biodiversity Program of the Center for Marine Conservation in Washington, DC. Estimates run as high as 250 new species to be identified from this island, which is only 5.2 square kilometers (2 square miles) (Science 1998). Puerto Rico undoubtedly would yield many new finds should such a study be conducted on such a diverse island landscape. According to Helmer et al. (2002), tropical areas with complex topography are particularly important for biodiversity conservation. Tropical mountainous areas made up 11 of 25 biodiversity "hotspots," and 7 hotspots included or consisted of complex tropical islands (Myers et al. 2000). According to Myers et al., the Caribbean region is one of the hottest hotspots where 11.3 percent of the region's original primary vegetation contains 2.3 percent of the world's endemic plants and 2.9 percent of the vertebrates.

As far as terrestrial vertebrates are concerned, the birds are the largest group by species numbers (see section on "Birds" of Puerto Rico that follows). The second

Table 10—Vertebrate species by major group

Group	Species
Birds (class aves): (50 families)	269
Reptiles (class reptilia):	54
Turtles	6
Snakes	9
Lizards	38
Crocodiles (introduced)	1
Mammals (class mammalia):	32
Bats	14
Marine (manatees, whales, porpoise)	8
Introduced (mongoose, rats, etc.)	10
Amphibians (class amphibia)	25
Toads	2
Frogs	23

largest group is reptiles. Mammals are third, followed by **amphibians**. These rankings include introduced species (table 10).

The Antilles Islands' bird life is probably the best known of any section of the Neotropics. According to Bond (1971), the **avifauna** of the West Indies is predominantly North American tropical, with its greatest connection to the Central American bird groups. There is also very good representation of the continental North American groups owing to the winter range of Neotropical migratory species (see section on Neotropicals that follows). Two bird area groups or provinces represent the Greater Antillean province and the Bahamian-Lesser Antillean province. Puerto Rico has no endemic bird families, and less than 1 percent of the genera are endemic. However, it does have 14 endemic species.

On the other hand, Puerto Rico's herpetofauna (amphibians and reptiles) is highly endemic. Only seven (9.2 percent) of its native species are found in other island systems. They are mostly related to genera from the Greater Antillean chain. Five genera are exclusive to the Greater Antilles, with the Puerto Rican crested toad (*Peltophryne lemur*) a good example. The other 11 genera are primarily Greater Antillean. According to Thomas and Joglar (1996), there are 80 species of amphibians and reptiles in Puerto Rico, 90 percent native and 10 percent introduced this century. No genera of amphibians and reptiles are endemic to Puerto Rico. Puerto Rico has no species of true **salamanders** (order Caudata). There is a gecko (*Hemidactylus* spp.) called "salamander," but it is a lizard.

There are four amphibian frog and toad families present: Bufonidae, Hylidae, Ranidae, and Leptodactylidae. This latter family includes the **genus**

Eleutherodactylus (tree frogs), which has 16 species in Puerto Rico, with numerous endemics (see section on "Tree Frogs" that follows). The family Bufonidae (toads) has only two species present, the endemic Puerto Rican crested toad (*Peltophryne lemur*) and the notorious giant marine toad (*Bufo marinus*). *Bufo marinus* was introduced to control the white grub that attacks sugarcane. As has been the case so many times in the past, this well-intentioned introduced alien is now naturalized and has spread throughout the island. It can grow to the size of an average man's foot. The Ranidae consists of one genus and species, *Rana catesbeiana* (bullfrog). This, too is an introduced alien species.

The class Reptilia (reptiles) has three orders present: Chelonia, Squamata, and Crocodilia. Chelonia includes the turtles and tortoises; Squamata includes the lizards and snakes; and the Crocodilia includes the crocodiles, alligators, and caimans. In Puerto Rico, the Squamata is the largest reptile group and includes six families of lizards, with 38 species present. There are three families of snakes, with nine native species. Both groups include alien species. The large common green tree iguana (*Iguana iguana*) is now found in many places in Puerto Rico. It is native to Central and South America and was introduced via the pet trade. It is not uncommon to see individuals greater than 1 meter (3 feet) in length along roads or in trees. They can grow to 2 meters (6 feet). They look fierce, but in fact are harmless and primarily **herbivorous**. There are at least three introduced snakes, including the common watersnake (*Natrix sipedon*) and the common garter snake (*Thamnophis sirtalis*) from the United States, and the African python (*Phyton regius*). Undoubtedly, there are other released and escaped snake species that are present, but to date not naturalized. The native snakes include three members of the Boa family (Boidae). The Puerto Rican boa (*Epicrates inornatus*) is endemic to the island. It is the largest native species attaining a length of 3.6 meters (12 feet). Most are less than 2 meters (6 feet). Its population is now restricted as a result of earlier massive habitat destruction. It is most common in the karst areas of the north coast and the volcanic Luquillo Mountains, although it occasionally shows up on the dry south coast. Its color varies from dark brown to tan, with crossbars or spots present. It uses the ground and trees while feeding on rats, mice, and bats. It will consume frogs, lizards, and insects. They in turn are preyed upon by hawks, domestic pigs, and cats. Puerto Rico also has blind or worm snakes (of the genus *Typhlops*), which are subterranean and feed extensively on ants and **termites** (see the section on termites that follows).

The lizards constitute the largest group of the Reptilia. This group includes the geckoes, anoles, iguanas, skinks, and blind lizards. The genus *Anolis* is quite large

L. Miranda Castro

Figure 8—A green Anole (*Anolis cuvieri*) with its brilliant dewlap expanded.

with an estimated 300 species, 11 of which are present in Puerto Rico. This is the lizard group most observed by students and visitors alike. They seem to be everywhere. They come in a variety of colors and their colors can change as the background color changes. Some are bright chameleon green. The most common species is *Anolis cristatellus*, commonly found in houses and nearby vegetation. The males are larger than females and have flexible colored dewlaps (expandable lower throat-neck skin) that they use in defense and courtship (fig. 8). They prey on a variety of insects and use the sit-and-wait technique of hunting. They in turn are prey to a variety of birds, the larger of their own species, and snakes. They are abundant in many habitats, from the coast to the high mountains, and some of the species are altitudinally zoned. They are **diurnal** and appear to occupy roughly the same **niche** diversity as birds do in larger continental systems in terms of habitat **zonation**, feeding, and microclimate preferences. They consume vast quantities of insects. The larger (body size) species group hunt over greater distances and consume larger prey. The smaller species seek out smaller prey over shorter foraging distances.

The Chelonia representatives in Puerto Rico consist of six species of turtles. Of the six species, only one is native and freshwater, *Trachemys stejnegeri* (locally called, *hicotea*). It is omnivorous and inhabits lowland freshwater habitats such as rivers, **lagoons**, and ponds. It is uncommon, but can be found in Lake Tortuguero

and drainage ditches in the Guánica area. It grows to about 25 centimeters (10 inches). The locals love its good tasting meat. Two introduced species of freshwater turtles are in Puerto Rico. They arrived via the pet shop trade. They are *Trachemys scripta* (red-eared turtle) and *Chrysemys picta* (eastern painted turtle). Their reproductive status and population distribution are poorly understood. The remaining turtle species are sea turtles and are all listed as endangered species. The two most important to Puerto Rico are *Chelonia mydas* (green sea turtle) and *Caretta caretta* (loggerhead turtle). Both have been heavily overfished this past century and are still being taken illegally, in spite of their protected status. These were all-purpose animals prized for their meat and shells, which could be made into useful objects such as jewelry (bracelets, earrings, necklaces, and hair pins). Possession of any part of these animals today can result in a substantial fine and even jail time. Green turtles used to be common to coral reefs and seagrass beds prior to the 1970s. Today they are rarely seen as a result of fishing pressures and loss of nesting habitat. For more information on the status of these two sea turtles, see Ehrhart et al. (1991 and 1993). There are a variety of educational wall charts and brochures available from government agencies describing sea turtles and their protected status. (See app. 4 for contact information). There are no native resident populations of tortoises, but some pets have likely been released in various places in Puerto Rico.

The third order in the Reptilia is the Crocodilia. Puerto Rico has only one species from this group, the introduced *Caiman crocodilus* (spectacled caiman). It is a species found in Central and South America and was released in Puerto Rico as a result of pets that grew too large to be accommodated by their owners. There are now four known populations in Puerto Rico, with one of them at Tortuguero Lagoon (see the "Wetlands" section). *Caiman crocodilus* can attain a length of 2.6 meters (9 feet), although most are less than 1.8 meters (6 feet). It gets its name from the presence of a bony ridge between its eyes that resembles the nosepiece of eyeglasses. The spectacled caiman is a popular reptile sold in the animal trade, especially after the United States designated the American alligator (*Alligator mississippiensis*) legally protected under the Endangered Species Act. For a complete review of the amphibians and reptiles of Puerto Rico, see Rivero (1998). Joglar (1998) presented a review of the amphibians, with special attention to the genus *Eleutherodactylus*, in his book *The Coquies of Puerto Rico: Their Natural History and Conservation*.

The mammal fauna in Puerto Rico is quite **depauperate**. The largest terrestrial group is the bats, with 14 species (see section on bats that follows). The next

largest group is the marine mammals of which there are 10 species that can be found in waters in the vicinity of Puerto Rico. This group includes whales, dolphins, and porpoises. There are at least eight alien terrestrial mammal species in Puerto Rico, including rats, mice, mongoose, and four species of monkeys. The mongoose was introduced from Jamaica (origin is India) to control rats. Unfortunately, it did not control the rat population, but it did become a pest in its own right and is a major predator of native birds and reptiles. The mongoose is active during the day, whereas the rat is most active at night. The monkeys escaped from rearing colonies of the Caribbean Primate Center for use in medical research. On occasion, small troops can be seen crossing roads and feeding in trees on the south coast. Puerto Rico recently received a large grant to be used for the recapture of the monkeys. Some **domesticated** mammal species have escaped and these **feral** populations are reproducing. According to Waide (1987), the introduction of mammals to islands with no native mammals has historically been most destructive for native wildlife.

The last native terrestrial mammals of any size were the giant tree shrew and a large rodent. The giant tree shrew (*Solenodon paradoxus*) has not been seen since the early 1800s. It is thought to be extant in Cuba. It was a large **insectivore**. The large rodent, *Isolobodon portoricensis*, has not been seen since the early 1800s. Again, it is thought to be extant in Cuba, but on the verge of extirpation. The fossil record also showed another 10 or so mammal species that were present in Puerto Rico in the past.

In the freshwater and marine environments around Puerto Rico and east to the U.S. Virgin Islands, there are nearly 800 fish species from the classes Chondrichthyes and Osteichthyes. The fish fauna of Puerto Rico is a complex mixture of Atlantic, Caribbean, and alien species. The north coast has a narrow shelf, with deep water near shore and the coastline receiving heavy surf. It has little coral or well-developed seagrass beds. The south coast's shelf is wider with lots of **fringing reefs**, seagrass beds, and adjacent mangrove swamps. The south coast receives much less heavy wave action off the Caribbean, especially in the winter. The freshwater fishery has a number of human introductions associated with it. The Chondrichthyes (cartilaginous fishes) include the sharks, dogfish sharks, skates, and rays. There are 20 species of sharks and rays in Puerto Rico's waters. The Osteichthyes are the true bony fishes, of which there are more than 18,000 species worldwide (some estimates run as high as 40,000 species). They represent the largest group of vertebrates and comprise about half of the world's species of living vertebrates. There are 80 freshwater fish species and nearly 300 marine species

common in Puerto Rico. Most species are associated with coral reefs. In 1970, Puerto Rico had an estimated 1,000 commercial fishermen, 400 full time. At that time, Puerto Rico produced around 2.4 million pounds of **shellfish** and fish. Virtually all of it was consumed locally. It was valued at $780,000. Even then, when the coral reefs were in good condition (see "coral reefs" section), Puerto Rico was importing $24 million in fish and shellfish from the United States. There are many fewer fishermen today, and the island is even more reliant on imports to satisfy its seafood demand. Many commercially valuable species such as Caribbean lobster, grouper (bluehead wrasse), and snapper can only be found in more distant and deeper waters.

Of the 80 freshwater fish species, 20 are alien species introduced for sport fishing and food. These include two species of bass (*Micropterus* spp.), three species of sunfish (*Lepomis* spp.), and four species of catfish (*Ictalurus* spp.). Numerous species of tropical aquarium fish, such as guppies, swordtails, and mollies, have been imported and subsequently released and introduced to the rivers and lakes of the island. There are also species such as the American eel (*Anguilla rostrata*), which grows to an adult in freshwater rivers and then returns to the sea for reproduction. These organisms are referred to as **catadromous**. They exhibit a fantastic migration to the Sargasso Sea where they spawn and die. Their offspring then return to freshwater completing this long roundtrip journey. Freshwater trout (*Salmo* spp.) were also introduced in 1938 via a trout hatchery established in Maricao, but because the water temperatures are too high, their introduction did not take. Table 11 presents some of the alien animals now found in Puerto Rico and some of the problems they are producing.

See appendix 2 for suggestions on viewing animals in Puerto Rico. For further reading on the fauna of Puerto Rico, see Diaz 1983, Erdman et al. 1985, Erdman et al. 1986, Martin and Patus 1984, Nellis 1999, Nieves 1980, Thomas and Joglar 1996, Torres 1994, Torres and Gaud 1998, Wallace 1989, and Wolcott 1948.

Tree Frogs

Puerto Rico has 23 species of frogs, of which 16 belong to the genus *Eleutherodactylus*, the group known as the tree frogs. They are unlike many other amphibians in that they do not have to return to water to complete their life cycle. They do not produce a free-living, water-requiring tadpole stage, but instead undergo rapid direct development to the adult stage. They are referred to as coquíes because of their calls, and specifically *E. coqui* whose call sounds like its genus name (Ko-key). Wherever you go in Puerto Rico from dusk to early morning you are likely to

Table 11—Examples of alien animal species in Puerto Rico

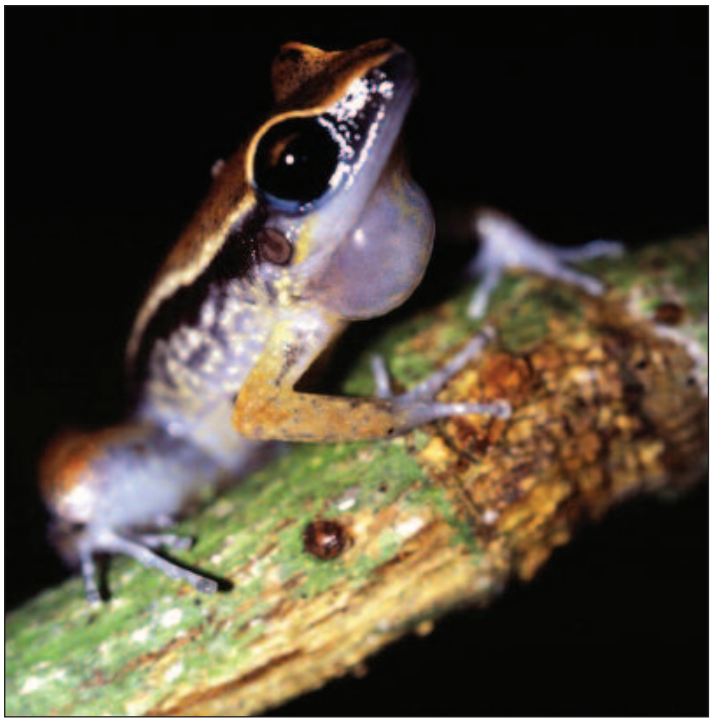
Scientific name	Common name	Location	Problem
Macaca mulatta	Rhesus monkey	Southwest	Will bite while being captured; may become major predator of local species
Herpestes auropunctatus	Indian mongoose	Islandwide	Major competitor to anything smaller
Rattus rattus	Black rat	Islandwide	Major competitor to anything smaller; preys on eggs and young of birds, including the endangered Puerto Rican parrot
Iguana iguana	Common iguana	Islandwide	Crop destruction
Caiman crocodilus	Spectacled caiman	Tortuguero Lagoon	Possible threat to humans—as subadults and adults
Python regius[a]	African python	Caribbean National Forest	Constrictor; could take domesticated animals
Margarops fuscatus	Pearly-eyed thrasher	Islandwide	Threat to native birds, especially Puerto Rican parrot and other cavity nesters; may have contributed to extinction of white-necked crow (*Corvus leucognaphalus*) in 1960s
Micropterus salmoides	Large-mouth bass	Freshwater	Top of aquatic food chain; could affect native fish species
Apis mellifera	Honey bee	Islandwide	Interferes with bird nesting—for example, endangered Puerto Rican parrot

[a] Not known to be a reproducing population.

hear the chorus of coquíes calling. Their call is almost the national anthem. The animal is the unofficial national symbol, in that it appears in fine jewelry shops as necklaces and pins, and on schoolkids' backpacks and t-shirts. The coquí is the animal most identified with in Puerto Rico and results in millions of dollars in sales of coquí products to islanders and tourists alike.

These small vertebrate animals are primarily insectivorous. Each species has a niche, and each niche has specific insects living there. Some feed at the base of tree trunks in the **litter** zone, whereas others use the trunk, branches, and leaves. Males usually feed higher up and usually will make their calls from a different location above the location of the females. Most are **nocturnal**, but they can be located during the day. At night they are easily spotted with a spotlight as you zero in on their calling position (see app. 2 for information on how to catch a tree frog).

Eleutherodactylus coqui is endemic to Puerto Rico and is found throughout the island. It is the second largest of the lowland species and is usually brown, to gray-brown, and it may be mottled. They sometimes have a w-shaped mark on the **nape** and a **chevron** mid-back. They frequently show a **dorsolateral** band and a stripe



J. Puente Rolón

Figure 9—*Eleutherodactylus coqui* (coqui) calling.

that may extend laterally to their knees. They are nocturnal and frequently inhabit tank bromeliads and curled leaves. They call at night and forage from the ground to the subcanopy (fig. 9). Males are territorial and they will defend their territory by biting and butting male invaders. Once a male attracts a female, **amplexus** occurs. Fertilization is internal and eggs are laid in nests of curled leaves. Typical nests will bear 26 eggs in the clutch and the male will provide parental care, which includes brooding and defense. Brooding maintains the needed moisture level and prevents desiccation. Egg and young predation occurs from other *coquíes* and **invertebrates**. Juvenile frogs develop directly without a tadpole phase in 17 to 26 days. *Coquíes* are very sedentary and will maintain the same territory for several years. Movement is usually associated with moving to calling perches and foraging. Coquíes are sit-and-wait predators of insects. Their vast numbers, coupled with the other species of amphibians and reptiles, make the herps the major predators of the forest. It is interesting that while in many areas of the world amphibians are in decline, not so in Hawaii. In the last decade, two small Caribbean frogs were introduced (probably on plants) and they have successfully invaded a number of the islands. Hawaiians want them eradicated because their vocalizations are perceived as noise. Most people of the Caribbean love their calls and generally find their melodic choruses sleep inducing.

For further reading see Joglar 1998, Reyes 1971, Rivero 1998, Schwartz 1991, Stewart and Pough 1983, Townsend and Pough 1984, Woolbright 1985. The Joglar reference has very good closeup photography of adults, egg masses, habitats and range maps, and Drewry's vocalization descriptions.

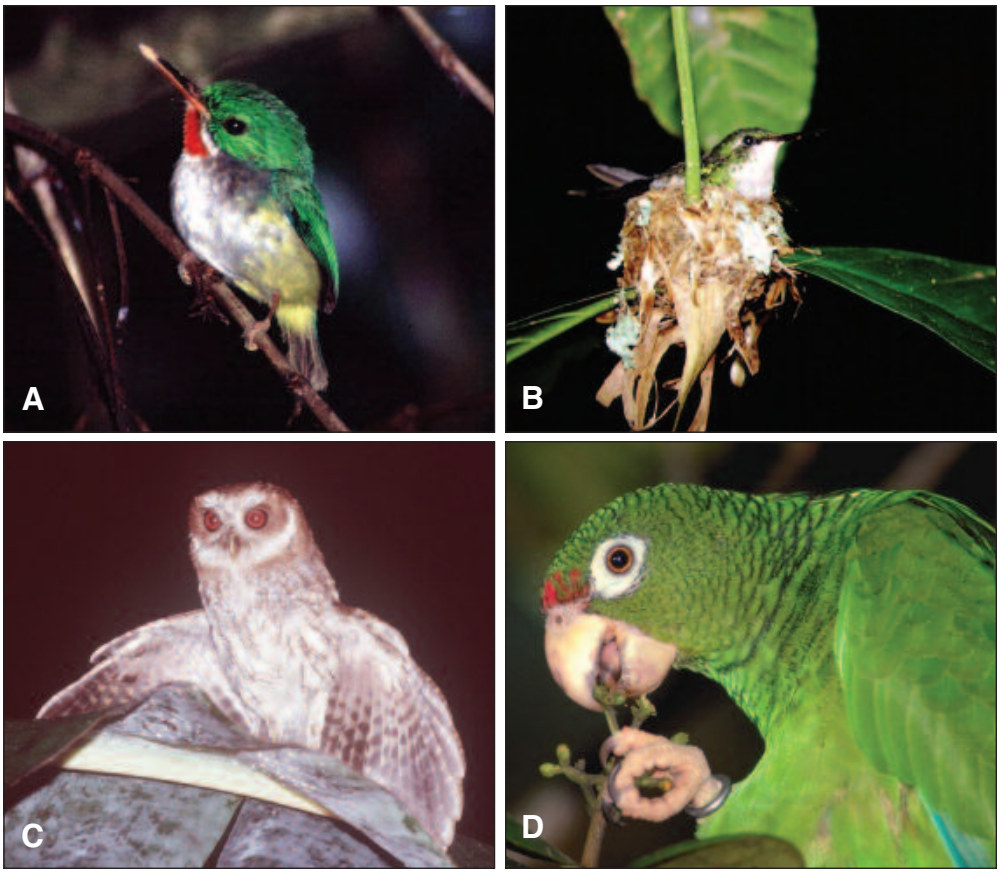
Birds

Herbert Raffaele (1983) in his *Guide to the Birds of Puerto Rico and the Virgin Islands* indicated the avifauna of Puerto Rico consists of 269 species. There are 50 bird families and 149 genera. Ninety-five of the species are permanent resident breeders, 126 species are nonbreeding migrants or visitors, 36 species are introduced aliens, 11 species use Puerto Rico for breeding, and 1 recently became extinct (white-necked crow [*Corvus leucognaphalus*]). Puerto Rico's avifauna diversity is second only to that of Cuba for the West Indies. It has the largest number of breeding alien species of any island in the West Indies. Why so many aliens? In Puerto Rico, many people have pet birds, resulting in many escapes as a result of the pet trade. For instance, the Dominican parrot population has been exploding in many areas. It is a very popular house pet and many escape into the wild. In addition, habitat alteration in the past 150 years has produced a considerable increase in grassland habitats and crop fields. This has resulted in a tremendous increase in edge habitat. Puerto Rico has many more seed-eating birds needing grassland or crops today than 150 to 200 years ago when forests dominated the landscape.

Puerto Rico has 14 endemic bird species (fig. 10) which include the:

- Puerto Rican parrot (*Amazona vittata*)
- Puerto Rican whip-poor-will (*Caprimulgus noctitherus*)
- Puerto Rican lizard cuckoo (*Saurothera vieilloti*)
- Puerto Rican tody (*Todus mexicanus*)
- Puerto Rican woodpecker (*Melanerpes portoricensis*)
- Puerto Rican tanager (*Nesospingus speculiferus*)
- Puerto Rican hummingbird (*Anthracothorax dominicus*)

One genus, *Nesospingus* (tanager), is found only in Puerto Rico's higher mountain forests, mainly in El Yunque and the Maricao Commonwealth Forest. The presence of endemics such as these makes for an interesting discussion of island biogeography, species dispersal, niche, speciation, and disjunct populations. Of great interest to humans today is the whole issue of species extinction and the problems that humans produce in the natural world, which can lead to animal and plant endangerment. In the case of birds, islands are at the heart of this debate because



Photos a-c by L. Miranda Castro, Photo d by T. Carlo

Figure 10—Four of the endemic birds of Puerto Rico: (a) Puerto Rican emerald (*Chlorostilbon maugaeus*), (b) Puerto Rican tody (*Todus mexicanus*), (c) Puerto Rican screech owl (*Otus nupides*), and (d) Puerto Rican parrot (*Amazona vittata*).

more than 75 percent of all bird extinctions have occurred on islands. Why? Very simply, islands are usually small, and thus many organisms found on islands have no additional habitat to escape to when their primary habitats are altered. In other cases, they have narrow specializations owing to their development in isolation, and may have no defense when new alien predators are introduced or humans decide to "use" them or exterminate them. Many are not exceptional flyers, thus there can be little chance for successful migration to new distant habitats. In some cases, island-dwelling birds may lose their immunity to disease, and as new organisms invade or are introduced by humans, diseases are introduced. Most bird extinction in the Caribbean is associated with humans and not alien species.

In the case of birds, the three most important causes of endangerment are habitat loss, introduced alien species, and hunting. In some cases all three may simultaneously affect a species, as was the case with the endangered Puerto Rican parrot.

Raffaele (1983) reviewed extirpations, both pre- and post-Columbian, and cited the current reasons for species being classed as threatened (T) or endangered (E). Of the 269 birds in Puerto Rico, 51 species are classed as either T or E. This represents 22 percent of the total. The vast majority is being severely affected by habitat disturbance or destruction (49 species). Seventeen species are affected by hunting, and three by the introduced mongoose or rats. There is overlap in these statistics, as some species may be affected by two of the population reduction factors. For example, all six species of breeding ducks were suffering from drainage of freshwater wetlands and, at the same time, they were being hunted. It is only recently that Puerto Rico has developed and enforced hunting laws for protected species. Enforcement continues to be a problem. There is need for additional officers in the field. In addition, some hunted species have well-defined seasons for breeding, whereas others do not. Thus, when some species are being legally hunted, others are breeding, which results in breeding interruption by guns, dogs, boats, and so forth, for some species. Six bird species have been introduced for hunting, for example, the partridge. About 75 species in Puerto Rico are used for sport or food. In other cases, growth of population centers and tourism is resulting in both habitat destruction and interruption of breeding in remote beaches, offshore islands, and mangrove swamps. Also, although it is illegal, many wild birds are kept in cages as house pets.

Bird sanctuaries have not been well developed or secured until recently. Major U.S. government sanctuaries exist in the El Yunque National Forest, the Cabo Rojo National Wildlife Refuge, and other national wildlife refuges at Laguna Cartagena, Desecheo Island, and Culebra. Commonwealth of Puerto Rico refuges have grown out of the 14 commonwealth forests, with Guánica especially significant to Neotropical migrants described in the section that follows. Additional sanctuaries have been developed at Boquerón Forest, Aguirre Forest, Piñones Forest, Humacao Refuge, *Las Cabezas* Reserve in Fajardo, *Caja de Muertos* Island Reserve, and the Boquerón Bird Refuge. All totaled, there are 13 commonwealth refuges on the island.

As throughout most countries of the world, ecological interest in birds and bird watching as an avocation is growing in Puerto Rico. Today, Puerto Rico has active bird watching clubs and a growing ecotourism industry that offers specialty trips centered on the island's wildlife. Mixed populations of exotic parrots, including the brilliantly colored macaws can be seen at the University of Puerto Rico's main campus in Río Piedras. Hundreds may be there at any given time. They are frequently in the area between the bell tower and the student union. You find them by

listening for their calls and chatter. They get to be quite loud! They all result from escapes or releases from homes or pet stores.

For places to bird watch, see app. 2. For further reading see Bond 1971, Nellis 1999, Oberle 2000, Philibosian and Yntema 1977, and Snyder et al. 1987.

Neotropical Migrants

In his poignant book titled *Where Have All The Birds Gone?* John Terborgh (1989) of Princeton University brought to the world's attention the fact that birds do not respect political boundaries and that they may reside in a series of countries in their long migrations to and from summer breeding and wintering areas. They are creatures of instinct and as such migrate according to the complex rhythms of nature. They are the birds that may be the summer songbirds in people's backyards or interior forests in eastern North America, and the winter songbirds in coffee plantations or dry forests of the American tropics—thus the term Neotropical migrants. Unfortunately these birds are under enormous pressure, and their populations are succumbing to a variety of **stressors**, chief among these is habitat destruction on both ends of the migration routes. Terborgh pointed out that even though bird populations have changed drastically in some areas of the Eastern United States, the physical places themselves have not. This raised the question of "Why?" Today, of course, we know why. In some instances it was the drastic alteration of habitat in the tropics, in other cases it was **fragmentation** of forests in the temperate zone. Following is a partial list that can account for most of the changes in Neotropical species populations.

Agents of stress include:

- Habitat destruction
- Forest fragmentation with increased edge
- Introduced species
- Pesticides
- Technology effects (lights, vehicles, and so forth)
- Changing agricultural practices
- Increased numbers of feral domestic cats
- Loss of **riparian** zones
- Destruction of wetlands
- Changing silvicultural patterns
- Monocultures
- Towers (power, radio, TV, phones)
- Highrise buildings

- Large plate-glass doors and windows
- Lack of fire or too much fire in the landscape
- Disease
- Nest predation
- Switching from shade- to sun-grown coffee

The genesis for Terborgh's book was a winter holiday to Puerto Rico in the late 1960s. It was during this first trip to the tropics that he noticed that many of the birds typical of the Middle Atlantic States were spending the winter in Puerto Rico, especially certain species of warblers, water thrushes, and ovenbirds. That was the advent of the study of Neotropical migrants. Over the years he has been tracking the status and destination of some 250 migratory species that spend time in 15 tropical countries. Surveys were conducted in habitats ranging from rain forests to deserts, and from coastal mangrove forests to mountaintop elfin forests.

One of the primary sites where Terborgh and his colleague at the USDA Forest Service, International Institute of Tropical Forestry (Wayne Arendt) conducted some of their initial research is the Guánica Commonwealth Forest (see app. 2, p. 373). Neotropical migrant surveys are still going on, and in any given January you are likely to see crews in the field sampling extensive arrays of mist nets as they stretch through various sections of the Guánica Forest.

Today, there are many groups working on the Neotropicals issue, including the U.S. Fish and Wildlife Service, the USDA Forest Service, and their counterpart agencies in Canada, the countries in the tropics, and the various state government groups in the United States and Puerto Rico. There are numerous nongovernmental organizations (**NGOs**) also vitally involved including the National Audubon Society, The Nature Conservancy, and The National Fish and Wildlife Foundation, to name just a few. Many public and private agencies cooperate in the Neotropical Migratory Bird Conservation Program, also called "Partners in Flight." This program was initiated in 1940 to promote Neotropical bird research, develop conservation programs, and promote habitat protection and enhancement. Cooperative programs are also in development with the counterpart agencies and NGOs in the birds' winter range countries.

The effort to protect these species must truly be an international effort. Without concern and efforts on both ends of this delicate migratory chain, conditions will only worsen. To be sure that half the birds that breed in the United States and Canada, and spend 6 to 9 months in the Neotropics, have the chance to continue these ancient migratory patterns, we have to reduce those agents of stress mentioned earlier. In addition, Neotropicals are at a distinct disadvantage reproductively

because many are small bodied and have difficulty in defending nests from predators. Many build open ground nests where they are more subject to detection. Many have difficulty in producing a second brood if the first is lost owing to weather, predation, or parisitism. Some species may not breed at all if the special requirements for isolation in the interior of extensive forests of critical stand age are not met.

Some migratory birds are permanent residents, that is, they stay put and do not migrate except for very short distances (Cardinals [*Richmondena cardinalis*] and Blue jays [*Cyanocitta cristata*] in North Carolina, Puerto Rican parrot [*Amazona vittata*] in Puerto Rico). They are able to cope with a variety of changing habitat conditions, and all their resource needs are met in one geographic area. Other species are short-distance migrants, that is, they move from mountain habitats to valleys as the seasons change, such as slate-colored Juncos (*Junco hyemalis*) or Robins (*Turdus migratorius*). True migrants may migrate great distances, thousands of kilometers (miles) or more, in order for their life cycle needs to be met as in red-eyed vireo (*Vireo olivaceus*). The common ruby-throated hummingbird makes a nonstop journey of 1300 kilometers (800 miles) to cross the Gulf of Mexico to its winter range in Central America. Long-distance migratory species require a vast storage of energy (up to 50 percent of body weight) or frequent refueling stops along the way in order to supply the energy necessary for the long distances to be traveled (fig. 11). Twenty-eight species of shorebirds have been recorded in Puerto Rico, 24 of which are migrants. Fourteen waterfowl species that breed in North America spend their winters in Puerto Rico, including Mallards (*Anas platyrhynchos*), blue-winged teal (*Anas discor*s), American widgeon (*Mareca americana*), and pintails (*Anas acuta*). A total of 132 Nearctic-Neotropical migrants have been identified in Puerto Rico (Watson and Martínez 2002.)

There are some distinct disadvantages to migration, so why migrate?

- It permits the birds to avoid the cold periods in the northern climates and hot/humid periods in the tropics.
- It reduces **intra** and **interspecific** competition for food in the winter pinch period at a time when the total bird population would be highest, that is, after the breeding season.
- It provides for opportunistic feeding during migration.
- The changing day lengths in the north greatly hamper food availability in the winter.
- Long daylight periods during the breeding season foster access to more food supplies.

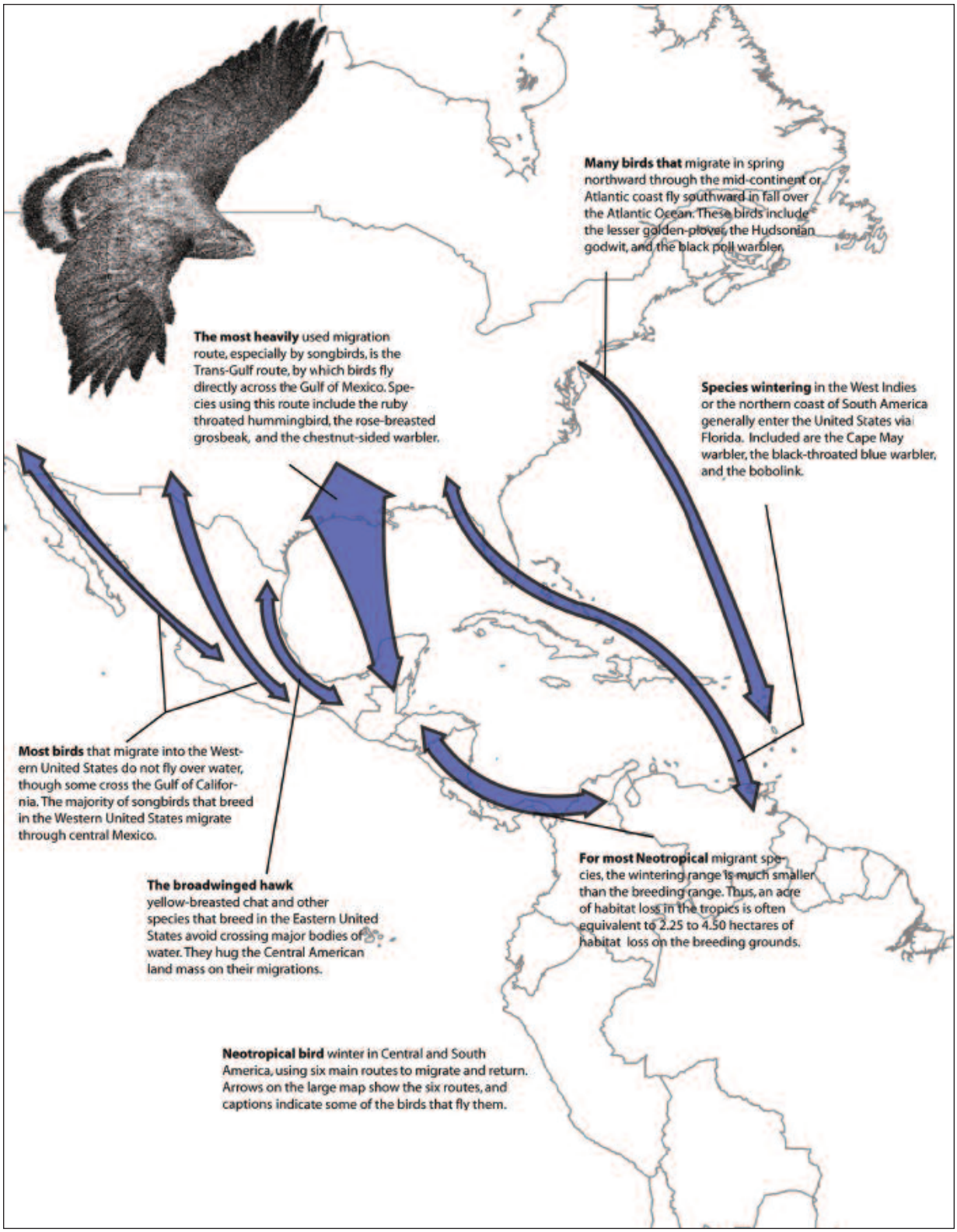


Figure 11—Neotropical migrants use a variety of fly ways to reach their summer/winter range destinations.

- It provides genetic advantages of large mixed populations, not just those of one highly restricted area.
- It allows ecosystem recovery in areas not continuously occupied 12 months a year by the entire bird assemblage.

As previously cited, there are many stressors of Neotropical migrant populations. One that is producing great habitat change in the tropical mountain **agroecosystems** is the switch from shade-grown to sun-grown coffee. This relatively simple shift in cultivation practice may be responsible for substantial declines in Neotropical migrants. Coffee has traditionally been grown under a **canopy** of other trees including citrus, breadfruit, bananas, **nut**-producing trees, and others. Mature trees full of epiphytes and **lianas** provide many microhabitats for a diverse animal **community**. Most coffee grown in the New World (32 percent of world production) comes from northern Latin America where coffee lands make up approximately 44 percent of the permanent crop land (Perfecto et al. 1996). New varieties of sun-loving coffee give higher yields per plant; as a result, the old plants are being replaced with new varieties, and the canopy species are being cut, highly simplifying the ecosystem. In addition, in this newly created coffee monoculture, more pesticides and fertilizers are required to produce the desired yields. Half of all shade-grown coffee has been replaced with sun-grown coffee. Environmentally friendly coffee companies can market shade-grown varieties and pay premium prices for them, thus encouraging coffee farmers to preserve existing shade coffee plantations and return coffee plantations to shade. They also give purchasing preferences and price incentives to vendors who grow coffee in accordance with the Conservation Principles for Coffee Production. These principles emphasize protection of biodiversity, soil conservation, water quality, minimization of agrochemical use, and appropriate waste management (Johnston 2001).

The previous multilevel shaded agroecosystem supported many more species of birds, with some studies indicating 150 species or more. As Wunderle (1997) put it, “diversity begets diversity,” that is, structural diversity of the vegetation promotes a biologically diverse animal community, thus contributing to a rich biologically diverse coffee plantation. In addition, these plantations may serve as refugia for forest-dwelling birds in a region that may be largely agricultural including native nonmigratory species. In the new simplified sun coffee plantation monocultures there is a drop in both total species present and numbers of individuals of a species. In some areas there has been a 90 percent decline in species presence. In Puerto Rico, where little shade-grown coffee land has been converted, the traditional coffee plantations are thought to have served as a critical refuge during a

human-caused habitat bottleneck. It appears that Puerto Rico experienced a low rate of avian extinction during recent periods of deforestation owing in part to their traditional agroecosystem plantations acting as refuges. Not only was bird loss minimized, it appears that rare orchids also survived on the coffee farms. The 9 percent of the island covered in traditional coffee served as a refuge even though 99 percent of the original forest had been destroyed or disturbed (Perfecto et al. 1996).

Coffee is the world's most widely consumed beverage; therefore, it has wide economic impact all the way through its delivery system. At all levels, various business people are making bottom-line decisions based on yield, supply, and profits. With slim profit margins, any increase in yield or profit is bound to produce pressure to switch to sun-grown coffee. Unfortunately, the short-term decision is likely to produce increased erosion, greater reliance on expensive chemicals, loss of water quality, and substantial long-term effects on the animal community, especially Neotropical migratory birds. The cost of operating coffee plantations also increases, and in cases, leads to bankruptcy.

Why should you be concerned about Neotropical birds?

- They eat vast quantities of insects.
- They disperse seeds for many plants.
- They are beautiful.
- Their songs are wonderful to listen to.
- Their migration ability represents one of the true wonders of nature.
- They are part of the complex web of life.
- Their place in the web of life is not completely understood.

For further reading on Neotropical migrants, see Franzreb and Phillips 1996, Raffaele 1983, Rappole 1995, Tangley 1996, Wille 1994, and Wunderle and Latta 1996.

Bats

Bats dwell in the secret world of the night. As a result of much misinformation, they are feared by many and poorly recognized for the vital roles they play in many ecosystems around the world, especially in the tropics. Mythology, world folklore, popular literature (Stoker's *Dracula*), and Hollywood movies have contributed to a reputation that portrays bats as evil and spreaders of disease. They fly at night, some live in caves (the netherworld) and, yes, some even suck blood (less than 1 percent). Thus, for many people "the only good bat is a dead bat." The truth is that these small flying mammals from the order Chiroptera (which means "handwing")

should be treasured because of all the good they do in nature. Some fruit-eating bats have wingspans approaching 1.8 meters (6 feet). The smallest bat is the bumblebee bat of Thailand, weighing less than a U.S. penny.

Many cultures have historically valued bats. In China they are a sign of happiness. In México and northern South America, they are a sign of fertility. Unfortunately, throughout much of Europe and North America they are associated with death, disease, blood sucking, and evil and are thus highly persecuted and classed as a pest. Some people think they are blind ("as a bat"), but in fact they have a highly evolved form of "vision by sound" called echolocation. This allows bats to locate prey, walls, vegetation, or whatever is in their path with extreme accuracy. They emit high-pitched sounds and then detect the echo that rebounds from any structure or organism in their flight path. Some can discriminate between echoes arriving only two-millionths of a second apart and can echo-separate objects that are only 0.3 millimeter (less than 1/90 of an inch) apart. These abilities are three times better than current military sonar, according to James Simmons of Brown University (1998).

Bats are the only flying mammals and are distributed all over the world. They comprise 25 percent of all mammal species and currently include nearly 1,000 species. Eighty-eight percent of all bat species are found in the tropics, mostly the Neotropics. There are as many bats in the tropics as all other mammal species combined. Their value is enormous and without them some species and whole ecosystems would be in jeopardy. Why are they valuable?

- They eat vast numbers of insects and rodents (70 percent of species are carnivorous and eat up to 50 percent of their body weight in one evening).
- They serve as primary **pollinators** for thousands of tropical plants while searching for nectar, pollen, and fruit (30 percent of species). Below are just a few of the plants that bats pollinate:
    - Bananas
    - Mangoes
    - Guavas
    - Avocadoes
    - Dates
    - Figs
    - Cashews
    - Cloves
    - Cacti
    - Kapok
    - Agave
    - Peaches
    - Durians
- They are fruit eaters that vector seeds throughout their range.
- They supply large quantities of guano fertilizer.
- They are important to research on blood clotting factors (anticoagulents produced by blood-sucking species).

- ➢ They are important to research in antibiotics because they show few diseases.
- ➢ They are important to ecotourism; many people are recognizing their ecological importance and want to see them and their habitats.
- ➢ Sonar research is looking at their exceptional ability to locate objects in flight.

Because of their vital importance in both pollination and seed distribution, bats are considered **keystone** agents. Should bats disappear or decline, other species would likewise decline or disappear. Their influence on the community or ecosystem is much larger and more influential than you would expect from their presence or abundance alone. Humans derive 450 commercial products from bat-dependent plants.

Unfortunately, wherever they are found, bats are under attack. Threats to their survival include:

- ➢ Lack of understanding of their value
- ➢ Disturbance of roosts such as caves by cavers, hikers, and researchers. Disturbances cause young to drop from the cave's ceiling and adults to fly and use up food reserves in winter periods.
- ➢ Habitat destruction (deforestation, fire, cutting snags in forests)
- ➢ Destruction of their food supply
- ➢ **Food chain** contamination with pesticides (DDT)
- ➢ Being classed as vermin in most countries and killed on sight
- ➢ Being eaten as human food in the Far East
- ➢ Vandalism whereby people intentionally disturb roosts or destroy habitat
- ➢ Flooding owing to hydroelectric dam construction

Puerto Rico has 14 species of bats. Some tend to be more coastal, such as the bulldog fishing bat (*Noctilio leporinus*), seen at Boquerón on the southwest coast where it feeds on insects and fish. It roosts in hollow trees and caves. Others, such as the endemic red fig bat (*Stenoderma rufum*) will be found in the tabonuco montane rain forest where it is a **frugivore** (fruit eater). It is classed as a sensitive species by the U.S. Fish and Wildlife Service. The tabonuco forest has populations of seven bat species, with the red fig bat accounting for nearly 25 percent of the total bat population (fig. 12). Eleven of Puerto Rico's 14 species are associated with the El Yunque National Forest (Weaver 1994). The largest bat found in Puerto Rico is the Jamaican fruit bat (*Artibeus jamaicensis*). As its common name implies, it is a frugivore, but it will also feed on insects. Four of Puerto Rico's bats feed

A. Puente Rolón

Figure 12—The red fig-eating bat, an endemic species to Puerto Rico.

mainly on fruits, pollen, and leaves. The others feed primarily on insects and fish. The majority of bat species roost in cool caves, and Puerto Rico has a vast network of caves, especially in the karst region on the north side of the island where roosting habitat is almost unlimited (see app. 2, p. 373). The karst belt is home to 13 species of bats, 10 of which use caves as preferred roosting sites (Rodríguez Durán 1998). Some caves support single species, whereas others house mixed species such as the Cucaracha Cave with its mixed populations of three species, numbering 700,000 individuals (Lugo et al. 2001).

One of the industrial world's most successful and recognizable logos is Bacardi Rum's bat silhouette. When you fly or cruise to Puerto Rico, you can immediately locate the Bacardi distillery in Cataño as a result of the highly visible bat-like outline of the visitors center (See app. 2, p. 372). Why use a bat for a logo? It is a very simple story. When Bacardi was still located in Cuba where the company started, bats were symbols of good luck, good fortune, and excellence. The garage where the first alcohol still was set up had bats in it. When the time came for a distinctive logo, the owner's wife fondly remembered the bats and said that it would bring luck and stand for an excellent product, thus the bat logo.

For further reading see Diaz 1983; Emmons 1990; Findley 1985; Fleming and Heithaus 1981; Gannon 1991; Gannon and Willig 1994, 1998; Hill and Smith 1988; Kunz 1982; Richards 1996; Science News 1994; Starrett 1962; Tuttle 1995; U.S. Department of the Interior 1985, 1998; Weaver 1994; and Willig and Gannon 1991.

Additional information on bats can be obtained by contacting: Bat Defenders, 1101 14th Street, NW, Suite 1400, Washington , DC 20005; or Bat Conservation International, P.O. Box 162603, Austin, TX 78716

Termites

Termites are a complex group of social insects. Most people associate termites with damage to wooden structures, when in fact the majority of the species of termites are not involved with these problems. Termites are highly beneficial to the natural environment. Less than 10 percent of the species has been identified as pests. Negative economic importance has masked the enormously important ecological role termites play in the breakdown of vegetation in the landscape and in nature's food chains. All termites are herbivores and decomposers. They exhibit a variable diet with some feeding on firm deadwood; others on decayed wood, and others on grass, dung, and leaf litter; some cultivate fungal gardens. They, in turn, are eaten by most predators around them such as amphibians, reptiles, birds, mammals, and a variety of invertebrates. Most termite swarms are heavily predated. Ants may be their largest predator. They also exhibit tremendous variation in social behavior, physiology, and regulation. Interestingly, this ancient group of animals is linked to our current greenhouse effect controversy because they generate considerable amounts of methane (CH_4). Methane is a greenhouse gas 20 times as effective at trapping heat as carbon dioxide (CO_2). Humans are altering environmental conditions and habitats in many areas of the world, making it possible for termite populations to expand, thus further increasing their methane production.

Termites are mostly tropical in their distribution. They exhibit many unique relationships, including:

- Complex social behavior
- **Polymorphism**
- Symbiotic relationships
- Intricate nest construction
- Being consumers of vast quantities of wood and other forms of cellulose
- Being consumed by many predators in a complex **food web**
- Special associations with **fungi** and **termitophiles**
- Nitrogen fixation

Taxonomically, termites belong to the order Isoptera. There are over 2,000 identified species of termites, grouped into six families. Five of the six families possess symbiotic protozoans necessary for cellulose digestion. They differ from other social insects such as bees, ants, and wasps in that they do not exhibit lower

social groups, their **castes** contain both sexes, and their digestive system involves protozoans or bacteria as the true digesters of cellulose, a condition known as hemimetabolism.

For those species that build aboveground nests, the nest wall serves as protection and as a thermoregulator. Nests are usually quite striking, and anyone who has ever traveled to the tropics has probably observed them. They appear as large mounds coming out of the soil or large ball-like structures positioned on limbs or trunks of trees. In Puerto Rico, large brown mounds in trees dot the landscape. When examined closely, each mound will have a series of covered trails called galleries leading from the colony to active deadwood feeding sites up to 30 meters (98 feet) away. These are protective pathways used by workers in securing food for the colony. Most feeding occurs at night, and termites use pheromone deposits for direction. Termites have little protection against desiccation; thus they must reside within the controlled environment of the nest. In the nest, temperature, humidity, and CO_2 are regulated. Relative humidity is generally in the range of 90 to 99 percent, and the temperature is higher than the outside temperature.

There are a variety of other organisms associated with termite colonies. Beetles, flies, fungi, and protozoans have developed highly interdependent associations. These organisms are called termitophiles. The relationships between **host** and termitophile are species-specific. Some termite colonies have fungus gardens in them. The fungus grows on the termites' excrement and may contribute nutritionally to the colony or be a source of heat and humidity. The five families of termites that possess protozoans in their hind-gut have evolved a classic example of endosymbiosis. It is mutualistic in that both the host termites and the endosymbiont gain from the relationship. The protozoans supply the needed enzymes for cellulose digestion, and the termites supply the cellulose. As mentioned earlier, not all termites possess protozoans as digester symbionts. The sixth and largest family use bacteria in cellulose digestion. Seventy-five percent of all termites have evolved this relationship with bacteria. As termites grow and molt, the essential digester symbionts are lost, thus they must be reinfected. The reinfection occurs as a result of the close feeding and cleaning relationships between nonmating individuals within the colony; thus there is intergenerational and intercaste dependency in these complex communities. In addition, large numbers of the microbial symbionts are digested by the termites, providing an important source of protein to their diets.

Puerto Rico has 17 species of termites, four of which are economically important (Torres 1994). Two of those species are dry-wood feeders. The other two are subterranean species and feed on a variety of cellulose substrates. The termite

G. Miller

Figure 13—A large *Nasutitermes costalis* (termite) nest (height approximately 60 centimeters or 23 inches) at the base of a red mangrove (*Rhizophora mangle* L.) near La Parguera.

species you will commonly see as you explore Puerto Rico is *Nasutitermes costalis*. It builds large arboreal nests on the trunks of trees such as the *flamboyán*, on major tree branches, fenceposts, and other raised substrates. These nests are very obvious because they are quite large and chocolate brown in color. This termite primarily harvests dead wood from tree branches. It will have a complex array of tunnels that protect workers as they forage for cellulose sources. The tunnels are also brown. The nest has to be located in an area where the termites have a dependable supply of ground water, otherwise the colony will fail. It is a dry-wood-consuming species, thus it causes considerable damage to houses, furniture, and other wooden structures. Colonies can easily be destroyed by pesticide injection or mechanical breakup. In one day, while driving through rural Puerto Rico, you will likely see 20 or more of these termite mounds. This species has bacteria in its gut.

Some of the nests of *Nasutitermes* will measure close to a meter (3 feet) in size. The nest material is referred to as **cartón** (fig. 13). The *cartón* nests are constructed by the workers and are composed of saliva, liquefied fecal materials, and

soil. The *cartón* contains lignin, cellulose, and hemicellulose. Functioning nests have been known to last 18 years or more (McMahan 1996). Termite colonies are almost immortal in that they keep making new nests as food supplies are used up.

One of the reasons most housing and business construction in Puerto Rico is of cement today is because of the threat from termite infestation. Only dense hardwoods like mahogany, which has highly lignified heartwood, resists termite infestation. Some farmers harvest termite nests and feed them to their chickens or hogs.

For further reading on termites, see Graham 1952 and Krishna and Weesner 1969.

Endangered Species

Although biological extinction is a natural evolutionary process, it has been accelerated by human actions in the environment. As humans modify the vast number of environmental settings throughout the world, species may become locally exterminated and then exterminated at the regional level, thus producing extinction of a species. In 1985, E.O. Wilson wrote the following:

> The worst thing that can happen during the 1980's is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process ongoing in the 1980's that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly that our descendants are least likely to forgive us.

What is driving habitat loss? Much of it is associated with maintenance of our current world population. Although birth rates are falling in some areas of the world and some countries are experiencing negative growth, the big crunch is yet to come because it will take another 50 years before the number of people and their impact reaches its peak. Our current 6.3 billion humans will likely mushroom to somewhere between 7.3 and 10.7 billion by 2050. As indicated by United Nations projections, Puerto Rico may see an increase in its population in the next 25 years although its current birth rate is falling and the population has not grown as predicted.

Another major reason for the loss of species relates to black market activities. Many plants and animals are sold because they are beautiful, exotic, dangerous, rare, or bizarre. The rarer an organism becomes, the higher its value in the black market. Many plants and animals are also used in patented and folk medicines. Unfortunately, many are perceived as aphrodisiacs putting enormous pressure on

many rare species such as bears, big cats, and the rhinoceros. The sale of endangered species and their parts is second only to drugs in the international black market.

Historically, there has been no documented plant extinction in Puerto Rico. On the other hand, there have been animal extinctions, including frogs, birds, and mammals. Today, the U.S. Fish and Wildlife Service and Puerto Rico's Department of Natural and Environmental Resources are tracking the status of 79 protected species in Puerto Rico and the Virgin Islands. Thirty of the species are animals, which include mammals (5), birds (11), reptiles (11), and amphibians (3). Table 12 has a complete list. Forty-nine species of plants are on the protected species list and include trees and shrubs (33), ferns (8), cacti (2), orchids (2), and herbaceous species (4). Table 13 has a complete plant list. Descriptions of these species and their habitat requirements (boxes 7 and 8) and, in some cases, published **recovery plans**, are available from the two lead management agencies mentioned above. Most of Puerto Rico's endangered species are found in karst habitat.

The primary reasons for species endangerment throughout the world are:

- Habitat destruction/alteration
- Introduction of alien species
- Commercial hunting and harvesting
- Pest and predator control
- Collection of plants and animals for human enjoyment, research, trade, and others
- Pollution
- Ecological/biological changes

All of these activities take place in Puerto Rico. Many people are unaware of the impact their activities have on species and their habitats; therefore, more education is needed at all age levels so this problem can be better understood and individuals can make the best decisions in terms of how they interact with the environment.

Puerto Rico is currently facing a major controversy involving endangered sea turtle species and the proposed development of a series of four north coast hotel and residential resort complexes in the Luquillo-Fajardo area covering 1300 hectares (3,200 acres). In March 2002, the U.S. Fish and Wildlife Service raised major objections based on the danger of losing the most important sea turtle nesting beach on the island. In 2001, biologists counted 346 leather back turtle (*Dermochelys coriacea*) nests. The areas in question also contain protected mangrove forests, habitats for the endangered brown pelicans (*Pelecanus occidentalis*),

Table 12—Animals in danger of extinction

Scientific name	Common name (Spanish)	Common name (English)
Amphibians (3):	Amphibians:	Amphibians:
[a] *Eleutherodactylus jasperi* (HC)	[a] Coquí dorado	[a] Golden coqui
[a] *Peltrophryne lemur*	[a] Sapo concho	[a b] Puerto Rican crested toad
[a] *Eleutherodactylus cooki*	[a] Guajón	[a] Puerto Rican rock frog
Reptiles (11):	Reptiles:	Reptiles:
[c] *Ameiva polops* (HC)	[c] Lagartijo de Santa Cruz	[c] St. Croix ground lizard
[c d] *Anolis roosevelti* (HC)	[c d] Lagartijo gigante de Culebra	[c d] Culebra giant anole
[a] *Caretta caretta*	[a] Cabezón o Caguama	[a b] Loggerhead sea turtle
[a] *Chelonia mydas*	[a] Peje blanco	[b] Green sea turtle
[a] *Cyclura stejnegeri* (HC)	[a] Iguana de Mona	[a c] Mona ground iguana
[b] *Dermochelys coriacea* (HC)	[c] Tinglar	[b c] Leatherback sea turtle
[b] *Epicrates inornatus*	[c] Boa puertorriqueña	[b c] Puerto Rican boa
[b] *Epicrates monensis granti*	[c] Boa de Islas Vírgenes	[b c] Virgin Islands tree boa
[a] *Epicrates monensis monensis* (HC)	[a] Boa de Mona	[b c] Mona Island boa
[c] *Eretmochelys imbricata* (HC)	[c] Carey de concha	[b c] Hawksbill sea turtle
[c] *Sphaerodactylus micropithecus* (HC)	[c] Salamanquita de monito	[b c] Monito gecko
Birds (11):	Birds:	Birds:
[c] *Accipiter striatus venator*	[c] Falcón de sierra	[c] Sharp-shinned hawk
[c] *Agelaius xanthomus* (HC)	[c] Mariquita	[c] Yellow-shouldered blackbird
[a] *Amazona vittata vittata*	[c] Cotorra puertorriqueña	[c] Puerto Rican parrot
[c] *Buteo platypterus brunnescens*	[c] Guaraguao de bosque	[c] Broad-winged hawk
[b] *Caprimulgus noctitherus*	[c] Guabairo	[c] Puerto Rican nightjar
[c] *Charadrius melodus*	[a] Playero melódico	[b c] Piping plover
[c] *Columba inornata wetmorei*	[c] Paloma sabanera	[c] Puerto Rican plain pigeon
[c] *Corvus leucognaphalus*	[c] Cuervo pescueciblanco	[c] White-necked crow
[a] *Falco peregrinus tundrius*	[a] Falcón peregrino	[c] Peregrine falcon
[c] *Pelecanus occidentalis*	[c] Pelícano pardo	[c] Brown pelican
[a] *Sterna dougallii*	[a] Palometa	[c] Roseate tern
Mammals (5):	Mammals:	Mammals:
[c] *Trichechus manatus manatus*	[c] Manatí antillano	[b c] Antillean manatee
[c] *Physeter macrocephalus*	[c] Cachalote	[c] Sperm whale
[c] *Megaptera novaeangliae*	[c] Ballena jorobada	[c] Humpback whale
[c] *Balaenoptera physalus*	[c] Ballena de aleta	[c] Finback or fin whale
[c] *Balaenoptera borealis*	[c] Ballena sei	[c] Sei whale

[a] Species threatened.

[b] See appendix for sources of educational wall charts describing endangered West Indian manatee, Puerto Rican toad, marine sea turtles, and Puerto Rican boa.

[c] Species in danger of extinction.

[d] Probably extinct.

Table 13—Plants in danger of extinction

Scientific name	Common name (Spanish)
Trees and shrubs (33):	Trees and shrubs
[a]*Auerodendron pauciflorum* Alain	
[a]*Banara vanderbiltii* Krug & Urban	Palo de ramón
[a]*Buxus vahlii* Baill.	
[a]*Callicarpa ampla* Schauer	Capá rosa
[a]*Calyptranthes thomasiana* O. Berg.	
[b]*Calyptronoma rivalis* (O.F. Cook) Bailey	Palma de manaca
[a]*Catesbaea melanocarpa* Krug & Urban	
[a]*Chamaecrista glandulosa* var. *mirabilis* (Pollard) Irwin & Barneby	
[a]*Cornutia obovata* Urban	Palo de nigua
[a]*Cordia bellonis* Urban	
[a]*Crescentia portoricensis* Britton	Higuero de sierra
[a]*Daphnopsis helleriana* Urban	
[a]*Eugenia haematocarpa* Alain	Uvillo
[a]*Eugenia woodburyana* Alain	
[a]*Goetzea elegans* Wydler	Matabuey
[a]*Ilex cookii* Britton & Wilson	
[a]*Ilex sintenisii* (Urban) Britton	
[a]*Juglans jamaicensis* C. DC.	Nogal
[a]*Lyonia truncata* Urban var. *proctorii* Judd	
[a]*Mitracarpus maxwelliae* Britton & Wilson	
[a]*Mitracarpus polycladus* Urban	
[a]*Myrica paganii* Krug & Urban	
[a]*Ottoschulzia rhodoxylon* (Urban) Urban	Palo de rosa
[a]*Pleodendron macranthum* (Baill.) V. Tieghem	Chupacallos
[b]*Schoepfia arenaria* Urban & Britton	
[a]*Solanum drymophilum* O.E. Schulz	Erubia
[b]*Stahlia monosperma* (Tul.) Urban	Cóbana negra
[a]*Styrax portoricensis* Krug & Urban	Palo de jazmín
[a]*Ternstroemia luquillensis* Krug & Urban	Palo colorado
[a]*Ternstroemia subsessilis* (Britton) Kobuski	
[a]*Trichilia triacantha* Urban	Bariaco
[a]V*ernonia proctorii* L.E. Urbasch	
[a]*Zanthoxylum thomasianum* (Krug & Urban) Krug & Urban	St. Thomas prickly ash
Ferns (8):	
[a]*Adiantum vivesii* Proctor	Ferns
[a]*Cyathea dryopteroides* Maxon	
[a]*Elaphoglossum serpens* Maxon & Morton ex Maxon	Helecho arbóreo de bosque enano
[a]*Polystichum calderonense* Proctor	
[a]*Tectaria estremerana* Proctor & Evans	Cactus
[a]*Thelypteris inabonensis* Proctor	Higo chumbo
[a]*Thelypteris verecunda* Proctor	
[a]*Thelypteris yaucoensis* Proctor	
Cactus (2)	
[b]*Harrisia portoricensis* Britton	Orchids
[a]*Leptocereus grantianus* Britton	

Table 13—Plants in danger of extinction (continued)

Scientific name	Common name (Spanish)
Orchids (2):	
[a]*Cranichis ricartii* Ackerman	
[a]*Lepanthes eltoroensis* Stimson	
Herbs (4):	
[a]*Aristida chaseae* Hitchc.	Herbs
[a]*Aristida portoricensis* Pilger	
[b]*Gesneria pauciflora* Urban	Pelos del diablo
[a]*Peperomia wheeleri* Britton	

[a] Species in danger of extinction.
[b] Species threatened.

Puerto Rico plain pigeon (*Columba inornata* Wetmorei), and the Puerto Rico boa (*Epicrates inornatus*). In addition, the National Marine Fisheries Service has indicated that the proposed projects are not in keeping with the Puerto Rico Coastal Zone Management Program. This series of projects could involve a couple of kilometers (miles) of critical coastal habitat and would require a zoning change from mangrove forest and conservation area to high-density development and use. The change would likely result in the loss of critical nesting habitat and important fishery resource areas. There are an estimated 40 rare, threatened, or endangered species present in this complex of wetlands and coastal fauna habitats in this vital "northeastern ecological corridor." Because much of the land is controlled by the Puerto Rican Development Corporation, it could effectively be permanently protected. One of the most crucial issues facing Puerto Rico today is the chronic need for setting aside presently owned lands and the continued need to purchase additional lands deemed critical habitats for the large number of endangered, threatened, and rare species on both federal and commonwealth lists. This is one of the most important environmental decisions to be made in the first decade of this century. Hopefully, Puerto Rico's leadership and natural resource management agencies will decide on behalf of protecting critical habitats and species, and protecting vital water supplies in an area notoriously short of meeting its current water demands. Unfortunately, in July 2003 a lawsuit filed by environmental groups and local citizens against the Department of Natural and the Environmental Resources claims that this lead environmental agency failed to inform other agencies about the ecological significance of the lands in question prior to their consideration for lease or sale. The case is under Superior Court review.

Prior to his death in May 2000, John Sawhill, head of the Nature Conservancy, wrote the following poignant statement: "In the end our society will be defined not only by what we create, but by what we refuse to destroy."

Box 7. *Stahlia monosperma* (Tul.) Urban (cobana negra)

Stahlia is a monospecific genus (only one species in it). This small tree was listed as an endangered species in 1990. It, like so many other listed species, has been greatly affected by the loss and modification of its habitat and the fact that its wood had utility. It is typical of dry coastal limestone woodlands, such as at Guánica and Cabo Rojo in southwestern Puerto Rico and on Vieques Island. It was thought to be endemic to Puerto Rico, but is now reported to be present in a very restricted area in eastern Dominican Republic.

The leaf, flower, and fruit of *Stahlia monosperma* (Tul.) Urban (cobana negra)

It can grow to 20 meters (65 feet) in height, but most individuals are smaller because the largest individuals in the small populations had been previously cut. The leaves are compound, alternately arranged, with 6 to 12 leaflets. Inflorescences are terminal racemes 10 to 15 centimeters (4 to 6 inches) long and the petals are light yellow. Flowering occurs from February to June, with fruits maturing from June through September. The fruit is a small, red to purple, fleshy legume about 5 centimeters (2 inches) long, with one seed.

The wood of *cobana negra* is very hard, dense, durable, and termite resistant. The heartwood is dark brown, whereas the sapwood is light brown in color. It had value as furniture wood, but today, because of its listed status and the fact that so few large trees remain, it is no longer used for that purpose. Historically, cobana negra was mainly a construction wood species. It is successfully being propagated at the tree nursery in the Cabo Rojo National Wildlife Refuge and outplantings are being made there, since they are attempting to ecologically restore significant sections of the refuge by using native species. Previously, most of the area had been converted to pasture or agricultural land. A variety of introduced forage species and exotic woody plants have dominated the area in recent decades. Other groups concerned with cobana's status are working on developing seedling nurseries and establishing new populations.

For more information about this species see Liogier 1997 and Little and Wadsworth 1964.

Box 8. *Juglans jamaicensis* C. DC. (Jamaican walnut) (Locally known as *nogal*)

According to Manning (1979), there are 59 species in the genus Juglans. They are distributed throughout the world including North, South, and Central America, and the Greater Antilles. *Juglans jamaicensis* is the only native walnut found in the West Indies. It is an extremely rare tree found in moist mid-elevation mountain habitats in Puerto Rico. Its regional distribution includes the neighboring islands of Hispaniola and Cuba. Its rarity in large part is due to its primary habitats being coincident with areas of human habitation and deforestation associated with montane zone agriculture and grazing. In all likelihood, this species was already rare at the turn of the last century owing to local cutting pressures and the establishment of coffee plantations.

The leaf, flower, and fruit structures of *Juglans jamaicensis* C.D.C. (Jamaican walnut)

Francis and Alemañy (1994) indicated that Jamaican walnut (locally known as *nogal*) only occurred in three forests in Puerto Rico in 1928. By 1974 it was highly restricted to one relict stand of just 14 individual trees. It is now listed as a U.S. endangered species. It is also classed as an endangered species in the Dominican Republic, but there its population is larger. Although the specific epithet (*jamaicensis*) suggests that it is from the island of Jamaica, it is now thought to be extinct there. Some question whether it ever occurred in Jamaica.

This species prefers cool, moist montane sites, on well-drained clay soils. The one existing stand in Puerto Rico is located at an elevation of 975 meters (3,200 feet). In other islands it has been associated with flood plains at lower elevations. Today it is found in secondary forests and in Puerto Rico's case, the stand is in an old coffee plantation. In the Dominican Republic it can be found in old agroecosystems.

Box 8. continued

Jamaican walnut produces small green flowers in catkins, with both male and female flowers on the same tree (monoecious). Flowering can occur from February to April. By June, ripened, round walnuts are formed, which fall in early summer. Trees can produce up to 100 large one-seeded fruits 4 to 5 centimeters (1½ inches) in diameter. Today, fruit dispersal is largely by humans. Walnuts native to the United States are frequently distributed by squirrels, but Puerto Rico has no equivalent animal, so it is likely that this species may have always had a restricted range. Seeds produced in flood plains are likely vectored by water.

Tree growth can be rapid, and medium to large trees result with maximum heights being up to 30 meters (98 feet). No trees in Puerto Rico are this large. As is the case for other walnuts, leaves are large, **odd pinnately** compound, and alternately arranged. There are 16 to 20 fine-toothed, **lanceolate** leaflets. Small buttresses develop at the root/shoot interface. Jamaican walnut is thought to be shade tolerant so it is likely to be a primary forest species should the ecosystems it inhabits have a chance to fully recover.

The wood of walnuts is generally considered of high value because it has been used extensively for the creation of some of the finest and most expensive furniture and specialty crafts. Walnut furniture is highly prized for its special dark brown color and graining. Many of these products are passed from one generation to another and are a part of the thriving antique fine furniture market. If properly cared for, these wood products can be useable for hundreds of years. The good wood qualities and high value have caused this species to disappear from much of its range. Unfortunately, *Juglans jamaicensis* populations are so small today that its wood is no longer available for commercial use throughout its West Indian range. If it could be grown in large volumes, this species would have great commercial value in today's competitive wood market. It is being propagated today in both Puerto Rico and Cuba.

This species has a variety of uses. It is valued as a nut food for humans and wildlife. Its wood is used for fine furniture, craft production, and general carpentry and interior finish wood. The juice from the fruit wall is used as a fabric dye, and bark and leaf extracts are used for home medicines.

For more information on this species, see Francis and Alemañy 1994, Little et al. 1974, and Manning 1960.

There is no more important issue than that of protecting our planet's biodiversity, that is, its genetic, species, and ecological richness. Everyone plays a role in the destruction; therefore, everyone must play a role in the conservation and protection.

For further reading, see Delgado-Mendoza et al. 1990, Meffe and Carroll 1994, and U.S. Department of the Interior 1997.

Continue

Chapter 3: Terrestrial Ecosystems

Subtropical Forest Life Zones of Puerto Rico

At the time of discovery, most of Puerto Rico's 890 000 hectares (2.2 million acres) of land was forested. By 1900, forest cover had been reduced to 189 000 hectares (467,000 acres) largely as a result of clearing for agriculture, timber harvest, and pasturage. By the late 1940s, deforestation was greater than 90 percent. In the 1950s, forest recovery began, and by 1990, forest cover had grown to 287 000 hectares (709,000 acres) (Franco et al. 1997). Forests now cover 40 percent of Puerto Rico. Older mature vegetation covers only 1 percent of the island, whereas older successional vegetation covers 10 percent. The remaining forest cover is young mixed-species stands. Today, the forests of Puerto Rico are very important because they supply the habitat for thousands of species of plants and animals. In addition, they are vital in helping to provide life support for nearly 4 million people. This is especially true for water supplies for municipalities, agriculture, and industry. They are also becoming important as recreation destinations for a growing urbanized population. The changes in forest dynamics intensively studied in Puerto Rico may be useful in gauging changes that will be experienced in many tropical islands throughout the world as the human population continues to expand. Insular systems make interesting case studies for a variety of environmental changes produced by human activities. Puerto Rico's forested ecosystems have been highly altered in the last 200 years owing to introduction of various economically important plants such as sugarcane,[1] coffee, bananas, tobacco, pineapples, and others. Considerable forest clearing also took place for pasturage and charcoal production. Today, forests and old agricultural lands are disappearing as a result of construction of highways, transmission lines, ports, refineries, mines, powerplants, industrial developments, and many other activities associated with extensive urbanization. Trends toward urbanization and industrialization are producing an opportunity in Puerto Rico to study what happens to large areas of a tropical island when released from intensive agricultural use. Successional sequences are being documented to understand natural recovery of forested ecosystems in areas massively degraded in the past.

Ewel and Whitmore (1973) published a USDA Forest Service monograph, *Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands*. Much of what follows in this section was initially described in that document. Their work was a

[1] See appendix 1 for Common and Latin names.

seminal document that pulled together our understanding of the life zones at that time. Since then, considerable new research has added insight to the structure and function of these forested zones. Much of the research has been carried out through the auspices and cooperation of the USDA Forest Service's International Institute of Tropical Forestry in Río Piedras, Puerto Rico.

We now know that the forests of Puerto Rico are extremely diverse for a landmass the size of the island. The forests range from dry forests to rain forests, lowland forests to lower montane forests, saltwater to freshwater forested wetlands, and forests on alluvial, karst, volcanic, and **ultramaphic** substrates. These forests occur in stages of succession including those influenced by human activities, those recovering from hurricanes or other natural disturbances, and those in mature stages of development. More forest variation is added by topography, rainfall, soil conditions, and aspect. Each of these categories of forest type intermix in such a way that the actual number of forest types on the island is quite large, and there is no systematic record of the full diversity of forest types. The most recent map of conditions for forest growth in Puerto Rico contains 28 geoclimatic zones. This new map is much finer in its site definition than the original descriptions at the life zone level, which depict only climate.

Puerto Rico lies at approximately 18º N latitude in what Holdridge[2] [3] classified as the subtropical latitudinal region. This system of classification is for climate-based life zones and is presented in figure 14.

Holdridge's theses are that:

- Mature, stable plant formations represent physiognomically discrete vegetation types that are easily recognized throughout the world.
- Vegetation and geographic boundaries correspond closely to climatic zones.
- Vegetation is determined largely by the interaction of temperature and rainfall.

Holdridge's life zones for the world are arranged by latitudinal region, altitudinal belt, and humidity province. Each zone is defined by mean annual precipitation and mean annual biotemperature. Biotemperature refers to all temperatures above freezing, with all temperatures below freezing adjusted to 0° C. Also important are available moisture and potential evapotranspiration. In general, rainfall ranges are associated with the following forest types:

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[2] Leslie Holdridge was the first scientist appointed at the USDA Forest Service Experiment Station in Río Piedras.

[3] Figueroa Colón, J.C. 2001. Map for the geoclimatic zones of Puerto Rico. On file with: the International Institute of Tropical Forestry, Río Piedras, Puerto Rico.

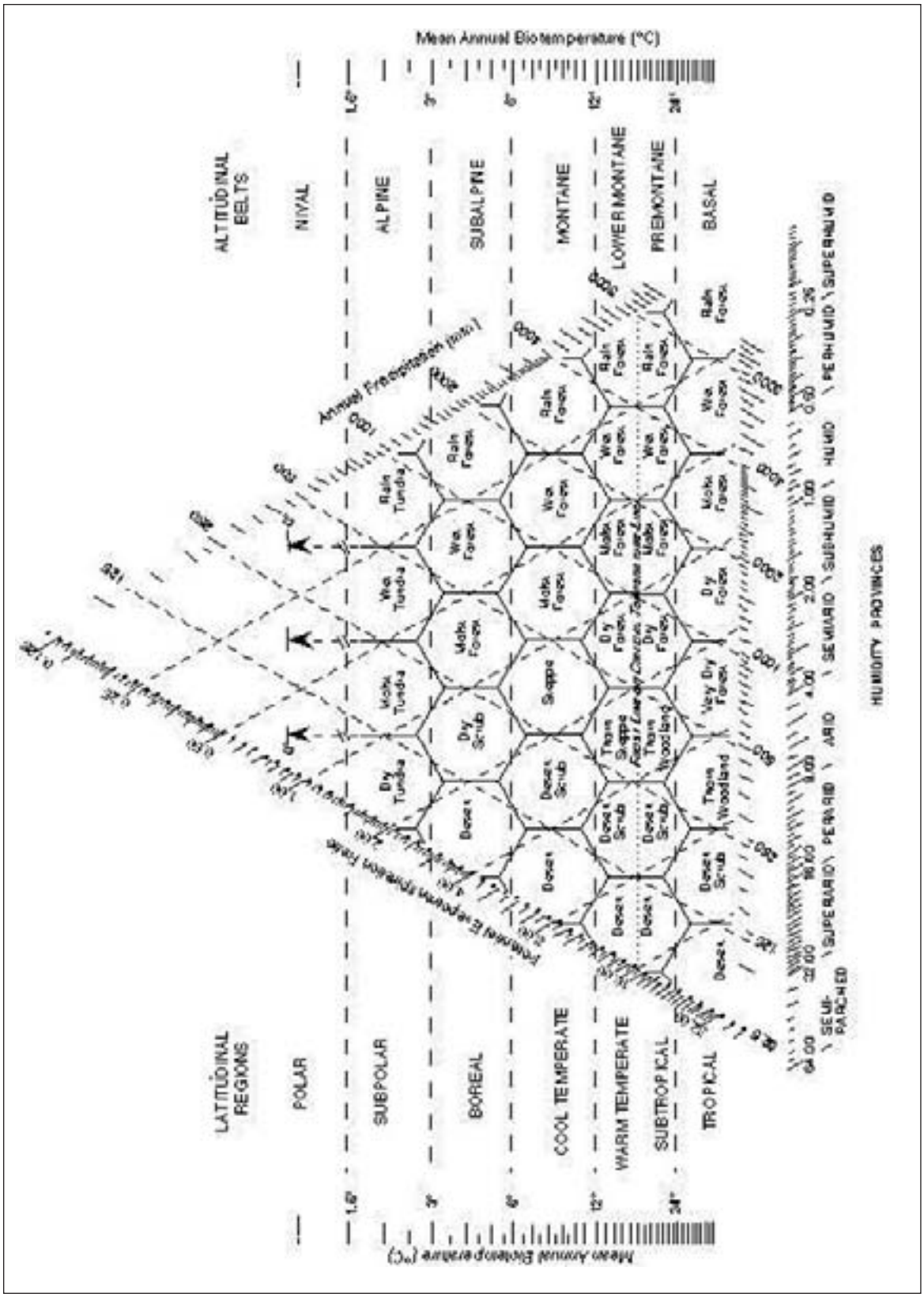


Figure 14—The Holdridge life zone system for classifying plant formations.

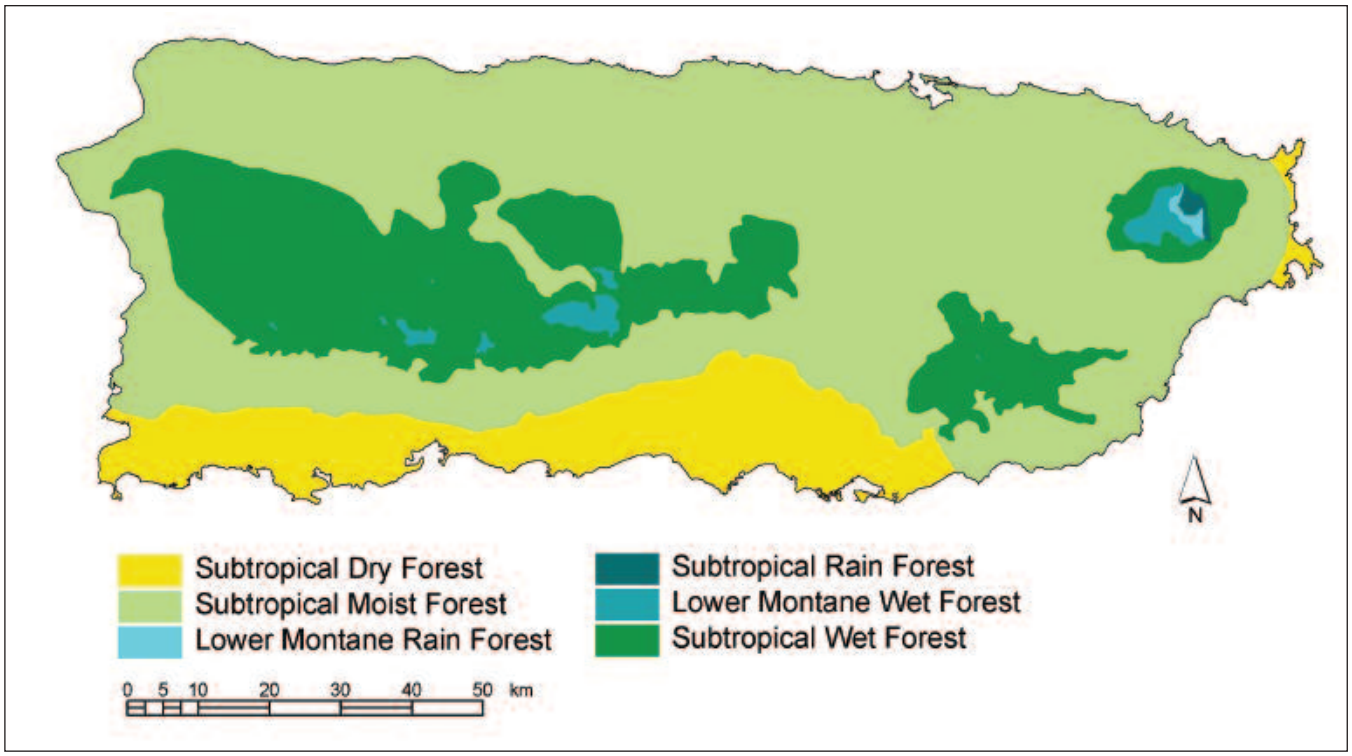


Figure 15—Ecological life zones of Puerto Rico.

- 500 to 1000 millimeters (20 to 40 inches) - dry forest
- 1000 to 2000 millimeters (40 to 80 inches) - moist forest
- 2000 to 4000 millimeters (80 to 160 inches) - wet forest
- 4000 to 8000 millimeters (160 to 320 inches) - rain forest

According to the Holdridge system, Puerto Rico has six subtropical life zones ranging from dry through moist forest zones in the basal, or sea level belt. In the wet and rain forest zones of the lower montane altitudinal belt, there are four forest zones. Figure 15 shows the major forest life zones of Puerto Rico.

The area occupied by each life zone is presented in table 14. The subtropical moist forest is the largest life zone, covering more than 59 percent of Puerto Rico, whereas the subtropical lower montane rain forest is the smallest life zone. Unfortunately, most forests of the subtropical moist forest zone have been destroyed.

The forest zones described in this section can all be seen in the 14 commonwealth forests and nature reserves located throughout Puerto Rico. See the location map and short descriptions in the “Commonwealth Forests and Nature Reserves” section that follows.

Table 14—Area (square kilometer) occupied by each life zone[a] in Puerto Rico

Island	Percentage of total area	Dry forest	Moist forest	Wet forest	Rain forest	Lower montane wet forest	Lower montane rain forest	Total area
					Square Kilometer			
Puerto Rico	97.46	1,216.4	5,326.1	2,124.8	13.2	109.1	12.3	8,801.9
Vieques	1.53	93.1	44.8	0	0	0	0	137.9
Mona	0.63	56.1	[b]0	0	0	0	0	56.1
Culebra	0.36	32.7	0	0	0	0	0	32.7
Desecheo	0.02	1.6	0	0	0	0	0	1.6
Total	100.00	1,399.9	5,370.9	2,124.8	13.2	109.1	12.3	9,030.2
Percentage of total area in life zone		15.50	59.48	23.53	0.15	1.21	0.13	100

[a] All life zones are tropical.
[b] 0 entries in the table indicate the absence of the life zone on that particular island.
Source: Modified from Ewel and Whitmore 1973.

The large diversity of ecosystem types in such a small island means that no ecosystem type covers a large area. The island is a mosaic of diverse ecosystem types. Because of Puerto Rico's high population density and intense human development activities, these ecosystems are highly fragmented. The steep topography and abundant rainfall results in a high degree of coupling between ecosystems. For example, when it rains in the mountains, rivers swell rapidly and quickly discharge nutrients and sediments on coastal ecosystems. Within hours, events in the mountains impact coastal ecosystems. This degree of connectivity, coupled with the small size of many types of ecosystems, has enormous implications for their management and conservation. Tropical ecosystems of Puerto Rico are ecologically resistant and resilient to numerous environmental disturbances, but are very vulnerable to improper human activities.

The Subtropical Dry Forest

For the last 30 years there has been a continuous debate throughout scientific, political, and economic circles regarding the devastating loss of tropical rain forests and their diverse assemblage of species. By comparison, very little concern has been expressed until recently about the loss of dry forests. One reason was because by the 1970s most of the dry forests of the world had already been severely altered. Some estimates indicate that up to 42 percent of forests in the tropics were originally dry forests. In addition, possibly 60 percent of current scrub forest and **savanna** may have been dry forests prior to human alterations. In some areas today, dry forests are only historical remnants, whereas many other areas have only 1 to 5 percent left. There are still large functional dry forests in Africa and tropical islands

where they cover 70 to 80 percent of lands that are still forested. In Central America, of the land still forested, 50 percent may be covered in dry forest, and South America has an estimated 22 percent in dry forest cover (Murphy and Lugo 1986).

Dryer conditions are generally much preferred by humans to the very wet humid parts of the tropics, and in many dry forest zones, large human populations have been supported for millennia. It is in such places that anthropologists theorize the transition to an agriculture-based human society may have taken place.

Dry forests can occur in areas with roughly an even split of 6 months wet and 6 months dry. They also occur in other wet/dry ratios of 4:2 and 5:1. This is thought to be one of the reasons why dry forest zones exhibit high species diversity, that is, there may be two groups of plants and animals adapted to the different water and vegetation regimes present. The conditions in dry forest zones are generally very different from the wet zones in the following ways:

- Lower rainfall that may be erratic
- High air and soil surface temperatures
- Low humidity
- Drying winds
- Extensive amounts of sun

The dry zone is the driest of the six life zones in Puerto Rico (fig. 15). It covers sizable areas in southwestern Puerto Rico and Vieques, plus all of Mona Island, Culebra, and Desecheo Islands. Mean annual rainfall ranges from a minimum of about 600 millimeters (24 inches) to a maximum of 1100 millimeters (43 inches).

The vegetation of this life zone tends to form a complete ground cover and is mostly semideciduous on most soils. At the tops of ridges, the forest will be more **deciduous**, and in valley bottoms, it will be mostly evergreen. Palms are usually absent from the canopy, leaves are often small and succulent or **coriaceous**, and species with thorns and spines are common. Tree heights do not usually exceed 15 meters (49 feet) and **crowns** are typically broad, spreading, and flattened, with sparse foliage. Fire is common on the better soils in many parts of the world, where the successional vegetation includes many grasses, and large amounts of organic debris accumulates on the soil surface during the dry season. Fire is not a natural factor in Puerto Rico, but is now being used in Puerto Rico as a control for alien species along the roads in the Guánica Commonwealth Forest. **Coppicing** is a common means of regeneration of many of the woody species found in this life zone. Successional forests, therefore, often consist of an almost-impenetrable maze of tangled, close-growing, small stems.

A dry forest is an excellent habitat in which to observe a variety of special adaptations of both plants and animals. Plant **adaptations** to observe are:

- Water conservation (**hairs**, spines, folded leaves, dropped leaves)
- Succulents (plants that can store water, for example, cacti)
- Cladophylls (plants that use green stems for photosynthesis)
- Ephemerals (plants that complete their life cycle rapidly)
- Deciduousness (leaf drop in the driest period[s])
- **Phreatophytes** (deep roots, may penetrate to a ground-water source)
- Vertical orientation of leaves (to avoid direct rays of the sun)
- Microphylly (small leaves)
- Heat control (spines and stem design)
- **Stomata** that open at night
- **Convergent evolution** (cacti as opposed to euphorbs, look alike but are from different parts of the world)

When compared to a wet forest, the structural traits of a dry forest will also vary where the following can be observed:

- Smaller stature (50 percent or less)
- May be floristically less complex (although dry forests can be species rich too; in fact, some dry forest zones may rival rain forests in diversity)
- Fewer layers to the forest
- Few trees common to the wet forest
- More abundant understory vegetation
- Higher percentage of the plant's total **biomass** in roots
- Annual diameter growth of stems is less than in wet forests

As indicated earlier, the dry forest life zone has historically been the preferred area for human settlement in many tropical countries. The pressure to alter these habitats has been ever increasing owing to:

- Agriculture
- Fire (**prescribed** and natural)
- Introduced species (goats, cattle, horses, pigs, and others)
- Firewood collection
- Increased human population growth and its attendant need for housing, transport corridors, businesses, use of available surface, and ground water supplies

One of the premier examples of a Neotropical subtropical dry forest ecosystem is in the Caribbean on the south coast of Puerto Rico near the town of Guánica (see app. 2). Fortunately, its unique qualities were recognized early on and it was set

aside as a commonwealth forest in 1917. It was still used locally for coppice wood harvesting, charcoal production, **grazing**, and so forth, until the early 1960s. It was also the site of an introduced West Indian mahogany plantation, which is still there and is being monitored to date. The Guánica Forest has received much better protection since the mid 1960s, and today it is a prime example of a Caribbean dry forest, with full protection by the Puerto Rican government. In 1981, the 4000-hectare (10,000-acre) forest was recognized by the United Nations for its special habitat qualities and was declared an International Biosphere Reserve. Today, there is a full-time reserve director and support staff that helps to monitor, promote research, and actively educate the citizens about the unique features typical of dry forest ecosystems. Recently, it added a marine sanctuary section under its control, as it borders the Caribbean Sea. The Guánica reserve now includes mangrove swamps, turtle grass beds, and coral reefs. This makes it one of the most unique management schemes in the Neotropics, where terrestrial and marine ecosystems are married together for management purposes, from the top of the watershed to the sea. This reserve has more than 700 plant species, 16 of which are reported to be endemic. It has more bird species than any other island forest.

Why is it so dry in the Guánica Forest when just a few miles away to the north some mountainous areas may receive more than 5000 millimeters (200 inches) of rain? The answer is relatively simple. The *Cordillera Central* Mountains that run east-west through the middle of Puerto Rico produce an orographic rain shadow. The prevailing trade winds bring moisture-laden clouds to the north side of the island and, as they rise in altitude, more rain falls on the north side of the island. As the clouds pass over to the south side, little water falls as rain, thus creating a rain shadow with the driest section of the island situated in the area near the Cabo Rojo lighthouse on the southwest coast. Figure 16 illustrates the differences in rainfall distribution in the wet versus dry zones in Puerto Rico. To visit sites at the two extremes of this gradient see app. 2.

Guánica's driest period is December to April when nearly 50 percent of the trees drop their leaves. For this reason, this forest is often called a deciduous forest. New leaves and flowers generally reappear from August to November. Temperatures fluctuate little at Guánica, with daily temperatures averaging 25 ºC (79 ºF). Guánica is in a windward area in that winds frequently come off the Caribbean Sea in this low topographic system and may create a drying effect. Dry forests in Puerto Rico extend inland up to 20 kilometers (12 miles). Water deficits may occur up to 10 months of the year. Guánica has a variety of succulent plants that exhibit special adaptations for coping in a heat/water stressed environment. Plants to look for are:

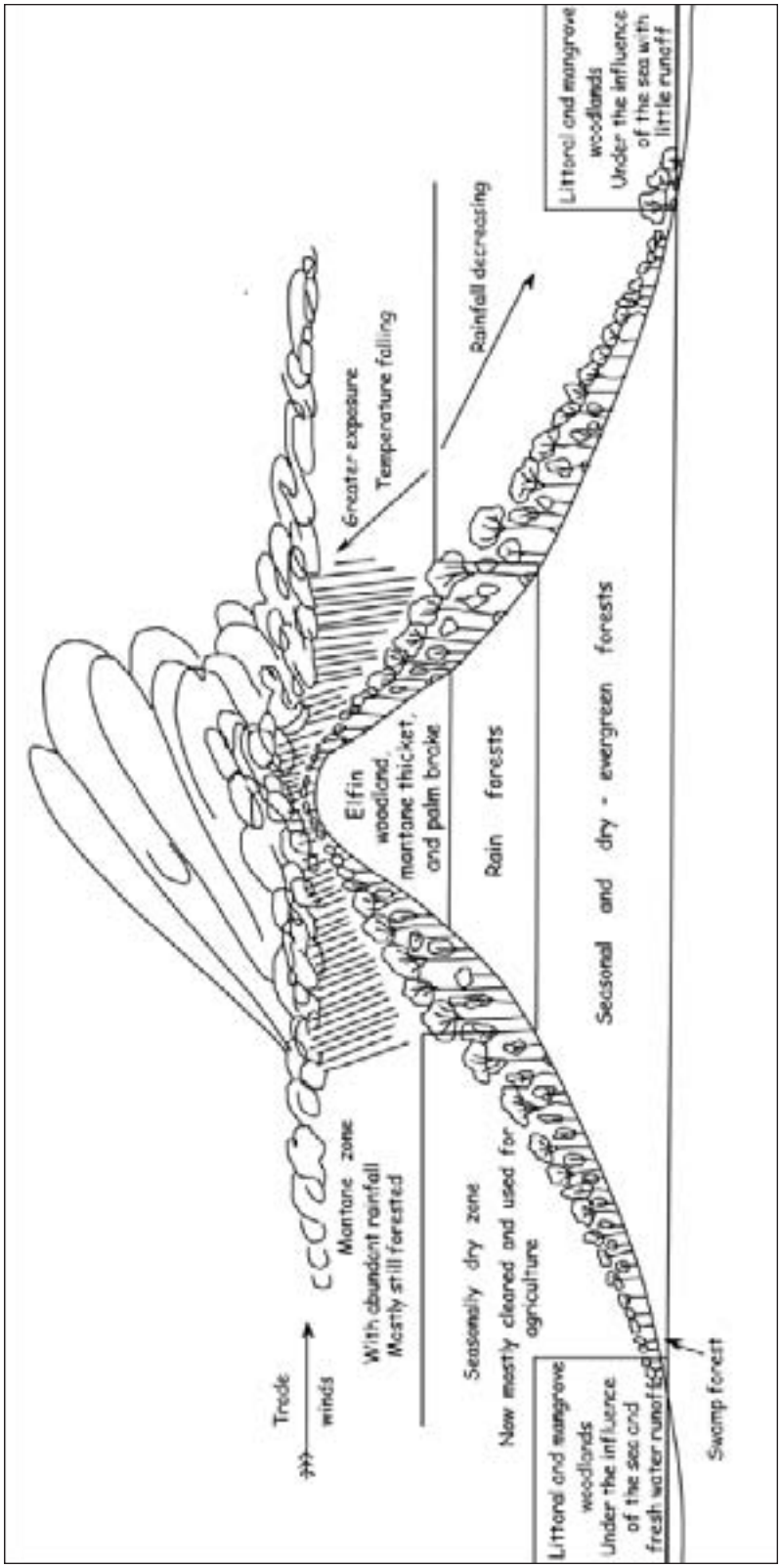


Figure 16—An idealized transect through a Caribbean island in the Lesser Antilles.

- *Opuntia dillenii* (Ker-Gawl) Haw. (prickley pear cactus)
- *Opuntia rubescens* Salm-Dyck ex. DC (tree opuntia cactus)
- *Cephalocereus royenii* (L.) Byles & Rowley (large pipe cactus)
- *Lemaireocereus hystrix* (Haw.) Britton & Rose (pipe organ cactus)
- *Melocactus intortus* (Miller) Urban (Turk's cap cactus)
- *Euphorbia lactea* Haw. (African cactus—it is really a euphorb in the family Euphorbiaceae)

The Guánica Forest is not structurally tall, but quite dense (fig. 17). There may be 12,000 tree stems per hectare. Most have relatively narrow diameters at breast height (d.b.h.). Many trees are either natural or coppice regrowth from past use for grazing, household wood collection, or charcoal pits. Species diversity of trees and shrubs in Guánica is comparable to that found in the rain forest in the Caribbean National Forest. Figure 18 illustrates species zonation in the Guánica Forest.

Some of the low alluvial areas on the south coast of Puerto Rico contain **saline** soils, such as the Santa Isabel series, and vegetation on these sites is dominated by *Prosopis juliflora* (Sw.) DC. (mesquite), an introduced tree. *Parkinsonia aculeata* L. (Jerusalem thorn) is another alien leguminous tree that often forms nearly pure stands on coastal alluvial soils.

Interesting dry forest plants to look for are:

- *Acacia farnesiana* (L.) Willd. (sweet acacia)
- *Bursera simaruba* (L.) Sarg. (Gumbo limbo) (box 9)
- *Calotropis procera* (Aiton) W.T. Aiton (African milkweed tree)
- *Comocladia dodonaea* (L.) Urban (*chicharrón* "poison ivy"—very common in Guánica forest)
- *Guaiacum officinale* L. (lignum vitae)
- *Parkinsonia aculeata* L. (Jerusalem thorn)
- *Plumeria rubra* L. (frangipani) (box 10)
- *Prosopis juliflora* (Sw.) DC. (mesquite)

There are many more bird species present in the Guánica Forest than in the montane rain forests (31 versus 20 species per 1,000 individuals). There is almost four times the bird density with 190 in Guánica versus 57 per linear kilometer (0.6 mile) in the rain forest. In discussing the greater number of insect-eating birds at Guánica, Kepler and Kepler (1970) pointed out that the wetter Luquillo Forest had well-developed lizard and frog populations, which might be performing the same function in the Luquillo Forest as insectivorous birds do in the drier Guánica Forest. In looking at the broader question of why the structurally simple dry forest

G. Miller

Figure 17—A general view of the Guánica Dry Forest in the south coast of Puerto Rico.

should have more birds, numerically and taxonomically, than the complex wetter forest, they state:

> The answer may well lie in the greater relative ability of xeric land birds from potential source areas to colonize oceanic islands, the larger number of xeric, compared to mesic, islands that could serve as stepping stones for dispersion in the Caribbean, and the proximity of the xeric forest to island coasts where potential propagules would first land.

Animals will also exhibit interesting adaptations to dry forest conditions. Consider the following:

- High percentage of nocturnals
- Many-scaled species that prevent desiccation
- Water sources from prey and vegetation
- Hibernation
- Burrowing or use of natural grottos (e.g., Puerto Rican crested toad, *Peltophryne lemur*)
- Low perspiration
- **Pallid** colors
- Ground/shrub nesters

Agriculture in the subtropical dry forest life zone is, at best, a marginal business, except under irrigation. The amounts of water that must be added to maintain crops and pastures in Puerto Rico are low, compared with irrigation demands in

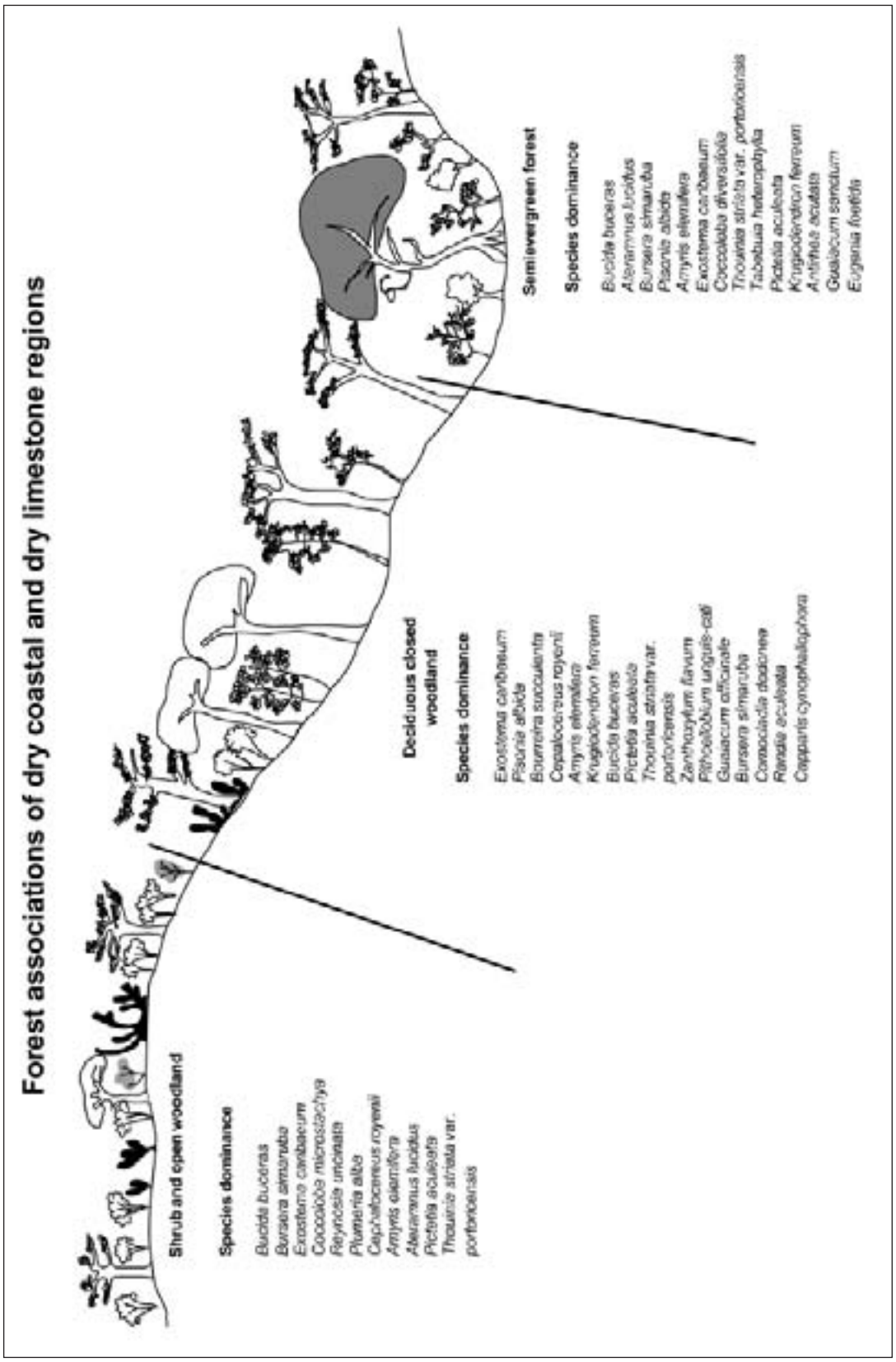


Figure 18—Zonation of species in a dry forest such as Guánica.

Box 9. *Bursera simaruba* L. Sarg. (gumbo limbo) (Locally known as *Almácigo*)

The leaf, flower, and fruit of *Brusera simaruba* (L.) sarg. (gumbo limbo)

This tree is typical of dry habitats. It has a thin copper-colored bark resembling the skin color of American aboriginals. It is somewhat unique in that under the coppery bark there is a chlorophyll-bearing layer that permits its bark to photosynthesize when it is leafless, which can be up to 6 months of the year. This chlorenchyma layer can be exposed by scraping the paper thin outer layer with your fingernail or small pocket-knife. Also notable is that it grows throughout the Caribbean Basin and Florida, and in each country or area it has a different common name. There are more than 50 local common names for this tree.

This medium-sized tree is native to Puerto Rico and the Virgin Islands and can achieve a height of 12.2 meters (40 feet) in well-drained alluvial valleys. It has a wide crown with crooked branches and thin foliage. The leaves are odd pinnately compound, with 3 to 7 ovate leaflets with oblique bases. Its slender flowers are white to yellow-green, arranged in a panicle. Most trees are male or female (dioecious), although occasionally bisexual. Flower parts are in fives, with a three-celled ovary that produces a diamond-shaped drupe-like fruit that eventually splits into three parts. Flowering and fruiting usually occurs from March to June prior to renewal of leaf growth.

The tree produces an aromatic sap with an odor like turpentine when the bark is cut. The odor is also present in the leaves and fruit. On some islands, its common name is turpentine tree. The wood is both light in color and density, without growth rings, and is susceptible to insect attack, especially by drywood termites. The wood is used for low-end products such as toothpicks, boxes, matches, charcoal, plywood, particle board, and basic construction. The resins are used in glue, varnish, incense, and folk medicines. The trees are also used as living fence posts, and are easily propagated via cuttings. It is salt spray tolerant. Because the coppery bark is attractive, it is used as a landscape plant, especially in dry zones. This tree is common throughout the dry zones

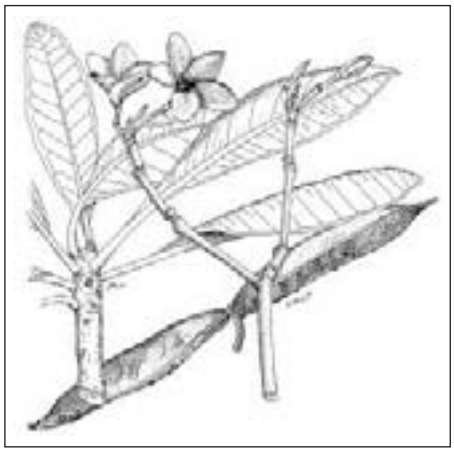
Box 9. continued

of the south coast of Puerto Rico and is readily found in the Guánica Forest. These trees exhibit pronounced trunk swell as a water storage mechanism for the dry season. They also produce a deep tap root that can absorb ground water. It does well in strong winds as it will lose its leaves, thus preventing windthrow. The largest gumbo limbo is located in Coamo and has a height of 14 meters (46 feet), a crown spread of 12 meters (39.2 feet), and a circumference of 2 meters (6.5 feet).

For more information on this species, see Francis 1990, Little and Wadsworth 1964, and Schubert 1979.

Box 10. *Plumeria rubra* L. (frangipani)

As you move across Puerto Rico you will see this small tree in many people's yards, and if you visit the Guánica Forest, you will see it in the wild. It is frequently planted because of its delicate and wonderfully scented flowers.



The leaf and flower of *Plumeria rubra* L. (frangipani)

Frangipani is a small tree, rarely taller than 7.6 meters (25 feet). Its crown is open, with a few spreading branches that have leaves clustered at their ends. Its bark is smooth and gray. In most areas it is evergreen, but in dry areas it may be deciduous. The leaves are entire, elliptic, leathery-shiny green, and densely alternate in arrangement. The bottom leaf surface is hairy. Its most distinguishing feature is its waxy flowers, which are 5 to 7 centimeters (2 to 3 inches) across, with an overlapping set of lobes. The terminal flowers produce a flat-topped **cyme** inflorescence. The stamens, petals, and sepals are in fives, with two pistils. The fruits that result are leathery brown follicles that open on one side releasing many small winged seeds. Flowering and fruiting goes on throughout the year in Puerto Rico. In dry areas, the tree may flower when there are no leaves present. Flower color is variable from red, to rose, and white to yellow in cultivated varieties. There is another white-flowered species,

Box 10. continue

P. alba L., which has lance-shaped leaves, with dense hair on the bottom surface. It is very common in the southern and western parts of Puerto Rico. Frangipani flowers do not wilt rapidly, and as a result, they are often picked for displays.

This tree's main use is as an ornamental in gardens, parks, and cemeteries. It flowers throughout the year and produces large clusters of fragrant flowers that persist. It produces only a minimum of leaf debris. It does not grow into a large tree, thus it is not likely to produce residential damage in tropical storms.

Frangipani gets its name from the French word *frangipanier*, which means coagulated milk, descriptive of the white latex that exudes from its branches or petioles when cut or damaged. It may be poisonous and is said to be used in folk medicines.

Frangipani grows easily from cuttings and can do well in very dry, to drained moist conditions. It is salt tolerant and can be found near beaches. It has been distributed throughout the tropical world, but was originally derived from Jamaica in the West Indies. Its life expectancy is about 30 years.

For more information on this species, see Little and Wadsworth 1964 and Schubert 1979.

many drier parts of the world. However, the better soils in this life zone are already under cultivation. Potential evapotranspiration is greater than rainfall in the subtropical dry forest life zone, so the repeated use of irrigation water can sometimes result in salt accumulation in the upper soil horizons. In the Lajas Valley of southwest Puerto Rico, for example, use of ground water for irrigation resulted in the loss of agricultural productivity on some soils, until the mid 1950s when water from another area was made available for irrigation.

Goats are pastured on the poorer soils, but to a much lesser extent than in years past. Charcoal production, a common land use process in many tropical environments, was once common in this life zone in Puerto Rico, but this practice is now almost extinct in Puerto Rico. The Guánica Forest, which has been protected from charcoal wood **cutting**, goat grazing, and subsistence farming for more than 50 years, is perhaps the best example anywhere in the world of natural vegetation in a subtropical dry forest. Commercial forestry has little prospect in this life zone, except in the limited production of exceedingly durable fenceposts and a few high-quality specialty woods such as *Swietenia mahagoni* (L.) Jacq. (West Indies mahogany) (fig. 19).

G. Miller

Figure 19—West Indian mahogany plantation in Puerto Rico.

Mangrove ecosystems may be present along the coast in dry forest zones. For further information, see the mangrove ecosystem section later in this document.

The Subtropical Moist Forest

This life zone in Puerto Rico covers more area than any of the other five life zones. It accounts for almost 5500 square kilometers (3,418 square miles), or 59 percent of the total. It is delineated by a mean annual rainfall of 1000 to 1100 millimeters (39 to 43 inches), that ranges to about 2000 to 2200 millimeters (78 to 86 inches) and a mean biotemperature between about 18 and 24 ºC (64 to 75 ºF).

Most of the subtropical moist forest zone in Puerto Rico has been deforested at one time or another owing to numerous human activities, but primarily because the climatic conditions defining its boundaries also make good conditions for growing a wide variety of crops. With the exception of the regions of serpentine- and limestone-derived soils, most of the land in this life zone remains in some form of nonforest use. A sizeable tract of cutover forest in the subtropical moist forest is in

the Caribbean National Forest (Luquillo Experimental Forest). This and other scattered remnants of this zonal association are characterized by trees up to 20 meters (66 feet) tall, with **rounded** crowns, like those of the mango tree. Many of the woody species are deciduous during the dry season, and epiphytes are common but seldom completely cover branches and trunks. Grass-covered pastures form one of the dominant landscape uses in the subtropical moist forest zone in Puerto Rico today. Figure 20 illustrates the many forest types and land covers present in Puerto Rico today (Helmer et al. 2002).

Karst—

The moist karst limestone hill region of northern Puerto Rico produces an interesting association in the subtropical moist forest zone. Puerto Rico's karst region was formed late in its geological history. After the mountains had formed, there was a secondary island sinking. The adjacent shallow seas, with abundant sea life associated with coral reef formation in the **Oligocene** and **Miocene** periods, formed the present coastal plain area from the Loíza area west to Mayagüez.

Numerous areas of the world exhibit karst topography. Puerto Rico has an extensive karst belt on the north coast extending from Loíza (east of San Juan) to the northwest coast (see app. 2). It extends south into the foothills of the Cordillera Central Mountains for 25 kilometers (15 miles). Karst is also present on the south coast, but more fragmented than and not as extensive as on the north coast. Karst covers more than 27 percent of the island (Lugo et al. 2001). Karst regions are characterized by the presence of rocky ground, caves, sinkholes, and underground rivers. Puerto Rico has an incredible network of rivers, streams, and creeks (fig. 21). Only in the karst region are surface rivers absent. There, the drainage is through underground rivers and aquifers that yield over 100 million gallons of freshwater to the ocean each day. One of the largest underground sections of river in the world is the *Río Encantado* found in the karst region of Puerto Rico. The river runs 16 kilometers (9.6 miles) underground. Rivers in Puerto Rico appear small to the casual observer. However, after heavy rains, all recipient rivers swell to enormous proportions and flood most of the coastal zone of the island. Instantaneous discharges of thousands of cubic feet or cubic meters per second are common during hurricane-induced floods. Floods can be instantaneous given the island's steep topography and the steep gradients of rivers. In 1998 during Hurricane Georges, the Río Camuy River, which runs underground through the Río Camuy Park, rose 45.7 meters (150 feet) and flooded the major room of the Río Camuy Caves. It was the greatest increase ever recorded for a river in Puerto Rico. The previous record increase inside the cave was 24.4 meters (80 feet).

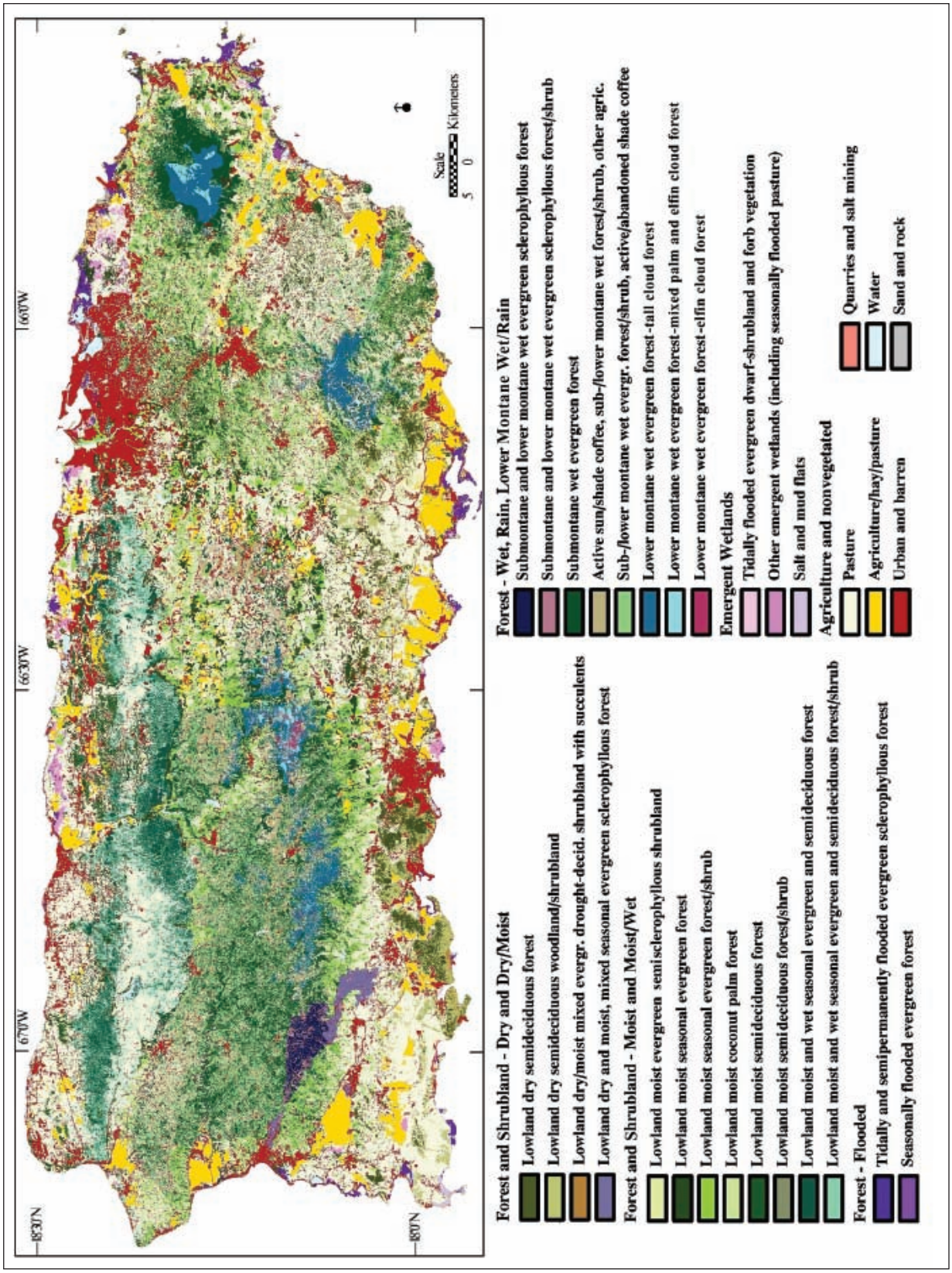


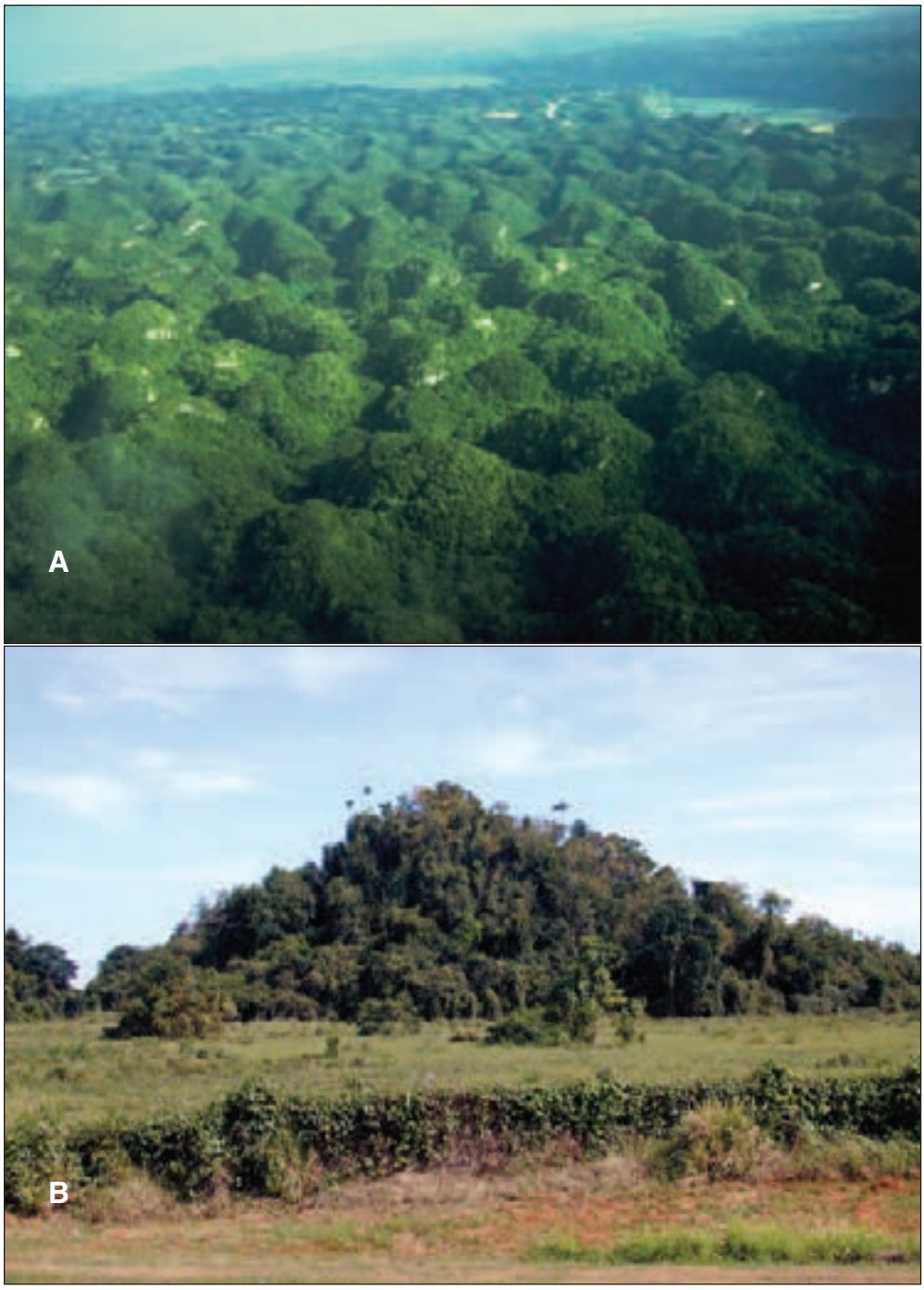
Figure 20—Forest sites and land uses of Puerto Rico.

Figure 21—The rivers of Puerto Rico. Each small line of this map represents a river.

In many karst areas, haystack-shaped hills are present (fig. 22). The landscape is often called egg-carton topography. This unusual landform results from the effect of water running over and through massive deposits of soluble limestone or calcium carbonate ($CaCO_3$). For karst to develop, there must be a soluble base rock near the surface. There also has to be a humid climate for maximum development, with moderate to heavy rainfall to produce the ground water circulation and the dissolution of the $CaCO_3$. The naturally acid rain then percolates through the calcium carbonate via cracks and carries it away in solution. As the cracks enlarge over long periods, they can become small single caves, cave systems, or underground stream systems. Most of the cave areas of the world are in karst regions. Puerto Rico has thousands of caves. Often the roof of one or more caves will subside and this can produce natural bridges or, more likely, sinkholes. Puerto Rico's karst region is an area of rolling rough surface with numerous haystack hills, sinkholes, and caves of various sizes. Some haystack hills are well over 100 meters (328 feet) high, whereas sinkholes may be hundreds of meters (hundreds of feet) deep and broad. As will be mentioned later, the Arecibo Ionospheric Observatory is built over a giant sinkhole (see app. 2). Some of the streams that originated on the surface periodically disappear, only to resurface kilometers (miles) later as they make their way to the coast.

The haystack hill region is one of the best displays of this formation in the world. Haystacks, called mogotes in Puerto Rico, are not pure limestone. Mogotes have sands and clays eroded from the Cordillera Central range mixed in. Much of the $CaCO_3$ was dissolved and ran off in the rainwater leaving the clays and sands behind. There is a difference in the degree of slope on the haystacks, with the western sides being steeper and the east and north sides more gently sloping. Why the difference? The reason is that the east sides are warmer and dryer, whereas the west and north sides are cooler and moister. This produces more solution and movement on the west sides. The haystack hills have an external limestone cover that results from a dissolution → evaporation → precipitation cycle much like what goes on in the formation of stalactites. This $CaCO_3$ precipitate is much harder than the original limestone and thus the mogotes keep their shape. The limestone precipitate may be up to 3.5 meters (12 feet) thick. This same process is involved in the formation of large deposits of beach rock at the ocean's edge.

Haystack hills are also ecologically interesting. They are excellent examples of the changes in microhabitat conditions that take place as you move up in altitude and soil and moisture conditions are altered. In the wetter part of the year they are dark green, whereas in the dry season they appear gray-green and deciduous. Many



L. Miranda Castro

Figure 22—Aerial (a) and ground (b) views of limestone hills on the north coast near Arecibo, Puerto Rico.

L. Miranda Castro

Figure 23—Dry woodlands on the tops of mogotes and mesophytic forest at the base.

of the mogotes are 91 to 122 meters (300 to 400 feet) tall and exhibit quite distinctive zonation of physical conditions, **morphological** variation, and species composition as you move from top to bottom. For example, the tops of the haystack hills are considerably dryer than the middle and lower sections, so much so that the top may be covered by deciduous vegetation, the middle by semievergreen, and the base by evergreen vegetation (fig. 23). Keep in mind that the rainfall is not any different (average 192 centimeters [77 inches] per year). Species composition, physical structure, morphology and density all change from top to bottom. Canopy height of trees typically ranges from 4.5 to 7.6 meters (15 to 25 feet) at the ridgetop, whereas in the middle slope it ranges from 12 to 18 meters (40 to 60 feet), and in the valley at the base of the hill 15 to 27 meters (50 to 90 feet). The d.b.h. will vary from 10 cm (4 inches) on top, to 15 cm (6 inches) in mid elevations, to 25 cm (10 inches) at the base of the haystack. Leaf morphology will also vary according to location.

As can be seen in table 15, all physical and vegetation features vary from top to bottom of a haystack hill. At the ridgetop it is more exposed with little soil, but with a good **duff** layer. It is rocky and there is less soil moisture. Vegetation is smaller in height and diameter, and plants express morphological features typical

Table 15—Haystack hill zonation and plant features

Physical or vegetation features	Ridge 69 to 122 meters (225 to 400 feet)	Slope 30 to 69 meters (100 to 225 feet)	Valley < 30 meters (< 100 feet)
Soil conditions	Dry litter in rocky crevices	Litter layer	Good soil profile and moisture
Available moisture	Low	Mid	High
Canopy height	4.6 to 7.6 meters (15 to 25 feet)	12 to 18 meters (40 to 60 feet)	15 to 27 meters (50 to 90 feet)
Tree diameter at breast height	10 centimeters (4 inches)	15 centimeters (6 inches)	25 centimeters (10 inches)
Leaf size	7.6 centimeters (3 inches and smaller)	15 centimeters (6 inches)	> 15 centimeters (> 6 inches)
Leaf characteristics	Small, sclerophyllous, often spiny, thick	Leathery, mesophyllous, moderately thick	Larger, leathery, membranous and thinner
Leaf apex shape	Rounded-obtuse	Acute-obtuse	Acute-acuminate
Shrub height	1 meter (3 feet)	1.8 meters (6 feet)	2.74 meters (9 feet)
Shrub species	Moderate	High	Lower
Vine species	High	Low	Moderate
Vine size	Small twiners	Mixed	Larger
Plant density (800 m^2 plot)			
Trees	200	180	86
Shrubs	354	460	256
Lianas	126	42	96
Herb presence	Few	Very low	High
Epiphyte presence	High	Few	Very low

of warmer and dryer conditions. These include smaller leaves, which are **sclerophyllous**, many that are spiny or with dense **pubescence**. The tree vegetation at the base of the mogote is much taller, with larger d.b.h., larger leaves, not sclerophyllic, and less thick. Most do not express the dense pubescence or presence of spines. Soils at the hill's base are deep and moist; in fact, in valley depressions it may be peaty, with ferns and mosses.

Haystack hills on an area basis are very species diverse. According to Lugo et al. (2001), the karst region harbors more than 1,300 species of plants and animals, including 30 federally listed threatened and endangered species. More than 75 species of Neotropical migratory birds use karst for wintering habitats. Reports indicate that large hills may have 500 to 800 species, whereas small hills could have 200 to 500 species. Large hills can have up to 200 tree species present, whereas small hills may have 50. Each haystack hill differs in species composition, but in general the structure is similar. In general, the larger/higher the hill, the higher the

species presence. Many species exhibit an altitude/**edaphic** preference and cluster out in each zone (fig. 24).

Puerto Rico has two common plant species that produce skin irritations similar to that caused by poison ivy, a plant species commonly found in the United States. Both species are present on haystack hills. *Comocladia glabra* (J.A. Shultes) Spreng. prefers moist habitats and can be found in the lower elevation of a hill or nearby sinkholes. *Comocladia dodonaea* (L.) Urban prefers dry areas and will be found in the upper elevation of a haystack hill. Both species are shrubs but can become tree-like. They produce **pinnately compound** leaves that have spiny margins. The **leaflets** of *Comocladia glabra* (Shultes) Spreng. (*carrasco*) are larger than those of *C. dodonaea* (L.) Urban. *Comocladia glabra* is more common in the moist karst area and other moist forest areas, whereas *C. dodonaea* is more common in the dry areas of the south coast. Detailed descriptions of each species were presented earlier.

Some haystack hills have the very tall and thin endemic palm *Gaussia attenuata* (O.F. Cook) Beccari (youmy palm). They stand out visually because of their height. Animals typical of these areas include birds, lizards, frogs, snails, scorpions, whip scorpions, and millipedes. There are 74 native fish and 25 fish species introduced to the waters of the north karst region. Nineteen caves have been investigated for their invertebrate faunas, and 151 species have been identified, many of which are endemic.

Serpentine—

Serpentine-derived soil (Nipe and Rosario series) is a second edaphic condition that results in an interesting plant association in the subtropical moist forest zone in southwestern Puerto Rico (a good example can be seen in the Susúa Commonwealth Forest). This soil supports unique vegetation, which contains a number of endemics, but does not support any significant agriculture or commercial forestry. The trees are slender, open-crowned, and usually less than 12 meters (39 feet) tall. The forest floor is open, for the excessively drained soil supports little herbaceous growth. Most of the species are sclerophyllous, and the vegetation is almost completely evergreen. Tschirley et al. (1970) found 105 species of woody plants larger than 2.5 centimeters (1 inch) d.b.h. on 0.9 hectare (2.2 acres) in this association, compared to the 85 species on 1.4 hectares (3.5 acres) in the wetter, more luxuriant Luquillo Forest. It is also an area rich in orchids. This surprising richness of woody flora on the serpentine soils contradicts most current ecological literature.

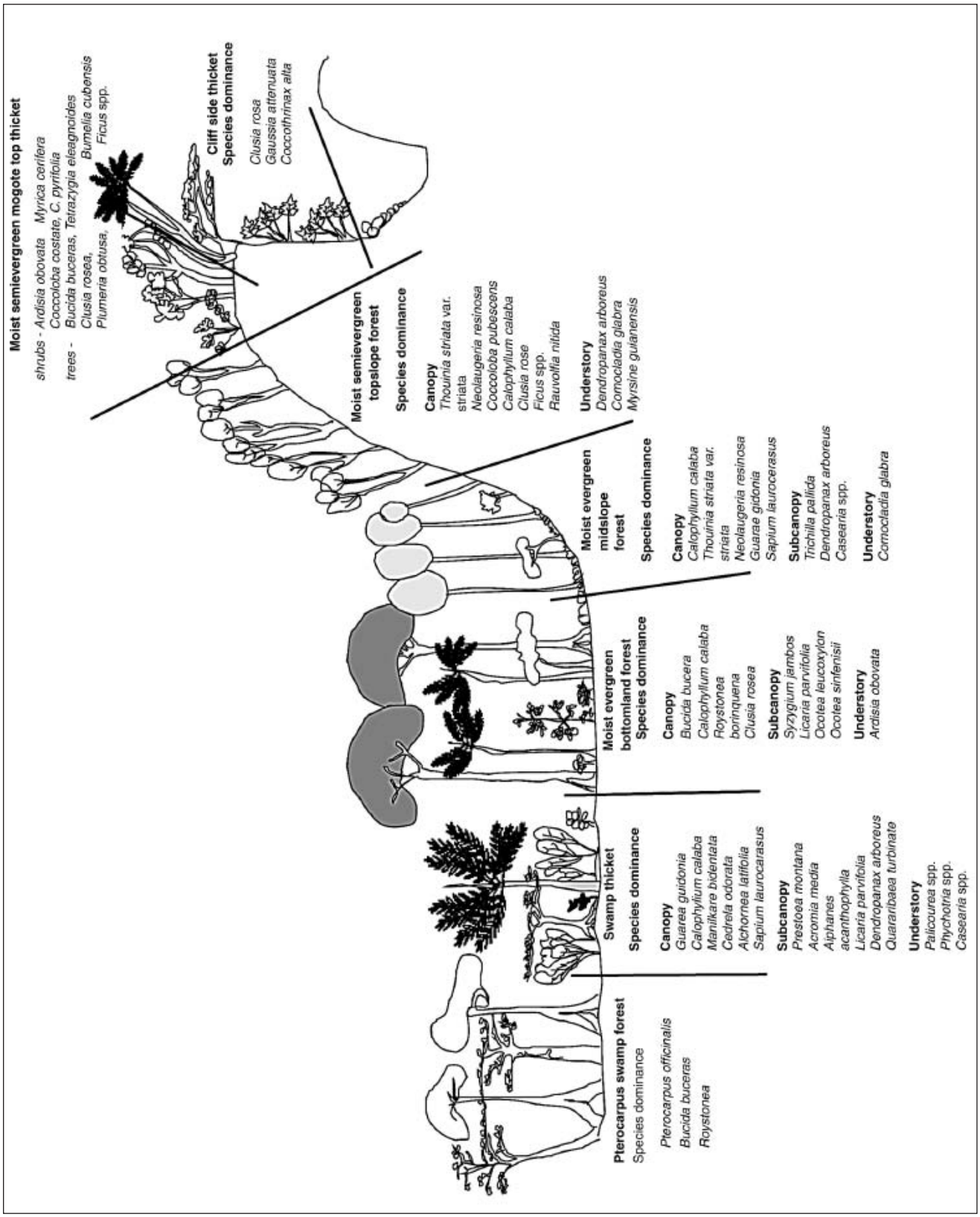


Figure 24—A profile view of a moist coastal and limestone forest.

L. Miranda Castro

Figure 25—Mangrove forest in Puerto Rico.

Mangroves—

Mangroves are found along the coast in the subtropical moist forest life zone where they appear to grow taller than in the subtropical dry forest life zone (fig. 25). Just inland from the mangrove forests are alluvial soils where the ground water may be slightly **brackish**. Most of these soils were cleared long ago for agriculture, but they probably supported impressive forests at one time. Gleason and Cook (1926) described a stand of *Pterocarpus officinalis* Jacq. (swamp bloodwood), with their impressive ribbon **buttresses**. Remnants of this alluvial swamp forest in the subtropical moist forest life zone remain near Dorado, on the north coast of Puerto Rico, and at La Boquilla, north of Mayagüez. *Pterocarpus* is reviewed in the wetlands section.

Throughout the tropical world, the subtropical moist forest life zones are among the most intensively used by humans. Pasture seems to be the predominant land use in this zone in Puerto Rico today, but sugarcane, which requires little or no irrigation, occupied a large part of this zone in the past. Some coffee is still grown, and pineapples are planted in drier portions of the subtropical moist forest life zone along Puerto Rico's north-central and northwest coast. Tobacco is also grown extensively in certain areas, notably in the Comerío-Cidra-Barranquitas region.

The subtropical moist forest life zone, with its intermediate moisture conditions—neither excessive rainfall, nor high irrigation requirements—is the life zone

G. Miller

Figure 26—Agriculture in the mountains of Puerto Rico.

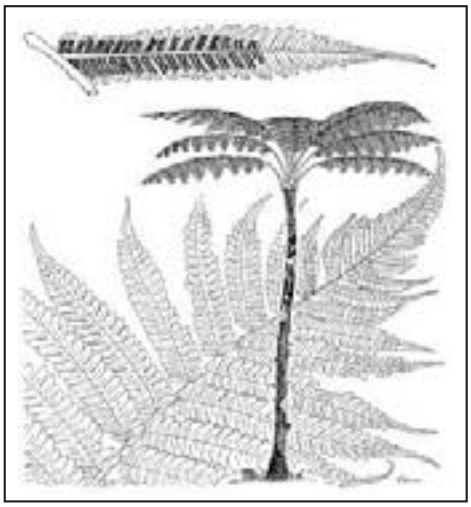
in Puerto Rico best adapted for a wide variety of land use systems, many of which offer potentially high yields (fig. 26). Intensive food production on the flats, forage production on the moderate slopes, and managed tree crops on the steep slopes are all possible here. A later section on agroecosystems describes this process and some of the economically important species typical of this zone.

The Subtropical Wet Forest

Wet and rain forests exhibit a variety of distinguishing features observed in the mountain communities of Puerto Rico, including:

- High species diversity
- Presence of tall broadleaf evergreen hardwood trees
- Stratification of forest species into layers such as canopy, subcanopy, shrubs, herbs, and ground cover
- Many lianas
- Diverse epiphyte groups
- Buttressed trunks
- Presence of **stranglers** such as *Ficus* spp. (figs) and *Clusia rosea* Jacq. (postcard tree)
- Many plants that exhibit drip-tip leaves
- Cauliflory and **ramiflory** (flowering from main trunks and woody branches)

Box 11. *Cyathea arborea* (L.) J.E. Smith (tree fern)



Cythea arborea (L.) Sm. (tree fern) stems, fronds, and sporangia

In the moist tropics, ferns achieve their greatest size, with some growing more than 18 meters (60 feet) tall. The fronds (leaves) of these trees may grow 3.65 meters (12 feet) long and exhibit a beautiful design. The fronds come out of the top of the trunk in a spray-like arrangement. It is said that God created ferns just to exhibit how creative He could be in designing leaves.

The trunks are not at all like those of true trees. They are not the result of accumulated wood over years of secondary growth. Instead they are composed of an upright rhizome (stem) surrounded by adventitious root bundles kept together by an outer layer of scales. The center is pith, with a ring of vascular bundles for conduction and support.

Tree ferns can be recognized by the characteristics they have in common with other ferns: lace-like fronds (leaves) divided into pinnae; crozier formation (that is, young leaves prior to expanding look like a fiddle head); fronds that unroll from a coil; lack of flowers, fruits, and seeds; presence of sporangia and spores on bottom surface of fronds. The main difference is that these ferns are tree-like in size. Puerto Rico has five evergreen tree fern species, with *Cyathea arborea* the most common and visually prominent.

At any given time, an adult tree fern will have 8 to 12 mature fronds, with another couple in the process of emerging. When they die and drop off, they leave a large leaf scar on the trunk. The trunk is rough and may be covered with epiphytes. They seem to do best in well-lighted areas and often succeed in areas following landslides and road construction. *Cyathea* is common to most of the montane wet forest zones in Puerto Rico.

Tree ferns can be seen throughout much of the Luquillo and *Cordillera Central* Mountain ranges. If you drive Route 191 to *El Yunque*, you see tree ferns as soon as you pass into the El Yunque National Forest. If you drive north to south on any road through the *Cordillera Central*, they will be prominently displayed along the road. Many people in the middle elevations of the mountains plant them near their homes because of their beauty.

Box 11. continued

The trunks are termite and rot resistant and are ground up and used commercially by the florist industry for planters and potting medium. They burn at low rates and historically were used for moving fire from place to place. If transplanted, they can grow on the hot and dry south coast where they are used as an ornamental. Unfortunately, many of the tree ferns seen out of the forest were probably stolen from a roadside somewhere in the mountains. Most illegally removed tree ferns probably die owing to transplant shock.

For more information on this species, see Little and Wadsworth 1964 and Proctor 1989.

The subtropical wet forest occupies much of the higher parts of Puerto Rico's mountains. This is a high rainfall life zone, encompassing areas with mean annual precipitation within the approximate range of 2000 to 4000 millimeters (78 to 156 inches) per year. At most, soil moisture drops below **field capacity** in this zone for only 3 months, and water deficit is very small. Significant amounts of runoff occur in this zone during at least 7 months and, in some cases, all year. The annual runoff in this life zone is greater than rainfall input in most areas of the subtropical dry forest life zone.

The abundant moisture of this life zone is evident in the character of the vegetation. Epiphytic ferns, bromeliads, and orchids are common; the forests are relatively rich in species; and the growth rates of successional trees are rapid. A mat-forming fern, *Gleichenia bifida* (Willd.) Spreng. and the common tree-fern, *Cyathea arborea* (L.) Sm. (box 11), form a common roadside plant cover (fig. 27). Mature forest remnants in this life zone exist in the Carite and Toro Negro Commonwealth Forests and in the Luquillo Experimental Forest. The zonal association of the subtropical wet forest in Puerto Rico corresponds to what is locally referred to as the tabonuco type, named for the dominant tree, *Dacryodes excelsa* Vahl (box 12). Two other very prominent species are *Sloanea berteriana* Choisy (motillo) and *Manilkara bidentata* (A. DC.) Chev. (ausubo or bulletwood). This is an impressive forest, containing more than 150 species of trees, and forming a dark, complete canopy at about 20 meters (66 feet). After disturbances, the trumpet tree, *Cecropia schreberiana* Miq. invades disturbed areas and rapidly closes the canopy (box 13). A massive volume edited by Odum and Pigeon (1970), and continuing research by the University of Puerto Rico and the International Institute of Tropical Forestry, makes this one of the most intensively studied forest types in

G. Miller

Figure 27—Species of *Gleichenia* (mat fern) [left] and *Cyathea* (tree fern) [right] along roadsides in the El Yunque National Forest.

the world. According to Brown et al. (1983), the tabonuco forest is found in the 15- to 550-meter (500- to 1,800-feet) altitude zone and occupies approximately 70 percent of the Luquillo Mountains (fig. 28).

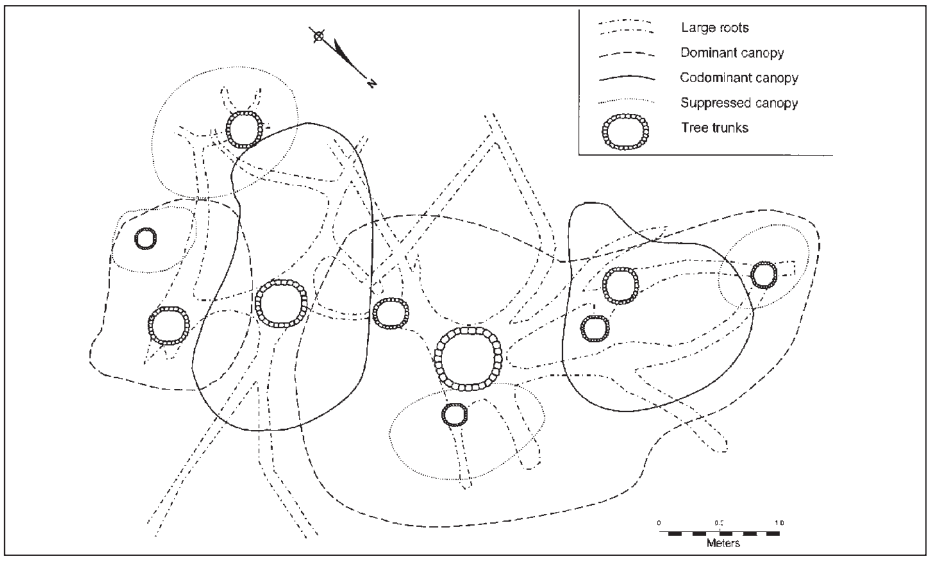
Serpentine areas, previously described for the subtropical moist forest life zone, are also found in the subtropical wet forest life zone. The vegetation on serpentine is similar in the two life zones, except that it is greener, denser, more lush, and most strikingly, contains more epiphytes in the subtropical wet forest life zone. The species are almost all evergreen and sclerophyllous, giving the impression of an anomalous wet desert or dry rain forest. Excellent examples of this association are available in the Maricao Commonwealth Forest in southwest Puerto Rico east of Mayagüez along Route 120 (fig. 29).

Much of the subtropical wet forest life zone in Puerto Rico is covered by successional vegetation as a result of emigration to cities of much of the former rural

Continued on page 112.

Box 12. *Dacryodes excelsa* Vahl (tabonuco)

As you move through the lower and middle sections of the Luquillo Mountains and similar areas in the *Cordillera Central*, you will encounter one of the native "dominants" of the subtropical wet forest zone. It is locally called tabonuco. Some locals also call it candlewood because its resins were used for candle and torch production. The tree is one of the largest in the forest and can reach heights of 35 meters (115 feet), diameters of 1.5 meters (5 feet) or more, and may live for hundreds of years.



Map of *Dacroydes excelsa* Vahl (tabonuco) tree union in the Bisley watersheds, Luquillo Experimental Forest.

It has a tall straight trunk (bole) and may exhibit buttressing. The bark is dark gray and frequently will show patches of accumulated white resin. If you encounter it on a trail, be sure to pinch off a piece of the resin and smell it. It has a distinctive odor like turpentine and, when burned, the resin acts as an insect repellent. The leaves are pinnately compound, with five to seven leaflets. It is referred to as a dominant because in the 200- to 850-meter (700- to 2,800-foot) zone, it is one of the trees with high basal area. It also has high commercial wood value.

It grows best on deep acidic clay-based soils that drain well. They frequently occur in groups on ridges where the trees are connected by their roots and form tree unions (p. 131, figure). Their habitat is usually on the top of ridges where they can secure themselves on large rocks. The formation of tree unions and the wrapping of roots around rocks allow tabonuco trees to resist hurricane

Box 12. continued

Dacroydes excelsa Vahl. (tabonuco) leaves, flowers, and fruit

winds. Tabonuco is a tree that produces distinctly male and female trees, a condition called dioecism (two separate houses). The flowers are small and green and result in a grape-sized, one-seeded fruit being formed. Flowering occurs from May through November, with the drupe fruit development occurring in the October to December period. The fruits are used by the endangered Puerto Rican parrot. After dispersal, the seeds germinate within a few weeks on the steep slopes of the mountains under the low light of the canopy. Most will not survive, but those that do may emerge from the seedling or transgressive state when a gap in the canopy occurs. The seedlings are quite tolerant to shade. The largest tabonuco in Puerto Rico is located in Luquillo. It is 38.4 meters (126 feet) tall, 14 meters (46 feet) in crown cover, and 4.2 meters (13.8 feet) in circumference.

This native hardwood species is excellent for furniture and cabinet production. It shows good working characteristics such as ease of planing, sawing, turning, and sanding. It finishes well and is sometimes used as a mahogany substitute because the wood has a reddish color.

Tabonuco was not significantly damaged in Hurricane Hugo. If you take the "Big Tree Trail" in the Luquillo Mountain Recreation Area, you will see many mature trees that resisted being blown over or snapped. More commonly, their crowns were blown away. The survivors are now well on their way to reforming their crowns, but there are still gaps and obvious evidence of serious crown loss in all of the tabonucos in that area of the forest. You will also be able to see the other trees profiled in this section along the trail or near the parking area. The "Big Tree Trail" can be accessed off Route 191 just below the main recreation area parking lot. Parking is available at the trail head. There are educational signs along the trail describing the forest and its inhabitants. At the bottom of the trail is located the beautiful La Mina waterfall. Plan on an hour or more for your round trip. Wear comfortable footwear.

For more information on this species, see Little and Wadsworth 1964, Lugo and Wadsworth 1990, and Walker 1991.

Box 13. *Cecropia schreberiana* Miq. (trumpet tree)

Cecropia schreberiana Miq. (trumpet tree) leaves, flower, and fruit

The American tropics has a group of trees very important in forest succession. When small gaps occur as a result of individual tree death or large gaps from landslides, hurricanes, or on the fringe of agricultural deforestation, one of the first trees to invade these sites is *Cecropia*. It is a very important Neotropical successional genus that has nearly 100 species. In Puerto Rico, the common species is *C. schreberiana* (or *peltata*).

Cecropia schreberiana is a common tree in Puerto Rico because much of the island is successionally responding to disturbance. It grows best in sunny openings provided they do not exceed a certain high temperature. Because of this, it will not invade pastures, certain landslides, or very large gaps. It produces shade and protects the soil. It is one of the fastest growing trees reaching heights of 4.6 meters (15 feet) in a couple of years. One of its interesting botanical features is that it has a hollow stem and trunk system when young. It can be cut down with a pocket knife. The branches remain hollow, but the trunk solidifies as it ages. Although *Cecropia* can achieve great size, its wood value is low because its early maturity and short life of 20 to 30 years, make it soft, weak, and brittle. It can be used for paper, model toy production, fishing floats, and for musical instruments (thus the name trumpet tree). The largest *C. schreberiana* is found in Adjuntas and is 27 meters (90 feet) tall, with a crown spread of 18 meters (59 feet).

The leaves and petioles are quite large, with widths of 0.3 to 0.76 meter (1 to 2.5 feet). Visitors to the rain forest often refer to them as “umbrella trees” because when caught in a rain shower they use *Cecropia* leaves as makeshift umbrellas. The leaf blades are simple with 7 to 11 lobes, with the same number of large veins arranged palmately. The leaf’s color is very prominent from a distance. The top (dorsal) is green, but the bottom (ventral) surface is white. The white color is due to dense white pubescence (hair). As the wind blows

Box 13. continued

these large leaves over, they switch position and whole hillsides may look like a field of lights as the white undersides show up. In the field you can use their presence to signify a successional site.

Cecropia produces large terminal buds. Individual trees are either male or female (dioecious). The female inflorescence results in large numbers of one-seeded fruits frequently eaten by frugivorous bats and birds, including the endemic Puerto Rican parrot. Flowering and fruiting goes on throughout the year, and the animal vectors continually add them to the forest seedbank.

For more information on *C. schreberiana* see Brokaw 1998, Little and Wadsworth 1964, Silander 1979, and Silander and Lugo 1990.

G. Miller

Figure 28—View of a canopy of the subtropical wet forest.

population. People left the land owing in part to the inappropriateness of most of the subtropical wet forest life zone for agriculture. On these abandoned lands, *Piper aduncum* L. (pepper or *higuillo*) often forms nearly pure stands.

During the 1800s, large tracts of forest were modified to plant coffee, which was heavily exported to the United States and Europe where it was considered a superior product. Much of this life zone, particularly in the western portion of the island, is still covered by coffee plantations, but to a lesser extent than formerly.

G. Miller

Figure 29—Vegetation cover, including an Agave, in the Maricao Forest in the mountains of western Puerto Rico.

A coffee plantation, consisting of an overstory of trees, a middle layer of coffee bushes, and a ground cover, is an agricultural ecosystem physiognomically resembling the forest it replaces. Shade-grown coffee has historically been a stable and successful land use in many wet, mountainous tropical areas. (See the discussion on coffee presented in the "Agroecosystems" section that follows.) Some sugarcane was also grown in this life zone, as no irrigation water was required. The dominant trend in land use, however, as in other areas of Puerto Rico, is grazing. Pasture management in the subtropical wet forest life zone can be difficult owing to both the vigorous growth of weedy herbs and **vines** and problems of soil compaction.

Perhaps the greatest value of the subtropical wet forest life zone in Puerto Rico is as a source of runoff that supplies water to the drier coastal areas where the population is concentrated. Future land use planning of areas within the subtropical wet forest life zone should certainly recognize the fact that any land and forest manipulations here may have very important effects on downstream water yield and quality.

The Subtropical Rain Forest

This is the wettest of the subtropical life zones with a lower rainfall limit of about 4000 millimeters (150 inches). It occupies very little area in Puerto Rico, occurring

only in a single crescent-shaped band on the windward faces of the Luquillo Mountains. It lies wholly within the Luquillo Experimental Forest. This life zone is characterized by a superabundance of precipitation. The water regime at La Mina indicates that the soil is at field capacity much of the year. The annual total of 3400 milli-meters (130 inches) of runoff is more than twice the annual rainfall input received by most areas of the world. The constantly wet soil eliminates water as a potentially limiting growth factor in this environment, but oxygen stress, which can inhibit root respiration, may exert an important influence on plant growth.

Figure 30—*Prestoea montana's* (Willd.) H.E. Moore (sierra palm) fronds, flowers and fruits.

The species found here are the same, for the most part, as those found in the surrounding subtropical wet forest. This may be due, in part, to the fact that water is not a limiting factor in either of these two life zones. The main features of the subtropical rain forest are the high frequency of *Prestoea montana* (Graham) Nichols (sierra palm, fig. 30) and a superabundance of epiphytes. No tree stem, building, or fencepost escapes colonization, and most leaves, even those in the upper canopy, are covered with epiphytes. One of the floristic components of this zone are orchids. The spiny tree fern, *Nephelea portoricensis* (Spreng.) Tryon, is more abundant here than in the subtropical wet forest. More detailed information on sierra palms (box 14), epiphytes (box 15), and orchids (box 16) follows.

Because of the small area it occupies, the subtropical rain forest life zone in Puerto Rico is primarily of academic interest, recreational purposes, and watershed and conservation value. Last year, nearly half a million people visited the recreation area at La Mina. The Baño de Oro Natural Area, much of which lies in this life zone, may be the only place in the world where an example of mature vegetation of a subtropical rain forest life zone is likely to receive long-term protection while still being readily accessible to the public.

Continue on page 125.

Box 14. *Prestoea montana* (R. Graham) Nichols. (sierra palm)

As this tree's common and scientific names imply, it is found in the mountains. This palm forms an almost continuous zone in sections of the upper reaches of the Luquillo and *Cordillera Central* Mountains along high-elevation streams, ridges, and steep slopes. It forms a community type sometimes referred to as the "palm brake." It is quite distinctive when viewed from the air or the observation tower on Mount Britton in the Luquillo Forest. These forests exhibit simple community structure and have few associated species. Its elevation ranges from 60 meters (197 feet) to 1000 meters (3,280 feet) and is found throughout most of the West Indies.

The tree is attractive throughout its life and is colorful when flowering and fruiting. Frequently the trunk is full of epiphytes, in particular the brilliant red bromeliad, *Guzmania berteroniana* (Schultes) Mez. Sierra palms do not attain the large size of many low-elevation palm species but will grow to 15 meters (50 feet) on good sites. Their trunks are straight and terminate in a cluster of a dozen or so attractive pinnately compound leaves that can grow to 6 meters (20 feet) or more in length. On average, four new leaves can be produced each year. When the old leaves drop, they leave a large leaf scar that circles the trunk. Just below the crown, one or more inflorescences (panicle) will develop full of hundreds of small white male and female flowers. This species is a prolific fruit and seed producer, with small and black fruits about the size of a small marble. They do not look like the fruits of coconut palms. Sierra's fruits are one of the primary foods in the diet of the Puerto Rican parrot and are also used by a variety of other birds. Sierra palms flower and fruit throughout the year. The palms are frequently anchored to boulders or the forest floor or stream edge by a large number of adventitious prop roots. When young, the roots appear pink and often show numerous large tubercles. This palm is a slow grower with vertical extension measured in centimeters (inches) per year and not meters (feet) as is the case for some tropical trees. According to Lugo and Battlle (1987), mean age of a population of 32 adult trees in the Luquillo Forest was 61 years.

Sierra palms are native to Puerto Rico (not endemic) and are the dominant tree in terms of sheer numbers in the middle and upper elevations of the mountains. Robinson (1997) estimated that there may be 800,000 mature sierra palms in the Caribbean National Forest and that the tree is present in higher numbers in both the tabonuco and palo colorado forest types than the species for which these forests are named. Sierra palms are not so much altitudinally controlled as they are controlled by soil conditions and degree of slope. They

Box 14. continued

tend to grow in areas that may be extremely wet, rocky, or subject to erosion, that is, streambanks and unstable slopes. As such, they appear as patches in these habitats in elevations above 457 meters (1,500 feet) and cover more than 10 percent of the Luquillo Mountains. Because they frequently occur in very wet areas, some people consider them to be a facultative wetland species. Strong winds, steep slopes, saturated soils, and periodic hurricanes are major contributors to sierra palm mortality. Its thin stems and ability to shed its leaves increases its survival rate. They are resilient following hurricanes and are able to leaf out fairly quickly. If they have large populations of epiphytes on their stems, they may be vulnerable to windthrow.

Sierra palms have limited economic value. On occasion they are planted ornamentally, the largest individuals may yield palm planks, the bud can be consumed for food, and their fronds have been used as thatch. The real value of this species is its ability to grow in and stabilize high-elevation soils, providing food for animals. For the student or the tourist it is also a pretty tree and adds to the tropical forest experience.

One thing that becomes evident as you move up in elevation through the various forest zones is the changing size of the sierra palms. In lower elevations of say 600 meters (2,000 feet) where there is less rainfall and warmer temperatures, the adult trees are considerably taller, many approaching the 15-meter (50-foot) size class. As you approach 915-meters (3,000-feet) their size decreases to 3 to 6 meters (10 to 20 feet). The areas where they grow as solid stands will be considerably cooler, moister, and windier and soil conditions will be less stable. These sites constitute the upper elevation palm brake forest type.

The easiest place to see sierra palms is probably in the *El Yunque* area of the Caribbean National Forest. Any trail leading away from the *El Yunque* Recreation Area will provide access to hundreds of them. Be sure to notice root structure with their pink root cap zone. Take a pocket knife along and cut longitudinally through a root in order to see the zones. Also, be sure to examine the many epiphytes, especially bromeliad "well" plants that will be growing on their trunks. As you change elevation, observe the changing size of the adult trees. If you are quiet—and lucky—you may be able to hear or see the endemic parrot feeding on its fruits.

For more information on this species, see Bannister 1970, Frangi and Ponce 1985, Little and Wadsworth 1964, Lugo and Battlle 1987, and Lugo et al. 1998.

Box 15. Epiphytes

G. Miller

Generalized view of epiphytic growth in a tropical rain forest.

Epiphytes are plants that grow on other plants or other objects and are frequently called "air plants" because they grow up in the air and are not directly attached to the soil. Although they look parasitic, they do not penetrate host tissue, so they do not cause direct harm to the host. They use the host for mechanical support in order to gain access to light. They are sometimes referred to as structural parasites, in that they will use space on a host which can reduce photosynthetic surface, and on occasion, may cause a host plant to loose limbs or fall over owing to the extra weight, especially during major storms. Epiphytes are photosynthetic and produce their own food. Their water and necessary nutrients are obtained from rain, dew, clouds, accumulated humus, and stem/leaf leachate from the host plant or other associated epiphytes. There are many types of epiphytes, and there are representatives from a number of flowering plant families, with the bromeliad (Bromeliaceae) and orchid (Orchidaceae) families two of the best examples. Lower nonflowering plants such as ferns, mosses, liverworts, and algae also exhibit many epiphytic species. There are even epiphytic cacti. Approximately 10 percent of all seed plant and fern species are epiphytic.

Canopy research is helping us to have a better understanding of the forest. The contribution of epiphytes is being investigated more thoroughly as we develop systems that permit safe access to the canopy. Many species will be described and new functional relationships will be discovered in the future. We suspect that over half of all orchids (more than 10,000 species) and up to 10 percent of all flowering plants and ferns are epiphytic. Some epiphytes are able to fix nitrogen, and many of the "well or tank" epiphytes may support more than 200 other species. A **well epiphyte** is one whose densely packed leaves collect water in their axils, creating small pockets of water such as

Box 15. continued

found in many bromeliads. Many animals are able to complete their life cycle in proximity to its host epiphyte. This ability to trap water and nutrients aboveground creates a small favorable microenvironment, often called miniecosystems. Algae, bacteria, fungi, protozoans, many insects, and even tree frogs are found there. They are often visited by lizards, spiders, scorpions, and birds for taking of prey.

Epiphytes are found in many habitats in the tropics. Any rain forest zone will exhibit a high abundance because most require high humidity, but they can also be found in dry forests. As you pass through any town in Puerto Rico, you are likely to see them growing on power and telephone lines or in the trees of the town's plaza. They are found throughout Puerto Rico from the highest and wettest zone in the montane rain forest, to the very dry habitat of the Guánica Dry Forest or even the coastal mangrove forest. Many species have special water-absorbing tissues on their roots and/or shoots, which promotes uptake of moisture from the atmosphere. Others will have swollen stems called pseudo-bulbs that permit water storage.

Many epiphytes exhibit unique growth forms that promote their existence aboveground. They have minimal roots mostly for attachment, but their overlapping leaves form a series of reservoirs (thus the name well or tank) that collects water along the central stem. Their leaves have specially adapted water-absorbing cells at their bases. The various water sources, accumulated dust, organic debris washed from above, and mycorrhizal fungi (in orchids) provide the necessary nutrients. Many epiphytes produce brightly colored flowers or bracts to attract pollinators. Orchids are notable for this and the bizarre animal designs that their flowers exhibit (see box on orchids that follows). Many bromeliads produce sticky seeds that glue the seed or seedling in position until it is established on its host.

The size of epiphytes is highly variable, and they are classed accordingly. *Macroepiphytes* include the larger vascular plant groups: orchids, bromeliads, cacti, and ferns. *Microepiphytes* include the lower plants: mosses, liverworts, lichens, and algae. Those that grow on branches and trunks are referred to as *epixylous*, and those that inhabit leaf surfaces are referred to as *epiphyllous*. There are four classes of epiphytes. All are common to Puerto Rico.

Box 15. continued

- **Proto-epiphytes** are least specialized and least protected against drought. They exhibit a velamen (water-absorption structure around roots), and some are succulent or with bulbous stems as in many orchids.
- **Nest or bracket epiphytes** form complex root masses interwoven with accummulated organic debris. They produce large multiple-branched fronds that aid in debris collection. Ex.: *Platycerium bifurcatum* (staghorn fern) and *Asplenium serratum* L. (bird's nest fern).
- **Hemiepiphytes** develop long aerial roots that can reach the ground where they may gain access to water, as in some *Ficus* (fig) species.
- **Tank epiphytes** are representative of one family, the Bromeliaceae (found only in the Neotropics). Bromeliads create miniature water tanks in the axils of their leaves in which water, debris, and nutrients are trapped and thus create a favorable environment for many other species. The genera *Guzmania* and *Vriesea* are described later in this section.

Some unusual tropical plants start out as epiphytes. Stranglers are trees, such as certain figs (*Ficus*), that ultimately "strangle" their host and assume their structural position in the forest. They start as epiphytes in an old canopy tree and then outlive their structural host. All the while they send down roots that eventually grow together forming a new outer trunk, thus producing the appearance of the strangling effect. *Clusia rosea* Jacq. (autograph tree) described earlier is another good example of this growth strategy.

In Puerto Rico, one of the most interesting places to see epiphytes is along one of the many trails associated with the *El Yunque* Recreation Area in the Caribbean National Forest. Access to the recreation area is via Route 191 at the town of Palmer. Palmer is on Route 3, 30 kilometers (18 miles) east of San Juan. A brochure with maps is available at *El Portal* as you enter the forest. Trail sections near the parking area are improved and may have a paved surface. As you get farther from the trail heads, trail surfaces become more rutted.

Hiking shoes are recommended for those planning to hike to one or more of the summits in the area. On any given day, you should expect a rain shower.

Box 15. continued

An interesting exercise is to find a recently downed tree in one of these habitats and try to determine how many different types of epiphytes are present. How are they distributed on the tree or branch? Look for any "well" plants present and examine their structural features, as well as animals present. Other features to look for are trapping of organic matter, water conservation mechanisms such as succulent leaves, leaf/stem scales, waxy covering of the epidermis, aerial roots that photosynthesize, bright colors in the inflorescence that helps to attract pollinators, and evidence of the presence of stranglers. Many trees in the El Yunque area have their trunks totally covered in epiphytes.

Puerto Rico has a diverse epiphytic flora, including 36 species in the Bromeliaceae family. Some of the common species that you will likely encounter as you visit different ecosystems are:

Tillandsia—This genus has 15 species in Puerto Rico. The most common is *Tillandsia recurvata* (L.) L., often called ball moss. It can be seen growing as a small ball on power or phone lines along roads in the coastal plain. It is especially common in trees on the south coast. *Tillandsia usneoides* (L.) L. or Spanish moss is the common epiphyte found in dense populations throughout much of the outer coastal plain of the Southeastern United States growing on live oaks and bald cypress trees. Spanish moss is much rarer in Puerto Rico but can be seen in some of the coastal hills near La Parguera and hanging in some trees south of Arecibo in the karst region. Both species are bromeliads and exhibit special adaptations to conserve water. Although they appear to be lichen or fungus-like, they are photosynthetic and are higher flowering plants. They produce capsule fruits and plumed seeds that are wind dispersed. This is the largest bromeliad genus with the greatest geographic range. One of their primary dispersal agents is the wind associated with hurricanes.

Guzmania—This is another very common bromeliad epiphyte found in most forested mountainous areas of Puerto Rico. There are four members of this genus in Puerto Rico. The common species is *Guzmania berteroniana* (Schultes) Mez. This tank epiphyte can be seen throughout the montane rain forest on El Yunque, which is its type habitat. It ranges from 365 to 1158 meters (1,200 to 3,800 feet) in Puerto Rico and nearby Dominican Republic. On occasion, you will see it growing on the ground as a terrestrial plant. The inflorescence consists of brilliant red bracts, with small yellow flowers. The

Box 15. continued

leaves are dark green and form a well-developed axillary tank system. When in flower, they look like red candles hanging off tree trunks. This genus is common throughout the Andean cloud forests of Ecuador and Colombia where they can grow at elevations exceeding 3050 meters (10,000 feet).

G. Miller

Common epiphytes (*Guzmania berteroniana* [Schultes] Mez.) growing on tree trunks in the mountains of Puerto Rico.

Vriesea—This is another bromeliad native to high-elevation and elfin cloud forests where it is quite cool. The El Yunque area is the type habitat for *Vriesea sintenisii* (Baker) L.B. Sm. & Pitt. It has green leaves in shady habitats but turns bright red in well-lighted areas. It also is a "well" plant and produces a large one-foot spike inflorescence of white flowers and red bracts. This genus is widespread throughout cloud forest regions of the Neotropics. Some of the species of this genus are important in the commercial house plant trade. They grow to elevations of 3050 meters (10,000 feet) in mainland Neotropics. Most are epiphytic, but some are cliff dwelling.

For more information on epiphytes, see Lüttge 1989, Padilla 1973, Patzelt 1973, Richards 1996, Royal Botanic Gardens 1996, and Zahl 1975.

Box 16. Orchids

Orchids belong to the monocot family Orchidaceae. This family is very species diverse, with more than 20,000 species (some estimates say 25,000) distributed throughout the world, especially in the tropics. Puerto Rico has 144 species of native orchids (5 percent of the flora). The flowers are unique, beautiful, and in some cases, bizarre. They are bizarre in terms of their shapes and colors, which may resemble their animal pollinators. They are among the top six plants sold by the cut flower industry. Some rare species are worth

Box 16. continued

G. Miller

Cultivated orchids of today were selected and bred from tropical forest species

$500,000, and, on several occasions, deaths have occurred in their procurement or possession. Rare orchid collectors are periodically taken hostage and held for ransom, as recently happened in Colombia, South America. Orchid poaching and smuggling is an international business today. Many rain forest trees will be cut in order to access the orchids growing as epiphytes on their branches. Over half of all orchids are epiphytic.

Orchids are mostly concentrated in the Asian and Neotropics where the majority are epiphytes (hundreds of genera) growing on trunks or branches of trees. They also occur in the temperate and Arctic zones where they are mostly ground dwellers. Flower morphology reaches its zenith in complexity and specialized parts in the orchids. Many orchids have evolved very special symbiotic relationships with their pollinators, and many produce flowers in the shape or color of the species that pollinate them. Various flies, bees, wasps, ants, moths, butterflies, beetles, and hummingbirds all serve as orchid pollinators, and each group is attracted to a different type of flower. Probably the best example of this is found in the euglossine orchids, which are singularly pollinated by euglossine bees after a pseudo-copulation. The orchid flowers smell, look, and feel like the female of the bee species.

When successful pollination and fertilization has occurred, the embryos develop inside a fruit that is typically a capsule. Thousands of seeds about the

Box 16. continued

size of dust specks develop. When mature, the seeds are spread by wind. The seeds lack nutritive endosperm, essential for normal embryo and seedling development. Because of this, it is critically important that the tiny seeds be blown to a suitable substrate with an essential fungus present. To grow and develop, the orchids must have a mycorrhizal relationship with the fungus. This is another example of a mutualistic symbiosis. The fungus is thought to receive vitamins or other growth substances, and the orchid benefits by receiving carbohydrates for its initial growth and development into a seedling that can then support itself through photosynthesis. This mycorrhizal relationship is one of the reasons why home gardeners find it difficult to raise their own orchids.

Without these specialized pollinators, sexual reproduction cannot occur. These elaborate floral/animal designs and colors give these plants added allure and economic value. Many orchids are very large and persist for weeks after opening, others are quite small and inconspicuous. Orchid flowers are typically small. Most of the orchids used for commerce are the result of hybridization or are some of the rare larger flowering wild species. Because of protection and increasing rarity, many orchids are being reproduced by tissue culture today. This allows many individuals to be grown quickly from expensive hybrids. Not all orchids are valuable for their flowers. Some are valuable for their fruit, with the vanilla orchid as the best example (*Vanilla planifolia* B.O. Jackson). Vanilla comes from the fruit of an epiphytic vine, and in Puerto Rico it is found in places such as the Guánica Forest. Guánica Forest is one of the dryest habitats in Puerto Rico and only five orchid species have been identified from there. The wettest areas in the tops of mountains also have reduced numbers of orchids. Greatest species diversity of orchids occurs in middle elevations, with moderate rainfall, such as in the Maricao Forest in the western end of the *Cordillera Central* Mountains. Again, it appears that Puerto Rico's geographic position as the easternmost island of the Greater Antilles chain places it furthest away from orchid-rich mainland Central and South America. It has the fewest species of orchids of any of the Greater Antilles. Puerto Rico has 14 endemic orchids, about 10 percent of the orchid flora. There have been recent alien introductions of orchids to Puerto Rico, and they are locally naturalized (Ackerman 1992). Unfortunately, Puerto Rico's largest and most showy orchids are the objects of collectors of wild orchids and most are suffering under this pressure. In some instances, their populations have been greatly

Box 16. continued

reduced, as in the case of *Psychilis kraenzlinii* (Bello) Sauleda (red butterfly orchid). This is an endemic orchid, and it is naturally uncommon. It is typical of the moist karst and lower elevation mountain forests. It grows as an epiphyte and occasionally on the ground. It produces large, bright red flowers, which form all year long. It takes years for this species to reach sexual maturity, one of the reasons for its vulnerability.

In Kathryn Robinson's (1997) research on the Luquillo Mountains, she found that "more people ask about orchids than about any other flowering plants, but few actually see them." This relates to the fact that, as indicated earlier, most orchids are small, and the majority are epiphytes, in other words, growing off the ground on tree branches in the canopy. In many cases it takes a trained eye to even spot a wild orchid, except for a few of the very large flowering species, which in most cases are rare. As is the case with many plants and animals, the more rare a species is, the more someone desires it or is willing to pay for it. Certainly this applies to orchids. Puerto Rico has a rich flora and, as cited earlier, the orchids are second in abundance in the monocots and fourth largest family overall. To help the native flora:

- Get educated about rare, threatened, and endangered species.
- Help to promote preservation of critical habitats.
- Do not take wild plants—most will die before they are successfully transplanted.
- Enjoy them in the wild—hopefully, future generations will be able to find them and appreciate them just as you have.
- Do not buy plants from local vendors that do not have verification tags as to species name and growth information. They are likely taken from the wild.

Two places will guarantee the visitor an opportunity to see orchids. One is in the wild, the other is a garden. The easiest place to see them in the wild is along the trails in the *El Yunque* Recreation Area of the Luquillo Mountains. There are 80 species native to this area. Many will be growing at ground level along the trails of the recreation area. These will be 25 to 37 centimeters (10 to 15 inches) tall, with an upright flower stalk (raceme) and numerous small white flowers. Two common ground-dwelling orchids are (*Octadesmia montana* (Swartz) Bentham) and the common genus *Spiranthes* spp. (Ladies tresses). Other species will be growing as epiphytes above your head on the major branches of the trees. To see these, you will probably need binoculars.

Box 16. continued

The other place to see orchids is in the garden display area of the Botanical Garden associated with the University of Puerto Rico at Río Piedras described earlier in the "Flora of Puerto Rico" section. In the upper section there is an outdoor display area with various species of large showy orchids. They are easy to access to take photographs. There is no entrance fee and parking is adjacent to the access trail through the garden. Many other species of native and introduced species are on display, as well as numerous other epiphytes. Unfortunately, many of the orchids were severely damaged during Hurricane Georges and funds have not been appropriated for their replanting.

For more information on orchids, see Ackerman 1995.

The Subtropical Lower Montane Wet Forest

There are two lower montane life zones in Puerto Rico (wet and rain). Figure 31 illustrates the typical species and forest types in this and adjacent zones. The wet forest zone is by far the most extensive. It occurs in both the eastern and central parts of the island up to the summits of most mountains above 1000 meters (3,280 feet) and occasionally extending down to almost 700 meters (2,300 feet). No peaks in Puerto Rico are high enough to encounter low temperatures necessary for the occurrence of the next highest, or montane altitudinal belt. The soil is at field capacity all year, and runoff occurs each month, but the total of 1700 millimeters (67 inches) annually is only about half of that at La Mina.

The colorado forest type, named for the common tree *Cyrilla racemiflora* L. (*palo colorado* or swamp cyrilla), corresponds to mature vegetation of the zonal association in the subtropical lower montane wet forest. *Cyrilla racemiflora* (box 17) is the same species that grows as a shrub or small tree in the wet swamps in the Southeastern United States. However, in the mountains of Puerto Rico it can grow into a large, reddish-barked canopy tree, and the hollow trunks of the older individuals are the main nesting sites for the nearly extinct Puerto Rican parrot (*Amazona vittata*). This forest is characterized by open-crowned trees, many of which have their leaves grouped toward the ends of branches. This forest is poorer in species than the adjacent tabonuco forest. Wadsworth (1951) reported that only 53 species have been found in this forest type, compared to more than 150 species in the adjacent tabonuco forest type in the subtropical wet forest. The colorado forest covers

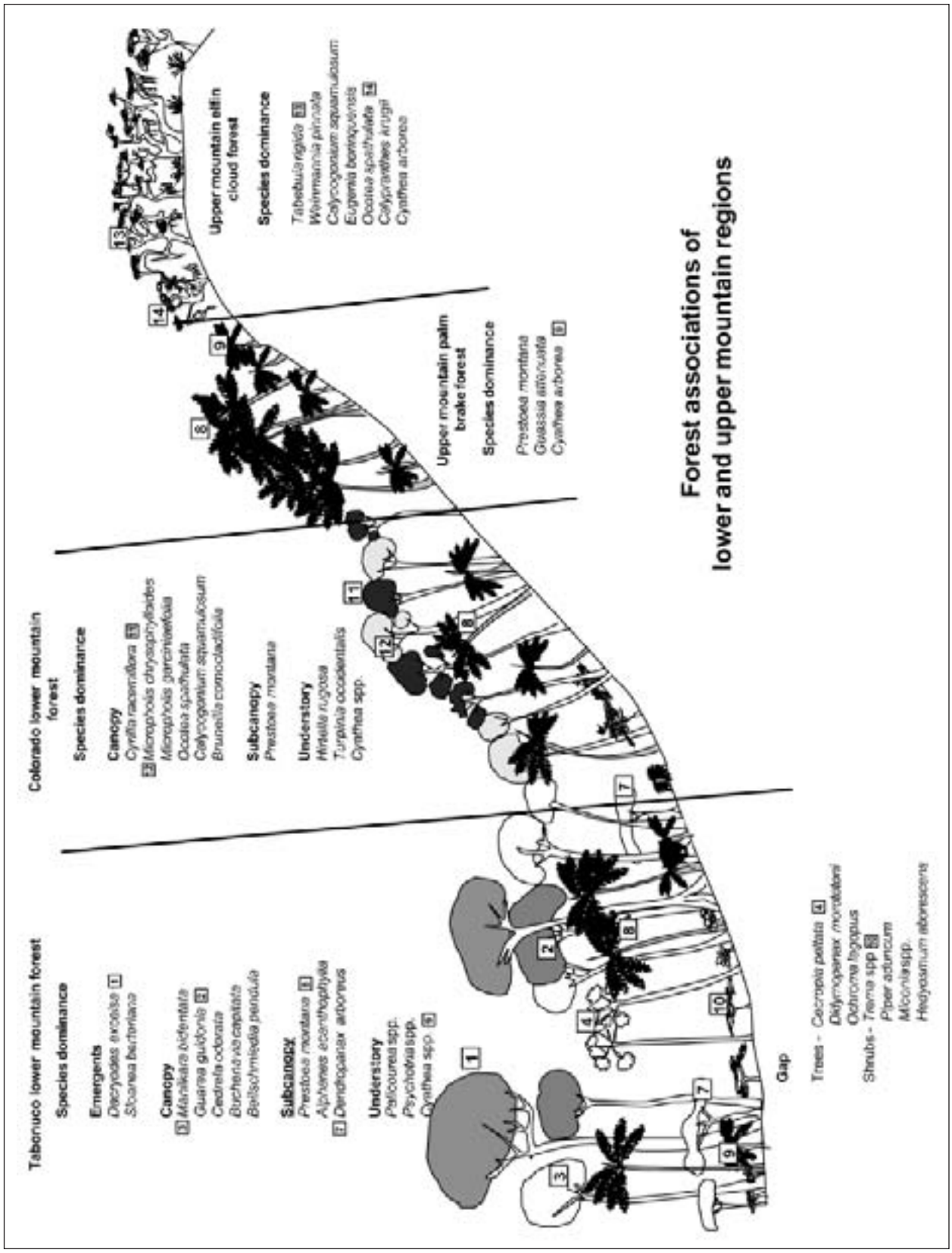


Figure 31—Species and forest types typical of the lower and upper elevations of Puerto Rico's mountains.

Box 17. *Cyrilla racemiflora* (palo colorado)

This tree is the species typical of the wet montane *palo colorado* forests. It has red bark and leaves at maturity, thus its common name *palo colorado* or "red tree." This is the preferred species for nesting by the endangered Puerto Rican parrot. It is said that this species has individuals older than 1,000 years in Puerto Rico and that some achieve greater than 2.5 meters (8.2 feet) in diameter. Examination of these giant individuals in the field indicates that many of these large individuals are the result of coalescence of multiple stems.

The stems, leaves, and inflorescence of *Cyrilla racemiflora* L. (Palo colorado)

This is one of the largest diameter trees in Puerto Rico. Interesting is the fact that in the temperate zone, this same species grows no larger than a head-high shrub and never achieves tree size in North Carolina and adjacent coastal states. This is a wetland species typical of coastal bogs called pocosins and goes by the common name of "Titi." In Puerto Rico, *Cyrilla* may grow up to 20 meters (60 feet), but on exposed ridges it may grow in the shrub form. The largest *palo colorado* in Puerto Rico is in Luquillo, and it measures 21 meters (69 feet) tall, has a canopy spread of 10.4 meters (34 feet), and a circumference of 6.45 meters (21.2 feet).

The leaves are simple and its flower is an easily recognized raceme, with numerous densely packed white flowers. The small ovate shaped fruits are drupes. Reproduction occurs throughout the year. Its growth and wood characteristics make it low value for commerce. Its primary value is as a fruit producer and nesting cavity supplier to wildlife. The species undergoes heartwood rot, thus many trunks and damaged branches have hollows needed by birds such as the Puerto Rican parrot, as they cannot fabricate their own nest cavities.

The species initially appeared to be a primary forest species owing to its size and presence, but further investigation seems to indicate that it also functions as a secondary species that takes advantage of gaps. There seems to be

Box 17. continued

strong correlation with the stand values of *Cyrilla* and the frequency and size of hurricanes, that is, more time between hurricanes seems to lessen *Cyrilla* seedling regeneration and produces larger diameter classes of older individuals (Weaver 1986). They may be primary species in extremely wet sites like *Prestoea montana* (R. Graham) Nichols. (sierra palm) is in the palm brakes and *Rhizophora mangle* L. (red mangrove) is along the coastal fringe.

For more information on this species, see Little and Wadsworth 1964 and Weaver 1996.

A.E. Lugo

Figure 32—Colorado forest at 700 meters (2,300 feet) on the windward aspect of the Luquillo Experimental Forest.

nearly 17 percent of the Luquillo Mountains and is found above 600 meters (2,000 feet). A description of the palo colorado follows. Figure 32 illustrates a typical stand in the Luquillo Experimental Forest.

Two additional associations are commonly found in the lower montane wet forest life zone in Puerto Rico. The first of these is a cloud forest, generally referred to as the elfin woodland, mossy forest, montane thicket, or dwarf forest (fig. 33). The most exposed ridgetop vegetation is characterized by twisted gnarled

A.E. Lugo

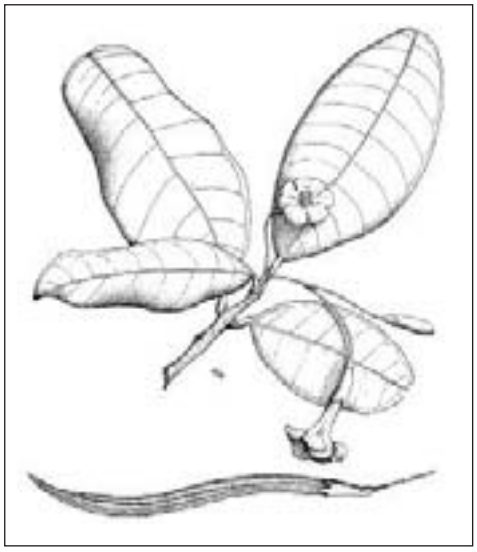
Figure 33—Elfin forest at 1050-m (3,400 feet) near Pico del Este in the Luquillo Experimental Forest.

trees less than 7 meters (23 feet) tall, with small diameters, a large number of stems per unit area, and extremely slow growth rates. All trees here are evergreen and sclerophyllous, and the leaves tend to be grouped near the ends of the branches. Common trees found in the elfin forest include: *Ocotea spathulata* Mez. (nemocá), *Eugenia borinquensis* Britt. (*guayabota*), *Tabebuia rigida* Urban (*roble de sierra*), *Magnolia splendens* Urban (magnolia), and *Clusia rosea* Jacq. (autograph tree). Box 18 describes *Tabebuia rigida* Urban. This forest is unique in that more than half of its dicotylodonous trees are endemics. In protected areas on mountain ridges, elfin forest will grow much taller and straighter. Weaver (2000) refers to it as Puerto Rico's endemic forest.

Decomposition is apparently slow in this association, and the upper soil cover seems to be almost pure organic matter, whereas the subsurface soils are clayey and oxygen-deficient. Tree roots form a tight, complete mat on the surface and do not appear to penetrate the soil very deeply. Another impressive feature of this association is the epiphyte load of ferns, mosses, liverworts, **algae**, and bromeliads, which cover almost all stems, even those perfectly vertical and smooth-barked. This forest is restricted to ridges and peaks above 750 meters (2,460 feet) and covers about 2 percent of the Luquillo Mountains.

Box 18. *Tabebuia rigida* Urban, (*roble de sierra* or mountain oak)

Tabebuia is one of the trees typical of the elfin forest found in the highest elevations of the Luquillo Mountains. It is a small evergreen tree found in eastern Puerto Rico. It may grow to 9.2 meters (30 feet), but frequently in the upper wind-swept, cloud-draped mountains it is dwarfed and twisted, sometimes growing to only 2.4 meters (8 feet). The leaves are opposite, simple, elliptic, with the margins curled under. The leaves are frequently covered with microepiphytes, while their branches and trunks tend to be full of macroepiphytes. They produce red flowers that are tubular and five-lobed, and the fruits are long cigar-like brown capsules. A distinguishing bark feature is its white inner bark. They reproduce throughout the year. Owing to its twisted growth form, the wood has little value. An unusual feature of this plant is that it also shows a disjunct distribution pattern as it is present in the Guánica dry forest.



The leaves and flowers of *Tabebuia rigida* Urban (roble de sierra).

For more information this species, see Little and Wadsworth 1964.

In an event entirely unexpected for an area as well known biologically as Puerto Rico, Kepler and Parkes (1972) discovered a new bird species, *Dendroica angelae* (Elfin woods warbler), which is apparently endemic to this association in Puerto Rico. It is also the habitat for rare species of tree frogs.

Several theories have been proposed to explain the low stature of the trees in this association. Murphy (1916) felt that exposure to strong winds affected the physiognomy of this vegetation, which he referred to as the “hurricane hardwood” type. For a description of the impacts on the elfin forest by Hurricane Hugo in the Luquillo Mountains, see Weaver (1999). Gleason and Cook (1926) and Beard (1942) also attributed it to the high winds that continually buffet these peaks, which, when coupled with the wet soils, might produce physiological drought. Wadsworth and Bonnet (1951) discussed water-saturated soils, with their impeded

A.E. Lugo

Figure 34—Well-developed prop root systems of *Prestoea montana* (Graham) Nichols (sierra palm) in the Luquillo mountains.

drainage, as factors influencing tree growth in the adjacent palo colorado type. Odum (1970) considered the elfin forest to be transpiration-limited, in that the continual cloud cover and saturated air impede transpiration, resulting in limited flow of essential mineral nutrients from the soil into the leaves. That theory was bolstered by the findings of Weaver in 1973 when he measured extremely low transpiration rates for several tree species in the elfin cloud forest association. Figure 33 illustrates the elfin forest in the Luquillo Experimental Forest.

A second azonal association in the lower montane wet forest life zone is the palm brake, consisting of nearly pure stands of the *Prestoea montana* (Graham) Nichols. (sierra palm). Box 30 describes the development of sierra palms. Examples of this association are readily accessible in both the Luquillo and Toro Negro Forests. Some of the characteristics of the palm brake include its high dominance (almost a monoculture) and a sharp **ecotone** with adjacent associations. Sierra palms also extend across life zone boundaries, reaching down into the subtropical wet forest and subtropical rain forest life zones. Beard felt that the occurrence of a palm brake was related to rates of erosion and that some of the areas where the palm formed pure stands were probably former landslides. Destruction of all trees by hurricanes, except the sierra palm, which sheds its **fronds** (leaves) in high winds and therefore does not uproot, might be another factor accounting for pure stands in Puerto Rico. They also develop a vast network of prop roots (fig. 34) that support them well in strong winds and heavy rains. In addition to forming

G. Miller

Figure 35—A view of the palm brake forest and elfin forest in the Luquillo Mountains.

nearly pure stands on steep soils, *Prestoea* is also an important component of the mature, mixed forest. Altitudinally, palm brake forests are interspersed between *palo colorado* and tabonuco forests and cover nearly 11 percent of the Luquillo Mountains (fig. 35). The sierra palm forest is present in the 730- to 915-meter (2,400- to 3,000-foot) altitude zone.

Because of high rainfall here, the lower montane wet forest life zone is not too vulnerable to damage by commercial forestry or agriculture, although in some areas dairy cattle are pastured, mostly on molasses grass (*Melinis minutiflora* Beauv.). Here again, as in other life zones with exceedingly high rainfall, primary value lies in water yield.

The Subtropical Lower Montane Rain Forest

This life zone occupies less area than any other in Puerto Rico and is found only in a narrow band on the windward slopes of the Luquillo Mountains, immediately above the subtropical rain forest life zone. Baynton (1968) measured several standard weather variables for 1 year, from March 1966 through February 1967. He reported a mean annual temperature (based on the mean of average daily maximum and average daily minimum) of 18.6 ºC (66 ºF), an annual rainfall of 4533 millimeters (178 inches), and a mean relative humidity of 98.5 percent. This area is subjected to strong winds and extensive exposure to clouds.

The vegetation of this life zone in Puerto Rico is very similar to that of the lower montane wet forest life zone. The distinguishing characteristics between the

A.E. Lugo

Figure 36—View of the high-elevation elfin forest.

two are greater abundance of epiphytes, palms, and tree ferns in the lower montane rain forest. Most of this life zone in Puerto Rico is in the elfin cloud forest association, where much of the vegetation on the exposed ridges has a windswept sculpted appearance. Gill (1969) documented the formation of aerial roots, extremely abundant on many species in this association. The water-saturated soil is covered with a soil-free root mat. Epiphytes, most of which are leafy **hepatics** (liverworts), cover everything. This forest of twisted and stunted trees and shrubs is found on the highest peaks in the 760- to 1070-meter (2,500- to 3,500-foot) altitude zone (fig. 36).

The lower montane rain forest life zone in Puerto Rico is primarily a biological curiosity, but an invaluable one since it represents an environmental extreme and, as such, is an excellent opportunity for investigating the response of natural ecosystems to environmental stress. It is indeed fortunate that the limited amount of this life zone in Puerto Rico is located in the El Yunque National Forest, specifically the Baño de Oro Natural Area.

The term cloud forest is often used to describe forests in wet mountainous areas in the tropics. Some authors use the term for a specific forest type, whereas others use it generically. In general, clouds start to form in the Luquillo mountains when moisture-laden air masses rise above 600 meters (1,970 feet). The clouds then enter all forests at or above that elevation. Thus the elfin, palm brake, and *palo colorado* forests are all “cloud forests.”

Table 16—Common plants that can be found along roads and trails in the El Yunque recreation area

Trees:	Shrubs:	Herbs/forbs(cont.):
Cecropia schreberiana (trumpet tree)	*Hisbiscus rosa-sinensis* (rose hibiscus)	*Spiranthes* (ladies tresses orchid)
Cyathea arborea (tree fern)	*Palicourea riparia* (cachimbo)	*Sansevieria* (snake plant)
Cyathea pubescens (small spiney tree fern)	*Piper aduncum* (common pepper)	*Begonia* spp. (begonias)
Prestoea montana (sierra palm)	*Bambusa vulgaris* (common bamboo)	*Andropogon gerardii* (broomstraw)
Dacryodes excelsa (tabonuco)	*Miconia prasina* (camasey)	*Mimosa pudica* (sensitive plant)
Magnolia splendens (laurel magnolia)	*Miconia impetiolaris* (camasey shrub)	
Manilkara bidentata (ausubo)	*Lobelia portoricensis* (Puerto Rican lobelia)	
Clusia rosea (postcard tree)	*Psychotria berteriana* (cachimbo)	Ferns:
Buchenavia capitata (wild olive)		*Adiantum latifolium* (maidenhair)
Sloanea berteriana (motillo)	Epiphytes:	*Thelypteris deltoidea* (eared woodfern)
Cyrilla racemiflora (swamp cyrilla)	*Vriesea sintenisii* (red leaf bromeliad)	*Dennstaedtia bipinnata* (mountain fern)
Tabebuia rigida (mountain oak)	*Guzmania berteroniana* (bromeliad)	*Nephrolepis multiflora* (flower fern)
Tabebuia heterophylla (white cedar)	*Philodendron oxycardium* (common	*Dryopteris* spp. (shield ferns)
Spathodea companulata (African tulip tree)	philodendron)	*Gleichenia pectinata* and
Artocarpus altilis (breadfruit or breadnut)	Philodendron giganteum (large philodendron)	*Gleichenia bifida* (common roadside ferns)
Musa paradisiaca (banana tree)	*Pitcairnia* spp. (Pitcairn's bromelidad)	*Polypodium crassifolium* (strap fern)
Inga vera (guaba)	Many mosses, ferns, and other lower plants.	*Hymenophyllum rigidum* (green filmy fern)
Ficus citrifolia (shortleaf fig)		
Didymopanax morototoni (matchwood)	Herbs/forbs:	Other lower plant groups:
Ocotea spathulata (nemoca)	*Impatiens sultana* (touch-me-nots)	*Marchantia* spp. (liverworts)
Mangifera indica (mango)	*Heliconia caribaea* (lobster claws)	*Polytrichum* spp. (haircap moss)
Citrus paradisi (grapefruit)	*Coleus blumei* (common coleus)	*Lycopodium* spp. (clubmoss)
	Ichnanthus pallens (grass)	*Selaginella* spp. (spike moss)

If you are visiting the El Yunque National Forest/Luquillo Experimental Forest, see appendix 2 and table 16.

For further reading see Ashton 1989; Baynton 1968; Bridsey and Weaver 1982; Brooks 1987; Daly 1995; Dansereau and Buell 1966; Farnsworth 1991; Holdridge 1967; Mares 1992; Miranda-Castro 2001; Murphy and Lugo 1986, 1995; Robinson 1997; Russell and Miller 1977; Wadsworth 1951; Weaver 1979, 1994, 1995; and Weaver et al. 1999a, 1999b.

Agroecosystems

Throughout the tropical world today there is great interest in **agroforestry** and **agroecosystems**. These involve sustainable practices that have evolved over the millennia in the tropics where local indigenous people developed forestry and agriculture in a mixed polyculture, sustaining aspects of both the forest's structure and function, and the continuous production of food crops. Agroecosystems are important because they produce many benefits such as:

- Locally available and constant source of wood fuel
- Source of small timbers for local use
- Source of locally grown and sold food
- Source of shade for crops such as coffee
- Litterfall to maintain or increase soil productivity
- Reduced soil erosion because of intact forest canopy and tree roots
- Interactive nutrient pump between deep-rooted and shallow-rooted species
- Continuous sustainable yields vs. shifting cultivation
- Shelterbelt provided by canopy species for adjacent open land agriculture
- Habitat for a variety of nonagricultural species
- Helps to maintain good soil moisture relations
- Sources of fodder for domestic animals

Many of these systems also serve as vital wildlife habitat, especially for Neotropical migratory bird species, many of which are common songbirds of eastern North America. A discussion of Neotropical migrant birds was presented earlier. For a review of how these habitats have been misunderstood in the temperate zone and mismanaged in the tropics, see Jansen's (1973) paper on tropical agroecosystems.

Unfortunately, in the case of Puerto Rico, no indigenous people remain nor is there any real record of prior polyculturing in their population centers. There are,

G. Miller

Figure 37—Overview of agroeocosystem with coffee as the understory crop.

however, some small limited examples of this process being conducted by contemporary farmers in the mountains of Puerto Rico. Mixed broadleaf canopy species with an understory of citrus (oranges, limes, grapefruit), breadfruit, bananas, and coffee (fig. 37) can be observed in some of the more rural areas along the roads between Adjuntas and Maricao and Lares and Utuado. Nearby mango trees frequently overhang the roads, papaya can be seen next to residences, and oftentimes on the forest floor, cassava will be present. All of these are very useful and heavily consumed fruits and vegetables in the tropics and require little attention other than harvesting when mature, and periodic replanting, as in the case of bananas and cassava. Frequently, free-range chickens and possibly a tethered pig, goat, or cow will be used to graze the area.

These small plot agroecosystems incorporate annual crops (bananas and cassava) and perennial tree crops (breadfruit, citrus, coffee, mango, and papaya). Note that all are introduced species to Puerto Rico. All can be bought commercially at roadside stands in the region or local markets throughout Puerto Rico and, in general, can be found in most produce markets of the tropical world.

These systems are important locally because they supply a vital, inexpensive, readily available food supply. In addition, they reduce nutrient loss in mountain soils, reduce compaction and erosion, and help maintain water quality. They provide vital forest structure that serves as wildlife habitat because they are not mass harvested, as in the case of tree monocultures or forest clearcuts. The forest

products are sustainable and have a relatively high per-unit commercial value when taken to local markets. Rural areas often exhibit high unemployment, thus income is generated from labor-intensive, rather than energy-intensive systems such as a commercial monoculture, so both human and wildlife food chains are maintained in these agroecosystems. This promotes maintenance of higher species diversity not found in monocultures.

Following are some basics about many of the plants we now take for granted in our local food stores, things that people may consume daily or weekly. Six plants that grow in the tropics and are shipped throughout the world for human consumption were arbitrarily selected. Some of these, such as coffee, sugarcane, and bananas, have such international significance that whole national economies are dependent on their harvest with prices derived in the international commodities markets. The so-called banana and sugar republics are well-known. They get their names because governments in the past rose and fell based on the price of the commodity. Fixing a satisfactory price for bananas and sugar is still a very contentious international issue and certainly affects the quality of life for millions of people in Central and South America as well as the Caribbean. Hurricanes can have enormous impact on most of the crops, especially species like bananas and coffee, important to family and national incomes. For instance, in 1996, Hurricane Hortense, a low-intensity hurricane with winds of 120 to 130 kph (75 to 80 mph), caused $128 million in damage to coffee and plantain crops in Puerto Rico.

Six economically important plants will be reviewed including sugarcane, coffee, banana, citrus, pineapple, and mango. Literally hundreds of fruits and vegetables could have been selected for review, but the ones selected are commonly grown and used in Puerto Rico and throughout the Neotropics. All are now readily available in produce markets in the United States and Europe.

Typical Crops of the Tropics

Sugarcane—

Scientific name—*Saccharum officinarum* L.

Plant family—Poaceae (Grass family)

Growth form—Perennial grass

Origin—South Pacific islands

Domesticated—India

Historical significance—Spread from India through Arab trade routes. In the 15th century, it replaced honey as the principal sweetener in Europe where it was largely used to disguise the bitter taste of herbal or other medicinal concoctions.

Caribbean spread—Brought to the Caribbean in 1493 on Columbus's second voyage, it was thought to be grown in Puerto Rico shortly after 1510.

Slave trade—Growing and harvesting of sugarcane was largely what gave impetus to the establishment of slave trade in the New World. Sugar, rum, and slavery became interdependent during the colonial period and formed the infamous "tragic triangle."

U.S. Revolutionary War—The imposition of the Sugar Act by British Parliament in 1764 caused extensive smuggling of sugar into the colonies from the Caribbean and resulted in the sinking of the British custom boat, the *Gaspee*. This was the first major action by colonists leading to the American Revolution.

Growth cycle—Sugarcane is grown as a monoculture throughout much of the lowland tropics and subtropics. The name "sugarcane" relates to the fact that the plant's stem has a high percentage of sucrose (10 to 15 percent), and the growth form of the aerial stem is botanically referred to as a cane. The aerial stems may grow up to 6 meters (20 feet).

Sugarcane was the dominant crop in Puerto Rico for more than 300 years. Free access to U.S. markets for sugar and large investments of American capital revolutionized the agricultural economy of Puerto Rico. It turned the island from subsistence agricultural economy, with some commercial success in tobacco and coffee, to one based primarily on sugar for export. The level coastal plain with its excellent soils and the rolling foothills adjacent to the mountains on the north and west sides were ideal for sugarcane growth. In addition, there was a good network of access roads. The dry south coast from Aguirre to Cabo Rojo could be irrigated to produce excellent yields. At the height of its sugar economy in the 1930s, Puerto Rico annually harvested 87 000 hectares (214,000 acres) of sugarcane, and in 1940, there were 22 sugar processing mills. By 1969, cane harvest had dropped to 68 800 hectares (170,000 acres). In 2002, there were only two cane mills operating, one at Yabucoa (Roig sugar mill) on the east coast and the other at Aguada (Coloso sugar mill) on the west coast. The mills are owned and operated by separate groups of sugarcane farmers, but are heavily subsidized by the Puerto Rico government.

Sugarcane harvest and processing into its various derivative products is all but a thing of the past. Vast acreages of cane in most coastal areas of Puerto Rico go unharvested even though raw sugar has to be imported for processing in order to meet the 40,000 tons of table sugar consumed in Puerto Rico each year. Sugar prices are politically regulated and highly subsidized. As a result, U.S. consumers pay sugar prices that are over two times the average world sugar price resulting in $1.9 billion in added food costs yearly. Sweeteners today include a vast array of

products, most not having their origin in sugarcane; cane sugar supplies just 50 percent of the world's supply of sugar. As a result of precarious price fluctuations, rising costs, and continual labor problems, it became no longer economical for U.S. sugar companies to maintain sugar operations in Puerto Rico. Vast areas in Texas, Louisiana, and Florida are now devoted to cane production using the most advanced mechanization systems available to the industry. Many former cane fields near metropolitan areas in Puerto Rico such as Bayamón, Caguas, Arecibo, Mayagüez, and Ponce are rapidly falling to urban sprawl, highway development, and conversion to other agricultural uses. Large sections of cane fields are reverting to nature by natural succession. Most of the raw sugar processing mills are now closed and wasting away in the tropical sun as sentinels to a time when Puerto Rico was a sugar colony for both Spain and the United States. Some of the mills were sold lock, stock, and barrel, dismantled, and shipped to large plantations in Brazil. There is currently a proposal to bring sugarcane production back to life in Puerto Rico. This new initiative will provide both table sugar and generate a new product, bio-ethanol, which can be blended into gasoline. The group proposing to do this is the Puerto Rico Bio-energy Cooperative. Ultimately, they hope to produce 45 million gallons of bio-ethanol and 59,000 tons of table sugar (*azúcar*).

There is a small photo museum devoted to the sugar industry at the old mill in Aguirre. There one can observe some classic plantation overseer houses, office buildings, and the processing mill. As there are tens of thousands of acres of sugarcane in Puerto Rico, we will next examine its biology and historical significance.

Sugarcane grows as an annual crop, although in some areas a crop may require 18 months to mature. Growth of a crop is from **vegetative** stem cuttings. Segments of a cane with three to five **nodes**, each with a bud, are placed in shallow soil depressions. Buds rapidly grow up and roots down from the vegetative buds. Depending on growing conditions, a grower may be able to get 2 to 10 crops from one well-established **rhizome** in subsequent years. Planting may be by hand, but in developed countries it is mechanized. Herbicide and fertilizer applications will accompany the planting process. Shortly after flowering, a crop matures and harvesting begins (fig. 38). Traditionally, the sugar harvest season in Puerto Rico runs from late January to early summer. Usually, fire is employed to rid the plants of leaves (chaff), leaving just standing canes. In less developed countries, cutting and gathering may all be done manually and cane may be taken to a nearby mill via ox carts or narrow gauge railroad (fig. 39). In the main growing areas of Puerto Rico, ox carts and trains became rarely seen as most cane was taken to the mill by large trucks.

G. Miller

38—View of sugarcane field in flower.

In sugar mills, the canes are put on conveyors and crushed with large-fluted metal rollers, the juice squeezed out, and the vegetative residue (**bagasse**) discarded. Bagasse can be used as a fuel supplement, as compost, or in paper production.

Cane juice requires removal of impurities by filtering and boiling. This produces a syrup which is heated, forming crystals. Centrifuges separate the crystals from the remaining syrup. At the end, two products are produced—sugar crystals and sugar molasses. Raw sugar (brown) has some impurities and a little molasses in it. Refined sugar (granulated white) has the impurities removed. Molasses is vital to the production of a variety of other products. Most importantly in Puerto Rico, it is the basis for rum production. Rum is one of Puerto Rico's main exports, with the United States as the major importer. Bacardi is the number one brand of hard alcohol consumed in the United States where 21 million cases are sold per

G. Miller

Figure 39—Transport of sugarcane in preparation for milling was frequently done by ox carts.

year. All federal taxes collected on the sale of rum in the United States are returned to Puerto Rico. This economic stimulus pumps over $250 million into Puerto Rico's economy.

Pineapples—

Scientific name—*Anana comosus* (L.) Merrill
Plant family—Bromeliaceae (Bromeliad family)
Growth form—Biennial rosette with a **multiple fruit** and armed leaves
Origin—South America
Domesticated—Prior to 1500

Historical significance—Throughout the world, pineapples are used as a symbol of hospitality. They appear in the stone carvings of many public buildings, and their likenesses are used in home decorations (bedposts, wallpaper, and fabric design).

Growth cycle—Pineapples (piña) belong to a unique family of plants, the Bromeliads. This is a family dominated by epiphytes, the so-called "air plants." Most of these plants grow on other plants, such as forest trees. Pineapples are ground-dwelling bromeliads. Most cultivated forms of this plant are seedless, reproduced by asexual cuttings. The upper leafy branch or axillary branches are detached and planted. Plants grow as a cluster of spiny rosette, bayonet-shaped leaves. The upper extensions of the stem will bear one- or two-flower stalks consisting of up to 200 individual flowers. Flowers, subtending bracts, and the flower

G. Miller

Figure 40—The multiple fruit of a mature pineapple.

stalk all fuse together to form a complex multiple fleshy fruit (fig. 40). When the fruit turns yellowish, it is ready to harvest. Today, fruit development and ripening are controlled by spraying plant hormones or carbide gas onto the field at a precise time in anticipation of when the fruit is to be shipped and served. It takes approximately 4 to 5 months for a mature fruit to develop. Commercial plantations replant every 3 to 4 years because root death and diseases cause fruit size to decline.

Pineapple, locally known as piña, is one of the fruits everyone associates with the tropics. It is native to the Western Hemisphere and is thought to have been domesticated by the Guarani people of present day Southern Brazil. By the time of Columbus' second voyage in 1493, it had spread to the Caribbean where he bartered for it in Guadeloupe.

It was taken back to Europe and spread to India by the mid 1500s and was introduced to the East Indies shortly thereafter. It was initially grown for European royalty. Royal English gardeners built special greenhouses for propagation and selective improvement. By the late 1800s, the modern pineapple, and the subsequent development of the pineapple-growing industry, started in Hawaii, where

today most of the U.S. commercial production occurs. Its common name is the result of the fruit resembling the outward appearance of a pine cone, with a soft fleshy center, like an apple.

Puerto Rico grows pineapples commercially on the north coast in the Arecibo-Manatí area. It is the third most important crop on the island. Prior to expansion of the *autopista* (toll road) in the area and commercial development along Highway 2, there were large pineapple fields on both sides of the road. To see fields today, you will have to exit off these roads. Many small farmers grow pineapples as a cash crop and sell them from roadside stands throughout the island. Sweet, ready-to-eat, field-ripened pineapples are especially abundant in the Cabo Rojo area where they may grow to 9 kilos (20 pounds). They are generally much better quality than those available in Puerto Rico's supermarkets, because supermarkets often sell imported pineapples that were harvested green. A description of the plant's biology follows.

Pineapples grow best in light soils, with good drainage, and a pH around 6.5. These soil conditions are found in the karst area of Puerto Rico's north coast. As is the case with sugarcane, many of the commercial pineapple fields are located in areas undergoing rapid development (housing, strip malls, and transportation corridors), and as a result, the land values are ever on the increase. There are three varieties of pineapples grown, with cayenne and red Spanish being the two grown in Puerto Rico. The cayenne variety has a smooth leaf, whereas the red Spanish exhibits a spiny leaf. Pineapples are mostly known for their delicious, fleshy fruit. Their juice is also widely consumed throughout the world. The fruit and juice contains bromelin, a digestive enzyme, often used in tenderizing meat. This crop requires fertilizers and pesticides. Weed control is effectively accomplished by growing plants in a black plastic soil cover. The main growth problems in Puerto Rico are soil nematodes and bacterial wilt associated with wet soils.

Coffee—

Scientific name—*Coffea arabica* L. (90 percent of world production)—
(*C. robusta* and *C. liberica*—10 percent of world production)

Plant family—Rubiaceae (Madder family)

Growth form—Perennial shrub, small tree

Origin—Ethiopia

Domesticated—13th century in Arabian Peninsula (Yemen)

***Historical significance*—**A major tradable commodity heavily controlled by Arab traders who sterilized all beans harvested so the beverage could not be grown by other trading groups. Coffee was introduced by the Dutch into the New World tropics in the 1720s.

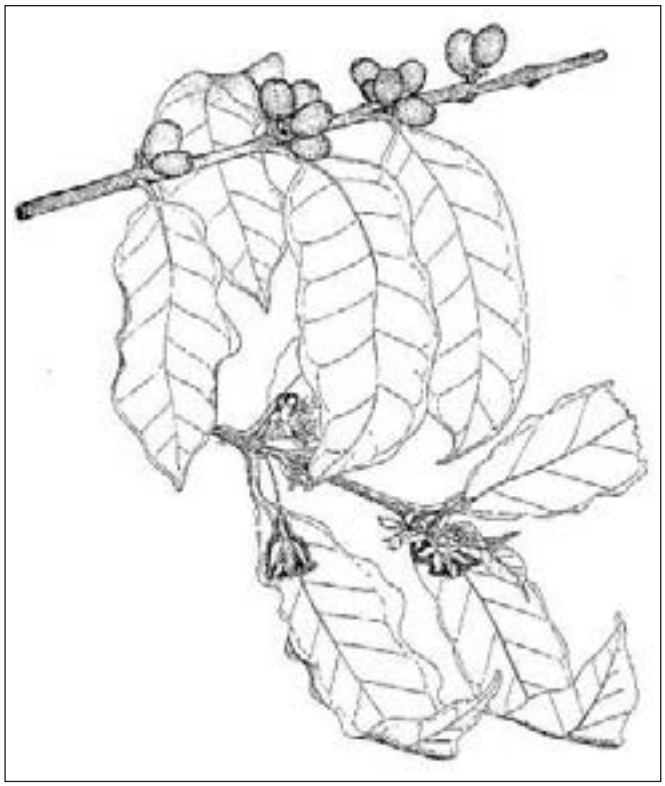


Figure 41—The leaves, flowers, and fruits of *Coffea arabica* L. (coffee).

Growth cycle—Coffee (*café*) is now grown throughout the tropics (20º N and S of the equator). It frequently grows best in mountainous terrain, but can be grown close to sea level. As was the case with sugarcane, this plant's culture was very labor intensive and gave rise to increased slave trade in the New World, but not in Puerto Rico. It is a plant influenced by cold weather; thus wild price swings occur as cold periods affect bean production in countries such as Colombia or Brazil. In northern Latin America, it is the leading source of foreign exchange.

Coffee "trees" are usually grown from seeds and planted into the field as young shrubs (fig. 41). Individual trees will bear fruit at 3 to 5 years of age and can bear harvestable fruit for 40 years (fig. 42). Mature plants typically produce 5 to 6 pounds (2 to 3 kilograms) of fruit per year. Approximately 2,000 beans are in a pound (less than 1 kilo) of coffee. One pound of coffee beans ready to roast will require 5 to 6 pounds of freshly picked raw fruits. Because most plantations are located in mountainous highlands, gathering of beans is done by hand. Mechanical harvesting is possible on flat or gently rolling landscapes. Mechanized harvesters do the equivalent work per day of 100 pickers. At the height of the harvest season, pickers may be able to pick up to 200 pounds (10 kilograms) per day.

G. Miller

Figure 42—Closeup view of the leaves, flowers, and fruits of coffee.

Traditional coffee cultivation is best in frost-free areas, receiving 1500 to 2500 millimeters (60 to 100 inches) of rainfall, and growing in a shaded environment. Coffee is frequently grown in an agroforestry setting with a variety of other fruit and vegetable species in the same system. Coffee grows best in fertile, well-drained soils. The major pest of coffee is the coffee leaf rust (*Hemileia vastatrix*) that, once introduced, is very difficult to control, so coffee is grown in areas free of the rust. Ceylon lost its entire coffee-growing area to the rust in the late 1800s. Unfortunately, the rust was introduced into Brazil in 1970 and Central America in 1976 (Perfecto et al. 1996).

Recently, many coffee-growing regions have started to switch to sun-loving trees, which produce slightly larger yields, but have shorter life expectancy. This switch has serious ecosystem and watershed implications, as it requires all canopy tree species to be eliminated, which results in a serious decline in the complex agroecosystems that serve as vital wildlife habitat. The implications of this change to a true coffee monoculture are discussed in the section on Neotropical migrants.

By 1990, half of the 2.7 million hectares (6.7 million acres) of coffee plantations in northern Latin America had already been converted to high-yield sun plantations. Sun-grown coffee is considerably more expensive to produce than traditional shade-grown coffee. However, owing to environmental problems and shorter tree lifespans—which requires expensive replanting—many farmers are returning to shade coffee plantations.

Once the coffee berries are picked, they are depulped (fruit wall and seedcoat removed) and the two beans per fruit (mostly food storage/endosperm) are gathered en masse and dried. Once dry, the beans are roasted. Roasting is critical because it imparts the aroma and flavor to the finished coffee. Both temperature (184 to 188 ºC or [392 to 400 ºF]), and time (5 to 15 minutes) of roasting, are critical to chemical reactions involving starch, sugars, and caffeine that take place as the bean is roasted.

At the end, a once light green bean is now dark brown to black, and a specific aroma and taste is imparted as the coffee is ground and brewed in water. Espresso coffee involves forcing steam through deep dark-roasted ground coffee. Espresso bars are very common in Europe and throughout Latin America. Americans tend to prefer light or medium roasted and less strong coffee. Many Puerto Ricans drink *café con leche*, an equal mix of boiled milk and dark roasted coffee. Either type of coffee contains 1.5 percent caffeine. Decaffeinated coffee has the caffeine removed by solvent extraction prior to roasting. The caffeine is then crystallized and sold as a food additive in soft drinks, and in headache and cold medicines. Twenty percent of U.S. coffee consumed is decaffeinated.

Coffee is an important beverage to many people in the world. It is the most important beverage commodity imported into the United States and one of the most important commodities traded internationally, ranked second after oil. Coffee is consumed most heavily in the United States (330 million cups per day). Nearly 50 percent of the world's coffee beans are purchased by three American multinationals (Kraft, Sara Lee, and Proctor and Gamble) and the Swiss food giant, Nestlé. More than 50 percent of the U.S. population drinks coffee. The U.S. coffee industry is worth an estimated $18 billion per year based on the 2.4 billion pounds of coffee that are imported. It is also heavily consumed in countries of Western Europe and throughout the tropical Americas. It was once the beverage of aristocrats, but today is the preferred morning and after-dinner beverage of people the world over. Coffee comes from a tropical shrub (small tree) with its center of origin in the highlands of east Africa. Today, most of the world's coffee production is grown in Colombia and Brazil. There are 80 countries in the tropics that grow coffee for export and their

Table 17—Approximate area of coffee production by country or region in northern Latin America

Country/region	Area	Percentage in sun coffee[a]
	Hectares (acres)	
Colombia	1 million (2.47 million)	> 60
Central America	750 000 (1.85 million)	> 20
Mexico	700 000 (1.73 million)	15
Caribbean countries	300 000 (741 thousand)	< 5
Totals	2.7 million[b] (6.79 million)	

[a] Data for percentage in sun coffee are 1990 estimates.
[b] 7 percent of usable land and 44 percent of total area of permanent cropland.
Source: Modified from Perfecto et al. 1996.

own domestic consumption. More than 25 million people are employed around the world in this $50 billion industry. Table 17 shows the approximate size of coffee-growing area by country or region in northern Latin America. In 2002, 117 million bags of coffee weighing 60 kilograms (132 pounds) each were harvested worldwide.

Puerto Rico still has many small coffee plantations centered in the Cordillera Central Mountains. There are 20 coffee-producing municipalities in Puerto Rico. One of the coffee-growing areas near Adjuntas convinced the Puerto Rico government to create a new national Park—*El Bosque del Pueblo* (people's forest) to save one of the best coffee-growing areas from strip mining for copper and other metals (Gómez 2001). Many small plantations can be accessed along Route 10 as one travels north from Ponce to Arecibo. Throughout the mountains, there will be plantations in full flower (white), while others will be exhibiting ripe red fruits (cherries). Naturally sun-dried beans are often seen lying along the road on burlap cloth. Many roadside stands and all community produce markets will have locally grown beans for sale. Puerto Rico has a series of island brands available as beans, ground, or instant coffee. All are very good, and one brand is notable because it is referred to as "the coffee of the popes" and has been a staple beverage in the Vatican for years. Pope Leo XIII designated Puerto Rican coffee an excellent drink. Unfortunately, Puerto Rico's great coffee exporting period ended in 1899 when Hurricane San Ciriaco severely damaged coffee plantations throughout the island. Shortly thereafter the United States barred Puerto Rico from conducting foreign trade; thus, the export of one of its most profitable products went into steep decline from which it never recovered (see app. 2).

In the United States, coffee is frequently used as a loss leader by large food chains in order to attract customers. Thus, on the same shelf, the customer may see

prices vary from $0.99 to $13.99 for the same quantity of coffee offered under different brand names. Today, specialty coffee labels and coffee restaurants dedicated to a wide array of coffee-based beverages are available. Dozens of adulterants, additives, and flavor enhancers are added to coffee to produce the current trend of designer coffees now available at specialty coffee houses. A fresh 6-oz cup of coffee may range from $0.69 to $6.00 on the same city street in the United States depending on who is selling it and what additives are in it. Good old-fashioned regular is usually the truest in terms of taste and cheapest in price.

In Puerto Rico, fresh coffee is frequently sold as *café con leche* or *pocillo* (a pocillo is a demitasse of coffee). Many visitors to Puerto Rico enjoy local brands and often take bags of island coffee products home to share with family or to give as gifts. Any large food store will have a complete array of local brands.

Bananas—

Scientific name—*Musa paradisiaca* L. (plus numerous other cultivars and species)

Plant family—Musaceae (Banana family)

Growth form—Upright herbs that appear tree-like; up to 10 meters tall (33 feet)

Origin—India

Domesticated—India and other Asiatic countries for at least 2,500 years; introduced into the Caribbean early in the 16th century.

***Historical significance*—**Bananas are important economically throughout the tropical world, especially in Central America where most countries were referred to as "Banana Republics" owing to intertwining of bananas, economies, the military, and large U.S. fruit companies (Jenkins 2000).

Growth cycle—Annual herb that can resprout yearly from rhizomes.

Bananas (*guineo*) are the United State's number one snack or dessert fresh fruit. Interestingly, prior to the 1880s, bananas were largely unknown in the United States, but by 1910 they were common. The United States imports more bananas than any other country, and United States fruit companies early in the 20th century had enormous influence on most Central American and a few northern South American countries and transport systems. Large areas of land are still controlled by Dole, United Fruit, and others, in Ecuador, Colombia, Costa Rica, Panamá, El Salvador, and Guatemala. Today, Ecuador is the largest exporter of dessert bananas, with most destined for the United States. Bananas trail only grapes, citrus, and apples as the fourth largest fresh fruit crop of the world. It is the developing world's fourth most important food crop.

Banana trees (a woody plant is considered a tree when it exceeds 15 feet in height) are among the plants people conjure up in their minds when they think of the tropics. They are interesting plants in that they are the world's largest herb, achieving heights of 10 meters (33 feet). They are easily grown and typically produce a crop of fruit yearly.

Throughout Puerto Rico, bananas are grown both commercially and by individual families for their own consumption. Banana trees can be seen throughout the island, except in the most wet and dry areas. With the decline of sugarcane in the coastal plain, some of these lands are now being converted to commercial banana plantations. Most homeowners with a yard will likely have a couple of trees around their home for family consumption and decoration. Bananas in Puerto Rico are mostly eaten unripe and boiled.

The banana requires hot and humid conditions found in the tropical and subtropical latitudes. It is native to the Indo-Malaysian region where it was domesticated 3,500 years ago or more. The word banan is Arabic for finger and so applied to the fruit because of its shape. Bananas reproduce vegetatively via sucker sprouts from an underground rhizome (horizontal stem). The small brown seeds seen in a banana fruit are aborted because they are the result of triploidy (three sets of chromosomes), which interferes with normal development of the embryo. Thus, all plants derived from the same individual are **clones** and genetically identical. There are thought to be over 300 cultivars of *Musa* now in production throughout the tropical world. These clonal types have varied features relative to taste quality, texture, size, and color of the fruit, resistance to disease, and tree height.

As a bud develops off the rhizome, it grows aerially into what appears to be a tree trunk. In actuality, that trunk is a tightly wrapped group of leaf sheaths and is not woody. As it develops through the annual cycle, more and more leaves emerge from the center of the sheath and the blade expands out after emergence. The leaf blades are quite large, up to 1 by 3.66 meters (3 by 12 feet), oval, and when young, entire. Owing to weather conditions, most banana leaves will split into the mid vein throughout the blade. The leaves are frequently used in various aspects of food preparation and storage in the tropics.

Late in the annual cycle following development of the vegetative tree, the **apical meristem** converts to a flowering meristem and a large single inflorescence emerges out of the rosette of leaves. Along the flowering stalk a series of flower rows will emerge forming the so-called hands of bananas as they grow. Each row will initially be covered by a brilliant purple-pink bract, thus, banana flowers are large and colorful (fig. 43). The banana flower is perfect in that both male and

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Figure 43—Banana tree with maturing inflorescence.

female parts are present, but it is the pistillate (female) flowers that develop into individual banana fruits **parthenocarpically**, that is, asexually. Banana fruits are a modified berry and mature in 3 to 5 months. Bananas for direct consumption are normally tree ripened. Commercial bananas are packed green and shipped around the world in refrigerated container ships where relative humidity is controlled at 90 percent and the temperature is 13 ºC (mid 50s ºF). Bananas can be artificially ripened by applying ethylene gas. Once ripe, the useful shelf life of bananas is only a few days.

After fruit harvest, the tree is chopped down and either replanted via new suckers, or a new sprout from the previous rhizome will be allowed to grow. Throughout the process, fertilizers and pesticides are used to promote growth, control fungal wilt, and reduce loss by fungal infection in transit. Under good growing conditions, carbohydrate yields are similar to the yields of potatoes in the temperate zone. Each year, great losses of banana crops occur as a result of hurricanes and typhoons throughout the tropics. The economies and governments of some countries rise and fall based on storm frequency.

Bananas were introduced to Africa by Arab traders; then Spanish and Portuguese traders spread them to the Neotropics, the center of world production

of sweet bananas. Plantains, which are large, starchy, and not sweet, are commercially cultivated for world distribution largely in Africa. The plantain banana is a true staple and major supplier of carbohydrates throughout much of the tropics. They are similar to the Irish potato in the diets of people from temperate lands. Plantains are eaten more frequently in a variety of forms on a daily basis than are sweet bananas. They can be boiled, baked, and fried. All are good sources of energy and potassium. In Puerto Rico, one of the most common ways to prepare them is as *tostones*. Here, the plantain is sliced, pounded with a mallet, and deep fried. They are frequently served as a vegetable side dish when eaten at a restaurant. Today, bananas are also chipped and sold as a snack food like potato chips are in the United States. When there are excess bananas, they are frequently used as animal feed, whereby the entire banana is consumed.

In most banana-producing countries, there is great concern about the ecological and health implications of the use of pesticides. In many cases, pesticides are applied by men wearing swimming suits and plastic open-toed shoes; thus, by the end of the day they are covered in pesticides. Many communities exhibit high incidences of still births, malformed infants, and male sterility. Large plantations usually apply their pesticides via spray planes resulting in offsite migration of the chemicals. Frequently, these plantations are bordered by squatter communities. In addition, local water supplies may become contaminated with residues. There are lawsuits pending in some countries related to these issues.

In July 2001, it was announced that an international research consortium (Global *Musa* Geonomics Consortium) would attempt to sequence the entire banana **genome** by 2006 to isolate and develop disease-resistant bananas. One disease, black sigatoka caused by *Mycosphaerella* fijiensis fungus, is known to have devastating effects and can reduce yields by 50 percent. The bananas' genome is 500 to 600 million base pairs and represents the largest plant genome to be attempted thus far (Gewolb 2001).

Citrus—

Scientific name—*Citrus* spp. (*C. sinensis* (L.) Osbeck (sweet orange), *C. aurantifolia* (L.) Swingle (lime), *C. limon* (L.) Burm. (lemon), *C. paradis*i Macfayden (grapefruit), and numerous other species)

Plant family—Rutaceae (Citrus family)

Growth form—Tree

Origin—Southeast Asia (China to Australia)

Domesticated—Well before Greek and Roman times, probably in China and India

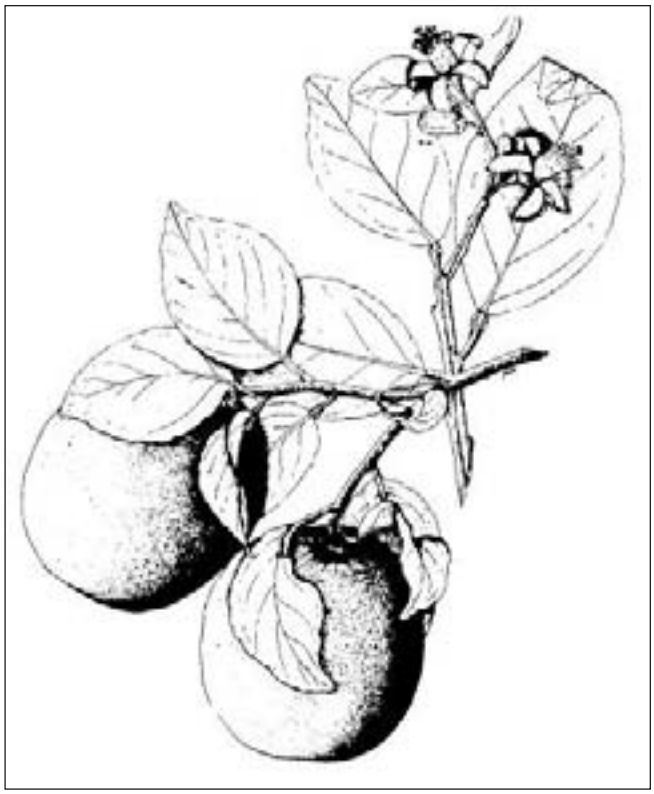


Figure 44—The leaves, flowers, and fruits of *Citrus sinensis* (L.) Osbeck (orange tree).

Historical significance—Citrus was brought to the New World by the Portuguese and Spanish. It was important to the health of sailors in preventing scurvy. English sailors were called "Limeys" because they carried fresh limes and kegs of lime juice on long voyages.

Growth cycle—Orange trees are easily grown from seeds, and trees will grow to 10 meters (33 feet) in height. They have broad evergreen leaves that are ovate, with **winged petioles**, and fragrant, white flowers (fig. 44). Growth can take place in a variety of soils from sandy to clay loams, but they prefer well-drained soils. Most new orchards result from small orange trees that are budded on stocks grown from the seed of specially-selected trees, having spent 1 year in a greenhouse and another year in a nursery. Profitable fruit production occurs at about age 6 to 8. Mature trees will bear fruit for about 80 years and, in some cases, centuries if free of disease and weather-related damage. The orange crop is normally picked when ripe (fig. 45). About 40 percent of the U.S. orange crop is made into frozen concentrate. Many fruit farmers in the U.S. have two chronic problems to deal with, one is threat of frost and the other is the rise in land values in the sunbelt states. To keep

G. Miller

Figure 45—Sweet orange tree in the mountains of Puerto Rico.

up with the ever-increasing demand, the industry had to go south into the tropics where cheap land was available.

Citrus fruits are among the most enjoyable products directly consumable from nature. Their original distribution was primarily the southeast Asian tropics, but today they are grown throughout the tropical world and throughout the southern tier states of the United States, with Florida and California being the major producer states. It is the number one tree fruit crop in the United States. There are a number of species that produce edible fruits, with four of them very common to Puerto Rico. Citrus can be seen throughout the island, including the dry areas of the southwest and the wet areas of the Luquillo Mountains. There are no extensive groves as you would see in Florida or California; instead they will more likely be 1 to 2 acres and frequently associated with other agroforestry species. Most people with yards are likely to have one or more of these species growing around their homes for personal use.

Citrus has become a huge commercial endeavor, and many U.S. fruit companies have established large holdings in Mexico, Brazil, and other tropical countries. Today, orange juice (*jugo de china*, as it is called in Puerto Rico) is frequently a mixture of juices originating in two or three countries.

The fruit of an orange tree is a modified berry called a hesperidium. The skin is full of aromatic glands and oils, as are the leaves. The oils are also a major product

used in the cosmetics and perfume industry. Most oranges produce viable seed and are easily grown from seed. Navel oranges are seedless, and it is thought that the southern California navel orange industry is based on two asexually **propagated** trees introduced in the early 1870s. The fleshy part of the fruit is divided into a series of sections filled with modified juice-bearing hairs, which we squeeze for juice or eat directly. Sweet oranges contain about 10 percent sugar in their juice. Pulp left over from processing can be used as an animal food, soil amendment, or in a variety of industrial products such as beverage flavoring, cleaning products, and medicinal additives. Orange juice is part of most American breakfasts, and grapefruits are likely to be on the menu for most dieters. Citrus is an excellent source of vitamin C and beta-carotene. Today, many commercial juices are also fortified with calcium and vitamins D, E, and C, as well as zinc.

Citrus was introduced into Puerto Rico in the early 1500s. Most of Puerto Rico's citrus is grown for local fresh consumption. In fact, most frozen orange juice in food stores is imported from Florida. Fresh oranges (locally called *chinas*) are available year round from roadside stands and street venders. For $3.00, you can buy 10 to 15 oranges (depending upon size). These are tree-ripened fruits and wonderful for sweet juice production. When buying fresh fruits, do not expect the perfect orange color typical of the American supermarket. Oranges from large commercial groves in the United States may be color processed and gassed with ethylene, which causes chlorophyll breakdown. Locally grown oranges in Puerto Rico are likely to be somewhat green. Some venders may not wash their fruits and they may have blackened areas as a result of microepiphytes growing on the fruits. These are easily washed off and do not present a health hazard.

Mangoes—

Scientific name—*Mangifera indica* L.

Common name—Mango

Family name—Anacardiaceae (Cashew family)

Growth form—Tree

Domesticated—Ancient period, southeast Asia

***Historical significance*—**Mangoes were introduced to the West Indies from South America in the mid 1700s.

***Growth cycle*—**Mango trees can grow to 23 meters (75 feet) tall; they have a broad canopy, with large, evergreen, lance-shaped, simple leaves. The flowers are a terminal complex inflorescence called a **panicle**. Flowers vary in color from green-yellow to purple-pink. Although many individual flowers are produced, generally

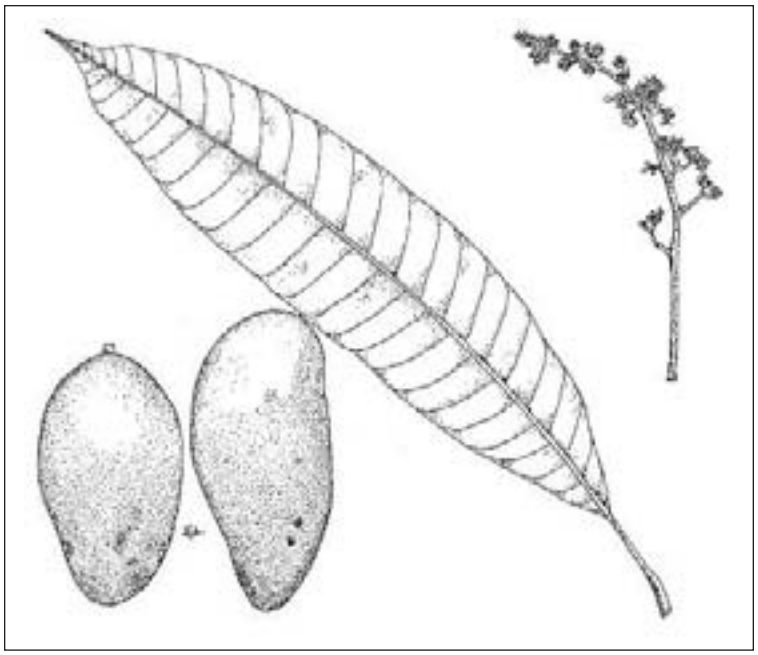


Figure 46—The leaf, flowers, and fruits of *Mangifera indica* L. (mango tree).

only one yellow **elliptic** fruit develops from each panicle. It is a large aromatic fruit called a **drupe**, with one seed (fig. 46). They are frequently planted as shade trees around homes. The largest mango tree in Puerto Rico, located in Arecibo, is 36.9 meters (121 feet) tall, with a crown spread of 18.9 meters (62 feet) and a circumference of 6.4 meters (20.9 feet).

Mangoes are ancient fruits found originally in a broad area of Southeast Asia. They belong to the same family as poison ivy and poison sumac, common plants in the Eastern United States that produce skin reactions in the form of dermatitis. In Puerto Rico, the two common poison plants of the genus *Comocladia* are also members of the Anacardiaceae family. Some people are also allergic to mango pulp and juice, especially if the fruit has not fully ripened. If you are allergic to poison ivy, be careful to take in only small quantities of the mango fruit. Some individuals will have gum, tongue, and throat reactions. Be sure to peel the fruit, as most allergic reactions are from contact with the latex in the skin.

Mangoes are very common trees throughout Puerto Rico, introduced via South America around 1750. Today, mangoes are extremely common along virtually all roads on the island because once the fruit is consumed, the large seed is generally thrown out the window of the vehicle or near someone's residence. In other cases, they were vectored by animals that ate the fruit and deposited the seeds randomly.

Mangoes typically flower in the "winter" in Puerto Rico, but flowering is variable from November to July, with fruits maturing May to September. Mangoes are a favorite fruit of many residents of the tropics and most homes have one or more trees in their yards. They are also grown commercially in small groves as a cash crop, often in combination with other fruit trees or shrubs. The flesh of the fruit is juicy and somewhat fibrous and is normally eaten fresh. It can be canned, pickled, or juiced. In the tropics, mangoes are as popular a fruit as apples in the temperate zone. Improved commercial varieties are sweeter, juicier, and less fibrous. Mangoes have carotenoids and possible anticancer properties. Mangoes are now sold widely in health food stores throughout the United States. They are heavily exported worldwide today and often used as a loss leader in the produce section of many U.S. supermarkets. Processed pulp residues can be used for animal feed, and seeds can be ground and used as flour. Mango fruits and leaves are important decorations in eastern cultures. The wood has a variety of uses from furniture, to box construction.

Many other tropical edible plants could have been selected for description, but these are species likely to be seen throughout Puerto Rico. Many more tropical agricultural products can be found at regional produce markets (See app. 2).

For additional reading see Franco et al. 1997, Gómez 2001, Jansen 1973, Leakey and Wills 1977, Levetin and McMahon 1999, Little and Wadsworth 1964, Parrotta 1993, Royal Botanical Gardens Kew 1998, Schery 1975, Simpson and Ogorzaly 1995, U.S. Department of Commerce 1972, and Wadsworth 1997.

Continue

Chapter 4: Freshwater Wetlands and Coastal Ecosystems

Wetland Ecosystems

Puerto Rico has a variety of freshwater and marine wetland ecosystems that range from the seagrass and mangrove ecosystems on the coast, to hundreds of wetlands associated with freshwater rivers and lakes, and even the wetland cloud forests high in the Luquillo Mountains.

What is a wetland? Wetlands are viewed as transitional areas between aquatic and terrestrial systems. According to Mitch and Gosselink (1993), wetlands are areas that exhibit certain distinguishing characteristics such as continuous or periodic presence of standing water, unique wetland soils, saturated soils, and vegetation adapted to or tolerant of saturated soils. Wetlands are not necessarily easily defined because they have a considerable range of hydrologic conditions and because they are found along a transitional gradient between upland (nonwetland) systems or deep water systems such as lakes and the ocean. Swamps, **marshes**, and **bogs** all fit the description of a wetland.

Wetlands in Puerto Rico are among this planet's most biologically productive ecosystems (fig. 47). Wetlands associated with montane rain forests in Puerto Rico contain rare plant and animal species and are species-rich (Lugo and Brown 1988). Runoff from these same mountains provides public water resources for human communities downstream. Once that water reaches the coast, it helps form critically important riverine, coastal marine, and estuarine wetland ecosystems (mangrove swamps, seagrass beds, and coral reefs). These are essential breeding and nursery habitats for many fish, crustaceans, and many other plants and animals in the complex food webs to be described later. Thus, there is a wetlands continuum that starts in the tops of the highest mountains and continues all the way through the coastal zone. A variety of organisms are tied to this aquatic continuum. Some of the species in mountain streams migrate to the ocean for reproduction and then migrate back upstream. They are called catadromous species. An example is the freshwater decapod (shrimp) that lives as an adult in the mountain streams. Its larvae float downstream and develop in the estuaries and ocean of the coast. Small shrimps then migrate in great numbers, usually at night, back up the mountain stream for their adult phase.

Figures 48 and 49 illustrate this wetland zonation continuum. Puerto Rican coastal wetlands are highly valuable wildlife habitats, such as those found at Cabo

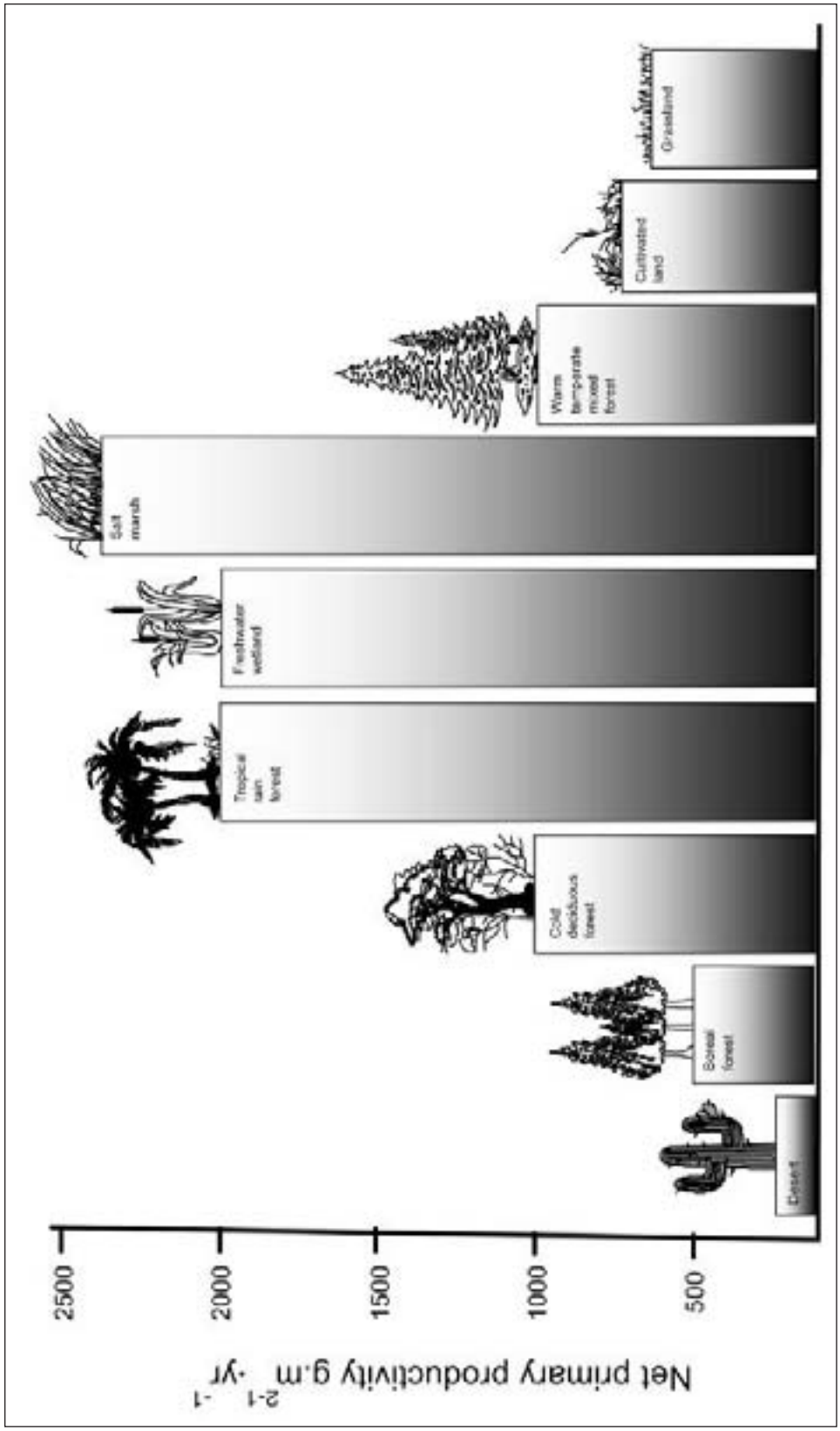


Figure 47—Relative productivity of wetland ecosystems in relation to others. From Newton, 1981.

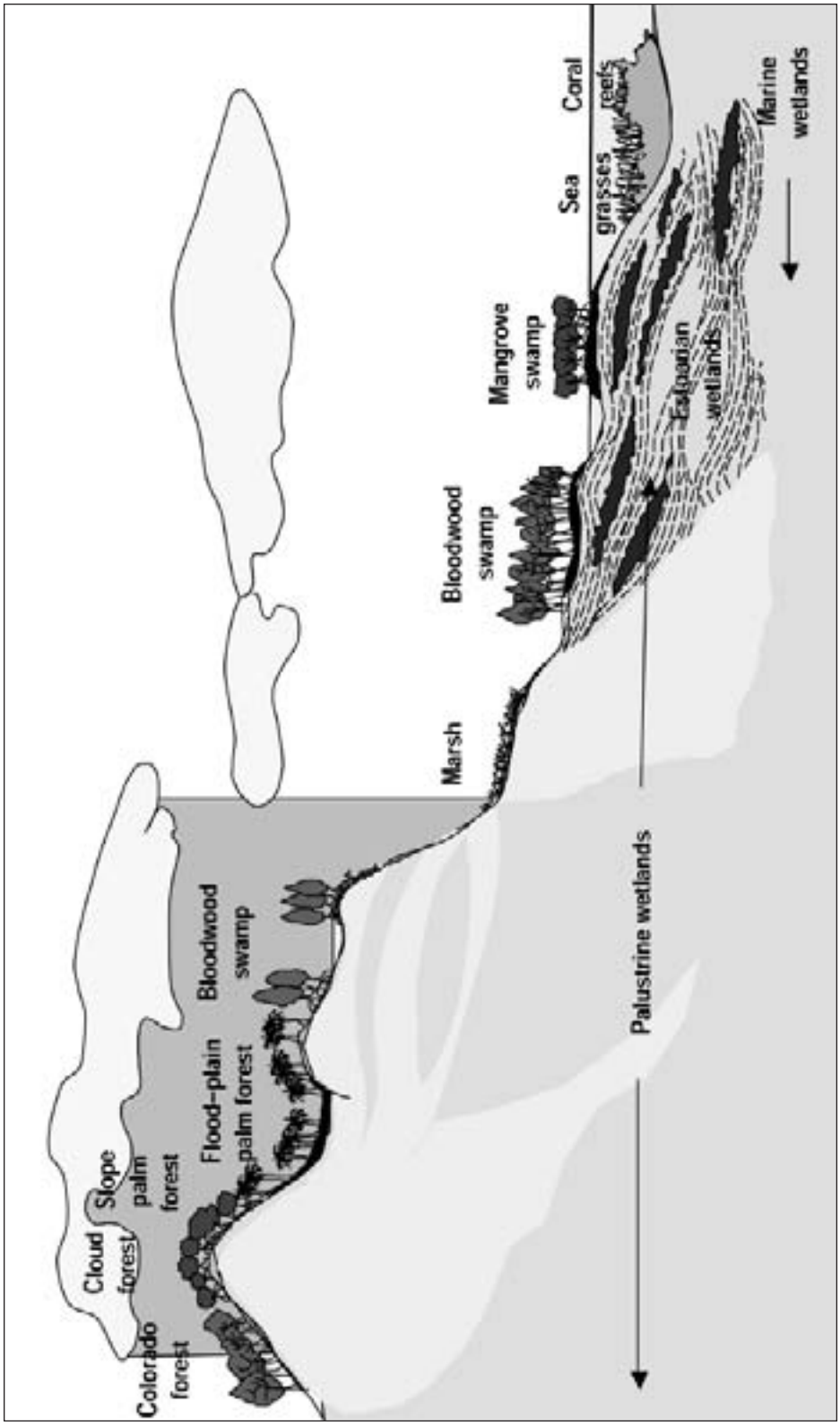


Figure 48—Generalized geohydrologic setting of wetlands in Puerto Rico. Wetland types from Lugo and Brown, 1988.

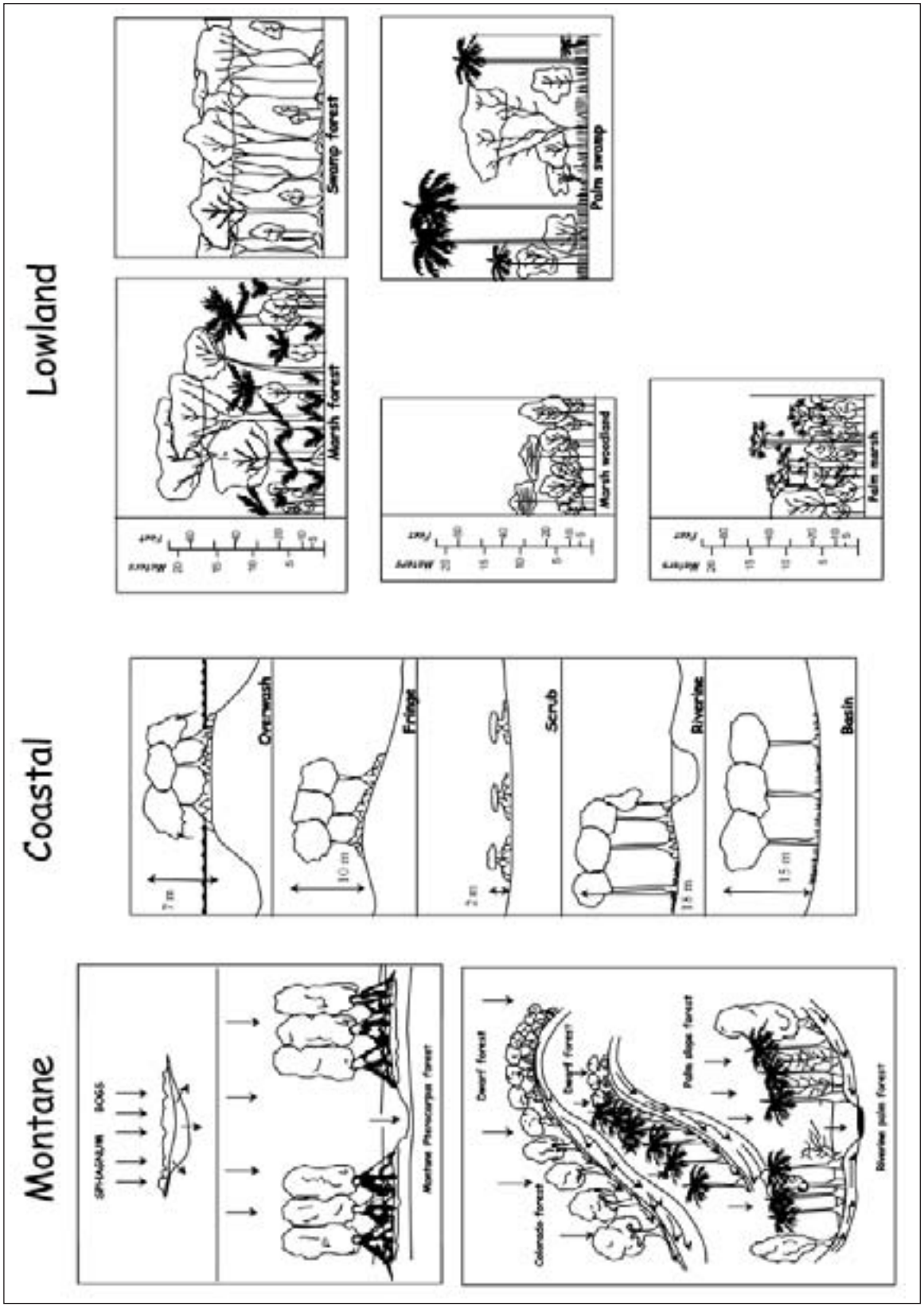


Figure 49—Profile diagrams of representative wetland ecosystems in Caribbean islands.

Rojo National Wildlife Refuge, the Laguna Cartagena National Wildlife Refuge, and the Laguna Tortuguero National Reserve (see app. 2 p. 376).

Throughout Puerto Rico's agricultural expansion period, wetland ecosystems were heavily degraded and destroyed as a result of dredging, filling, draining, **eutrophication**, and use of agricultural fertilizers and pesticides. Unfortunately, no one knows what the original freshwater wetlands coverage was in Puerto Rico at the time of Columbus. There is no realistic set of statistics available to compare current trends in wetland loss or growth in Puerto Rico. To give some perspective to wetland loss, in the continental United States, less than 50 percent of the original wetlands coverage remains today. In Puerto Rico, one low-elevation freshwater coastal swamp forest type dominated by *Pterocarpus officinalis* Jacq.[1] (swamp bloodwood, box 19) is quite rare today (243 hectares or 600 acres). It probably occupies no more than 5 percent of its original range making it deserving of special protection status. As a result of being a coastal plain ecosystem, the pterocarpus swamp has been reduced to only a few small remnant stands. The rest fell prey to coastal development and agriculture. Mangrove forests and **palustrine** freshwater wetlands continue to be at-risk wetland types throughout Puerto Rico.

With cessation of many agricultural activities throughout Puerto Rico, wetlands are starting to redevelop. Part of this unexpected ecological response is related to increases in the abundance of freshwater runoff to coastal areas as a result of reduced usage of water by agriculture for irrigation, and abandonment of maintenance of drainage canals. As a result, freshwater wetlands in the coastal zone are increasing in area. Figure 50 represents the current distribution of wetlands in Puerto Rico.

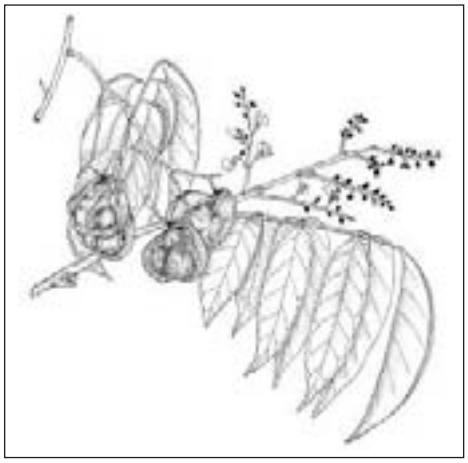
Wetlands serve many functions in nature, and humans derive many benefits from these special ecosystems. The following list identifies some of the values of wetlands, all of which apply to Puerto Rico's wetlands.

- Flood conveyance
- Barriers to waves and erosion
- Floodwater storage
- Sediment control
- Fish and shellfish nursery
- Habitat for waterfowl and wildlife
- Habitat for rare and endangered species
- Recreation
- Water supply
- Food production
- Timber production
- Education/research
- Open space
- Aesthetics
- Enhanced water quality

Wetlands are classified into the following types, according to their position on the landscape and their attributes. At times, wetlands are discrete ecological units and yet, in many instances, they are highly interrelated (fig. 51):

[1] See appendix 1 for Common and Latin names.

Box 19. *Pterocarpus officinalis* Jacq. (swamp bloodwood)



The leaves, stems, flowers, and fruit of *Pterocarpus officinalis* Jacq. (Swamp bloodwood)

This tree is an indicator species for a rare habitat in Puerto Rico, the freshwater swamp. A swamp is a wetland dominated by woody plants (trees and shrubs). Swamps exhibit full or periodic wet soil conditions. *Pterocarpus officinalis* can grow in areas that are slightly brackish and sometimes grows as a natural monoculture in habitats with sizeable yearly water fluctuations. At one point, this tree may have exhibited extensive coverage in wet areas of the coastal plain, but today its habitat and species coverage is greatly reduced, possibly to as little as 5 percent of its original coverage. Its greatest loss is thought to have resulted from land clearing for agriculture, especially for growing sugarcane, and more recently, resorts and golf courses. Swamp bloodwood exhibits a disjunct distribution pattern because there are small populations of this tree in stream borders in the mountains of the Caribbean National Forest. A more complete review of wetland types, their values, and problems in their maintenance is presented in the section on wetlands.

This tree is a Neotropical species ranging from southern Mexico to northern South America, the Greater Antilles, and much of the Lesser Antilles in coastal and interior swamp forests. As a result, it has many common names throughout its large geographic area. It is an evergreen species with alternately arranged, pinnately compound leaves. The oblong leaflets vary from five to nine. A pair of **stipules** subtend the petioles. Its yellow flowers form a raceme and are typical of the pea family in shape. Its pod-like legume fruits are round, dark brown, winged at maturity and measure 3.75 to 5 centimeters (1.5 to 2 inches) in diameter. Flowers form February through September, and fruits develop April to November. It can regenerate via root sprouting should it be damaged by hurricanes or cutting. The fruits float when released, and water and hurricanes may be the primary dispersal agents. Trunks are frequently buttressed and curved, almost snake-like, on the swamp floor. Its bark is smooth to lightly fissured and light brown. The inner bark is blood red, thus the name bloodwood.

Box 19. continued

A.E. Lugo

Bloodwood trees in *Pterocarpus* forest near Humacao, Puerto Rico.

Bloodwood sapwood is yellow-white, lightweight, and weak, thus it has little commercial value except for items such as fishnet floats. Its resins are used for medicinals such as astringents. It can be used as a shade ornamental, especially in moist areas. It can grow into a sizeable tree achieving heights of 40 meters (130 feet) and have diameters up to 90 centimeters (36 inches) above its buttressed lower trunk. Some buttresses can rise 4.5 meters (15 feet) off the swamp floor. It also produces pneumatophores at the ends of buttress development, which aid in gas exchange.

The largest swamp bloodwood in Puerto Rico is located in Luquillo and is 8.6 meters (28.2 feet) in circumference, stands 20.5 meters (67 feet) tall, and has a crown spread of 6.9 meters (22.6 feet). Most bloodwood species are much smaller than this record individual. Because it produces lightweight wood, it probably grows fast. Interestingly, this tree hosts lots of epiphytes, one of which is particularly noteworthy: *Psilotum nudum* (L.) Beauv. (wisk-fern). This is one of the most primitive and ancient of tracheophyte plants on Earth as most of its closest relatives are known only from the fossil record.

In review, bloodwood exhibits a series of adaptations for survival under wetland conditions, which include:

- ➢ Ability to grow under a variety of flood conditions
- ➢ Rapid growth rate
- ➢ Ability to sprout when damaged
- ➢ Production of pneumatophores for gas exchange
- ➢ Buttressed trunk growth for support
- ➢ Tolerance to brackish conditions
- ➢ Seeds that float

For more information on this species, see Álvarez López 1990, Little and Wadsworth 1964, and Weaver 1997.

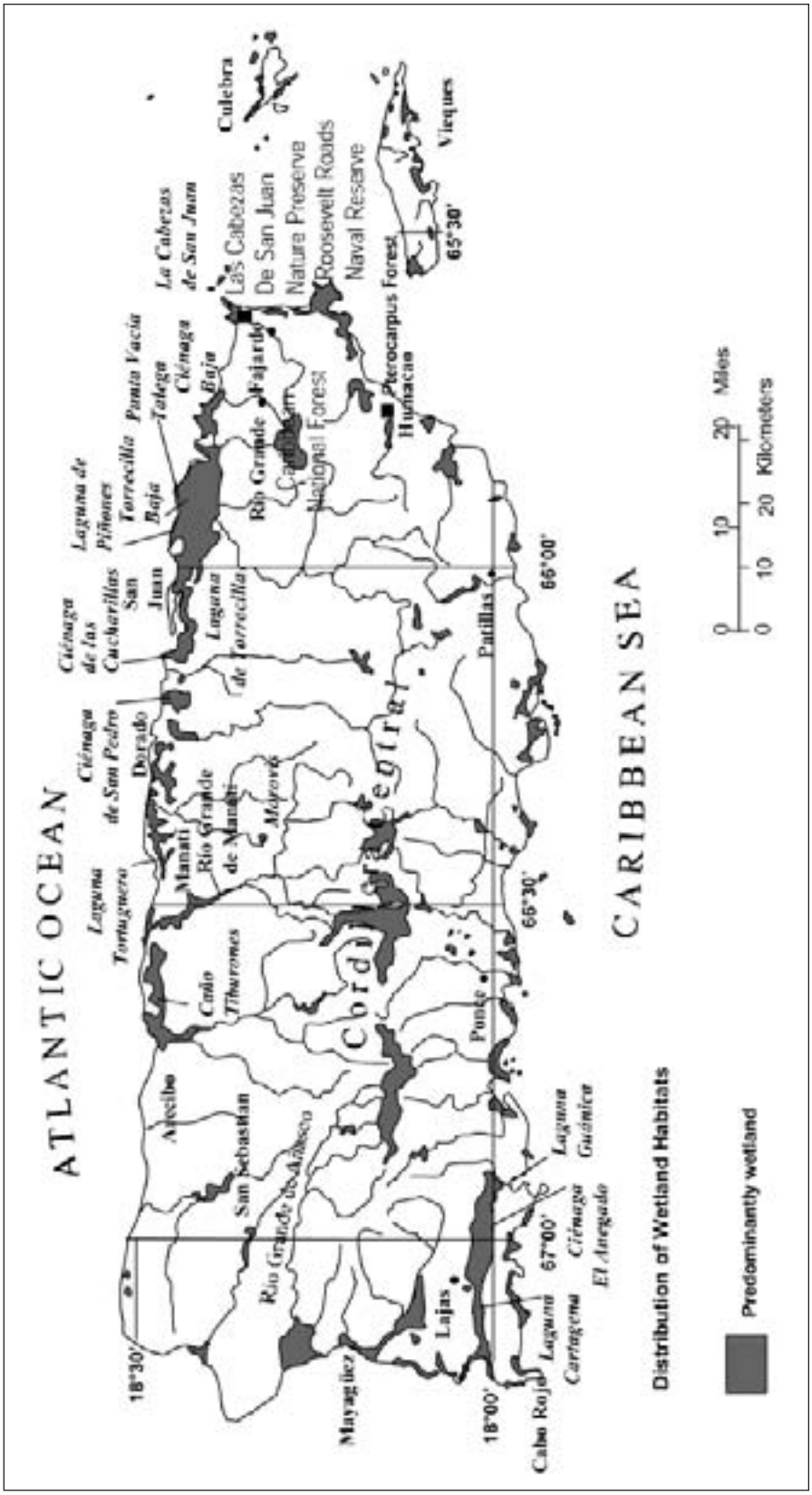


Figure 50—Current wetlands distribution in Puerto Rico.

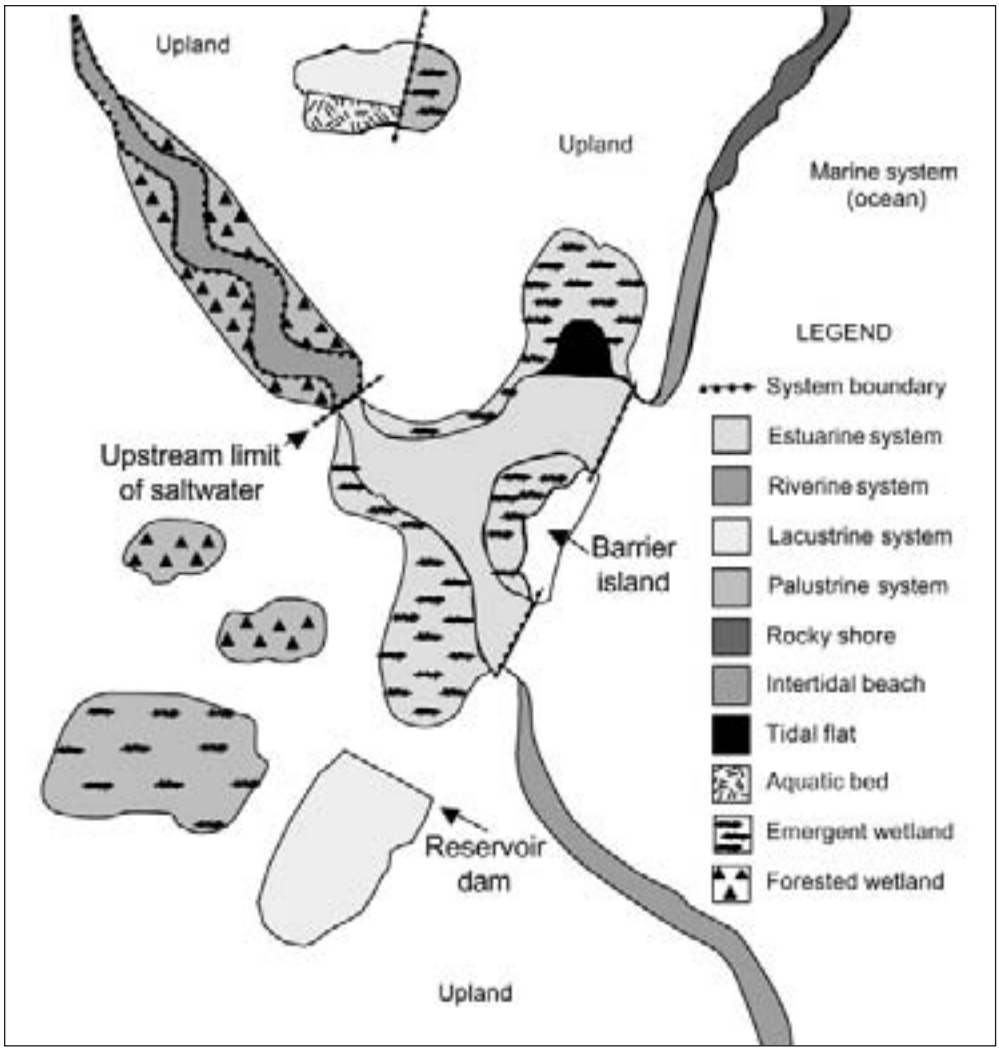


Figure 51—Diagram showing major wetland habitat systems.

Palustrine—All nontidal and tidal freshwater wetlands dominated by trees, shrubs, **persistent emergents**, and/or submerged aquatic plants—for example, marshes, bogs, and swamps. These are shoreward of lakes, rivers, estuaries, or islands in rivers and lakes and wet depressions (fig. 52).

Lacustrine—Permanently flooded lakes, ponds, and reservoirs greater than 8.1 hectares (20 acres) and deeper than 2 meters (6.6 feet). Vegetation is largely emergent and/or **submergent**/floating plants.

Riverine—Channelized wetlands bounded by riverbanks or human-made levees, or where persistent emergents, and/or submergent plants are present.

Estuarine—Tidal habitats and adjacent areas such as **bays**, **sounds**, and lagoons where salinity of the water is >0.5 parts per thousand.

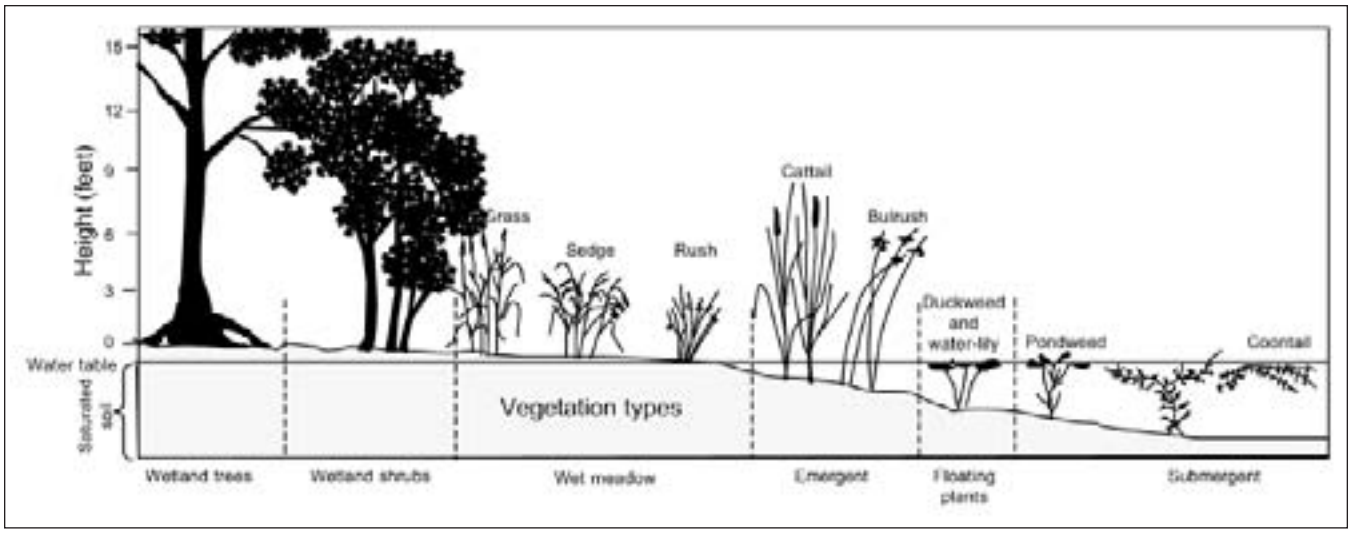


Figure 52—Typical cross section of a pond, lake, or marsh.

Marine—Extends from the outer edge of the island shelf to the high-tide mark on coastal beaches or where trees and shrubs extend to that part of the sea where the water's salinity is greater than 30 parts per thousand.

Plants typical of wetland habitats are generally adapted to the soil and moisture conditions found there. The following types of plants are found in the wetlands of Puerto Rico.

Submergent vegetation—Rooted or fixed plants, completely or largely submerged, such as:

- *Potamogeton nodosus* Poiret. (pondweeds)
- *Hydrilla verticillata* (L. f.) Royle (water hydrilla)
- *Thalassia testudinum* Konig (turtle grass)
- *Najas marina* L. (water naiad)

Free-floating vegetation—Unattached, floating, such as:

- *Lemna perpusilla* Torr. (duckweed)
- *Azolla caroliniana* Willd. (water fern)
- *Eichhornia crassipes* (Mart.) Solms (water hyacinth)
- *Pistia stratiotes* L. (water lettuce)
- *Utricularia gibba* L. (bladderworts)

Floating attached vegetation—Floating leaves, with attachments to bottom sediments, such as:

- *Nymphaea odorata* Ait. (white water lily)

Emergent vegetation—Rooted plants with their principal photosynthetic surfaces above the water, such as:

- *Typha angustifolia* L. (cattail)
- *Phragmites australis* (Cav.) Trin. ex Steud. (reed)
- *Sagittaria lancifolia* L. (arrowhead)
- *Cladium jamaicense* Crantz (sawgrass)

Woody plants—Trees and shrubs that can withstand water exposure to trunks and/or roots during periods of inundation, and soil conditions with reduced oxygen availability include:

- *Pterocarpus officinalis* Jacq. (swamp bloodwood)
- *Rhizophora mangle* L. (red mangrove)
- *Avicennia germinans* L. (black mangrove)
- *Laguncularia racemosa* (L.) Gaertn. (white mangrove)
- *Prestoea montana* (Graham) Nichols. (sierra palm)
- *Cyrilla racemiflora* L. (palo colorado)

Some wetland plant species have very close relationships to soil and water conditions found in wetlands, so much so that they are not found elsewhere; whereas other plants are never found in wetlands. Following are indicator categories for wetland plant species.

Obligate wetland—Species almost always found in a wetland under natural conditions (more than 99 percent probability), such as:

- *Typha angustifolia* L. (cattail)
- *Eichhornia crassipes* (Mart.) Solms (water hyacinth)
- *Thalassia testudinum* Konig (turtle grass)
- *Rhizophora mangle* L. (red mangrove)

Facultative wetland—Species that usually occur in a wetland, but are occasionally found in nonwetland habitat (67 to 99 percent probability), such as:

- *Boehmeria cylindrica* (L.) Swartz (false nettle)
- *Bucida buceras* L. (ucar)
- *Cyrilla racemiflora* L. (palo colorado)
- *Prestoea montana* (Graham) Nichols. (sierra palm)

Facultative—Species that are likely to occur in wetlands or nonwetlands habitat (34 to 66 percent probability), such as:

- *Myrica cerifera* L. (bayberry)
- *Cakile lanceolata* (Willd.) O.E. Schulz (sea rocket)

Facultative **upland**—Species that usually occur in nonwetland habitat (67 to 99 percent probability), such as:

- *Casuarina equisetifolia* L. (Australian pine)
- *Cocos nucifera* L. (coconut palm)
- *Andropogon gerardii* Vitman (broomstraw)

Obligate upland—Species that almost always occur in nonwetlands habitat (more than 99 percent probability), such as:

- *Clusia rosea* Jacq. (autograph tree)
- *Colubrina arborescens* (Mill.) Sarg. (coffee colubrina)
- *Mangifera indica* L. (mango)

Nonwetland—Species that never occur in wetlands, such as:

- *Cephalocereus royenii* (L.) Britton & Rose (pipe organ cactus)

To determine which category a species in Puerto Rico falls into, see the *National Wetland Plant List* (Reed 1988).

Most of Puerto Rico's wetlands are estuarine and palustrine. The most common wetlands on the island are described below.

Palustrine forested swamps—These are characterized by having more than 40 percent of the area in tree cover. They are situated in areas where they are occasionally inundated by freshwater as exemplified by the *Pterocarpus officinalis* Jacq. (swamp bloodwood) forests found at Dorado and Humacao and the high-elevation *palo colorado* and palm forests where *Cyrilla racemiflora* L. (*palo colorado*) and *Prestoea montana* (Graham) Nichols. (sierra palm) are the dominants.

Palustrine emergent marshes—These are dominated by herbaceous plants (25 percent or more cover) and woody plants (up to 40 percent cover). The freshwater inundation in these areas varies from occasionally to regularly with typical species. As exemplified by *Cladium jamaicense* Crantz (sawgrass) and *Typha domingensis* Pers. (cattail) found in marshes at Tortuguero Lagoon. Palustrine marshes are common throughout Puerto Rico. More freshwater marshes are found on the north coast of Puerto Rico owing to higher rainfall amounts and a more extensive river system.

Palustrine aquatic beds—These wetland areas are associated with freshwater rivers, lakes, and ponds. The aquatic beds will exhibit floating and/or submerged attached vegetation in an inundated habitat such as at Tortuguero Lagoon and Cartagena Lagoon. Plants such as *Lemna perpusilla* Torr. (duckweed), *Nymphaea odorata* Ait. (white water lily), *Eichhornia crassipes* (Mart.) Solms (water hyacinth), *Pistia stratiotes* L. (water lettuce), *Potamogeton nodosus* Poiret (pondweed), and *Utricularia gibba* L. (bladderworts) can be present.

Estuarine forested/shrub swamps—These swamps are found along the coast where there are tides, currents, and storm surges that expose the habitats to salty conditions as exemplified by the coastal forests dominated by *Rhizophora mangle* L. (red mangrove) and *Avicennia germinans* L. (black mangrove). Saltwater swamps can be seen in many areas of Puerto Rico, but particularly easy access is available at Piñones, Boquerón, Guánica, and Aguirre. Commonwealth forest cover can be up to 100 percent mangrove species. The lower reaches of Puerto Rico's rivers are estuaries where fresh and seawater mix. Saltwater can flow upstream in these rivers as far as several kilometers. This explains why mangroves extend kilometers (miles) inland on the north coast of the island. They grow as far as the presence of saltwater occurs. Mangroves are the most extensive estuarine forested wetlands. The largest is just east of San Juan in the municipality of Carolina and Loíza.

Estuarine emergent marshes—These coastal marsh wetlands are dominated by herbaceous plants (25 percent or more cover) and woody plants (up to 40 percent cover). They are inundated at different frequencies and intensities by saltwater and will have species such as *Acrostichum aureum* L. (mangrove fern), *Cladium jamaicense* Crantz (sawgrass), *Typha domingensis* Pers. (southern cattail), and *Laguncularia racemosa* (L.) Gaertn. (white mangrove) present. These wetlands are located in areas to the rear of coastal mangrove swamps. Estuarine marshes are uncommon in Puerto Rico because most of these habitats were destroyed by development and past agricultural activities or because mangrove forest species outcompete the salt marsh species in tropical coastlines.

Estuarine coastal flats—These salt flats or *salinas* are frequently positioned to the rear of coastal fringing mangrove swamps on the south coast of Puerto Rico in areas that have access to sea water. The sea water then evaporates and produces high salt concentrations in the water and soils. Species that can be present are *Avicennia germinans* L. (black mangrove), *Salicornia perennis* Mill. and S. virginica L. (glassworts), *Batis maritima* L. (saltwort), and *Sesuvium portulacastrum* L. (sea purselane). When flooded, these form **hypersaline** lagoons.

Estuarine aquatic beds—These wetlands are found in coastal waters and are sometimes referred to as underwater "marine prairies." Most aquatic seagrass beds are likely to have *Thalassia testudinum* Konig (turtle grass) present, but there are six other seagrasses in Puerto Rico's waters, including *Syringodium filiforme* Kutzing (manatee grass), *Halodule wrightii* Ascherson (shoal grass), and *Halophila* spp. (dwarf seagrass). These systems are frequently located in lagoons to the rear of coral reefs and in open shallow waters in front of red mangrove swamps. Large

estuarine beds are also found in the waters of La Parquera, Boquerón Bay, and the bay at Isla Verde. A more detailed review of seagrasses follows.

Estuarine and marine open water reef wetlands—Where reefs are exposed or near the surface, are classed as a wetland. When they are permanently inundated and in deeper water, they are considered deep water systems. A detailed description of coral reefs follows.

Why have we lost so many wetlands in Puerto Rico, the United States, and the world? In most instances the cause was simple habitat alteration. The largest percentage of habitat loss has been associated with agricultural activities. The following list describes the ways wetland ecosystems have been destroyed or degraded in the Puerto Rican landscape. These include both natural and human causes:

Natural causes:

- Sea-level rise
- Hurricanes and other storms
- Erosion

Human causes:

- Drainage for agriculture and mosquito control
- Dredging and stream channelization for navigation and flood control
- Filling for road construction and development of residential, commercial, and industrial sites
- Construction of dikes, levees, dams, and seawalls for flood control, water supplies, irrigation, and from storm protection
- **Effluent** and runoff from agriculture, domestic sewerage, industrial and commercial sites
- Mining of gravel, limestone, sand, and other materials
- Hydrological alterations resulting from road construction, drainage canals, dams, housing, industrial and port construction
- Cutting of mangroves for fuel sources for households and sugarcane mills

Wetlands Regulation

All of the above-mentioned activities were largely unregulated until the past couple of decades. Today, wetlands are protected and require permits if they are to be altered. There is no uniform national or commonwealth wetland legislation. Instead, wetlands are regulated by a series of federal and commonwealth statutes with regulations overseen by four U.S. agencies: the Environmental Protection Agency (EPA), U.S. Fish and Wildlife Service, National Resources Conservation

Service and the U.S. Corps of Engineers (COE). The Puerto Rico Department of Natural and Environmental Resources and the Planning Board of Puerto Rico are the primary commonwealth agencies overseeing wetland protection. Each agency has areas of vested interest and serves as the lead agency overseeing related wetland activities and oversight in these interest areas. Any operations related to dredge and fill projects are generally controlled by the COE who has the regulatory responsibility of issuing or denying construction permits in navigable waters of the United States based on the 1899 Rivers and Harbors Act, Section 404 of the 1972 Clean Water Act, and other legislation (Adams and Hefner 1994). The 404 legislation is the most often used federal legislation protecting wetlands because it regulates discharge of dredged or fill materials into wetlands. Large projects require full permit applications, whereas small projects less than an acre with minimal wetland impact are typically covered on the basis of simple permits issued under the Nationwide Permit System. These permits can be granted at the local field office of the U.S. COE. The EPA has final review and veto power for all permit applications. Full permit applications can be both time consuming and expensive as they have to be reviewed by all concerned oversight agencies and the public. This can lead to lawsuits that attempt to block the project and deny permit application. Frequently, larger and more complex permit applications will require **mitigations** as a part of the permitting process. In those instances, the permittee must minimize wetland impacts and, in some cases, rehabilitate nearby degraded wetlands or construct new wetlands at a different site to meet "no net loss" mandates for our national wetlands management program. Unfortunately, many wetlands have been filled without authorization, but less than half of the illegal fills have been restored. Many field offices of the U.S. COE have inadequate staff to handle the permit applications and the heavy case load investigating illegal activities. This also makes it difficult to enforce compliance with permit conditions when mitigation is required. The same is true with other responsible federal agencies in Puerto Rico.

As indicated previously, Puerto Rico's wetlands are valuable for the benefits derived by humans and for what they supply in terms of **ecological services**. They are especially valuable as wildlife habitat. The salt flats and marshes of southwest Puerto Rico are key to providing large numbers of migratory shore birds with resting and feeding areas as they migrate from North America and the Caribbean and South America and back. Freshwater marshes throughout Puerto Rico provide habitat for nearly 100 species of migratory and resident birds. The mountain wetland forests in the Luquillo Mountains are the last habitats with wild populations of the endangered Puerto Rican parrot. Areas associated with the island's wetlands

provide feeding and nesting habitat for endangered sea turtles and manatees. The majority of commercially important food fish and shellfish come directly from coastal wetlands or wetlands serve as the nursery habitat for these species.

One of the most important freshwater wetlands now protected is the Tortuguero Lagoon National Reserve. It is a spring- and seep-fed wetland with an open-water lake on the north coast, Puerto Rico's only natural lake (fig. 53). There are nearly 700 plants present, and it has a variety of palustrine wetlands, including a tropical bog with insectivorous plants. The description of this flora by Roy Woodbury[2] includes 217 marsh species, 78 grasses, 79 sedges, 17 orchids, and 38 ferns. There were 69 rare and endangered species, 17 endemic to Puerto Rico, 7 endemic to Tortuguero, and 26 species new to the flora of Puerto Rico (Lugo and Brown 1988). This is exceptional biodiversity for an area of 225 hectares (556 acres).

Wetlands are often referred to as the "landscape's kidneys" because they perform valuable functions related to eliminating or storing potentially harmful material. They are also called "nature's supermarkets" because of the extensive and complex food webs present and the vast array of species associated with them. Thankfully, wetlands appear to be on the rebound in Puerto Rico. It is hoped that greater protection will be provided to existing remnants and newly developing wetlands. Wherever possible, **reclamation** and mitigation procedures should be applied to permitted development sites, especially throughout the coastal areas. This is especially so for the north coast where most palustrine freshwater wetlands are located owing to the higher concentration and length of rivers there. The north coast is undergoing rapid and intense urbanization, and, because of all of the vital services supplied by the wetlands, it is essential that wetlands not be destroyed or degraded in this area of rapid growth. They are essential to maintaining water quality in the rivers, bays, estuaries, and open sea associated with the entire Puerto Rican coastal zone. Puerto Rico can ill afford to lose its wetlands. Wetlands in Puerto Rico are especially vulnerable because they are fairly small, interrupted in distribution, and often located in areas that people want to develop or alter in some way. Historically, wetlands have been looked upon as wastelands. Puerto Rico's wetlands need better oversight and protection because they represent habitats of concern and are not wastelands. Once gone, they will likely be gone forever, and with their disappearance will follow the loss of all those free ecological services and the many species they support.

[2] Woodbury, Roy, unpublished material available through A.E. Lugo.

L. Miranda Castro

Figure 53—View of Lake Tortuguero wetlands.

Many people, including professional scientists and elected officials, think that our problem of wetlands loss is no longer much of an issue because it is now possible to rehabilitate degraded wetlands or make totally new artificial wetlands. A report issued by the National Research Council (NRC 2001) indicated that current approaches designed to guarantee "no net loss" of U.S. wetlands are basically a failure. Artificial wetlands are a poor substitute for the real thing. Although 17 000 hectares (41,990 acres) of wetlands were created (on paper) between 1993 and 2000, many projects were never done, or only partially completed. Others had no postconstruction monitoring to verify they were working as designed. Why? The NRC says that the projects were not being adequately tracked. They also indicated that the difficulty in designing projects that require intermittent waterflows results in different mixes of plants and animals when the water regime is not correct. The NRC further indicated that wetlands difficult to reproduce, such as bogs, should be left alone. They also recommended:

- Permits be closely tracked
- Continuing research on design and reclamation be maintained in order to find out what types of wetland projects work
- Stricter enforcement standards be devised for all projects
- Improved long-term monitoring be implemented
- Permitting be at the watershed level, not on a simple project-by-project basis

Should these recommendations, especially the watershed approach, be implemented, it will require much better cooperation, coordination, and management by all agencies involved in the wetlands management program.

For further reading see Álvarez-López 1990, Cowardin et al. 1979, Dahl 2000, del Llano 1988, Frayer et al. 1983, Little and Wadsworth 1964, Lugo and Brown, 1988, Mitch and Gosselink 1993, Newton 1981, Reed 1988, Tiner 1984, U.S. Corps of Engineers 1978, U.S. Department of the Interior 1990.

Coastal Ecosystems

Puerto Rico lies slightly south of the Tropic of Cancer and environments are tropical owing to proximity of constantly warm ocean water and air masses. The warm waters make environmental conditions suitable for large numbers of tropical marine organisms, many not found above the Greater Antilles.

The surrounding ocean water plays an important role in moderating the climate of the island. Typical of a tropical climate, there are two seasons: a warm rainy season from May through September, with temperatures in the 30 ºC range (mid to high 80s ºF) and a mild dry season, October through April, with temperatures averaging in the mid to high 20 ºC (70s ºF). Occasionally temperatures drop into the low 20s ºC (70s ºF). Temperatures are rarely lower, except in the mountains. During these periods, there is only a slight change in water temperature.

As is true of most inhabited tropical islands today, Puerto Rico has experienced the pressures of agriculture, population growth, development, and construction in the entire coastal plain area (fig. 54). As a result, many natural habitats typical of the coastal fringe of the island and adjacent waters exist in a somewhat disturbed condition, or are heavily modified to the point where they are no longer natural. Coastal marine habitats constitute only 10 percent of the world's ocean area, but the coastal habitats contain an estimated 90 percent of all known marine species. As with many ecological systems, beach systems are zoned. Figure 55 illustrates the zones found in a typical beach front, and app. 3 recommends a location for viewing coastal habitats.

Sandy Beach Habitats

Rachel Carson (1955) in *The Edge of the Sea* wrote:

> The edge of the sea is a strange and beautiful place. All through the long history of Earth it has been an area of unrest where waves have broken heavily against the land, where the tides have pressed forward over the continents, receded, and then returned. For no two successive days is the shore line precisely the same. Not only do the tides advance and retreat in

J. Colón

Figure 54—Intensive coastal zone development.

their eternal rhythms, but the level of the sea itself is never at rest. It rises or falls as the glaciers melt or grow, as the floor of the deep ocean basins shifts under its increasing load of sediments, or as the earth's crust along the continental margins warps up or down in adjustment to strain and tension. Today a little more land may belong to the sea, tomorrow a little less. Always the edge of the sea remains an elusive and indefinable boundary.

Coastlines throughout the world are being affected both from human assaults as our population expands, and as a result of sea level rise associated with **global climate change**. Many areas are experiencing serious erosion problems as a result of the rise, whereas others are seeing natural coastal ecosystems degrade or disappear as a result of development pressures. These problems are important issues that need attention in Puerto Rico. Puerto Rico has major sand dune management problems because they are viewed as cheap, easy-to-access sources of sand for use in construction.

Sandy beaches and dunes make up only a small percentage of Puerto Rico's 518-kilometer (311-mile) coastline. Many tropical beaches are composed of carbonate sands produced from the disintegration of various shelled animals, **hard corals**, and **coralline algae**. There is very little sand on Caribbean islands because they have small **insular shelves** causing much of the sand to be lost to deeper areas of the sea. Puerto Rico has few long, straight beaches. Luquillo is the largest, and the reason it has sand is because it is locked in a bay. The same is true of Boquerón

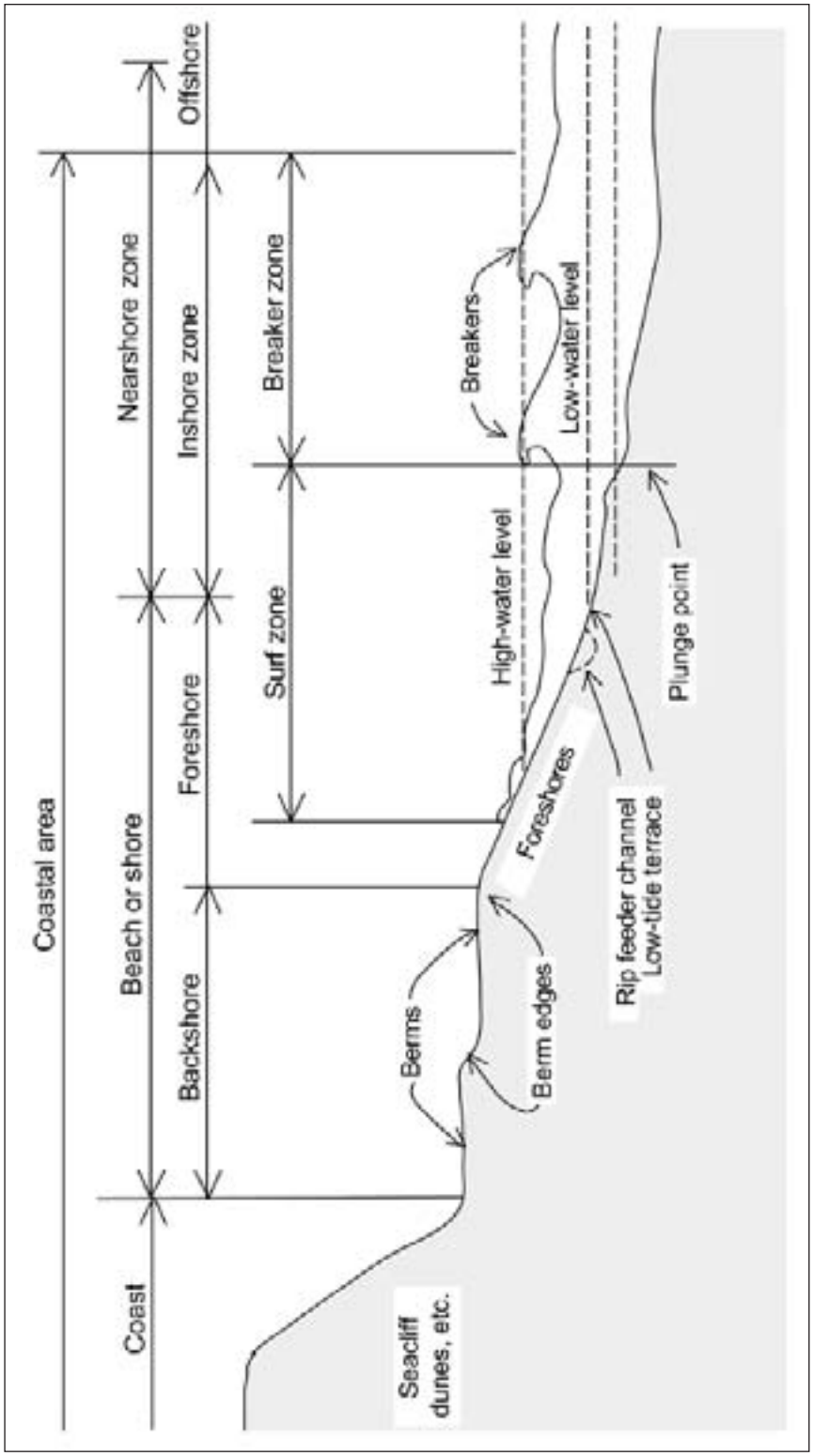


Figure 55—The anatomy of a typical beachfront.

Bay and its large sandy beach. Puerto Rico's north coast has more sandy beaches than does the south coast owing to its geographic configuration. Many of the shallow coastal sand deposits provide the necessary substrate for development of highly productive seagrass ecosystems.

Coastal sand systems appear to be all but lifeless, but, in fact, they are vital, constantly changing, and quite interesting, ecologically. They are much more than just a barrier to the sea. On open wet sandy shorelines, most of the inhabitants live under the sandy surface in tubes and burrows or in spaces between sand grains. They surface when waves pass over their habitats. This guide is not going to review the variety of plants and animals likely to be encountered in wet and dry portions of the sandy **littoral** (intertidal) zone, other than to indicate that there are a variety of worms, crabs, sand dollars, clams, amphipods, burrowing anemones, protozoans, fungi, bacteria, and plankton (**phytoplankton** and **zooplankton**), among others present. The main focus of this section will be to describe the higher plant species and communities likely to be encountered in the **supralittoral** zone, that is, from the high tide line into the adjacent sand dunes, and the outer true terrestrial zone, which may be forest covered.

The physical nature of a beach determines the type of vegetation present. Beaches and dunes are rarely permanent natural structures, they are constantly shifting and migrating based on wind, currents, tides, storms, and **anthropogenic** activities. Beaches build up when the weather is calm and retreat when exposed to large storm events. They are very dynamic habitats. Four factors affect beach stability: shape and orientation of the beach, sediment sources, wave energy, and sea level rise. At any given time, a beach is in dynamic equilibrium. Beaches and dunes are built by wind, waves, and currents, and then stabilized by specially adapted vegetation. If vegetation is present, it responds as the sand system is altered. Beach plants are adapted to colonize the shifting sands as long as the rate of sand migration is not too rapid. Many have spreading roots like *Coccoloba uvifera* L. (sea grape). They also have large leaves, which can reduce windspeeds and cause sand to drop at the base of the tree. Many grasses and herbs develop widespread rhizomes that promote extensive clonal populations and thus are referred to as dune builders.

Key features to look for in sandy beach organisms are adaptations that protect stems and leaves and help to reduce drying effects of wind, exposure to salt, and physical abrasion by sand. They include:

- Asexual methods of reproduction via rhizomes, runners, and stem tipping

G. Miller

Figure 56—General view of a rocky beach front in the Piñones Vacia Talega area.

- Protection from high heat (thick leaves, heavy cuticle, dense pubescence, rolled leaves, leaf position)
- Xerophytic water conservation adaptations (succulent stems, pubescence, heavy cuticle, leathery leaves, waxy leaves, and small leaves)
- Sand collection mechanisms (large leaves, fibrous roots, and multiple stems)
- Salt tolerance (sculptured growth form)

In general, beaches and dunes are zoned based on the degree that these environmental stress factors affect the plants present. The three general zones are open beach, fore dune, and rear dune. Each of these has a group of plants that produce a community typical of these zones (fig. 56).

The open beach supralittoral zone is a zone of extremes: cool/hot, salt/fresh, wet/dry. As a result, it exhibits low productivity because few organisms are adapted to the range of these variable conditions. This is the "dry" zone that most people will likely put their beach towel on when they go to the beach for recreation. Most of the organic matter present is deposited there by high tides or wind action. This zone is physically unstable, thus difficult for most terrestrial plants to inhabit. Fruits and seeds will be cast into the zone, and seedlings may become established or they may be removed owing to shifting wind and waves (fig. 57).

If the beach accumulates sand deposits, one or more dunes will likely develop. The first dune is called the fore dune. Fore dunes are also areas of extremes:

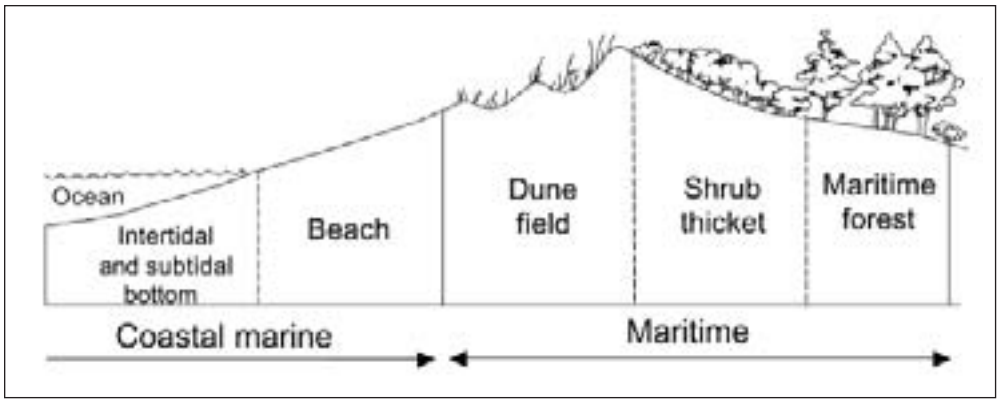


Figure 57—Generalized view of a sandy beach.

cool/hot, salt/fresh, wet/dry conditions, but they are at least semistable; thus plants can succeed in establishing permanent populations. Species diversity will be low and most organisms will occupy specific zones based on environmental factors at work on that habitat. Dunes typically have a couple of beach grasses and associated forbs present adapted to salt spray exposure and sand blasting, and exhibiting rhizomatous growth. They are salt tolerant and unharmed by occasional submergence or sea water overwash. Their seeds generally float. The species present can tolerate strong winds either by producing flexuous stems or growing prostate on the sand's surface. Plants typical of this zone in Puerto Rico are:

- *Sporobolus virginicus* (L.) Kunth. (beach dropseed or salt grass)
- *Paspalum vaginatum* Swartz. (sea paspalum)
- *Spartina patens* (Ait.) Muhl. (sea grass)
- *Cakile lanceolata* (Willd.) O.E. Schulz (sea rocket)
- *Canavalia maritima* (Aubl.) Thouars (sea bean)
- *Ipomoea pes-caprae* (L.) R. Br. (beach morning glory)
- *I. stolonifera* (Cyrillo) Poiret (fiddle-leaf morning glory)
- *Sesuvium portulacastrum* L. (sea purselane)
- *Cenchrus echinatus* L. (sandspur)

All of these species are sand stabilizers and generally extend into the supralittoral open beach from the fore dune via rhizomes or runners. If the fore dune is fairly stable, it may develop an evergreen hedge dominated by xerophytic woody scrub species. The "hedge" is rarely over 0.5 meter (1.5 feet) high. Typical species are:

- *Borrichia arborescens* (L.) DC. (sea ox-eye aster)
- *Chrysobalanus icaco* L. (coco plum)

- *Smilax coriacea* Spreng. (cat briar)
- *Coccoloba uvifera* L. (sea grape)

At the top of dunes, other woody species may include:

- *Plumeria alba* L. (frangipani)
- *Anthacanthus spinosus* L. (beach spine)

To the rear of the dune, especially if high and stable for an extended period, dry seasonal evergreen woodland may be present, including:

- *Scleria microcarpa* Nees (beach rush)
- *Calophyllum brasiliense* Camb. (Santa-María)
- *Annona glabra* L. (pond apple)
- *Coccoloba uvifera* L. (sea grapes)

In depression areas where salt content is high owing to evaporation, **halophytic** (salt-tolerant) species will dominate, such as:

- *Salicornia bigelovii* Torrey. (glasswort)
- *Batis maritima* L. (saltwort)

Trees and shrubs may be present naturally in these zones, or planted to reduce beach erosion. Woody species typical of beaches throughout Puerto Rico are:

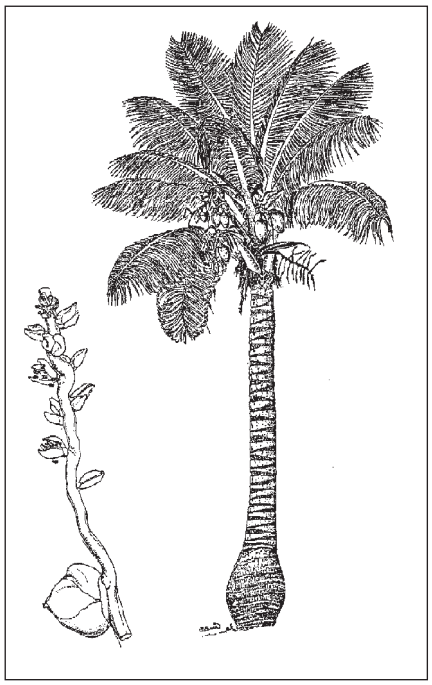
- *Cocos nucifera* L. (coconut palm)
- *Suriana maritima* L. (baycedar)
- *Casuarina equisetifolia* L. (Australian pine)
- *Coccoloba uvifera* L. (sea grapes)
- *Conocarpus erectus* L. (buttonwood mangrove)
- *Bursera simaruba* (L.) Sarg. (Gumbo limbo)
- *Chrysobalanus icaco* L. (coco plum)
- *Dalbergia ecastaphyllum* (L.) Taubert (chicken wood)

A profile of three trees typical of the beach community follows, including *Cocos nucifera* L. (box 20), *Coccoloba uvifera* L. (box 21), and *Casuarina equisetifolia* L. (box 22).

All of these species can colonize and maintain themselves on sandy shorelines. As indicated, they are salt tolerant and may exhibit salt and/or **wind shearing** or training. In other words, due to salt effects (**chlorosis**) on plant tissue, or sand/wind blasting causing death of windward buds and tissues, the plant exhibits a growth form that appears sheared or wind trained. The parts of the plant on the windward side grow little, whereas those on the leeward (protected) side grow more. This growth form is typical of beaches and mountains. Generally, salt spray is the most

Continue on page 186

Box 20. *Cocos nucifera* L. (coconut palm)



View of fronds, trunk, flowers, and fruit of *Cocos nucifera* L. (coconut palm)

When you hear the words "tropical island," 8 out of 10 times what comes to mind are white sandy beaches studded with palm trees. The coconut palm (*Cocos nucifera*) belongs to the Palmaceae family and is distributed throughout the coastal areas of the tropics and semitropics. Coconut palms are not native to Puerto Rico. They are thought to have been introduced to the Caribbean islands in the early colonial period. Their origin is thought to be Indo-Malayan. Coconuts are not only tall beautiful trees, but they are also very economically important. They are an all-purpose tree in that all parts have value. Often called "trees of life" on tropical islands, they rank as one of the world's top 10 most useful trees. Simpson and Ogorzaly (1995) quoted a southseas proverb, "He who plants a coconut tree, plants food and drink, vessels and clothing, a habitation for himself, and a heritage for his children." Their trunks can be sawed into termite-resistant boards for construction. Whole trunks are used for marine posts and can be lashed together to make rafts. Their giant leaves make excellent thatch and fencing, and their fruits provide both solid and liquid foods and oil. One of the most popular drinks in the tropics is cold coconut milk and sold as "*cocos fríos*" (liquid endosperm) along roads. Once solidified, the endosperm becomes the white coconut meat used for confections. The shell of the nut (coir) is often made into rope, floor mats, industrial filler, and road and riparian zone riverbank stabilizers. The hard seed coat is crushed and used for charcoal filters. Their immature flowers can be baked and eaten by humans or used for animal food. Many people plant them as ornamentals around their homes. This tree supplies jobs to many people in the tropics, especially in countries like the Philippines, Indonesia, and Mexico.

Box 20. continued

G. Miller

An "helado de coco" vendor in the Plaza at Guayama.

Coconuts can be seen throughout most of Puerto Rico's sandy beach zone, throughout much of the coastal plain, near roads, homes, and parks. Large commercial plantations have all but disappeared in Puerto Rico. Coconuts are regularly harvested by local drink stand operators and confection makers. Before leaving Puerto Rico, try a local ice cream favorite—*helado de coco*—sold on street corners from push carts.

Coconuts require a warm, wet climate with little diurnal or yearly temperature swings. In dryer areas, general size and fruit production decline. They grow best in deep, well-drained, sandy loam soils and can tolerate some exposure to saltwater, such as storm surges along coastal beaches. Coconuts will be seen well into the mountains of Puerto Rico and are common up through 800-meter (2,624-foot) elevations, especially along roads with nearby houses where they are planted for their fruit production and beauty.

Coconuts are majestic trees with some of the largest leaves (fronds) known to the plant world (up to 6 meters or 20 feet long). They have a unique growth form with 24 to 36 fronds growing out of the tall branchless trunk. The fronds are compound with many pairs of leaflets. About a dozen new fronds are produced yearly. When a frond dies and falls, it produces a scar on the tree's trunk. To age palms, count leaf scars and divide by 12. Trees in the tropics cannot be aged by counting annual growth rings in the secondary xylem (wood). Palms are unusual in that they are monocots. Most monocots are herbs with a different growth strategy than trees from dicot families. A coconut tree trunk is actually composed of overlapping sheathing bases of the fronds. If the

Box 20. continued

growing tip is damaged or eaten, the tree will die. Coconut trees may live for decades.

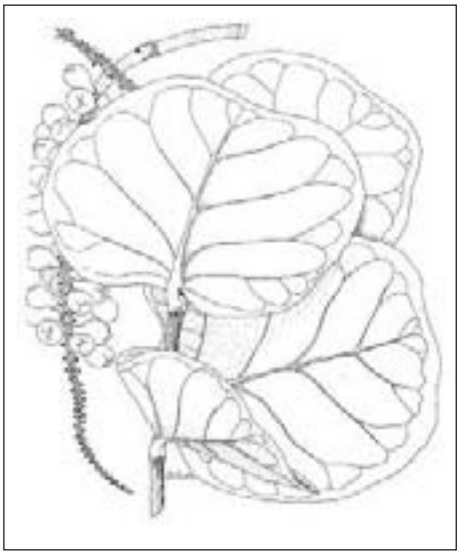
Coconuts begin flowering around 6 years of age, and at maturity may produce 40 to 100 nuts per year. The fruits grow for about 6 months and then take another 6 months to ripen, at which time they change from green to yellow, and when they fall they may be brown. If the nuts fall into the sea, they will float for months and sea currents are one of their primary vectoring agents. They may travel thousands of miles before being lodged on a foreign beach. They are easily germinated and may geminate while still on the tree. The young are frequently observed developing on the beaches of the island. Growth is related to nutrient and water relations in the soil. Under good conditions they may grow to a height of 30 meters (100 feet). They grow best in open habitats but can be used as a canopy species in a multicrop agroecosystem. Puerto Rico's largest coconut palm is located in Carolina. Its height is 28 meters (92 feet), it has a crown spread of 5.3 meters (17.4 feet), and its circumference is 121 centimeters (48.5 inches).

Root development is from the large swollen trunk base. Because they typically grow in wet places, deep taproots do not form; instead they are supported by a vast network of adventitious fibrous roots. They radiate for several meters from the base and do an excellent job in supporting the tree, even in hurricane winds.

A number of insects attack coconuts, such as scarab beetles, scale insects, and moths. The worst infection is a condition called lethal yellowing, which is caused by a mycoplasma-like organism. Many plantations have been destroyed in the Caribbean in the last few decades. The crown of the tree drops off and the dead trunk remains, producing an appearance of a tree killing zone. Once infected, the tree dies within 5 months. Many resorts that featured beautiful palm-lined beaches have had major infections including Miami Beach, Key West, Palm Beach in the United States, and on beaches in Cuba, Jamaica, the Cayman Islands, and Mexico. Fortunately, there are resistant varieties being used to replant the devastated populations. Puerto Rico has had lethal yellowing infections, and the dead trunks can still be observed standing at Caña *Gorda* on the south coast in the Guánica Forest. Puerto Rico has 13 native or naturalized species of palms, two of which are endemic.

For more information on this species, see McCoy 1988, Moore 1948, Parrotta 1993, and Royal Botanic Gardens at Kew 1998.

Box 21. *Coccoloba uvifera* L. (sea grape)



The leaves, flowers, and fruit of *Coccoloba uvifera* L. (seagrapes).

As you walk along most beaches in Puerto Rico you are likely to encounter trees that appear to have large clusters of green or purple grapes hanging from their branches. This tree is sea grape. It is a Neotropical species that occurs throughout coastal Bahamas, southern Florida, the West Indies, Central America, and both coasts of tropical South America. It has been introduced to various beach habitats in the Pacific region. It most often grows on sandy shorelines and dunes, but it can also be found on rocky shorelines such as the limestone outcrops in the Guánica Forest. Heavy winds may cause the tree to grow prostrate to the ground surface or as a bush. Often, it will have partially brown leaves, the result of exposure to salt spray.

It is easily recognized by the edible grape clusters and large, thick, alternate, orbicular leaves. Its trunk is rarely straight because its habitat is windswept. It is an early colonizer of shorelines and has high tolerance to salt spray exposure. It rarely grows away from the coast, although today it is being grown as a horticultural species around homes, businesses, public parks, and highway medians. It grows best in full sunlight.

Sea grapes have separately sexed trees (dioecious) and begin to flower at about age six. The fragrant flowers and fruits develop as terminal racemes, and their flowers are green-white. Fertile flowers mature into a fleshy edible fruit. They flower and fruit throughout the year. The fruits and seeds are dispersed by frugivorous birds and bats. Germination and new seedling growth can occur throughout the year.

Growth is strongly influenced by exposure to wind and salt spray, and many individuals may be misshapen and show wind shearing. Sea grapes rarely exceed 18 meters (60 feet), most are less than 7.6 meters (25 feet). The largest sea grape in Puerto Rico is in Guánica. It is 9 meters (29.5 feet) tall,

Box 21. continued

has a crown spread of 8.5 meters (28 feet), and has a circumference of 124 centimeters (49.5 inches).

The fruits of sea grapes are edible as a raw fruit, and are used for jellies, wine, honey, and native medicines. Tannins can be extracted from the bark, and the wood can be used for firewood, charcoal, and posts. Its primary value is ecological for beach stabilization along sandy coastlines. *Coccoloba uvifera* is native to Puerto Rico, and there are 13 other species in the genus; four are endemic to Puerto Rico.

For more information about this species, see Craig 1984, Little and Wadsworth 1964, and Parrotta 1994.

Box 22. *Casuarina equisetifolia* L. (Australian pine)

Another introduced coastal tree very likely to be encountered on the beaches of Puerto Rico is *Casuarina equisetifolia* L., commonly called Australian pine. Its common name relates to the fact that this tree grows in Australia, but it is not a pine. It is not even a gymnosperm. Casuarina is a fast-growing dicotyledonous evergreen tree requiring full sunlight that achieves heights of 45 meters (148 feet). Trees in Puerto Rico rarely exceed 30 meters (100 feet), although the tallest tree reported in Puerto Rico is a 43-meter (141-foot) Australian pine. Now distributed throughout much of the tropical world's sandy coasts, it is extensively used for reforestation on degraded lands and as a plantation monoculture from China to Africa and the Caribbean. It is widely planted throughout Puerto Rico's lower elevations, especially along the coast. They are often used to create windbreaks.

The stems and fruit of *Casaurina equisetifolia* L. (Australian pine)

Australian pine does not develop a wide full crown; rather it is slender and open, with drooping branches. One of its most distinguishing characteristics is

Box 22. continued

that the stem looks remarkably similar to that of the ancient genus *Equisetum* (horsetails). The stems are segmented and form a twig that appears to be needle-shaped, much like a true pine needle. Actual leaves are very small, scale-like, whorled at nodes, and less than 2 millimeters (1/32 inch) long. The main photosynthetic surface is actually the tree's twigs, which remain evergreen and are 22 to 45 centimeters (9 to 18 inches) long. Flowering and fruiting goes on throughout the year. Separate male and female flowers protrude from the scales on the same plant (monoecious). The pointy fruit is a multiple that produces a cone-like structure of achenes; which releases one-winged seeds at maturity. The tree and fruits are sometimes used for Christmas decoration.

The tree's main value is for beach stabilization, windbreaks, poles, posts, charcoal, and fuel wood. It produces a hard wood that cracks and splits easily. Its bark produces tannins, dyes, and home medicines. Because of its pine-like features, it is often planted as a horticultural species around homes and in parks. Australian pines in Puerto Rico have recently been attacked by a blight. Like leguminous species, *Casuarina* has nodules with nitrogen-fixers, which allows it to grow in degraded soils; thus it can be used in soil reclamation projects. Young trees are very resistant to wind damage and can survive hurricane force winds.

For more information on this species, see Little and Wadsworth 1964, Midgley et al. 1983, National Research Council 1984, and Parrotta 1993.

critical environmental factor limiting adaptability of plants in coastal communities both as related to salt buildup in the soil and tissue chlorosis in the aerial organs.

In Puerto Rico, the only significant sand dunes are on the northern coast because it is a high-energy coastline. Coastal dunes range from small sand mounds to dunes 15 meters (50 feet) tall, such as those at Isabela. Unvegetated dunes can be destroyed by wind or waves, the same forces that produced them. Coastal dunes build when sand is blown or washed into areas with vegetation. As long as the rate of sand deposition does not exceed that of the plant's ability to grow, the dune will be stabilized. Dunes are critically important because they act like bulwarks against surging sea waves and as a source of sand to replenish natural beach erosion. Unfortunately, many dunes have disappeared in Puerto Rico owing to illegal poaching of sand for commercial activities, as well as permitted overextraction activities

G. Miller

Figure 58—The giant sand dunes of Isabela showing the effects of illegal removal of sand.

(fig. 58). For a review of coastal zone and dune management issues, see Bush et al. (1995), *Living With the Puerto Rico Shore*. This is one in a series of books done in cooperation with Orrin Pilkey of Duke University, considered by many the United States' authority on human impact on the coast.

Dunes and beaches are important during hurricanes because they serve to dampen large waves and tidal surges when they interact with sand and wash it into the sea. To gain the benefits of dunes, they must be protected. Activities that degrade sand beaches and dunes include:

- Sand removal for construction and fill
- Flattening of dunes for building construction: homes, condominiums, and hotels
- Constant foot traffic in vulnerable areas that kills vegetation or breaks the dune line
- Hard stabilization projects such as jetties, sea walls, and groins
- Development of harbors, marinas, and docking facilities
- Dredging of channels that can affect long shore littoral drift of sand
- Oil spills

All these activities result in removal of the plants/communities and, in many cases, the sand itself, causing the loss of filtering, stabilization, protection, and productivity provided by the beach ecosystem. Puerto Rico's coastline is experiencing shoreline retreat (beach erosion). In some places it is negligible, such as on rocky

shorelines. On the other hand, on some of the best tourist sandy beaches, such as those at Boquerón or the Condado, retreat can be measured in meters after major storms.

Rocky Shoreline Habitat[3]

Rocky shorelines are found in many areas of Puerto Rico. Although the mean tidal fluctuation is only 0.5 meter (1.5 feet), exposed rocky shoreline areas of the Pleistocene reef formation can produce an intertidal platform up to 50 meters (165 feet) wide. This area of the coast exhibits unique zonation patterns and morphological, physiological, and behavioral adaptations by organisms present in this stressed environment. The upper zones and organisms are subjected to the greatest stress. Rocky shores are in direct contrast to sandy shores by the almost total lack of sand. As is the case with sandy shores, pristine unspoiled rocky shores are rare today. A rocky shore may exhibit rock that clearly shows its origin as coral with the elongated grooves representing each coral cup through time. The horizontal lines are basal plates, or the bases of the cups, as the **polyps** extended the cups by building new floors, constantly enlarging the size of the colony. Other rocky shores are beach rock formations resulting from cementing of sand, shell fragments, and precipitation of calcium carbonate coming into the sea from drainage out of the karst region.

There may be a number of *Chitons* and snails on the coral chunks. At the upper margins of this beach, in the **detritus**, many small hermit crabs in snail shells will likely be found. These are juvenile *Coenobita clypeatus* (purple-clawed land crabs). They are still located near the sea, but when they reach maturity, about 2 centimeters (three quarters of an inch) and larger, they will move inland, to return to the sea only to spawn. They are able to retain water inside their adopted shells to keep their gills moist. This lung-like apparatus allows them to carry on terrestrial respiration. These are the crabs sold in the United States in pet shops. Typical rocky zones and their species are described in this section. Their position is based on daily tidal fluctuation, which in Puerto Rico is only 0.5 meter (1.6 feet). Rocky shorelines provide one of the best natural stages for observers to see species zonation based on a series of physical and biological limiting factors at work on this ecosystem that is transitional between land and sea. Many of the organisms will exhibit special adaptations for maintaining themselves on this high-stress environment such as holdfasts, suckers, and glue.

[3] See appendix 2 for dangers to be aware of on rocky beaches.

Rocky beach conditions that will be present are:

- ➢ Hard stable substrate
- ➢ Water-wet/dry
- ➢ Salinity-salty/fresh
- ➢ Oxygen-air/water
- ➢ Wave energy-calm vs. storms
- ➢ Predation-aquatic/terrestrial
- ➢ Interspecific competition-*Balanus* and *Chthamalus*
- ➢ Temperature-hot/cool
- ➢ Human activities
- ➢ Oil spills
- ➢ Industrial effluents-air and water
- ➢ Collecting
- ➢ Construction
- ➢ Wind-vegetation response

On the open rocky shore, zonation is clearly depicted in the color of the rock. The white zone is revealed as a white patina on the very tips of the rocks. This region is inundated only by spring storm tides, so it is dry much of the time. Along the landward margin of the beach there may be gnarled, almost prostrate bushes of *Sesuvium portulacastrum* L. (sea purselane), *Batis maritima* L. (saltwort) and *Conocarpus erectus* L. (buttonwood mangrove), and other shrubs or trees. These are typical inhabitants of the white zone. They have been shaped by the strong wind and salty atmosphere of their environment. The rock may be covered by lichens or blue-green algae, which exude slime coatings to prevent desiccation. A snail that is an indicator organism of the white zone is the white or grayish white, **globose**, *Tectarius muricatus* (beaded periwinkle). This snail feeds at the waterline at night, but during the daytime it moves up into the white zone and beyond, sometimes 10 meters (33 feet) or more above the waterline (table 18).

Most of the beach is in the gray zone, indicated by pitted gray rocks, dissolved by extensive exposure to saltwater and rain. Limestone, formerly the calcium carbonate skeletons of corals, the calcareous alga (*Halimeda*), and other calcareous species, the shells and spines of sea urchins, and others, is quite soluble in water. It dissolves at a variable rate, resulting in the highly dissected appearance of the gray zone. Three snails are indicators of this zone: *Littorina zigzag* (zebra periwinkle), *Nodilittorina tuberculata* (common prickly winkle), and the large *Nerita peloronta* (bleeding tooth nerite). *Nodilittorina* is a small gray snail with pointed, randomly distributed **tubercles**. *Littornia zigzag* is usually less than 1 centimeter (less then or equal to one-half inch) long with a distinctive gray herringbone pattern on a cream background.

The *Neritas* are the best indicators of levels of the gray zone. *Nerita peloronta* (bleeding tooth nerite) is found high up in the gray zone. A smaller nerite with pink and black flecks and deep cords running the length of the shell is *Nerita versicolor* (four-toothed nerite). It is found lower down in the gray zone, sometimes in the

Table 18—Indicator organisms of each tidal zone on a rocky shore

White zone Beach	Gray zone Supralittoral	Black zone Periodic inundation	Yellow zone Intertidal	Pink zone Sublittoral
(Snails) *Tectarius muricatus*	Upper (snails) *Nerita peloronta* *Nodilittorina tuberculata* *Littorina zigzag*	In tide pools (Snails) *Puperita pupa* *Planaxis nucleus* *Batillaria minima* (Inside *B minima* shells are the tiny hermit crabs, *Clibanarius* tricolor)	Upper (Chitons) *Acanthopleura granulata*	(Snails) *Cittarium pica*
(Land plants) *Sesuvium portulacastrum* *Ipomoea pes-caprae* *Batis maritima*	Middle and lower *Nerita versicolor* *Nerita tessellata*	On rocks The snail, *Nerita tesselata*, becomes more common here	(Limpets) *Fissurella barbadensis* *F. nodosa* *Diodora listeri*	(Sea urchins) *Echinometra lucunter*
(Others) Insects Spiders	(Crabs) *Grapsus grapsus*		(Barnacles) *Chthamalus stellatus*	(Algae) *Caulerpa species*
	(Algae) *Bostrychia*	(Algae) *Bostrychia* common, giving zone its typical black color	Lower (Chitons) *Chiton tuberculatus* *C. marmoratus* *C. squamosus*	Corals *Millepora* spp. *Acropora palmata* *Siderastrea radians*
			(Barnacles) *Tetraclita squamosa stalactofera*	
			(Snails) *Purpura patula* *Thais haemastoma* *T. rustica* *Turbinaria turbinata*	
			(Algae of upper and lower Yellow zones) *Sargassum* sp. *Padina sanctae-crucis* *Valonia ocellata* *Dictyosphaeria* sp.	
			Short, fuzzy algae such as: *Cladophoropsis* sp. *Heterosiphonia* sp. *Champia* sp.	

black zone. *Nerita tessellata* (checkered nerite) is smaller than the other nerites and has a black and white checkered appearance. It moves up and down with the tide and will be found in the yellow zone or intertidal sometimes, but most of the time is an inhabitant of the lowest parts of the gray zone. The gray zone is submerged for only a few days a month during spring tides.

The black zone is a narrow band (often not visible on the island) inundated more often—more than half the days of every month. It is black because of the predominance of *Bostrychia* spp. (red alga).

The yellow zone is inundated daily. It corresponds to the term littoral or intertidal, more commonly used in northern waters where rocks do not exhibit such clear-cut color variations according to their degree of inundation.

In the lower black and upper yellow zones, the first of three common species of chitons can be found. *Acanthopleura granulata* (fuzzy chiton) is so called because its girdle is fuzzy, lacking the typical snakeskin appearance of other common chitons. The other two species of chiton are found in the lower yellow zone and rarely exposed. *Chiton tuberculatus* (West Indian chiton) has chevrons or diamonds of tubercles on its plates, one large chevron per plate. The *C. marmoratus* (marbled chiton) has a brown and tan marbelized pattern on its shiny plates. These water-covered zones may exhibit algae such as *Sargassum* spp. (sargassum), *Valonia ventricosa* J. Agardh (sea pearls), *Dictyosphaeria cavernosa* (Forsskal) Boergesen (green bubble alga), and *Caulerpa* spp. (feather algae).

At low tide, note the pink zone, another narrow band, this time covered with *Goniolithon strictum* (Foslie) Setchell & Mason (pink calcareous alga), and other coralline algal species can be observed. This zone is located at the base of the yellow zone. It is submerged except for a few days a month when low spring tides expose it. It may have hard corals such as *Acropora palmata* (elkhorn) and *Siderastrea radians* (shallow starlet) present.

Tide pools—

Tide pools are sometimes referred to as microecosystems of the sea. Tide pool water levels vary from ankle to knee-deep, and the pool may contain a number of *Diadema antillarum* (long-spined black sea urchins), thus one should be careful not to step on them. The pools may have wide swings in factors such as temperature, carbon dioxide/oxygen levels, pH, salinity, and water volume. *Stoichactis helianthus* (sun anemones), resembling greenish rugs, may be dominant organisms in the pool. There is usually a mat of *Padina sanctae-crucis Boergesen* (tan petticoat algae). It has thin calcareous bands running across a flat, encrusting, tan thallus.

Tide pools may contain a number of species of fishes. Most are damselfishes of one sort or another. Most common are beaugregories and sergeant majors (*Abudefduf saxatilis*). There are many types of gobies and blennies, usually well camouflaged and visible only when they characteristically dart from one rock to another. Sometimes you will see one sticking to the vertical wall of a tide pool by its ventral sucking disk. Some pools, usually those with little access to the sea and no tidal current, are covered by colonies of the famous *Acetabularia crenulata* Lamouroux (mermaid's wineglass), which looks like dusty green miniature umbrellas about 2 centimeters (1 inch) high.

Some tidepools and adjacent flats have crevices often containing the *Echinometra lucunter* (red rock urchin). These have medium-sized spines, usually blackish, contrasting with a bright red to reddish-black test. Do not make the mistake of trying to pick up a *Diadema*, thinking that it is just a particularly dark specimen of *Echinometra*. *Diadema's* spines are like hypodermic needles with backward pointing barbs at their ends.

Coastal scrub—

Some rocky shores have elevated cliff exposures that may have a dry coastal scrub community present. Some of these exhibit extreme wind/salt shear and may only be a few centimeters (inches) tall. There are three species likely to occupy the leading edge of this community: *Strumpfia maritima* Jacq. (bonzai plant), *Coccoloba uvifera* L. (sea grapes), and *Conocarpus erectus* L. (buttonwood mangrove). The stunting and salt/wind shear will be exaggerated to the point that the species will create a "carpet effect" over the rocky surface. Vertical growth is almost impossible owing to the stressors at work on the lead vertical meristems of the branches; thus virtually all growth is horizontal. In some cases, the vertical extension of the tree will be measured in centimeters (inches), whereas the horizontal growth will be in meters (feet). The low prostrate growth form exhibited by these trees is due to loss of their lead apical meristems causing a branched response similar to that achieved when a woody plant is pruned. Farther away from the cliff's edge and as the plants provide protection to each other, greater vertical extension is observed. Eventually, more normal vertical growth is achieved. Excellent coastal scrub can be observed in the Guánica forest along the coastal road.

Other plants typical of this community are:

- *Batis maritima* L. (saltwort)
- *Borrichia arborescens* (L.) DC. (sea ox-eye aster)
- *Melocactus intortus* (Miller) Urban (turk's cap cactus)

- *Opuntia rubescens* Salm-Dyck (tree cactus)
- *Opuntia dillenii* (Ker-Gawl.) Haw. (prickly pear cactus)
- *Plumeria alba* L. (frangipani)
- *Bursera simaruba* (L.) Sarg. (Gumbo limbo)
- *Comocladia dodonaea* (L.) Urban (poison plant)
- *Furcraea tuberosa* (Mill.) Ait. (Puerto Rican century plant)
- *Suriana maritima* L. (baycedar)

The exact species present will differ from habitat to habitat.

At the outer limits of this community, the plants will appear to be growing on exposed rock, which they are. However, their stem and root systems penetrate a dissolation depression in the limestone substrate where there are small accumulations of soil and moisture. Growth is extremely slow in this habitat, and it is likely these sea cliffs are just as they appeared at the time of European discovery. They are probably one of Puerto Rico's only examples of an **old-growth** community.

For further reading see Kaplan 1982, 1988 and Stephenson and Stephenson 1972.

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Chapter 5: Estuarine Ecosystems

Mangrove Forests

Some of the most intriguing forests found in the tropics are mangrove forests. They are unlike any other forest type in the world, as mangroves grow in sea water. These forests are often referred to as tidal **fringing forests** because they live in or create an ecotonal fringe along protected tropical coasts, lagoons, bays, and off-shore islands. They also create a riverine fringe in deltas and farther inland along riverine flood plains. They cover nearly 10 million hectares (25 million acres) worldwide.

The term mangrove does not directly refer to a specific family, genus, or species as when you say beech, spruce, or red oak. In the latter instances, members of a particular family, genus or, in some cases, species actually define the forest type. Mangrove is a general term that can refer to numerous families, genera, and species of totally different **taxons**. What they have in common is tolerance to salt, that is, they are halophytes. The term mangrove can refer to up to 19 plant families, 26 genera, and close to 80 species worldwide. Old World tropics have many more of each taxon in comparison to the Neotropics. There are four common mangroves typical to Puerto Rico and the Caribbean: *Rhizophora mangle* L.[1] (red, box 23), *Avicennia germinans* L. (black, box 24), *Laguncularia racemosa* (L.) Gaertn. (white) and *Conocarpus erectus* L. (buttonwood). Table 19 compares the taxonomic, morphological, reproductive, and habitat attributes of these species. All species are intolerant of frost.

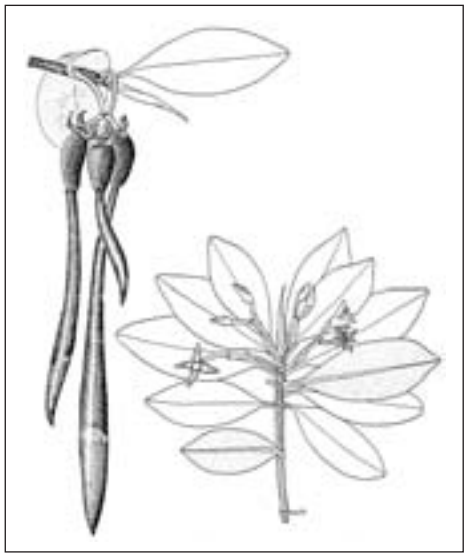
The buttonwood mangrove is probably the least common of the four. The red, white, and black mangroves owe their worldwide dispersal to their "sea-going" seeds. Red mangroves are unique because their seeds germinate while still on the parent tree. The flowers of red mangroves bloom for a few weeks on the tree while pollination and fertilization take place. The fruits then form consisting of a single seed. A shoot and root then sprout from the seed and grow until so heavy it drops off the parent tree. This condition is called **vivipary**. When it falls, it can either take root immediately or will float away with the tide. This seedling may float around for almost a year until it lands in a location suitable for anchoring. In time, the root tip becomes water-logged, turning the plant vertical. The suitable site is sometimes a sandbar, but it will as likely be a shallow coral reef. The seedling then anchors itself by sending out prop roots and grows rapidly, sometimes as much

[1] See appendix 1 for Common and Latin names.

Continued on page 200.

Box 23. *Rhizophora mangle* L. (red mangrove)

Most tropical forests have high species diversity. A distinct exception to this are coastal fringing forests composed of red mangroves and sierra palm forests in the high mountains of Puerto Rico. These are examples of natural monocultures. Monocultures are generally associated with intensive agriculture or silviculture such as tobacco or various species of pine trees.



Rhizophora mangle L. (red mangrove) leaves, flowers, and viviparous seeds.

Rhizophora mangle L. (red mangrove) is found throughout the tropical world from the Pacific islands to West Africa, the south coast of Florida, the Caribbean, and Central and South America. This distribution roughly approximates 30° N and S of the equator. It is a frost-sensitive species. It grows in diverse climatic areas, from very dry to wet forest life zones, with best growth occurring in wet areas. It prefers salty soils, with salty or brackish water present. It develops best in areas protected from high wave energy such as lagoons, or coastal river flood plains with tidal fluctuations, often referred to as "fringing wetlands."

Red mangrove is a very interesting tree, botanically and ecologically, because it exhibits a series of rare traits, such as:

- Tolerance to high salt concentrations
- Natural monoculture
- Vivipary
- Stilt (prop) roots
- Detritally enriched nursery habitat for many other species of plants and animals
- Seedlings spread by ocean currents
- Salt exclusion ability

Box 23. continued

The red mangrove gets its name from its reddish bark. Certainly the most obvious feature of red mangroves is their characteristic highly branched stilt or prop roots. These are not true roots. They are adventitious, that is, their origin is in stem tissue. The stilts appear to be "tree legs," thus they are sometimes called a walking forest. Very often these forests are at the water's edge, growing in very silty and anaerobic conditions. These trees can exchange oxygen via large and numerous lenticels on the stilt roots. They can exclude salt by concentrating cell sap and preventing salt uptake with water uptake from soil. High leaf fall rates add high quantities of biomass to the forest floor. The leaves and other organic matter from the forest are the basis for a detritally enriched food chain that ultimately yields some of the highest secondary productivity known. Up to 80 percent of all harvested fish and associated shellfish species in tropical coastal waters spend all or part of their life cycle associated with mangrove swamps. They are the ecological equivalent of salt marshes in the temperate zone and are truly nursery areas for a vast assemblage of animal species.

Red mangroves produce yellow star-shaped flowers and shiny leathery evergreen leaves. When mature and reproducing, their seeds germinate while still attached to the adult parent tree. This condition is called vivipary and is quite rare in the plant world. When mature, the young seedling drops and is most often spread by ocean currents. Some of the bayonet-shaped seedlings may stick in the mud if the tide is out. The seedlings may be more than 1 foot in length, with the first root (radicle) the bulk of its growth.

Red mangrove trunks are frequently used for posts or charcoal production. The bark is a commercial source of tannin for leather tanning. Fringing forests on windswept coasts may only be 10 meters (33 feet) tall, whereas in optimally protected areas they may grow to 50 meters (164 feet). They rarely exceed 20 meters (66 feet) in Puerto Rico.

For more information on this species, see Hogarth 1999, Jiménez and Lugo 1985, Little and Wadsworth 1964, and Tomlinson 1986.

Box 24. *Avicennia germinans* L. (black mangrove)

The leaves, stems, flowers, and fruit of *Avicennia germinalis* L. (Black mangrove)

Another mangrove important to the Neotropics is *Avicennia germinans* L. (black mangrove). It is not as easily distinguished as *Rhizophora mangle* L. (red mangrove), because it does not exhibit the easily recognized adventitious stilt (prop) roots or its red bark. This species does have an easily recognized morphological feature, that is, its pneumatophores (see below). They are vertical upward root growths that aid in gas exchange. This species is also ecologically very important. Black mangroves appear in coastal swamp forests throughout the New World tropics from the Gulf coast of the United States and Mexico, throughout the West Indies and is present on both the Pacific and Atlantic coasts of Central and South America (northern Perú and southern Brazil). Its leaves are oppositely arranged, elliptic, leathery, and yellow-green (see above). The leaves are salty to the taste. Its bark is dark, thus its common name, and fissured when old.

It grows in brackish to hypersaline waters and can grow in soils where salinities range from 0 to 100‰. In hypersaline conditions, individual trees may be stunted. In all saline habitat conditions, the plant is adapted to excrete salt through specialized glands on its leaves. Depauperate forms are best observed in depression areas away from the coast where high tide or storm water can be trapped producing hypersaline conditions. It also grows well in dry habitats. It grows best in wet riverine habitats and may achieve heights of 30 meters (98 feet) in Central America, whereas in Puerto Rico maximum heights rarely exceed 15 meters (49 feet). Throughout most of its range it will be found growing in a mixed mangrove forest. It, too, adds greatly to the detritally enriched food chain that enhances the complex food web associated with mangrove ecosystems. This results in the production of many commercially important species of mollusks, crustaceans, and numerous fish. Just as in red mangrove, natural monoculture black mangrove forests also occur. It is limited

Box 24. continued

in its distribution by frost. It grows best in full sunlight and will have reduced stature in a mixed mangrove forest.

Black mangrove is also viviparous in that its seeds germinate while still in the fruit (capsule) and attached to the parent plant. The tree's flowers are small spikes with individual white-yellow flowers. Flower-ing can take place throughout the year. Initially four eggs are formed, but three abort early and only one fully develops into a one-seeded fruit. Trees will produce hundreds of fruits per year. As in the case with red mangroves, black mangrove seedlings drop and are vectored by tidal change and currents. The seedlings need to locate above the low tide mark in the littoral zone. Sexual maturity is reached when the tree grows to about 3 meters (10 feet).

G. Miller

The pneumatophores of *Avicennia germinans* L. (black mangrove) growing on the south coast of Puerto Rico

One of the most interesting morphological features exhibited by black mangroves is their root development. They produce a shallow sinker root system typical of most plants that grow in wet areas. *Avicennia germinans* may also produce slender adventitious roots from their trunks up to 25 centimeters (1 foot) long. Pneumatophores are also produced growing vertically up from horizontal lateral roots in the substrate. Pneumatophores are small, pencil-like, vertical, upward extensions that serve in gas exchange. There may be hundreds of them under one tree and their height differs with that habitat's water depth. Up to 65 percent of a tree's total biomass may be in roots. Because of their extensive root systems, they are considered soil stabilizers along coasts and rivers.

Black mangrove is easily damaged by exposure to auxin-based pesticides, strong winds (especially hurricane strength), and alteration of its hydrological conditions. In September 1998, Hurricane Georges produced winds of 145 to 160 kilometers per hour (90 to 100 miles per hour), with gusts nearing 242 kilometers per hour (150 miles per hour). Most of the black mangroves in the

Box 24. continued

Boquerón Wildlife Refuge were blown over because they produce a ball root system, whereas the red mangroves, with their prop roots, were only minimally damaged. Black mangrove wood is used for charcoal production and firewood in developing countries. It also has a variety of other uses such as posts, power poles, framing, railroad ties, pulp, and fiberboard. Its bark yields tannins and medicinals. Cooked seedlings can be eaten, and its leaves can be used as a source of salt.

For more information on this species, see Jiménez and Lugo 1985, Little and Wadsworth 1964, and Lugo and Snedaker 1974.

as 0.6 meter (2 feet) in its first year. Mangroves sometimes root in mud lacking oxygen, so they send out aerial prop roots that allow for the exchange of gases required for respiration. Gradually this tree can form its own colony of mangroves.

The term mangrove can also refer to an ecological community type such as mangrove swamp, which may include trees, shrubs, herbs, ferns, and epiphytes in a complex mangal ecosystem. Mangrove communities are notable for their species diversity, salt tolerance, ability to colonize coastlines, and very high biological productivity. Life in a mangrove ecosystem is in a constant state of flux owing to changes produced by natural processes and increasing human interactions. Some human activities such as shrimp pond construction have resulted in vast areas of mangroves being destroyed, which is ecologically catastrophic.

Mangroves exhibit a series of adaptations that allow them to hold their positions in the coastal fringe. They include:

- Tolerance to high amounts of salt
- Specialized roots that allow them to establish in soft muds or saturated conditions
- Seeds that can germinate on the tree (viviparous) and when they fall, the seedlings can float
- Special structures that permit gas exchange in low oxygen environments, such as **lenticels**, **aerenchyma** tissue, and **pneumatophores**

Ecological Functions of Mangroves

Only recently have we been able to understand the complex mangrove ecosystem. We know that red mangroves provide a safe wildlife habitat both on land and around their prop roots in the water. They also dampen the power of storm waves.

Table 19—Taxonomic, morphological, reproductive, and habitat comparisons of the four species of mangrove in Puerto Rico

Scientific name and family	Common names	Morphological and reproductive features	Habitats
Rhizophora mangle L. Rhizophoraceae (mangrove family) Pantropical family and genus	Red mangrove *mangle rojo*	Viviparous Aerial stilt roots from branches and trunk Leathery leaves opposite, elliptical, and glabrous Stipules present Black dots on bottom surface Yellow flowers in fours Fruits olive green Large lenticels present on stilt roots Trees up to 30 meters (98 feet) tall Red roots and stems	Soft to firm organic mud Occupies outer tidal fringe, but can appear in transitional areas and exhibit dwarfing Grows best in areas of daily tidal change or in riverine habitats Hurricane resistant owing to stilt roots
Avicennia germinans L. Avicenniaceae (black mangrove family) Monogeneric family Pantropical family and genus	Black mangrove *mangle negro*	Viviparous (not obvious) Aerial root pneumatophores Leaves opposite and ovate to elliptic Bottom of leaves hairy and gray Salt-excreting glands on leaves Bark gray-black Petiole without glands May grow as tree or shrub Trees rarely taller than 20 meters (66 feet) White flowers in terminal spikes Fruit single-seed capsule	Occupies diverse habitats from frontal fringe to back fringe and hypersaline elevated basins May be heavily damaged during hurricanes because top heavy (balloon effect); they produce a root ball; At Boquerón Refuge, the black mangroves were toppled in Hurricane Georges in 1998. Flowers produce abundant nectar used by bees for honey production
Laguncularia racemosa Gaerth. Combretaceae (Combretum family)	White mangrove *mangle blanco*	Viviparous (not obvious) Facultative pneumatophores Leaves opposite and somewhat fleshy Bottom of leaf without hairs, with pits at minor veins Petioles red with a pair of glands near base of leaf Leaf elliptic shape with apex indented, glandular at the base Bark fissured and gray Inflorescence panicle of racemes with bell-shaped white flowers Gray-green fruit, single-seed nutlet Up to 13 meters (40 ft) tall	Found in the landward side of the fringe, although may form pure stands in disturbed sites Sites are usually elevated with lower tidal frequency (in riverine systems) Grow in low depressions; may grow in peat and soft mud

Table 19—Taxonomic, morphological, reproductive, and habitat comparisons of the four species of mangrove in Puerto Rico continued

Scientific name and family	Common names	Morphological and reproductive features	Habitats
Conocarpus erectus L. Combretaceae (Combretum family)	Buttonwood mangrove *mangle botón*	Leaves alternate Pits along main vein on bottom surface of leaf May have hairy leaves Petiole with pair of glands at base of blade Often grow as shrubs Bark rough Some call this a mangrove associate because it lacks vivipary and aerial roots, Flowers terminal, globose heads Fruit an aggregate of nutlets, round and purplish-brown Up to 6.5 meters (20 ft) tall	Brackish to fresh water communities inland, although present on dry exposed limestone cliffs in Guánica Forest where it forms a highly sheared old-growth forest rarely over 0.5 meter (2 feet) tall and growth is prostrate over the surface Tolerant of high salinity May grow on sandy berms as a beach shrub or small tree

Their prop roots stabilize land that would normally be eroded into the sea. William Odum (1969) demonstrated that the mangrove is actually the basis of an elegant detritus-based food chain supporting numerous tropical animals.

Mangroves produce a tremendous amount of leaf biomass each year, which they shed. The red mangrove in particular, has been shown to produce almost 3 tons (2.72 metric tons) of leaves per 0.4 hectare (1 acre) per year. This rate of biomass formation is equal to that of intensively cultivated agricultural lands and only slightly lower than that produced by coral reefs, marine seagrass beds, and tropical rain forests. This leaf biomass is the origin of the mangroves' unique and vital detritus-based food chain.

Bacteria and fungi begin to colonize the leaves while they are still on the tree. Within about 24 hours after the leaf falls, marine microbes invade the waxy cuticle of the leaf. These microbes stay on the leaf 2 or 3 weeks, or until the particular cellular nutrients they thrive on are exhausted. They coexist with, and are at times succeeded by protozoans, bacteria, and various fungi. In looking at the leaf with the naked eye, these bacteria and fungi look like a brown slime. It is this slime that attracts other marine animals, mostly marine worms and microscopic crustaceans called copepods. Small crabs and amphipods are soon drawn to the leaf by these worms and copepods. The worms, crabs, and amphipods also break down and consume the leaves.

The broken down leaf particles are called "detritus." This detritus can be eaten and excreted and eaten again by many different animals; mainly small mollusks, crustaceans, shrimp, sea worms, and crabs. Those animals then become prey for small fish, which are then eaten by larger fish. Many of those larger fish are commercially important for human food (protein). One commercially important fish, the striped mullet, feeds directly on mangrove detritus.

It is estimated that 75 percent of game fish and 90 percent of commercial species in Florida's waters depend in part on the mangrove ecosystem. There are no printed figures on the importance of mangroves to commercial game fish in Puerto Rico, but it is likely that they are at least as high as in Florida. Mumby et al. (2004) indicated that mangroves in the Caribbean strongly influence the community structure of fish on neighboring coral reefs. In addition, biomass of commercially important species is more than doubled when adult habitat is connected to mangroves.

Habitat zonation for plants and animals living in the mangrove is very striking. There are three distinct zones:

- Branches of the trees

- Terrestrial roots
- Submerged roots

The branches above the water line provide an excellent rookery for birds. Two birds, the golden warbler and the mangrove clapper rail, are true mangrove species (endemics). Other birds such as the cattle egret normally only roost in mangroves. Their flocks can be observed migrating daily to and from inland agricultural lands at dusk and dawn. The branches of the tree are structured as if the tree were an apartment building; with the larger birds like the egrets, herons, pelicans, cormorants, and frigate birds using the top of the canopy, and smaller birds using the area inside. The advantage of these island rookeries is that they offer protection from egg-robbing rodents and humans.

The terrestrial roots are dominated by mobile animals such as crabs and mollusks. A few examples of these are the *Littorina angulifera* (red snail), *Grapsus grapsus*, *Aratus pisonii*, *Goniopsis cruentata* (crabs), and *Cardisoma guanhumi* (the edible land crab). Throughout a mangrove swamp, large brown termite nests in the aerial branches can be seen. These are the nests of *Nasutitermes costalis*, which harvest the dead wood in the swamp. Other groups present are ants, spiders, moths, roaches, and mosquitoes. Lizards will likely be present feeding on these invertebrates.

The most densely populated and species-rich area in the red mangrove swamp is the habitat created by prop roots that penetrate the water of the subtidal zone (fig. 59). A wide variety of plants and animals form biological coatings that cover these roots and serve as food and refuge to many animals. The presence of these organisms may provide some protection from predatory root-boring animals. Rützler and Feller (1996) indicated a number of new species recently described from these **fouling communities**. They estimated that perhaps as many as 20 to 30 percent of the microbes, algae, sponges, and worms living on their research mangroves may be as yet undiscovered species in Twin Cays off the coast of Belize.

Underwater mangroves offer a veritable cornucopia of organisms to observe. In the narrow channels between the roots, are found green algae, jelly fish, the spotted cucumber, and the young of many fish. The submerged roots represent the least understood, but probably the most interesting zone (fig. 60). It is here that competition for living space is the greatest. Most of the sedentary animals are filter feeders. Algae are also present, but only to depths where light penetrates. Among those algae found on submerged roots are *Caulerpa mexicana* Kuetzing (green feather alga), *C. racemosa* (Forsskal) J. Agardh (grape alga), and *Acetabularia crenulata* Lamouroux (mermaid's wine glass). Other **benthic** algae present in the lighted

A.E. Lugo

Figure 59—The prop roots of *Rhizophora mangle* L. (red mangrove) on south coast of Puerto Rico.

channels are *Penicillus capitatus* Lamarck (shaving brush alga), *Halimeda opuntia* (L.) Lamouroux (coralline watercress alga), *Valonia ventricosa* J. Agardh (sea pearl), *Udotea flabellum* (Ellis & Solander) Lamouroux (hard fan alga), and *Avrainvillea nigricans* Decaisne (soft fan alga).

For additional details see the description of the littoral fauna, by Matthews (1967).

Zonation of Mangrove Communities

Mangroves have been estimated to dominate about 75 percent of the world's coastlines between 25° N and 25° S latitude. Mangroves are classified structurally many different ways. Lugo and Snedaker (1974) classified mangroves into five categories according to the geomorphology of their basins:

- **Riverine** mangroves grow on river flood plains and are involved with the lateral flow of water of low salt concentrations.

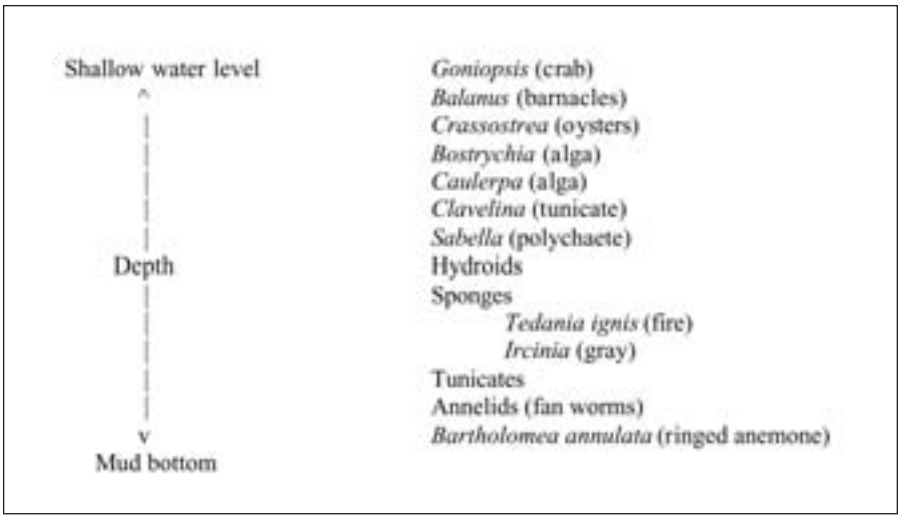


Figure 60—Vertical zonation of organisms along the underwater prop roots of *Rhizophora mangle* L. (red mangrove).

- **Basin** mangroves grow in depressions where waterflows are sluggish and the vertical flow of water prevails over its lateral flow.
- **Fringe** mangroves grow at the edge of the sea or other water bodies and are exposed to vertical water fluctuations or to broad wave fronts.
- **Mangrove islands** occur out at sea as overwash islands where tides flow over the islands or may develop inland as mangrove "hammocks" where water flows around the island.
- **Dwarf** red mangroves occur in humid areas over peats. The trees are dwarfed but have leaves of normal size. Mature trees of dwarf mangroves are not to be confused with scrub mangroves, which have reduced size as a result of harsh growing conditions such as hypersalinity.

Each of these different types of mangrove demonstrates a different set of environmental conditions that shape the landscape, and what types of flora and fauna will be present and what types of environmental stressors will have an impact. Stressors will be mentioned later.

Lugo and Cintrón (1975), classified Puerto Rican mangrove communities into two general categories: south coast and north coast types. The determinant factors in this classification were the intensity of wave action, rainfall, and freshwater runoff.

The environment of the south coast type mangrove forest is characterized by low rainfall, very little freshwater runoff, and a low wave energy regime. The predominant type of forest is the fringe mangrove forest. In general, south coast

fringing mangroves grow at the edge of the sea, have low structural complexity, low leaf fall, and low rates of tree growth. These forests are dominated by the *Rhizophora mangle* L. (red mangrove). The salt content of the south coast waterways (i.e., ocean, lagoons, and others) varies little throughout the year. North coast type mangroves on the other hand, show higher structural complexity and higher rates of leaf fall and tree growth. The salt content also fluctuates more in the waterways on the north coast than on the south owing to seasonal terrestrial freshwater runoff.

Lugo (1978) came to the conclusion that the smaller the mangrove, the higher the salinity of the environment. He found a rapid increase in mangrove tree mortality beyond a soil salinity threshold of about 65 ‰ (parts per thousand). Through this conclusion, Lugo has come up with another way of classifying mangroves, that is, through their succession rates. According to Lugo, in the American tropics the mangrove swamp forest consists of a series of zones each dominated by one species of mangrove. From open ocean and extending through to the area covered by maximum high tides, the red mangrove is dominant. Except for the red mangrove's prop roots and its seedlings, this forest floor is devoid of higher plant life. Vigorous growth of more red mangroves at the edge of the forest results in restriction of water circulation to the inner parts of the swamp. These areas can then be invaded by the more salt-tolerant black mangrove. Eventually, extensive areas of the inner swamp die, and a salt flat is formed. Lugo is quick to point out that severe storm or wave fronts could delay this succession indefinitely.

Although there is some animal life in the above-water parts of all mangrove forests, it is not abundant. Where the roots are submerged, massive **epifauna** populations are numerous.

Extent of Puerto Rico's Mangroves

Puerto Rico may have had 12 146 hectares (30,000 acres) of mangroves at the time of European discovery. By 1975, half had been destroyed. Much of the loss was associated with agriculture and a variety of human developments along the coastal fringe. By the mid 1980s, up to 75 percent of Puerto Rico's mangroves had been destroyed or highly altered. Naturally, most of the loss since 1975 was associated with continued development of the coast. Figure 61 shows the distribution of mangroves in Puerto Rico (see app. 2).

Mangroves are recovering in some places in Puerto Rico as a result of their protected status. In the last few years there has been a net gain in mangrove coverage. The Department of Natural and Environmental Resources of Puerto Rico

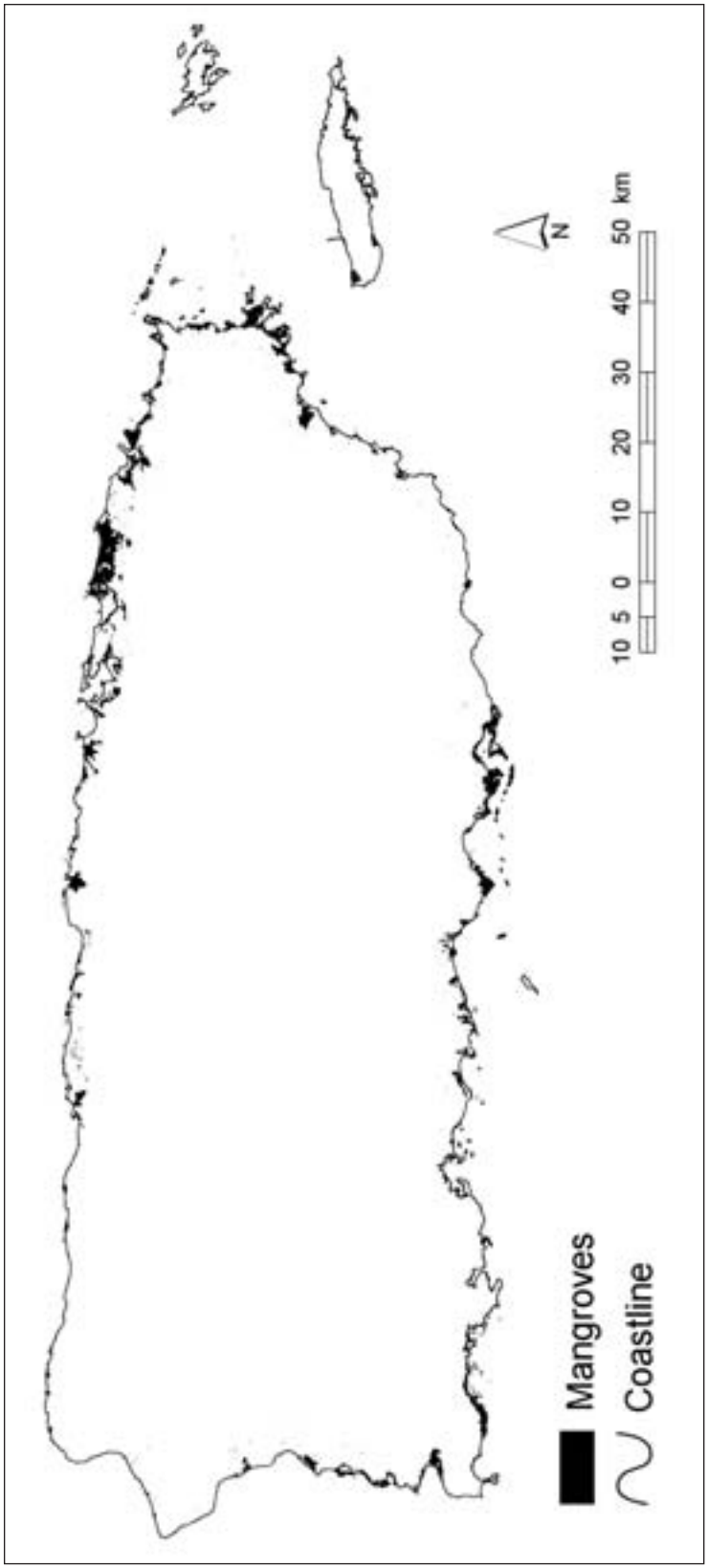


Figure 61—Distribution of mangroves in Puerto Rico. Modified from an unpublished map by the Puerto Rico Department of Natural and Environmental Resources.

currently estimates mangrove coverage at 9020 hectares (22,300 acres), distributed in 119 habitats. Twelve of these habitats are considered critical because of collateral construction, recreation or tourist activities, and urbanization. Their total coverage is 2196 hectares (5,425 acres). One of these is the mangrove complex surrounding the **Phosphorescent** Bay at La Parguera (see app. 2 p. 377). Mangroves compose a significant portion of Puerto Rico's public forests (see section on Puerto Rico's Commonwealth Forests). These forests have exceptional educational, recreational, and food value. Mangroves constitute both a wetland species and a wetland habitat. Today, permits are required to alter them in either case. They are covered by a variety of federal and Puerto Rican regulations that generally require permits to be issued prior to activities such as dredge and fill in mangrove habitat (see section on wetlands). Having said this, mangroves are still being damaged and removed largely because of ignorance of their ecological importance and of the law. Law enforcement is also limited.

Stressors

Lugo et al. (1981) described a stressor as any factor or situation that forces a system to mobilize its resources and spend more energy to maintain **homeostasis**. Lugo later said that "when all conditions are equal in the environment, ecosystem response to a stressor depends on the point of attack of the stressor on the system . . . and that if the stressor had interfered with the primary energy source of the mangrove system, recovery would be slow."

Factors that can produce stress in mangroves include:

- Low temperature
- Low nutrients
- Low O2 concentrations
- High wind
- Drought
- Storms
- A rise in sea level
- Predators
- Runoff
- **Allochthonous** inputs of pollutants
- Changes in salinity
- Changing depth
- Water temperature
- Pesticides
- Oil spills
- Human stressors

Lugo has classified stressors into five types:

- Those that alter the nature of the main energy source
- Those diverting part of the main energy source before it can be incorporated into the system
- Those that remove potential energy before it is stored, but after it is transformed by plant photosynthesis

- Those that remove storages, either in photosynthesis or in the ecosystem itself
- Those that increase the rate of respiration

One stress that the mangrove swamp has to endure is abnormal runoff. When a portion of land is developed bordering the mangrove swamp, increased rainwater runoff causes problems. What was once water-thirsty soil is now water-repellent pavement. The runoff washes more nutrients, pollutants, and sediment into the water. The extra nutrients result in increased algal growth that can directly clog the mangroves' "gas exchange" lenticels. Increased sediment may build up until it eventually forms a smothering black blanket that kills the trees.

Another stressor is the wood-boring isopod, *Sphaeroma terebrans*, which destroys the prop roots of mangroves, especially those of the red mangrove. *Sphaeroma* enters the prop roots of the mangrove. Reproduction then occurs inside the roots, with the young passing through all developmental states within the root. These young isopods then join the adults in wood boring. In time, in highly infested areas, all prop roots of the outer fringe of the mangrove colony are destroyed. This is as far as the isopod goes in destroying the tree, waves then take over, causing the tree to topple over.

Herbicides and insecticides are also stressors on mangroves. The amount of herbicides required to kill mangroves appears to be smaller than that required to kill other species of tropical trees. With application of as little as 1 percent of a herbicide, a 90-percent defoliation occurred in the mangroves after 1 month. Walsh et al. (1973) demonstrated the effects of herbicides and concluded that the mangrove was affected so extremely because, although the herbicides were applied to the bark of the tree, tides and storm waves washed them down near the prop roots, where the herbicides did their greatest damage.

Oil is another stressor. On March 17, 1973, the Greek tanker, the *Zoe Colocotroni*, spilled about 5,000 tons (4535.92 metric tons) of oil in the southwestern tip of Puerto Rico on Margarita Reef near Bahía Sucia. Wind and water currents pushed oil into the fringing mangrove forest of the bay, covering significant areas of mangrove forest. Mangroves are very sensitive to oil spills because of the dependency on their prop and aerial roots for respiration. The response of the mangrove to oil is a very rapid shedding of leaves, which then leads to the new leaves being susceptible to deformation and insect attacks.

A significant legal outcome was associated with this oil spill. In 1980, a U.S. Court of Appeals found that states and Puerto Rico had the right to sue and recover damages to their natural resources even though there was no apparent market value

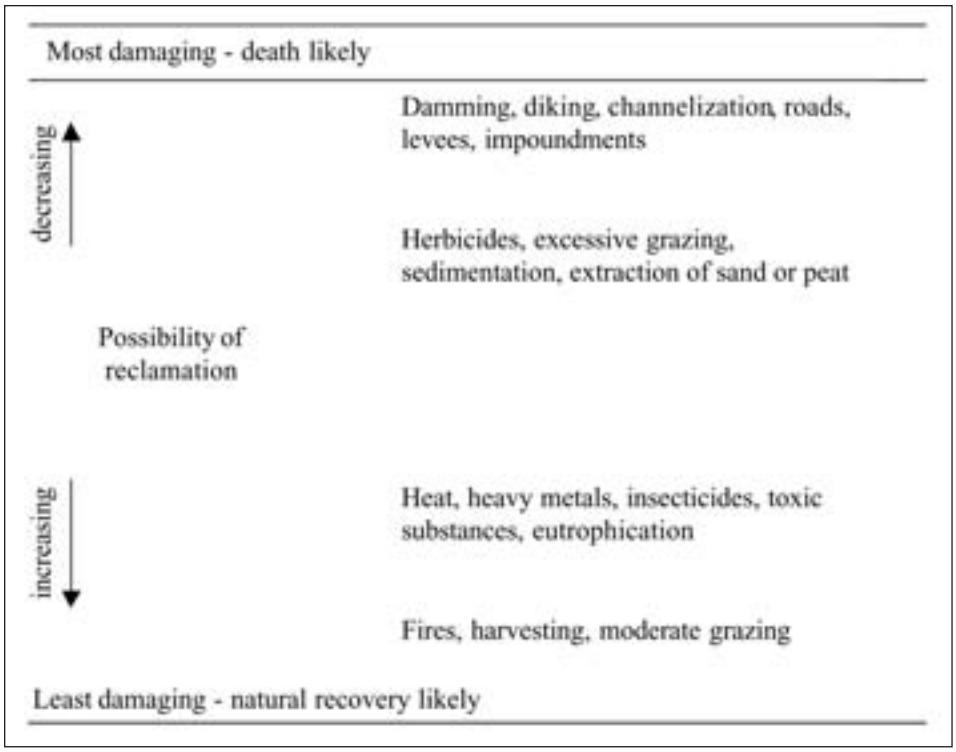


Figure 62—Effect of human stressors on mangroves.

(to the mangrove swamps). In addition, it was ruled that the $2.1 million awarded in 1978 to Puerto Rico had to be used for land acquisition of comparable ecological value for establishment of a public park. This was the beginning of the establishment of the Cabo Rojo National Wildlife Refuge that rings Bahía Sucia today.

Mangrove stressors produced by humans can be grouped based on severity of impact and likelihood of reclamation. Figure 62 expresses these on a sliding continuum with the top line being most severe and least reclaimable because they alter the habitat's soils and hydrology. Those on the bottom line are generally less severe and through natural regrowth or succession, are able to recover on their own.

Mangrove swamps and associated marshes in the San Juan area are newly incorporated into the U.S. Environmental Protection Agency's (EPA) San Juan Bay National Estuary Program. This is the only tropical ecosystem in the U.S. EPA Estuary program and the only one outside the continental United States. This complex estuary is a mosaic of marine and coastal ecosystems located in the San Juan metropolitan area. Many of its components have been destroyed or severely degraded. This new program, completed in October 2000, is designed to restore and conserve its present components. At its center is the Comprehensive Conservation and Management Plan, which involves local, state, and federal agencies,

as well as citizens, educators, and private groups. The plan has 49 action plans that address four priority areas:

- Water and sediment
- Habitat, fish, and wildlife
- Aquatic debris
- Public education and involvement (EPA 2000)

Values of Mangroves

Until the latter half of the 20th century, most people looked on mangroves as "junk" trees as they seemed to have little value except for charcoal production, as building or wharf posts, and as a source of **tannins**. Today we know that they are very valuable. Tables 20 and 21 list some of the many benefits derived from mangroves.

Tropical societies have been using wetlands for millennia, both directly and indirectly. Mangroves have been economically important throughout history, but unfortunately the values of mangroves have not been accounted for monetarily until recently. We now know they are worth millions of dollars per year. More and more of the human population (65 percent) live in the world's coastal zones, and that number is expected to grow significantly in the next 50 years. In the Caribbean, it is estimated that 85 percent of the population lives in the coastal zone. Coastal zones have not been well managed up to this point. It is incumbent upon us to recognize what is at risk when this exceptional ecosystem is being degraded.

Destruction of vast areas of mangrove ecosystems, with from 50 to 60 percent of all mangroves destroyed, is occurring in the tropical world. Currently, mangrove destruction is estimated to be 5 percent annually worldwide. Much of the recent destruction has been for the construction of industrial shrimp farms. Over 202 425 hectares (500,000 acres) were destroyed in Ecuador for this purpose. Once destroyed, all of these direct and indirect values that societies derive from mangroves are lost, maybe forever. In addition, locals do not benefit from mangrove conversion because most of the high-quality shrimp protein is largely exported to the United States or other industrialized countries. Developed nations are unwittingly putting great pressure on many natural ecosystems as the demand for high-grade products at low cost increases. Awareness is needed at both ends of this supply/demand system so the remaining 50 percent of this extremely beneficial and productive ecosystem is not destroyed.

Table 20—Economic values of mangroves

Activity	Use
Agriculture	Direct grazing or biomass gathered for fodder
Construction	Scaffolding, posts, pilings, railroad ties, and tool handles
Ecotourism/ education	Growing interest in using mangroves for water-related field trips, recreation, and education
Fishing	Net floats, poles, and fish harvest
Food	Honey, alcohol, bark condiments, consumption of fruits and secondary animal products (birds and eggs)
Fuel	Firewood and charcoal
Household	Water pipes, furniture, and dyes
Medicine	Bark, leaf, fruit decoctions, and incense

Table 21—Ecosystem values of mangroves

Activity	Value
Detrital-based food chains	Low direct use results in high secondary productivity through detrital enrichment
Ecosystem linkage	Proximal to other high-productivity ecosystems (coral reefs and seagrass beds)
Education/research	Exceptional habitat to explore productivity, symbiosis, food chains, competition dynamics
Nursery habitat	80 percent of commercially harvestable fish and shellfish spend part of life cycle here
Nutrient filter	Controls eutrophication
Sediment filter	Keeps water column clean
Storm buffer	Reduces impact on inland natural and human systems
Waste treatment	Effective in filtering and using human wastes
Wildlife habitat	High value as rookery for various shore and marine birds, small fish, and other marine organisms

Riverine Estuaries

Mangrove swamps, the lowland reaches of rivers, coastal lagoons, and bays are examples of Puerto Rico's estuaries. In all these places, upland freshwater runoff reaches the coastal lowlands where it mixes with seawater. An estuary is the zone where seawater and freshwater mix; the salinity area is lower than in the ocean, but higher than in freshwater. Estuaries are dynamic systems, and the location of the mixing zone changes year round owing to changing conditions of freshwater runoff and tidal energy. If rainfall is abundant, the salinity of the estuary decreases. Salinity increases if there is a drought or during periods of ocean storms and high waves and tides.

We already discussed mangrove forests as examples of estuaries. In this section, our focus is on riverine estuaries. Riverine estuaries are the zones

where freshwater and saltwater mix within the river channel. However, riverine estuaries include the mangrove flood-plain forests (riverine mangroves), which occur on both sides of the channel of rivers. In these flood-plain forests *Pterocarpus officinalis* Jacq. (swamp bloodwood) and other tree and fern species can also be found among the mangrove trees. They all become part of the riverine estuary.

During intense rainfall, rivers and aquifers overflow, and their discharge overwhelms saltwater intrusion such that most coastal systems have a freshwater layer. At this time, it is common to see freshwater plants floating in the ocean. However, sediments of rivers, swamps, or lagoons will contain saltwater buried by the weight of the freshwater column. In contrast, during the dry season, both river and aquifer discharges into the coast reach minimum values. Without a freshwater discharge to impede movement of sea water powered by tides, saltwater wedges push upstream and into bays, swamps, and lagoons and become saltwater systems. Saltwater wedges penetrate several kilometers inland through river channels. The limit of penetration is determined by the topography of the channel relative to the push of the tide. At peak dry season, a sandbar closes the mouth of many rivers (fig. 63). River discharge becomes a trickle, and the river estuary appears to be a lake in the flood plain. Heavy river discharges remove the sandbar following the onset of heavy rains during the wet season. At this time, the cycle of salinity change of the estuary starts again.

The changes in salinity and water movement through these estuaries—rivers, swamps, bays, and lagoons—drive the biota and ecological processes of estuaries. Species that live in estuaries have to survive wide fluctuations in salinity, water current, water depth, or combinations of all three. Many only visit the estuary when conditions are favorable for them. For example, marine organisms enter the river when salinities are high. Freshwater organisms visit the estuary when salinity is low. Others migrate in and out of the estuary according to their tolerance. Mangrove trees can survive the wide fluctuations of water and salinity in the swamp, but when conditions exceed their adaptations, they die massively.

This in- and outmigration of so many species makes estuaries very dynamic systems. Estuaries are known for high primary productivity, abundance of food for animals, and as a place where many types of organisms find optimal conditions for reproduction and development. In Puerto Rico, about 11 species of freshwater crustaceans, mollusks, and fish migrate from high-elevation streams to estuaries where they develop. These organisms require saltwater conditions to complete their life

A.E. Lugo

Figure 63—Typical mouth of an island river during the dry season. Notice the sand bar that forms and prevents freshwater discharge to the ocean. The river mouth is an estuary with a saltwater wedge that moves inland several kilometers depending on topography and tidal conditions.

cycles. Similarly, open ocean fish enter estuaries to reproduce and complete the early stages of their life cycles. The estuary provides protection and abundant food.

An example of a marine organism that reproduces and feeds in the estuary is the tarpon (*Megalops atlanticus*). This is a commercially important fish, favored by sports fishermen. Freshwater shrimp (fig. 64) are examples of montane organisms that float eggs and larvae to the estuary where they develop and then migrate upstream to montane habitats in stream pools. The upstream migrations are massive and subject to heavy predation by fish, birds, and people. Caribbean freshwater fish dominate the lower inner systems. Some of the same species will also be found in high-elevation freshwater streams.

Through research, fascinating facts about the ecology of the movement of these species are emerging, and these findings help us manage aquatic systems and water extraction from rivers. Below is a summary of the findings:

- Most aquatic organisms, particularly shrimp, are many times more abundant (even orders of magnitude more) at night than during the day.
- Even the drift of larvae and eggs to the estuary and the postlarval migration upstream follow a diurnal rhythm with greater numbers moving at night. At 1:00 p.m., the average downstream flow of larvae peaks.

J.G. Marsh

Figure 64—Freshwater shrimp (*Xiphocaris elongata*).

- Forty-two percent of shrimp larvae floating downstream are lost to intake pipes. Adjusting water intake to the schedule of larval and shrimp migrations, can greatly reduce loss of shrimp larvae and juveniles.
- River dams, even small ones, impact migrations and species composition upstream from the structures.
- Dead leaves from the forest (detritus) are an important food source for aquatic organisms in the river and estuary.
- Stream discharge, particularly large discharges, trigger migrations. Droughts affect the food webs in the river, particularly in pools.
- Conditions in pools influence the degree of reproduction of riverine fauna.
- Shrimp activity controls algae growth in the river and keeps rocks free of algal growth, which in turn increases safety to people using rocks to step across the river, as rocks are less slippery without algae. In fact, in the absence of shrimp, the species of algae change, as does the benthic community and its functioning.

The importance of healthy streams to a modern society transcends the water supply and sewage dilution services. Many values are derived from these systems including recreation, as well as aesthetic values. The population of Puerto Rico understands the value of natural systems. A study by González Cabán and Loomis (1999) found that Puerto Ricans were willing to pay up to $21 per year for maintaining the river-estuarine complex in the northeastern section of the island in

healthy condition. This translated to a $110 million value to the economy of Puerto Rico.

Posters that illustrate the complexity and biodiversity of the riverine estuary are available through the library of the International Institute of Tropical Forestry of the USDA Forest Service in Río Piedras.

For further reading, see Benstead 2000, Benstead et. al 1999, Benstead et. al N.d., Johnson and Covich 2000, March et. al 2001, March et. al 2002, Pringle 2001, and Scatena and Johnson 2001.

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Chapter 6: Marine Ecosystems

Submerged Seagrasses

In the shallow coastal **sublittoral** zone of Puerto Rico's bays, coral reef lagoons, and mangrove channels, soft marine sediments are frequently covered with a lush growth of submerged aquatic vascular vegetation (**SAV**). These perennial herbaceous plants are all adapted to exposure to a variety of saline and substrate conditions. There are 5 families, 12 genera, and 58 SAV species distributed throughout the world's tropical and temperate waters. All are higher flowering monocot plants (angiospermae). The majority of the tropical genera and species are found in Caribbean and Indo-Malaysian waters but occur in all coastal areas of the world, except Antarctica. Their distribution is affected by a variety of factors including depth, salinity, water turbulence, temperature, and **turbidity**.

The habitat these organisms form is classified as a marine aquatic bed wetland according to the Cowardin et al. (1979) *Classification of Wetlands and Deepwater Habitats of the United States*. Often intermingled in the seagrass beds will be **macrobenthic** algae, a few coral, and a wide variety of animals, many of which will be epiphytic. Ecologically, this community of plants and animals constitutes one of the most productive ecosystems on Earth (table 22). It forms a rich food web with hundreds of species of organisms that use seagrasses as physical substrate and food and serves as part of the complex coastal nursery for many fish and invertebrates that breed and develop in these waters. The values of these seagrass ecosystems include:

- Direct grazing by herbivorous predators
- Detrital enrichment of the food chain
- Nesting habitat for a variety of animals
- General habitat for an array of animals and other marine plants
- Predator escape for young, especially fish
- Stabilization of the substrate via large masses of interlocking rhizomes and roots
- Ability to dampen the intensity of storm waves
- Absorbtion of nitrogen and phosphorous
- Importance to the global carbon cycle
- Structural habitat for numerous **epibionts**
- Filtration of sediment from the water column
- Export of organic matter to other coastal ecosystems
- Source of human food

Table 22—Ratios of gross primary productivity (P) to aboveground standing crop (B) for mangrove forests, and for other systems that may succeed them

Ecosystem	Aboveground biomass	Gross primary productivity	P/B
	g/m²	*g/m² year*	
Riverine mangrove forest in Panama	27,921[a]	10,147[b]	0.36
Riverine mangrove forest in Florida	11,943[b]	8,760[b]	0.73
Fringe mangrove forest in Florida	7,933[b]	5,292[b]	0.67
Scrub mangrove forest in Florida	786[b]	1,022[b]	1.30
Subtropical moist forest in Puerto Rico	19,947[c]	11,972[c]	0.60
Tropical moist forests in Panama	36,320[a]	11,972[c]	0.45
	36,800[a]	11,972[c]	0.32
Saltwater marsh in Georgia	3,321[d]	3,285[d]	1.56
Freshwater marsh in south Florida	2,100[e]	4,745[f]	1.47
Thalassia beds	600–5,660[g]	1,825–13,410[g]	0.32–22.0
Coral reefs	846[h]	3,285–13,870[h]	3.8–16.0

[a] Golley et al. 1975.
[b] Lugo and Snedaker 1974.
[c] Odum 1970.
[d] Crip 1975.
[e] Steward and Ornes 1975.
[f] Bayley and Odum 1975.
[g] Odum 1971.
[h] Odum and Odum 1955.

Aquatic bed seagrasses develop best in shallow, low-energy, submerged sand flats and bays. Most seagrass beds are found in depths less than 10 meters (33 feet). They complete their entire sexual life cycle in seawater, and most are very adept at vegetative reproduction. Most species are well adapted to deal with wave action and shifting sediments in that they produce grass-like linear leaves and an extensive system of rhizomes. The creeping rhizomes produce erect shoots with leaves and roots at each node. The roots are **adventitious**. All species are clonal and rely heavily on asexual reproduction. In addition, they have thin leaves with a high surface-to-volume ratio, and aerenchyma tissue with extensive **lacunae** (air space) in their vegetative structures permitting rapid **diffusion** of gases. The high surface-to-volume ratios provide for maximum diffusion of nutrients between leaf blades and seawater, and maximum photosynthetic surface. The horizontal rhizomatous stems anchor and absorb nutrients. Flowers of seagrasses are incomplete, that is, separate male and female flowers, which causes cross pollination. Some species are **monoecious**, whereas others are **dioecious**. Submerged aquatic vegetation differs from algae in that it produces true flowers, fruits, and seeds; develops **vascular tissues**, and has true roots. (For information on access to seagrass beds in Puerto Rico, see app. 2.)

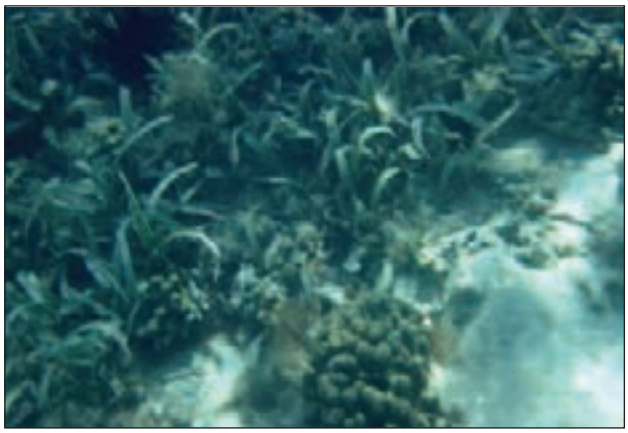
The predominant Caribbean seagrass is *Thalassia testudinum* Koenig[1] (turtle grass, box 25). Other important Caribbean seagrasses include *Syringodium filiforme* Kuetzing (manatee grass, box 26), *Halophila decipiens* Ostenfield (sea vine), *H. engelmannii* Ascherson (six-leaved seagrass), and *Halodule beaudettei* (den Hartog) den Hartog (shoal grass). None of the "seagrasses" actually belong to the true grass family Poaceae. They are grass-like in their external morphology, thus the common name. They often form dense blankets, much like a grass lawn, as a single species or in a mixed community. Most seagrass meadows are monospecific, that is, greater than 60 percent of the meadows have only one species present (Hemminga and Duarte 2000). They frequently are referred to as underwater meadows and, in fact, are grazed by a number of animals including sea turtles and manatees. The expanded surface area provided by the seagrass leaves, especially turtle grass, provides substrate for attachment of macro- and microepiphytic algae, as well as protistans, bacteria, and a variety of epifauna, that is, animals living on the leaf. These organisms are grazed by progressively larger free-swimming and surface-dwelling meio- and macrofauna. In many instances, this epibiotic community is so abundant that its biomass exceeds that of the seagrass leaf and, in fact, it may be difficult to see the leaf's surface. Ballantine (1971) identified 65 epiphytic algae on seagrass leaves in Florida. Although seagrass ecosystems are highly productive, as little as 5 percent of the accumulated biomass is eaten directly by herbivores. The remaining 95 percent eventually enters the detritus food chain. As seagrass leaves age, initial organic releases are most likely taken up by epibionts, and later, when the leaf detaches and floats free, it will gradually break down into smaller pieces and sink into sediments where bacterial breakdown is initiated. This degraded leaf substrate with its microflora will then be used by a variety of benthic detritus feeders. Some seagrass leaves float long distances and can even enter deep water food chains. Blades of seagrasses have shown up on pictures from the Puerto Rico Trench at a depth of 7860 meters (25,780 feet).

Of the 12 recognized genera of seagrasses in the world, 5 are present in waters around Puerto Rico, with 7 species present from 4 families (table 23). Two of the species, *Halophila decipiens* Ostenfeld (sea vine) and *Ruppia maritima* L. (widgeon grass), can grow in habitats that are brackish, and *Ruppia* can grow in freshwater. *Thalassia* and *Syringodium* are the most abundant and widely dispersed seagrasses in the sublittoral zone of Puerto Rico in the southwest, south, and east coasts, where the shelf is broader and more protected. The largest and most dense meadows are in shallow waters of 2 meters (6 feet) or less. *Halophila decipiens*

[1] See appendix 1 for Common and Latin names.

Continued on page 226.

Box 25. *Thalassia testudinum* Konig (turtle grass)



G. Miller

Views of *Thalassia testudum* Konig (turtle grass) in a shallow water habitat.

By far the most abundant seagrass species in Puerto Rico and the Caribbean is *Thalassia testudinum* Konig (turtle grass). This species gets its common name from the fact that it is eaten by green sea turtles. The family Hydrocharitaceae is a family of 16 genera and 120 species of submergent and emergent fresh and saltwater aquatic herbs. Only two of the genera are marine and both are found in Puerto Rico. Members of the family produce separately sexed male and female flowers. Flowering occurs in April and May. The leaves are produced in clusters or whorls at numerous points along the stems, which are horizontal and root-like rhizomes. The rhizomes act like roots to anchor the plant into the soft sandy bottom, and they periodically break, thus serving as a way to asexually propagate the species. Vast clonal populations of turtle grass are found throughout its range. Habitat coverage can be less than a meter square or up to hundreds of square kilometers (square miles). *Thalassia* grows in mud, sand, and broken shell accumulations. Storms may cause detachment of old leaves, and large **windrows** of the leaves are often found cast upon beaches. The leaves can be collected and used for mulch and fertilizer. General growth and accumulation of turtle grass biomass is controlled by available light, water quality, available nutrients, substrate composition, and wave action. In the Caribbean, biomass accumulation in the water near La Parguera in southwestern Puerto Rico ranges from 532 to 1,986 grams per square cubic meter per day, according to González Liboy (1979). This indicates very high productivity comparable to intensive high-yield agriculture. This is why this ecosystem is so vital to the complex grazing and detrital-based food webs found there and in all seagrass ecosystems. For a review of grazing relationships in *Thalassia beds*, see García Rios (1990).

Box 25. continued

The large, flat, strap-shaped leaves of turtle grass provide important vertical structural habitat for many small epiphytic plants and animals. Turtle grass and other seagrasses, with their associated flora and fauna, create a complex epibenthic community distinct from other marine habitats in the sublittoral zone.

Thalassia anatomically lacks well-developed support tissue, so can bend with the currents and wave action. The large leaves create drag on the water, reducing its velocity, reducing erosion, and allowing for organic particulates to settle in place, important to the detrital-based component of the food chain. Growth is optimal in gentle, clear lagoons in depths from 0.5 up to 30 meters (2 to 90 feet). Turtle grass can tolerate salinities ranging from 10 to 48‰, with normal sea water as the optimal (33‰) salinity. Leaves grow in clusters from nodes and are sheathed at the base. When excavated, the rhizome is hairy, and fibrous adventious roots are evident. The rhizomes are creeping and generally located 5 to 10 centimeters (2 to 4 inches) into the substrate.

They are easily removed by hand and require a gentle wash in order to see the various rhizome and root structures. If you slit the rhizome, it is possible to observe the aerenchyma tissue with the large lacunae. This porous tissue, with its large air spaces, promotes the movement of oxygen into the rhizome and fine roots. Frequently, the rhizome and roots grow in substrates with little to no oxygen available.

What conditions in the environment produce changes in turtle grass? Nutrient enrichment via human sources or seabird excrement can cause a shift to *Halodule wrightii* Ascherson (shoal grass). It is thought that shoal grass has an advantage in that it can grow vertically more rapidly. Infections can reduce or eliminate turtle grass. Higher water temperatures, altered salinity, and increased sedimentation can cause a decline in turtle grass. Algae blooms can block light and increase turbidity. As turtle grass dies out, bottom sediments are more easily disturbed by wave action, boats, and so forth, thus expanding the decline of turtle grass. In general, areas with frequent disturbance are likely to have a multispecies community. When the benthic environment is stable, usually a monospecific community such as turtle grass will be found.

For more information on this species, see den Hartog 1970, Hemminga and Duarte 2000, Howard 1979, and Littler et al. 1989.

Box 26. *Syringodium filiforme* Kuetzing (manatee grass)

G. Miller

Syringodium filiforme Kutzing (manatee grass) growth form.

All genera of seagrasses have fairly thin, blade-like, flat leaves, except *Syringodium filiforme* Kutzing (manatee grass). It has cylindrical leaves. It is frequently found growing mixed with turtle grass, but it can grow in a monospecific population. Manatee grass occurs in tropical waters of the western Atlantic Ocean, Gulf of Mexico, and the Caribbean Sea. It typically grows in water 10 meters or less (33 feet), but in extremely clear water it has been found at depths of 20 meters (66 feet). The cylindrical, stiff, light green leaf blades differ in length from 2 to 30 centimeters (1 to 12 inches) and in width from 1 to 2 millimeters (less than 1⁄16 inch). The rhizome of manatee grass is 2 to 4 millimeters (around 1⁄16 inch) in diameter and it serves as the primary food storage organ. It produces two to four roots with root hairs, scale leaves, and short shoots at each node. The small shoots then give off two or three thread-like (filiform) leaves, which are terete (round).

The plants are dioecious. Flowering is controlled by water temperature, with 25 °C (77 °F) being the critical temperature in the waters of Puerto Rico and the Virgin Islands. Flowers form on inconspicuous raceme inflorescences. Fruits are small, ovoid, beaked, and about 6 millimeters (4-inchs) long.

Manatee grass is thought to be intermediate in the succession sequence in seagrass communities in the Caribbean. Nutrient supply may be critical, with macrobenthic algae initially occupying open sediments, such as blowouts or areas opened by hurricane scouring. Manatee grass then invades, followed by turtle grass. Turtle grass, through **interference competition** for light and nutrients, replaces manatee grass. Turtle grass populations will then control that site until the next physical disturbance or pollution event creates a gap that manatee grass can invade.

For more information on this species, see Dawes 1998, Howard 1979, and Kaplan 1988.

Table 23—Names and characteristics of the seagrasses of Puerto Rico

Species	Common name	Family	Habitat	Distinguishing features
Thalassia testudinum Konig	Turtle grass	Hydrocharitaceae	0.5 to 20 meters (2 to 65 feet) deep, mostly in depths < 10 meters (33 feet); sandy bottoms; low disturbance climax species; east and southwest coast; common	Long, flat, strap-shaped leaves up to 1 meter (3 feet) long with 9 to 15 parallel veins, rounded apex; older leaves usually covered in epiphytes; creates an appearance of a vast green meadow
Halophila decipiens Ostenfeld	Sea vine or dwarf seagrass	Hydrocharitaceae	0.5 to 30 meters (2 to 100 feet) deep; quiet lagoons and brackish ponds; can tolerate turbid polluted water; soft bottoms; common	Slender vine-like stems; leaves opposite at the nodes, leaves oval and minutely toothed; one prominent midvein per leaf; grows as small patches up to 3 feet (1 meter) across
Halophila baillonis Ascherson	Midrib seagrass	Hydrocharitaceae	Shallow water; 1 to 3 meters (3 to 10 feet) deep; sandy or muddy bottoms; small distribution in Puerto Rico	Delicate, with thin rhizomes, leaves in two or four pairs at shoot apex forming a pseudo whorl, blades oblong to elliptic, apex obtuse, blade margin with fine hairs
Halophila engelmannii Ascherson	Six-leaved seagrass	Hydrocharitaceae	Shallow water; 1 to 3 meters (3 to 10 feet) deep; quiet lagoons, ponds or boat harbors; soft bottoms of sand or mud; restricted distribution	Resembles the alga *Caulerpa paspaloides*; leaves smooth, flat with distinctive midrib and veins; stalks erect in water; leaves in whorls of six to eight at top, up to 20 centimeters (8 inches) long; margins fine toothed
Syringodium filiforme Kutzing	Manatee grass	Cymodoceaceae	Shallow clear water; 1 to 20 meters (3 to 65 feet) deep; fine muds or sandy bottoms; east and southwest coast; common	Leaves cylindrical (terete); forms dense mats; leaves up to 45 centimeters (18 inches) long; may grow with turtle grass
Halodule wrightii Ascherson	Shoal grass	Zosteraceae	Shallow waters; 1 to 10 meters (3 to 33 feet) deep; fine muds to sandy bottoms; colonizer after disturbance like hurricanes; common	Leaves very narrow with flat blades, 4 to 10 centimeters (1.5 to 4 inches) long; leaf blade apex is topped by three teeth, with the mid tooth longer; forms extensive meadows
Ruppia maritima L.	Widgeon grass	Ruppiaceae	Shallow water of estuaries, lagoons, rivers, and freshwater lakes and ponds, wide salt tolerance; mostly brackish in Puerto Rico	Leaves narrow and lanceolate shaped, alternate arrangement, apex pointed, fine structure throughout body

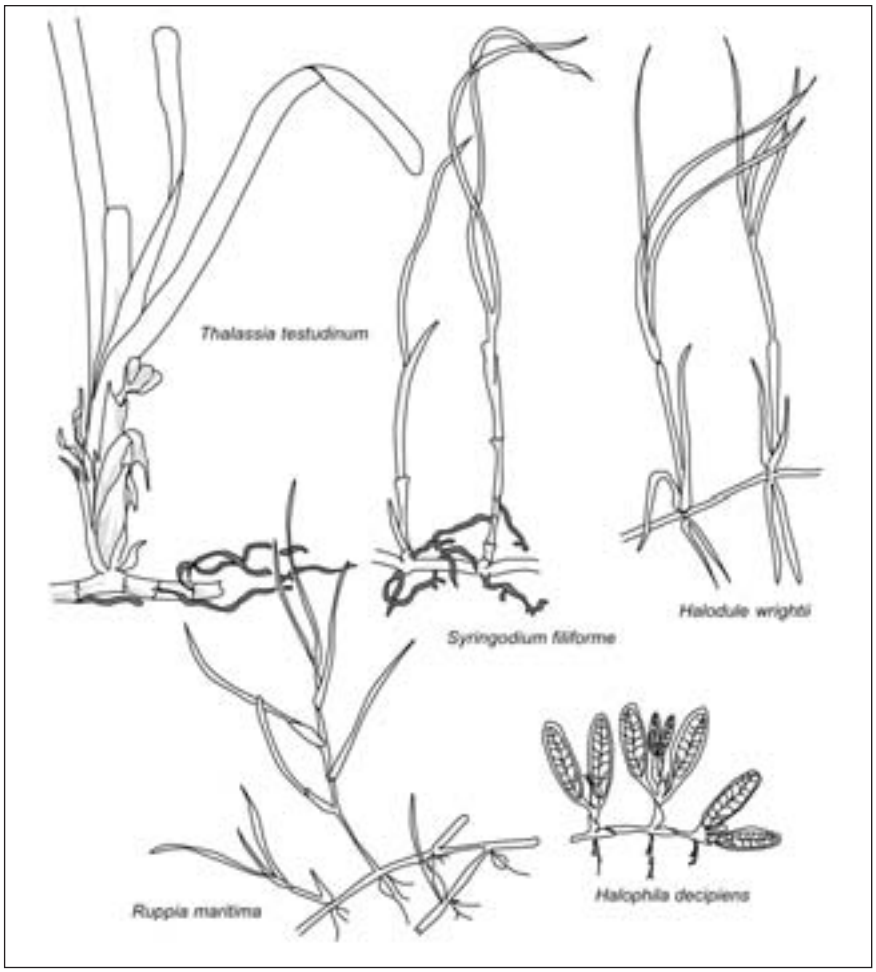


Figure 65—Morphology of five of the seagrass species found in Puerto Rican waters.

Ostenfeld and *Halodule wrightii* Ascherson (shoal grass) are also very common on the Atlantic and Caribbean shelves of Puerto Rico. Figure 65 illustrates the morphology of five of the species found in Puerto Rican waters.

Seagrasses and their associated macrobenthic algae are the basis for an extremely productive ecosystem. It provides animals with a wide variety of plants (macrobenthic and microepiphytic) to feed upon and space in which to live, hide, and reproduce. There are five groups of organisms associated with seagrass communities of Puerto Rico (modified from García Ríos 1990). These include:

- **Sessile** algae and animals such as diatoms and a variety of invertebrates
- Microfauna such as protozoans, flagellates, and various small invertebrates
- Animals that travel or crawl on the bottom of seagrass beds such as snails, small crustaceans, and echinoderms

- ➢ Animals that swim and settle on leaf blades such as shrimp, copepods, and small jellyfish
- ➢ Animals that swim among leaf blades such as a variety of fish species, especially larval and juvenile stages

Many animals present in these waters are valuable commercial species, such as fish, conch, and shellfish. Seagrass beds are also in proximity to two other ecologically critical and commercially valuable ecosystems: mangrove swamps and coral reefs (fig. 66). These also exhibit some of the same attributes of food chain and space values as cited for seagrass beds. Together these three proximal key coastal marine habitats are the heart and soul of the tropical nursery and feeding grounds for most of Puerto Rico's insular shelf. This is especially true of about 80 percent of the fish of commercial value that are fished from these waters. These unique underwater meadows are also critically important to endangered animals such as *Chelonia mydas* (green sea turtle) and *Trichechus manatus* (West Indian manatee). Both are known to graze these habitats heavily.

Most seagrass populations are well adapted for cloning, and by excavating their underground parts, this strategy can be effectively observed. See fig. 67 for the general morphology of seagrass. Some of these clonal populations are thought to be thousands of years old. Could they be considered a form of old growth? Remember that all marine SAV's are adapted to the following conditions:

- ➢ They are able to grow submerged.
- ➢ They are totally tolerant to saltwater.
- ➢ They show a well-developed anchorage system to cope with waves or tides.
- ➢ They can successfully reproduce underwater—both sexually and asexually.
- ➢ They are tolerant to cropping by herbivores.
- ➢ They compete in a stressful environment.
- ➢ They can absorb essential carbon dioxide, phosphates, and NO_4 via the leaf epidermis without the presence of stomata or through roots.

An interesting field exercise is to conduct a survey of macrobenthic algae encountered in SAV communities and how the algae differ from the flowering plants. In addition, seagrass beds have many animals associated with them. These, too, can be surveyed and discussed in terms of their life cycle stages, numbers, and position in the ecosystem, and so forth. The following list includes some of the

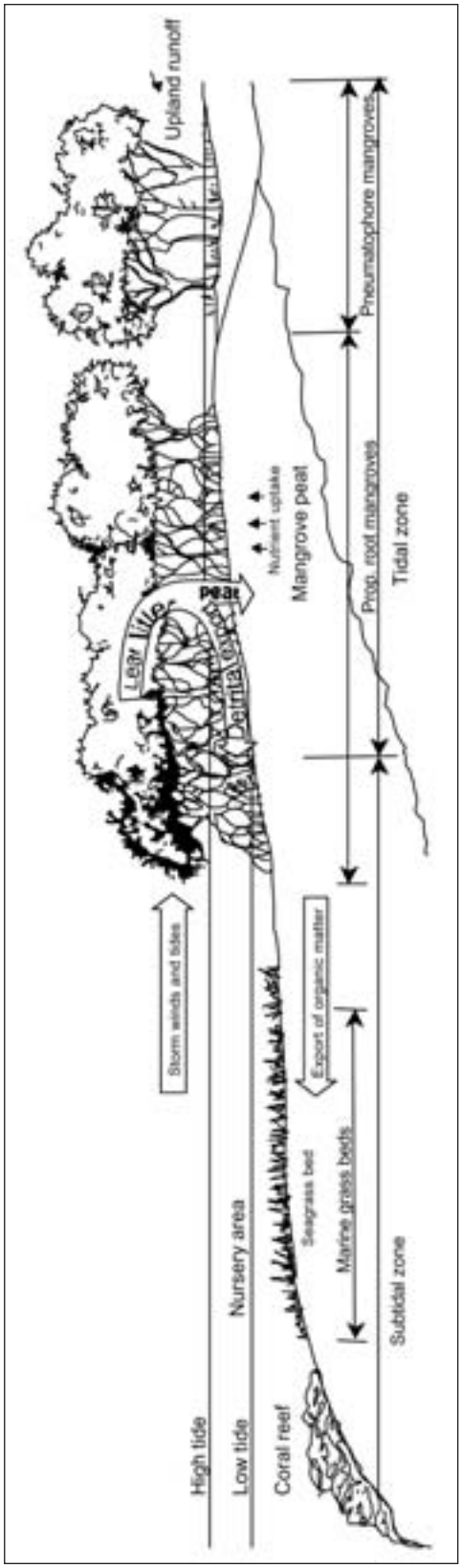


Figure 66—Typical partitioning of subsystems in a tropical coastal area. The mangroves and seagrasses retain the flows of nutrients from the land, ensuring clear water for the corals, which in turn constitutes a means of protection to counter erosion of the coast.

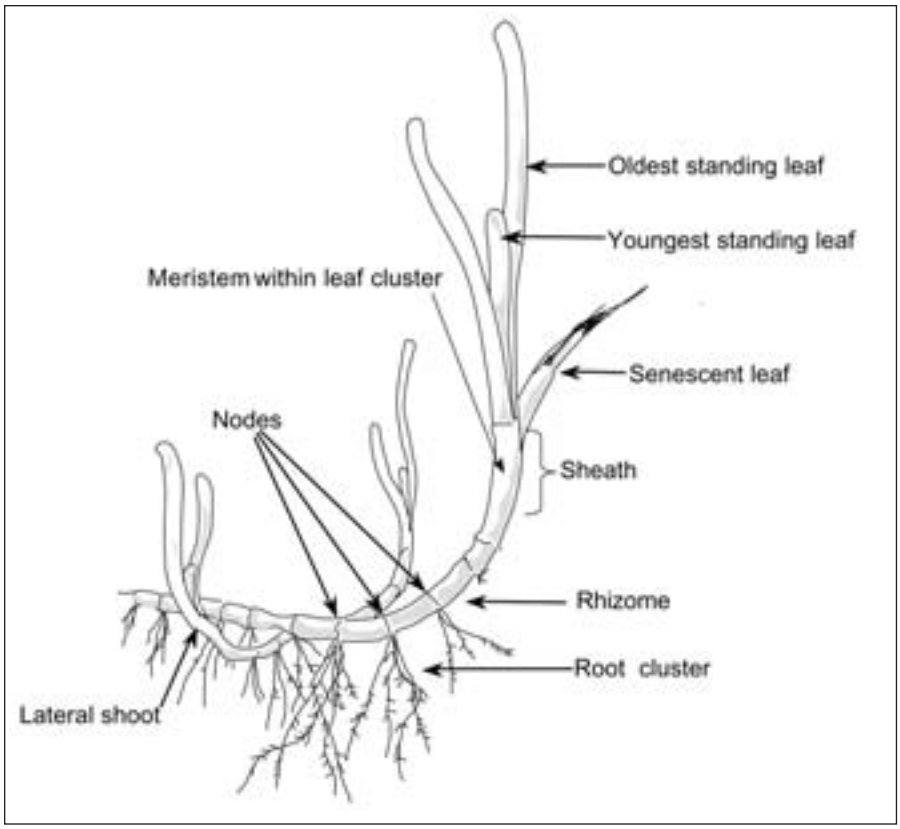


Figure 67—General features of the morphology of a seagrass.

many macrobenthic marine algae and animals likely to be encountered in seagrass beds of Puerto Rico.

Macrobenthic Algae

Green

- *Acetabularia crenulata* Lamouroux (white mermaid's wineglass)
- *Avrainvillea longicaulis* (Kuetzing) Murray & Boodle (paddle-blade alga)
- *Avrainvillea nigricans* Decaisne (soft fan alga)
- *Bryopsis pennata* (Harvey) Collins & Hervey (sea fern)
- *Caulerpa mexicana* Kuetzing (yellow leaf alga)

Animals

Fish (short list)

- *Sparisoma radians* (parrot fish)
- *Acanthurus chirurgus* (surgeon fish)
- *Sphyraena barracuda* (barracuda)
- *Megalops atlanticus* (tarpin)
- *Ablennes hians* (needle fish)
- Silversides, herring, anchovies (small silver-colored fish that form massive schools in calm waters of seagrass beds and mangrove channels)

- *Caulerpa racemosa* (Forsskal) J. Agardh (grape alga)
- *Caulerpa sertularioides*
- *Cladophoropsis* spp. (turf alga)
- *Codium decorticatum* (Woodward) Howe (dead man's fingers)
- *Dictyosphaeria cavernosa* (Forsskal) Boer. (green bubble alga)
- *Enteromorpha* spp. (green tube alga)
- *Halimeda incrassata* (Ellis) Lamouroux (three finger leaf alga)
- *Halimeda opuntia* (L.) Lamouroux (coralline watercress alga)
- *Halimeda tuna* (Ellis & Solander) Lamouroux (stalked lettuce alga)
- *Penicillus capitatus* Lamarck) (shaving brush alga)
- *Udotea conglutinata* Lamouroux (mermaid's fan)
- *Udotea flabellum* (Ellis & Solander) Lamouroux (hard fan alga)
- *Valonia ventricosa* J. Agardh (sea pearls)
- *Vaucheria* sp. (vaucheria)

Brown

- *Dictyopteris* spp. (brown strap alga)
- *Dictyota divaricata* Lamouroux (strap alga)
- *Sphaeroides spengleri* (banded puffer)
  Boergesen (green feather alga)
- *Holocentrus rufus* (squirrel fish)
- *Thalassoma bifasciatum* (bluehead wrasse)
- *Hemiramphus brasiliensis* (bally-hoo)
- *Hippocampus reidi* (seahorse)
- *Aetobatus narinari* (spotted eagle ray)
- *Synodus* spp. (lizard fish)
- *Epinephelus guttatus* (red hind seabass)
- *Dasyatis americana* (southern stingray).

Reptiles

- *Chelonia mydas* (green sea turtle)

Mammals

- *Trichechus manatus* (West Indian manatee)

Invertebrates

(Herbivorous predators)

- *Diadema antillarum* (long-spined sea urchin)
- *Lytechinus variegatus* (green sea urchin)
- *Tripneustes ventricosus* (West Indian sea egg)
- Echinometra lucunter (red rock urchin)

(Nonherbivorous)

- *Bartholomea* sp. (sea anemone)
- *Aplysia dactylomela* (sea hare)
- Amphipods

- *Padina sanctae-crucis* Boergesen (tan petticoat alga)
- *Sargassum natans* (L.) Gaillon (sargassum seaweed)

Red

- *Acanthophora spicifera* (Vahl) Boergesen (red brittle alga)
- *Ceramium* sp. (red banded alga)
- *Chondria* sp. (red tuft alga)
- *Dictyurus occidentalis* J. Agardh (red lace alga)
- *Gracilaria* spp. (red branched alga)
- *Polysiphonia* sp. (polysiphonia)
- *Spyridia filamentosa* (Wulfen) Harvey

Coral

- *Acropora cervicornis* (staghorn coral)
- *Millepora complanata* (flat-topped fire coral)
- *Porites* spp. (finger corals)
- *Siderastrea radians* (shallow-water starlet coral)
- *Manicina areolata* (rose coral)
- *Oculina diffusa* (ivory bush coral)
- *Agaricia agaricites* (lettuce-leaf coral)
- *Cassiopeia frondosa* (upside-down jellyfish)
- Gastropod snails
- *Strombus gigas* (green conch)
- *Strombus pugilis* (fighting conch)
- *Cassis tuberosa* (helmet conch)
- Isopods
- *Ludwigothuria mexicana* (sea cucumber)
- Nudibranchs
- *Octopus briareus* (reef octopus)
- *Oreaster reticulatus* (West Indian starfish)
- *Sabellastarte magnifica* (magnificent feather duster worm)
- Shrimp (eight species are common)
- *Sepioteuthis sepioidea* (reef squid)
- Various crabs
- *Stoichactis helianthus* (Sun anemones)
- *Panulirus argus* (spiny lobster)
- *Ophiocoma echinata* (spiny brittle star)
- *Pinna carnea* (amber pen shell)
- *Modulus modulus* (Atlantic modulus)
- *Codakia orbicularis* (tiger lucine clam)
- *Hermodice carunculata* (fire worm)
- *Haliclona rubens* (breadcrumb sponge)

As is the case for so many important natural ecosystems, seagrass beds are in a state of decline or disappearing in many areas of the world where an estimated 100 000 hectares (247,000 acres) have been lost. The rate of loss is poorly documented. However, in one of the most carefully documented cases—the Chesapeake Bay of the Eastern United States—less than 10 percent of the original seagrass beds remain. A similar dieoff of turtle grass occurred in Florida Bay in the 1980s. Puerto

Rico is no exception. To maintain the vital functions of these communities, it is essential that they be understood, appreciated, and protected. The coastal zones throughout the globe are undergoing the greatest increases in human population, and this is where seagrasses occur. Many anthropogenic activities will continue to degrade and accelerate the loss of seagrass beds. Following is a list of some of the important stressors that can cause the decline or extirpation of seagrass beds. Stressors are known to both reduce species diversity and cause species shifts (Hemminga and Duarte 2000). All of these are ongoing in the Caribbean, and most are affecting Puerto Rico's seagrass populations.

Anthropogenic stressors:

- Dredge/fill operations
- Industrial effluent (organic and inorganic)
- Municipal effluent
- Oil spills
- Agricultural nutrient enrichment (especially nitrates and phosphates)
- Sedimentation from construction and agriculture
- Motor boat props and wave scouring
- Harbor and marine development
- Commercial fishing techniques that disrupt the benthic zone
- Treasure hunting (use of sucker dredges and drag lines)
- Extirpation of large vertebrate grazers, such as sea turtles and manatees
- Power plants (temperature change)
- Effects associated with ***El Niño*** and global climate change
- Commercial cropping of seagrasses for aquaculture
- Recreation trampling and anchor scarring
- Introduced alien species

Natural stressors:

- Storm scouring (especially hurricanes)
- Excessive grazing by herbivorous predators
- Algae blooms
- Seasonal temperature changes
- Salinity change associated with storms
- Diseases, such as the slime-mold-induced wasting disease
- Excessive sedimentation from terrestrial erosion

The seagrass ecosystem constitutes a vital wetland in the marine waters of the United States, and more can be done to protect it.

For further reading see Austin 1971, Ballantine 1971 and 1977, Cowardin et al. 1979, Dawes 1998, Delgado González 1978, den Hartog 1970, González Liboy 1979, Harlin 1975, Jackson et al. 2001, Kikuchi and Peres 1977, Kjerfve 1998, Littler et al. 1989, McRoy and Helfferich 1977, Ogden 1980, Phillips and McRoy 1980, Scientific Committee on Problems of the Environment 1997, Thayer et al. 1975 and 1984, Vicente 1992, and Zieman 1976.

Coral Reefs

For many people, the term "coral reef" immediately conjures up images of crystal clear water filled with vast schools of beautifully colored fish, swimming over and within an underwater seascape filled with an array of colorful corals. This perception is only partially accurate. In fact, the coral reef and its inhabitants form a complex ecosystem filled with aggressive behavior, heavy predation, complex symbiotic relationships, and very specific species zonations. In addition, many organisms are nocturnal feeders and may rarely be seen. Coral reefs are frequently characterized as the species habitat equivalent of tropical rain forests, that is, the sea's most structurally complex and taxonomically diverse ecosystem. Estimates of coral reef species range from 600,000 to more than 9 million species worldwide (Knowlton 2001). Coral reef development is generally limited by water quality and temperature (fig. 68).

So, what is coral? Coral is the common name for a variety of invertebrate marine organisms that belong to the ***phylum Cnidaria*** (coelenterata). There are an estimated 9,000 species of cnidarians in three classes.

- Hydrozoa–hydras, Portuguese man-of-war, fire corals (3,000 species)
- Scyphozoa–jellyfish (200 species)
- Anthozoa–hard corals, sea anemones, sea whips, sea fans, sea pens (6,000 species)

The following list will help you understand the features of this animal group.

- They have external or internal skeletons.
- They exhibit stony, horny, or leathery consistency.
- The term coral is particularly applied to the stone-like hard corals, such as *Acropora* (order Scleractinia), of which there are over 1,400 species, and the horny corals such as *Gorgonia*, of which there are an estimated 1,200 species.

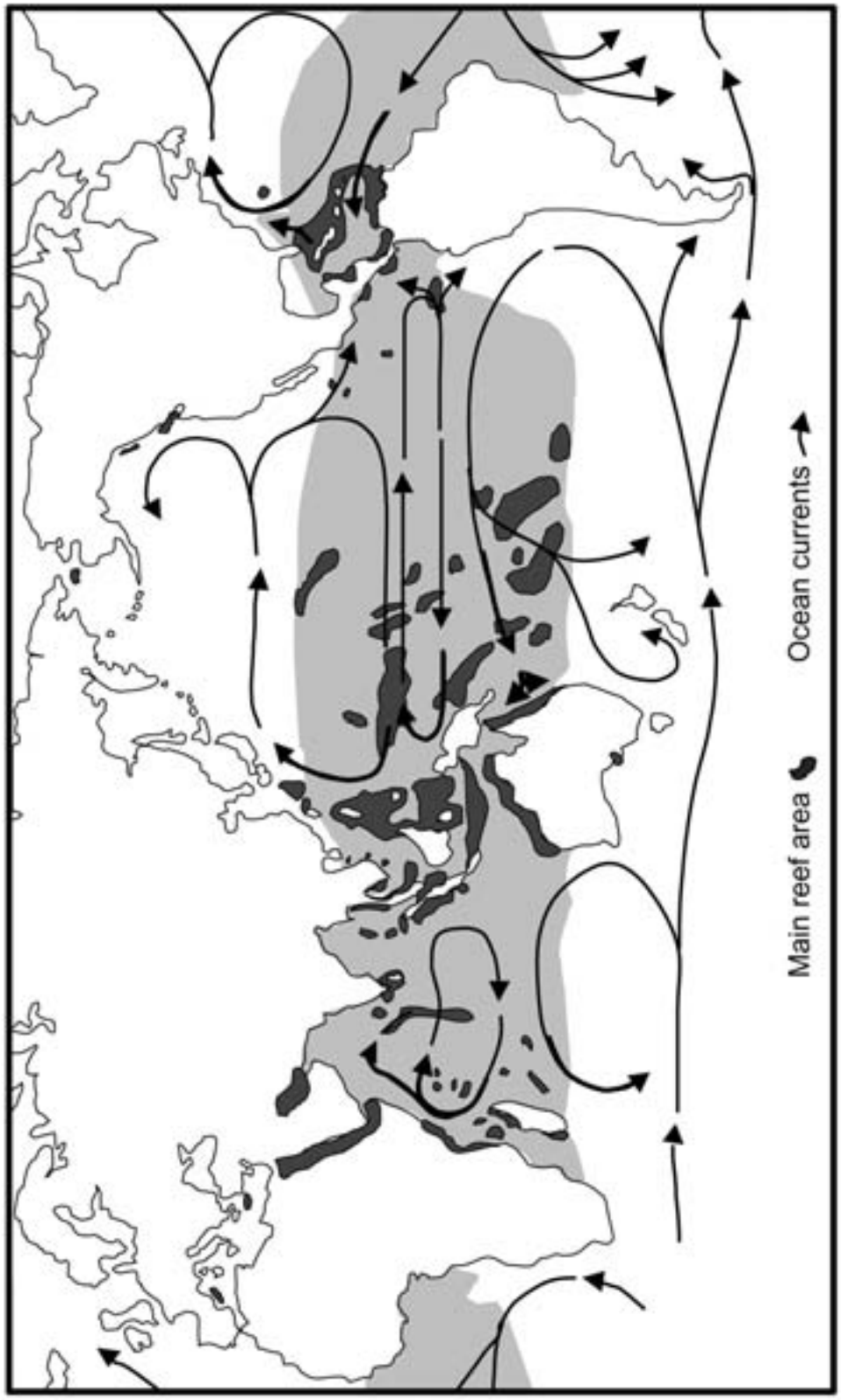


Figure 68—Global distribution of coral reefs (dark hatching), along with the major patterns of surface currents. Reef growth is generally limited by water temperature down to 18º or 20º C (the light shaded area is the 20º C isotherm band). Reefs are predominantly distributed on the eastern margins of continents where favorable currents (emphasized by thicker arrows), of clean low nutrient water are present.

- Most corals are named for their individual appearances:
  - Elkhorn
  - Star
  - Fan
  - Staghorn
  - Mushroom
  - Whip
  - Brain
  - Finger
  - Rod
- All cnidarians produce cnidocytes (stinging cells).
- Food capture is by the use of stinging cells for predation of zooplankton.
- They have primitive body organization surrounding a large hollow, central gut (**coelenteron**).
- Most corals are tropical and found in shallow marine waters.
- Reef-building corals are restricted to clear, warm water, generally less than 90 meters (295 feet) deep.
- They have a polymorphic life cycle (more than one phase).
- There are two body types:
- Medussae–free swimming.
- Polyps–sedentary with tentacles (fig. 69).
- Life expectancy varies from one season (hydra), to 90 years (sea anemones).
- Most have the ability to regenerate new body parts from damaged individuals.
- Many possess single-celled **endosymbiotic** algae in their tissues (section on symbiosis follows).
- Body plan is simple consisting of three layers:
- Ectoderm–protection
- Endoderm–digestive layer
- Central mouth surrounded by tentacles for food capture
- No brains or heads
- No organs formed, complexity is not beyond tissue level (fig. 70).

Corals are tiny animals that form vast colonies that attach to firm surfaces on the ocean bottom. The living reef is built upon vast layers of old calcium carbonate laid down by innumerable earlier generations. The living part of the reef is its outer layer. The individual animals are referred to as polyps. The polyps are able to generate calcium carbonate, which they use to build protective skeletal structures in many sizes and shapes. Some corals (hermatypic reef building) build complex skeletal structures that form the massive limestone deposits we call the coral reef. A large reef is actually composed of countless numbers of coral animals and literally tens of thousands of invertebrates and fishes. Also mixed into the reef are a vast number and coverage of algae. Not all cnidarians are reef builders. Many, in

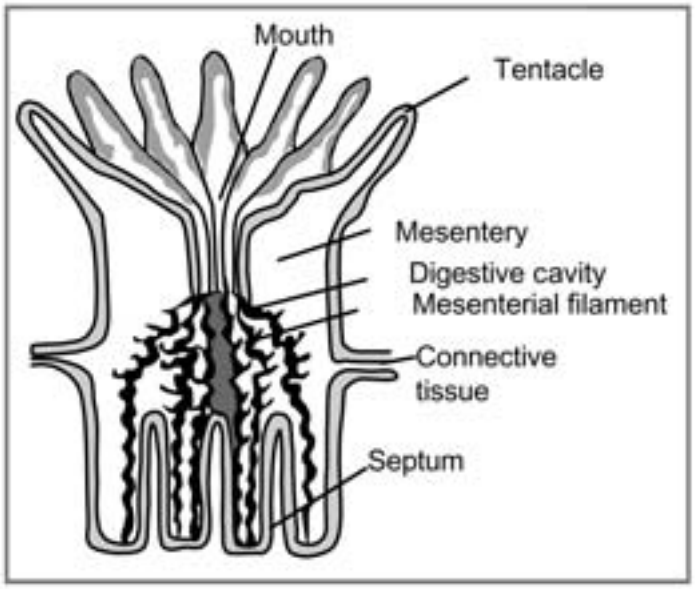


Figure 69—Cross section through a hard coral polyp.

fact, live singly and remain unattached, such as jellyfish and the Portuguese man-of-war. Many organisms on a reef are potentially hazardous to unprotected skin, especially these latter groups (Halstead 1967, Halstead et al. 1990). Many species can sting, bite, shock, puncture, and cause abrasions.

Various factors affect the growth and development of reef building (**hermatypic**) corals. The following list describes the narrow range of conditions that must be met in order for these corals to exist.

- Shallow water with waves and currents
- Firm substrates for polyp attachment
- Undiluted sea water (33 to 35‰ sodium chloride)
- High amounts of light
- Zooxanthellic symbiotic algae
- Water temperatures of 18 to 25 ºC (64 to 78 ºF)
- Low-turbidity, high-clarity water
- Waters with good circulation to provide high oxygen levels, remove wastes, and bring in food organisms

Oceanic reefs are autotrophic units operating at a high level of productivity, with fast turnover rates, short life cycles, and high efficiency in using and recycling

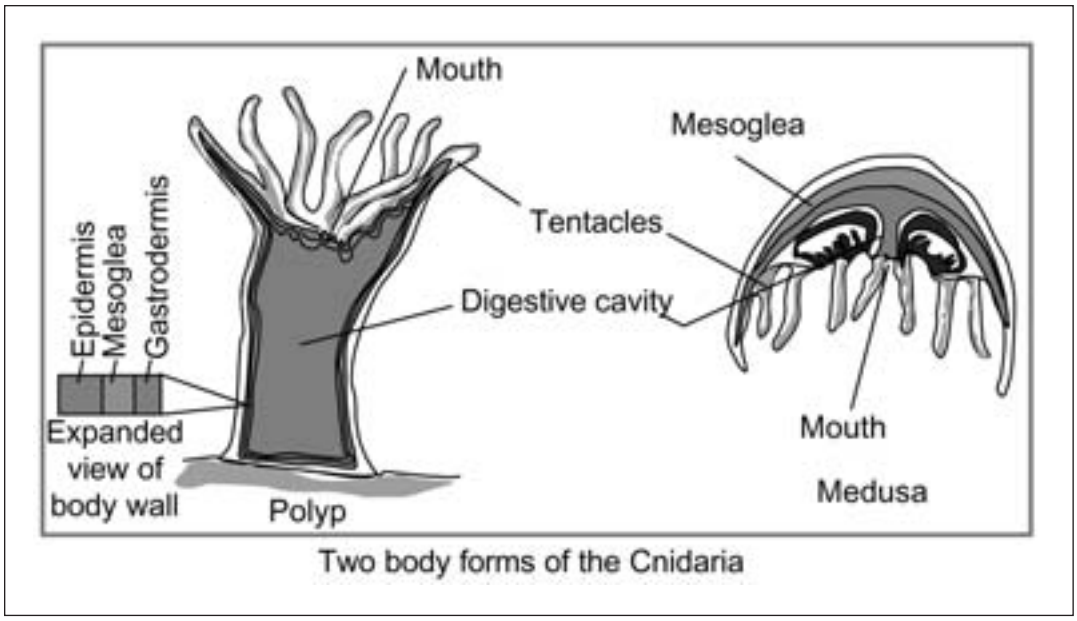


Figure 70—Body forms of Cnidaria.

nutrients. Vast amounts of endosymbiotic algae are present within the coral polyps. In addition, large quantities of other phytoplankton, macrobenthic attached algae, and submerged seagrasses may be present. All give off **metabolites** into the water column. As a result, the water circulating within the reef system has much higher amounts of organic detritus, dissolved nutrients, and concentrations of zooplankton than does the surrounding open ocean. Thus, the water surrounding the corals is nutrient enriched. These nutrients can be picked up by the microvilli covering the polyp's epithelium. As a result of these factors, coral reefs exhibit high productivity ranking them one of the Earth's highest producing ecosystems (fig. 71). Although coral reefs cover less than 0.1 percent of the area of the world's seas, they are home to nearly one third of all marine fishes.

Coral reefs are a seeming paradox in that they are highly productive ecosystems, or islands of productivity, frequently surrounded by large areas of inherently low natural productivity. This was brought to light recently in the case of Puerto Rico in a satellite view of the equatorial and north Atlantic Ocean on the cover of *Science* (2001). It showed that the islands of the West Indies are in large part surrounded by very low productivity ocean water. To the east of Puerto Rico, for over 1667 kilometers (1,000 miles), lie the least productive waters in the north Atlantic Ocean (fig. 72). In spite of this seeming biological desert to the east, Puerto Rico's shelf waters are quite productive thanks in large part to coral reefs, seagrass beds,

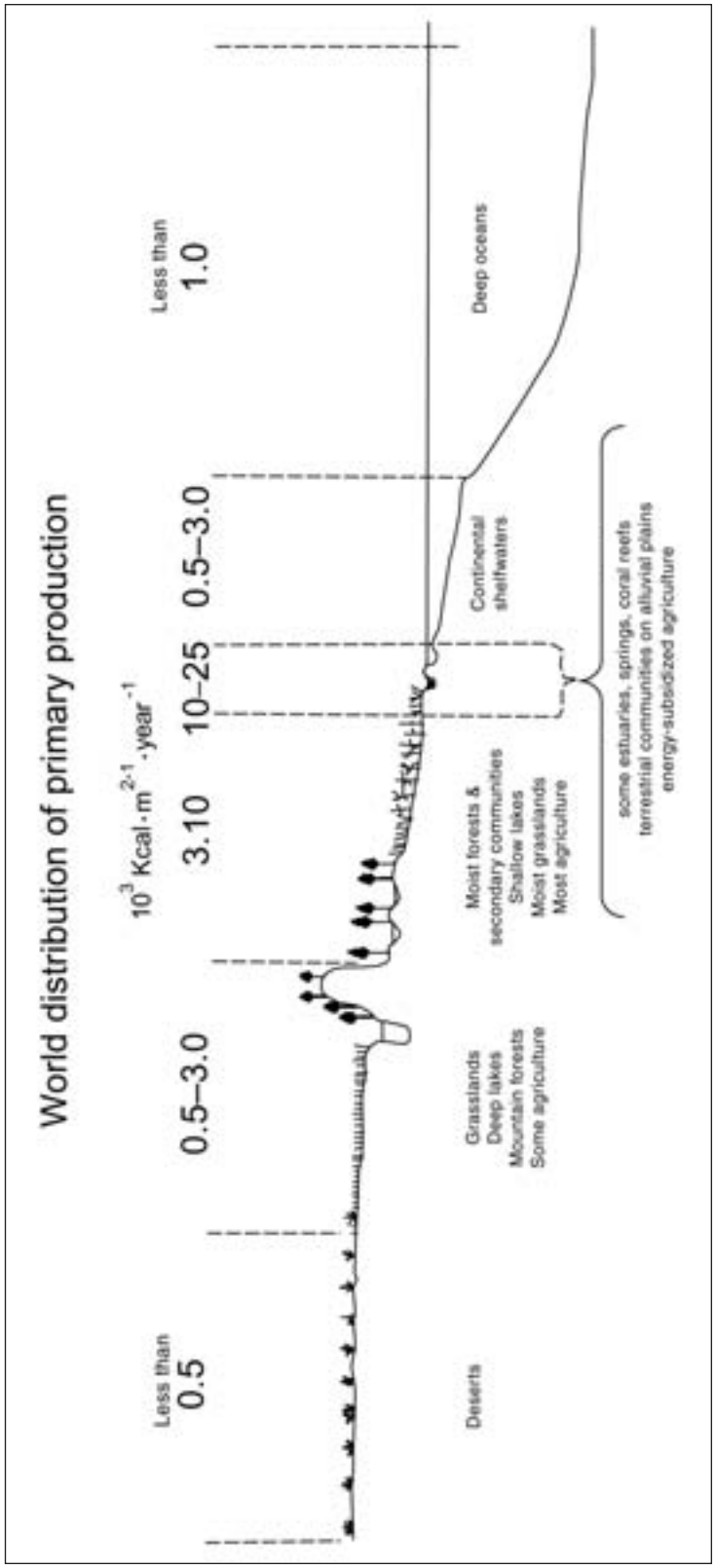


Figure 71—Comparative productivity of ecosystems.

G. Miller

Figure 72—Puerto Rico and adjacent waters.

and mangrove swamps (fig. 73). Therefore, from an ecological standpoint, the primary resource values of a reef are its high productivity, variable habitat, and high species diversity. Up to 180 species of edible fish are found on the reefs of Puerto Rico. The reefs contain an enormous amount of marine protein in a relatively localized area thanks to concentrations of nutrients and microhabitats for growth, and reproduction by a large variety of noncoralline animals.

When scuba diving, snorkeling, or looking through glass-bottomed boats, people are immediately struck by the zonation they view within the reefs. One of the first researchers to describe this phenomenon was Charles Darwin. In fact, the terms coined by Darwin in 1842 to describe the types of reefs are still used today. The main types of reefs are:

- **Barrier reefs** occur along continents such as Australia's Great Barrier Reef, which is 1935 kilometers (1,200 miles) long. This massive reef is separated from the mainland by large lagoons and channels (fig. 74).
- **Fringing reefs** occur around islands and are adjacent to continents. In some cases they are shoreline projections.
- **Atolls** are horseshoe-shaped ridges of reefs and islands, with a lagoon in the center and often are old sunken volcanic cones. They are typical of the Pacific and Indian Oceans, and generally not associated with continents.

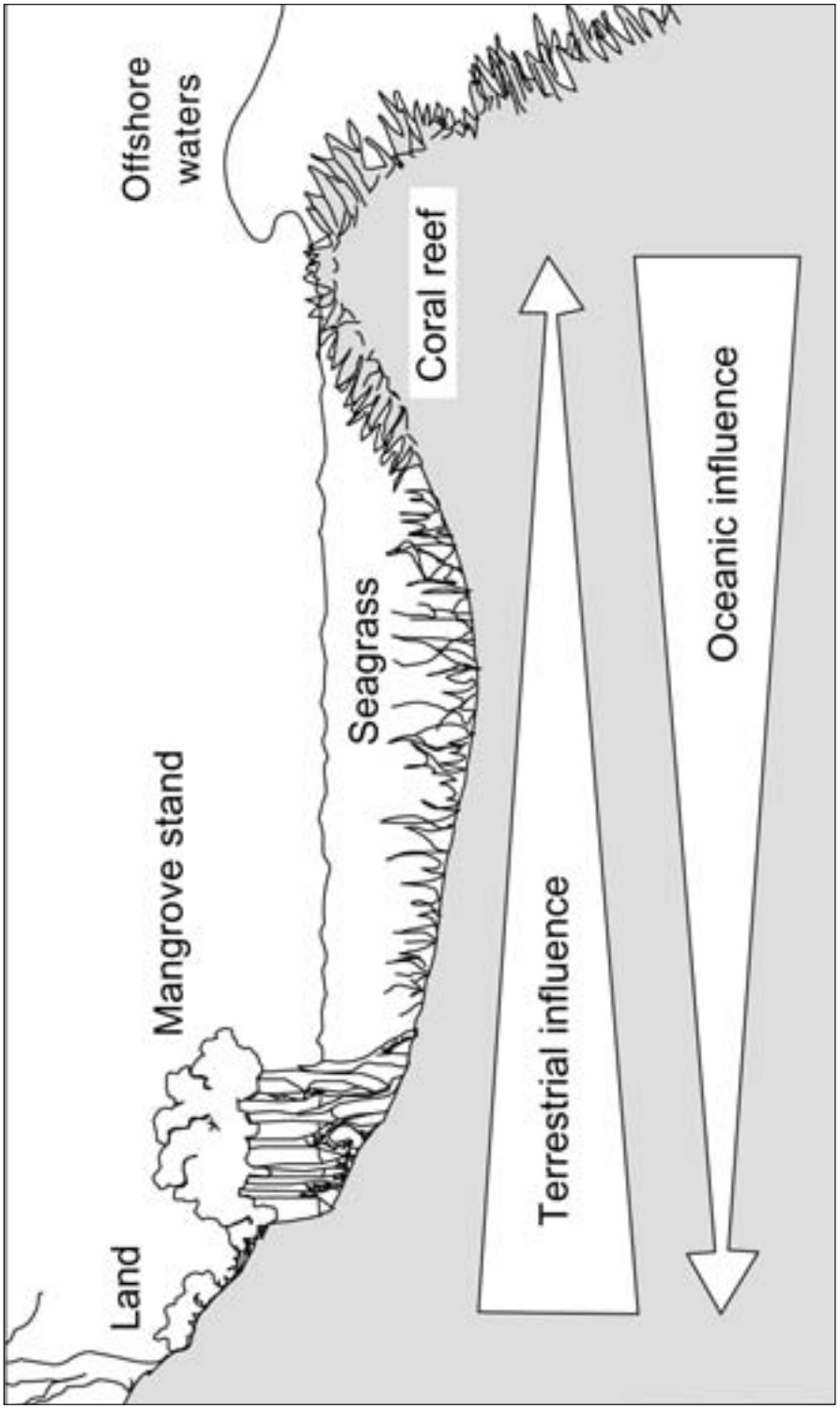


Figure 73—A diagrammatic representation of the different types of new coral reefs built on top of old previous reefs, over the underlying base rock, including volcanic rock and sediments. The major influences are marked as arrows indicating the direction of that influence.

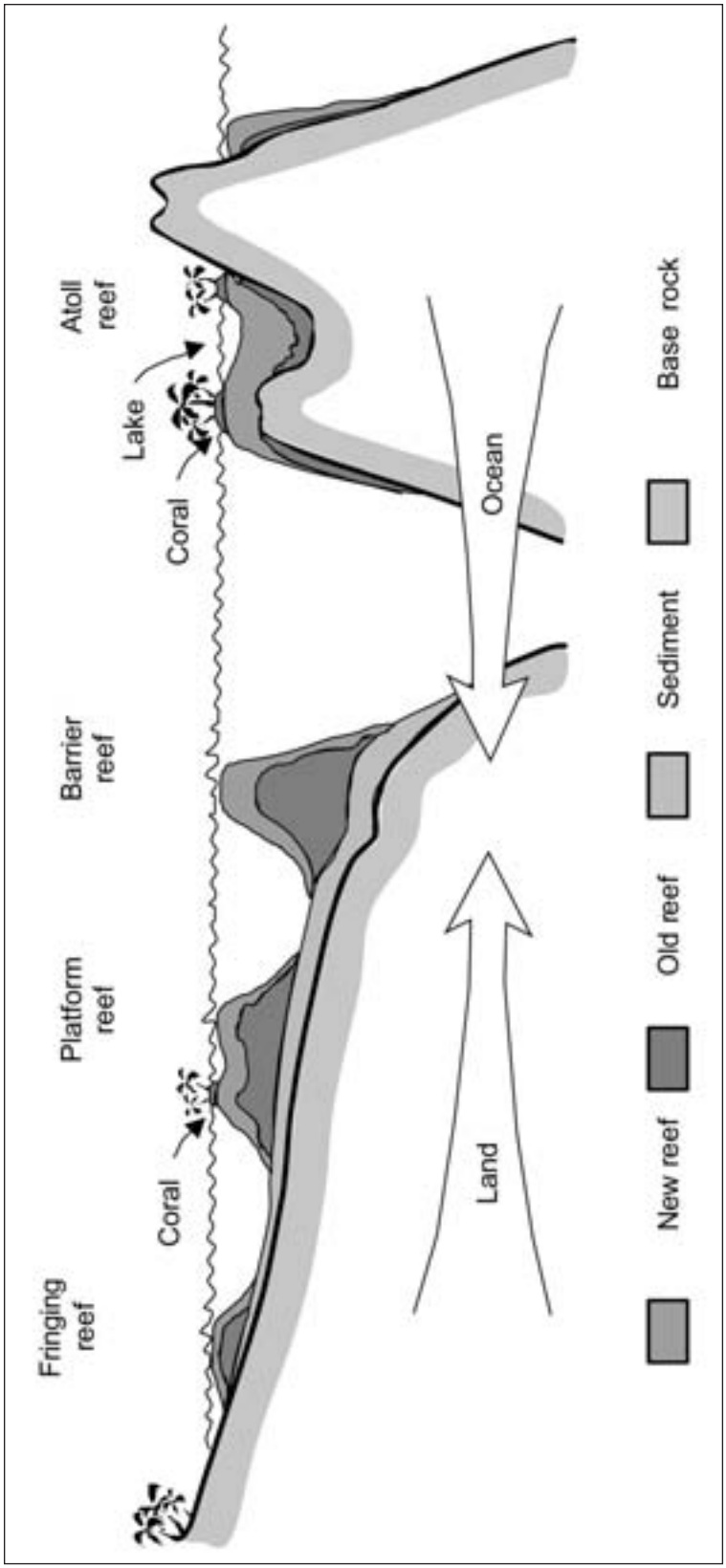


Figure 74—Schematic representation of interaction between the principal coastal marine ecosystems of the Caribbean.

- **Bank reefs** are open sea reefs without a central lagoon and generally surrounded by deep water, for example, the Great Bahama Bank.
- **Patch reefs** are generally small irregular-shaped reefs or accumulations of coral separated by a sandy bottom. They are frequently located to the rear of fringing reefs and may appear as coral mounds in seagrass beds.

Barrier reefs and atolls are not found in the waters of Puerto Rico, but are found off the coast of Belize in the western Caribbean. No matter what type of reef is being visited or studied, the organisms found will exhibit specific zonation patterns, that is, each species tends to show up in a particular area on a reef based on its needs and tolerances for the conditions controlling growth and development in these zones, such as wave action, light, salinity, depth, and sediment (fig. 75). The zones typically found on a reef are:

- **Lagoon.** A shallow, protected, calm, clear water area behind a barrier or fringing reef. It generally has large sand flats, seagrass beds, and dispersed coral groups.
- **Rear zone.** An area behind a fringing reef, usually protected where the water is calm. It may contain patch reefs, various shallow water corals, and seagrass beds.
- **Reef flat (crest).** The top of the reef. It can be subject to exposure. Many dead and fragmented hard corals are present.
- **Breaker zone (fore reef).** An area on the seaward side projecting toward deeper water, likely to have elkhorn corals.
- **Buttress zone.** A mixed coral zone in deeper water.
- **Terrace.** An area of mixed staghorn, star coral, and other large mound corals.
- **Slope zone.** An area of increasing water depth on the seaward side, gradual depletion of some coral owing to reduced light.
- **Deep forereef** (reef wall). Underwater cliffs that may drop at angles nearing 90º. This may signify the edge of an island's or continent's underwater shelf.

According to Jackson (1991), the total number of coral species recorded from different reefs decreases with depth, the number of species is greatest at intermediate depths and highest cover, and lowest diversity occurs at the shallowest depths where disturbance is greatest.

The upper limit of most **reef crests** is set by the level of low tides because dry polyps will die in a short period. Often this area contains macrobenthic algae, as

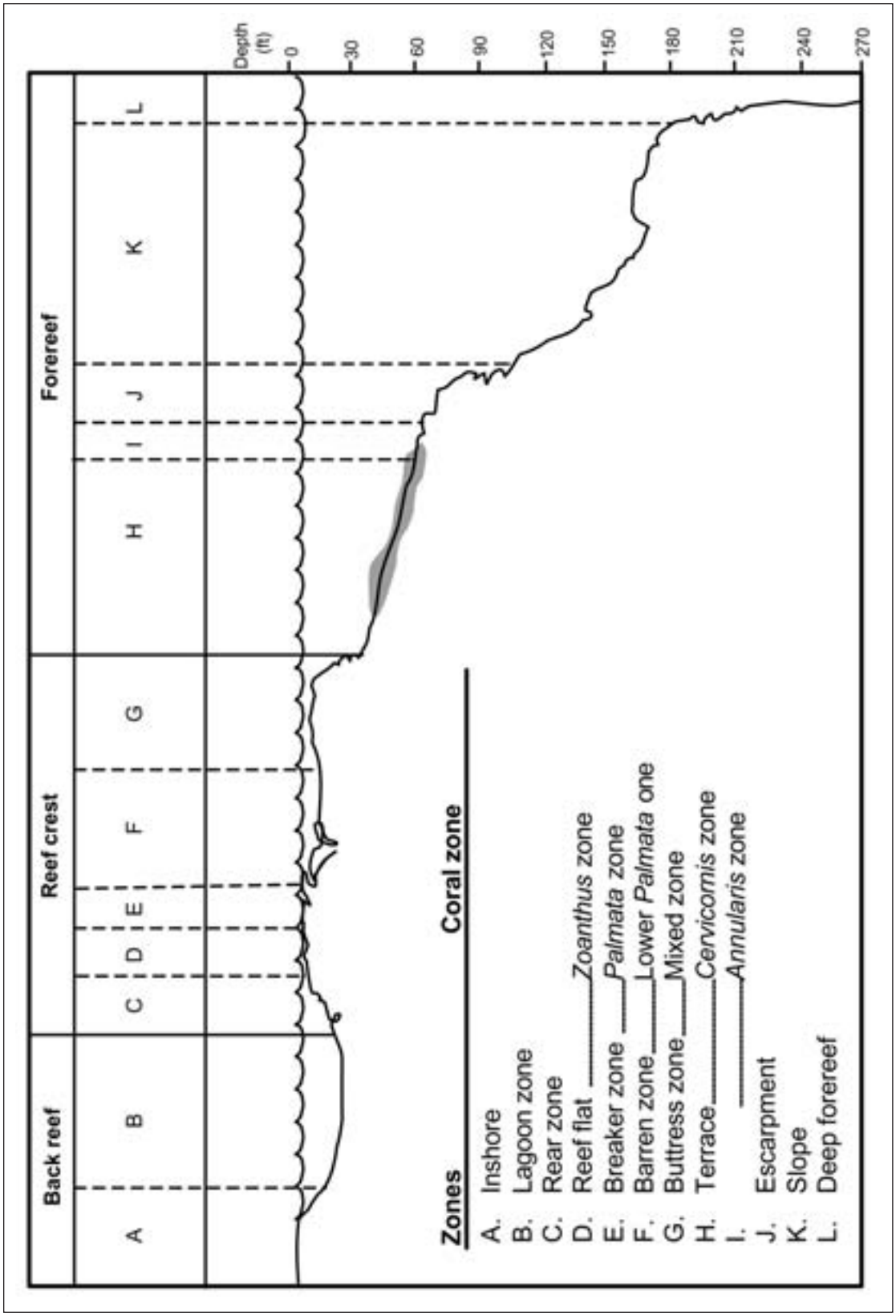


Figure 75—Generalized zonation of Caribbean reefs.

they are more tolerant to desiccation along the ridges and crest of this shallow area. Algae can cover more than 50 percent of the total area of many reefs. The algae form the bottom of the food chain for grazers, including many fish. There are certain groups of red and green algae particularly important to reef formation. Red coralline algae, like *Lithothamnion*, can be found encrusting on reef tops and wave breaking ridges. They grow rapidly and trap loose sand and shell fragments, cementing them to the solid reef underneath. The common green alga genus, *Halimeda*, which looks somewhat like an underwater cactus, is also calcified and has a segmented branching pattern. *Halimeda* spp. are some of the most common organisms on the reef. They are found in deep waters of reef slopes, reef passages, on coral in upper zones, and occur in carpets on the bottom of lagoons. *Halimeda* contributes both calcium carbonate and biomass to the reef. They are the source of much food for herbivores and the white coralline sediments that are produced when they die and degrade. Up to 25 percent of the limestone on a reef may be the product of *Halimeda* growth.

There are considerable differences in the coral fauna and general animal species composition found in reefs of the Caribbean compared to the Pacific Ocean region. There are few species of corals, mollusks, echinoderms, and fish common to both regions. Coral reefs of the western Pacific and Indian Oceans are comparatively richer in coral than those of the Caribbean. The Pacific has 100 genera compared to 26 in the Caribbean (75 percent more) and 700 species of coral compared to 90 in the Caribbean (85 percent more). Almy and Carrión (1963) found 38 species of shallow water **stony corals** in Puerto Rico's waters. On the other hand, when you look at the presence of the **soft coral** group (class Anthozoa, subclass Alcyonaria), the Caribbean Sea shows the highest abundance and diversity of Gorgonians (sea fans, sea whips) in tropical waters.

Coral reefs, with their diverse plant and animal species, are beneficial to natural processes and human society. The following list identifies some of these benefits and ecological services.

- Food for both reef and open water food chains, as well as the human food chain
- Living space for vast numbers of aquatic plants and animals, and on large coral islands for large numbers of tropical terrestrial plants and animals, and humans
- Coastal protection during storms
- Help to control sediments in coastal waters, and reduce coastal erosion

- Source of beach sands
- Importance for coastal nutrient cycles
- Marine carbon budget (atmospheric carbon dioxide extraction)
- Importance for local folk medicines and pharmaceutical research in anticoagulants, antimicrobials, anticancer properties, and mechanisms of drug action
- Construction materials for roads, walls, buildings, ports, and airport runways
- Recreation
- Ecotourism
- Ecological research
- Aesthetics (fantastic array of colors and forms)

Coral reefs provide an estimated $400 billion to fishing and tourism industries around the world (Normile 2000a, 2000b, 2000c). Unfortunately, today coral reefs and their many species are experiencing rapid changes in various aspects of water quality and species composition, which can only be viewed as negative. The health of most reefs is largely dependent upon what goes on in nearby adjacent continental or insular land masses. In addition, there are numerous diseases currently affecting many corals, and an increasing number of reefs and species are experiencing severe episodes of dieback (see **coral dieback** section that follows). It is estimated that as much as 90 percent of all coral reefs examined are negatively impacted, and ironically, up to 90 percent of the species on the coral reefs of the world remain poorly or largely undescribed. In addition, there are many potential and real threats to the very existence of reefs. Most of the reefs experiencing severe degradation are located in areas near human population centers or terrestrial areas being degraded by anthropogenic activities, such as large-scale agriculture. Nearly 27 percent of the world's coral reefs are considered at high risk, and up to 10 percent of the reefs have been declared dead. Southeast Asia's coral reefs contain the largest number of species and yet are the most threatened of any region (Raven and Berg 2001). Coral reefs cannot be viewed as isolated ecosystems. They are part of an interactive complex of ecosystems that can involve massive land and sea areas. They are linked to seagrass beds and mangrove swamps on the coastal fringe. In addition, alterations in terrestrial landscapes hundreds to thousands of miles away may threaten their productivity and general health. For a detailed review of the state of coral reefs in the Caribbean, see Goenaga (1989). The following list identifies some of the common threats to reefs. The majority affect coral reefs in the Caribbean and Puerto Rico.

- Vessel groundings and sinkings
- Anchor damage
- Oil spills
- Hazardous wastes
- Solid wastes
- Sewage wastes
- Siltation from deforestation (inland removal of upland forests and coastal mangroves)
- Beach nourishment activities for recreation beaches
- Dredging and filling
- Fishing-lines, traps, nets; overfishing
- Use of chemicals and explosives in fishing
- Tropical fish collections for aquarium trade
- Invertebrate collections for study and display
- Diving and snorkeling damage
- Tropical storms, especially hurricanes/typhoons
- Oxygen depletion
- Loss of predatory algae grazers
- Temperature changes (powerplant and industrial thermal effluents, and global warming)
- Ozone loss–increased ultraviolet radiation exposure
- Disease outbreaks (*Diadema* virus/bacterium and coral bleaching)
- Nutrient eutrophication
- Mass collections for sale as tourism trinkets and jewelry (U.S. imports 730 tons per year, world's largest importer) (fig. 76)
- Eruption of alien species ("crown of thorns")
- Offshore drilling and release of muds
- Harbor construction
- Tourist facilities development
- Pesticides
- Coral mining for construction materials
- Upland mine discharges (sediment and chemicals)
- Military activities (explosions, shock waves, sedimentation, and weakening of corals that will be easily damaged by subsequent storms)
- Shell collecting

G. Miller

Figure 76—Shell shop showing the effects of mass collection of shelled animals for sale to tourists.

There are roughly 453 000 square kilometers (177,000 square miles) of coral reef scattered throughout the world's tropical and subtropical seas (United Nations Environmental Programme 2001). Today, reef conservation is a high-profile international topic. About 50 percent of the countries with coral reefs have reserves in place to safeguard some of them. In most cases they are underfunded and understaffed. As of March 2000, 20 percent of all U.S. reefs were proposed off-limits and designated no-take zones by the U.S. Coral Reef Task Force. As a result, President Clinton, just prior to leaving office in December 2000, announced the creation of the Northwestern Hawaiian Islands Coral Reef Ecosystem Preserve extending 1935 kilometers (1,200 miles) long and 161 kilometers (100 miles) wide. This 35-million hectare (86.5-million-acre) preserve is the largest conservation area created in U.S. history and the second largest marine-protected zone on earth, second only to the Great Barrier Reef in Australia. This new area protects 70 percent of all U.S. coral reefs and an estimated 7,000 species of plants and animals. It will prohibit most consumptive uses of the ecosystem in 5 percent of the reserve, which will be set aside in 15 preservation areas. Other countries are also considering adding more preserves to curtail the rapid depletion of fish stocks and many other marine species associated with reefs. Without special protection, many of these areas are facing extinction. Less than 1 percent of the world's waters are protected in marine preserves. For those areas that have received special protection, recovery has shown to be quite rapid and biodiversity is conserved. In June 1998, President Clinton also issued Executive Order 13089, which directed all U.S. federal

agencies whose actions can affect U.S. coral reef ecosystems, to seek implementation of measures to reduce and mitigate degradation, and to restore damaged coral reef ecosystems.

Keeping Your Keel off Coral

More than 1 million snorkelers and scuba divers visit coral reefs yearly, and this number is growing as popularity of the sport and interest in ecotourism increases. Reefs are degraded by many people collecting specimens, anchoring boats, and standing on corals or algae. The following is a description of coral reef restrictions in place for protected waters in the U.S. Virgin Islands National Park. "No person shall cut, carve, injure, mutilate, remove, displace, or break off any underwater growth or coral formation. No digging in the bottom is permitted, and no rope, wire, or other contrivance should be attached to any coral, rock, or other underwater formation. No watercraft shall be operated in a manner, nor shall anchors or other mooring devices be cast or dragged so as to cause damage to any underwater features of the reef" (Allen 1992). These are all destructive activities to be avoided or minimized whenever possible.

For more information on reducing recreation impacts on coral reefs, contact Friends of the Sanctuaries, Center for Environmental Education, 624 9th Street, NW, Washington, DC (202) 737-3600 and see app. 4.

Puerto Rico's coral reefs are found in many areas of the insular shelf but are most concentrated in two areas: the southwest in the Cabo Rojo/La Parguera area and the northeast from Fajardo to Culebra, Vieques, and the many small islets going east toward the U.S. Virgin Islands (see app. 2). The two largest areas of the insular shelf are west of Boquerón, where it extends for 22 kilometers (13 miles), and east of Fajardo, where it extends all the way to St. Thomas, in the U.S. Virgin Islands. The reef at the mouth of Boquerón Bay is not well developed. There are numerous well-developed reefs in the eastern area around Vieques Sound. On the northeast coast, the best reef development occurs on the string of fringing reefs that run along a narrow 30-kilometer (18-mile) submarine ridge, which runs from the northeastern tip of Puerto Rico to Culebra in an east-southeast direction. Corals are present in most of Puerto Rico's marine waters, but these are the areas where they are extensive and relatively easy to access. In many areas on the west and north coasts, reefs have been killed or are absent owing to the higher number of rivers that discharge large quantities of freshwater, sediments, and pollutants into these marine waters. The north coast rivers carry greater loads of pollutants from construction, various industries, sewerage plants, and urban runoff. Fortunately for the north coast, there are still reefs present protecting the calm-water sandy beaches

found along Isla Verde, Piñones, and Luquillo. These extensive sandy beaches are protected from higher energy waves of the Atlantic by near-shore fringing reefs. Most reefs are degraded by sediments and runoff being released by the continued urban development going on in the north coast area. Corals are very sensitive to these materials as they increase turbidity or cover the corals, thus reducing their access to light and reducing their productivity. If the hard, exposed substrate is sedimented over, coral larvae cannot establish themselves, and sediments or other effluents may consume oxygen, causing a drop in the aerobic conditions needed for their survival.

We will now turn to the description of coral reefs found in the La Parguera area. La Parguera is in the municipality of Lajas on the southwest coast. The insular shelf is fairly extensive there and exhibits a complex array of mangrove swamps, seagrass beds, and coral reefs. This area of coastal Puerto Rico is dry and warm throughout the year, and exhibits relatively low urban development. The waters exhibit high clarity, have low wave energy, and in this area are relatively low in nutrients (**oligotrophic**). All are necessary conditions for coral reef development. The positioning of the three important and productive coastal ecosystems, that is, seagrass, mangrove, and coral ecosystems, made these waters quite productive historically. Unfortunately, many of the near-shore reefs today do not exhibit the once abundant fish populations seen prior to the 1970s. Some of this can be attributed to overfishing. Spiny lobsters are also rare except for juveniles, whereas they used to be quite common. The same is true for octopus and large conchs (various species). The reefs are still present, but their health has declined because of bleaching events that occurred in 1987 and 1990. García et al. (1998) indicated that more than 60 species of corals have been affected in the La Parguera area. In addition, hurricanes and other tropical storms have produced considerable physical damage to the reefs as a result of waves and currents associated with them. Because of reduced yields, fishing pressure on these reefs has greatly declined in recent years. Many fishermen are now employed in the tourist industry. Today, La Parguera's reefs are being used extensively for recreation. Many more Puerto Ricans have motor and sailboats and use the waters off La Parguera for a variety of water sports. The coral reefs, mangrove swamps, and seagrass communities are also used for field trip sites by educational institutions and ecotourism companies. Many of the activities just mentioned can have serious effects on these ecosystems caused by boat propellers, walking, sitting/standing on corals, collecting samples, spear fishing, pollution produced by gas-powered engines, improper solid waste disposal, and sediment disturbance.

The La Parguera area has the highest number of shallow-water stony coral species of any reef complex in Puerto Rico. The 38 shallow-water stony coral species identified for Puerto Rico by Almy and Carrión Torres (1963) are present on the reefs at La Parguera. Most species are located on the east ends of the reefs in open back reef waters. These areas are somewhat protected and yet turbulent enough to provide water with adequate oxygen and salinity content to promote growth of a variety of corals. Another 30 species of shallow-water Gorgonian **octocorals** have been reported by Yoshioka snd Yoshioka (1989). The insular shelf in the La Parguera area is 8 to 13 kilometers (5 to 8 miles) wide. At the edge of the shelf, water depth is around 21 meters (70 feet) deep. It then drops rapidly to 37 meters (120 feet) along the shelf wall and, at its outer edge, will be nearly 549 meters (1,800 feet) deep before dropping to the Caribbean abyss.

The shallow-water reefs at La Parguera are located in two arcs along the insular shelf and are frequently referred to as the "outer" and "inner" reefs. The outer reef arc is about 3.3 kilometers (2 miles) from shore; the inner reefs are approximately 1.6 kilometers (1 mile) from shore. The reefs are elongated east to west, which allows them to interface with waves coming from the southeast into the bay in front of La Parguera. The reefs are generally small, with the largest being Margarita, about 3.3 kilometers (2 miles) in length (fig. 77). Water depth between the two reef arcs varies from 12 to 21 meters (40 to 70 feet) in depth. The lagoons immediately to the rear of the reefs vary from 0.5 to 7.5 meters (1.6 to 25 feet) deep.

The two reefs easiest to access are Enrique and Caracoles (not labeled on the figure). They are about 1.6 kilometers (1 mile) directly out from the boat rental docks at La Parguera.

Organisms likely to be observed on coral reefs in the La Parguera area include the following:

Shallow-water stony corals

Porites porites (finger coral, box 27)
Millepora complanata (stinging fire coral)
Millepora alcicornis (branching fire coral)
Acropora palmata (elkhorn coral, box 28)
Acropora prolifera (fused staghorn coral)
Acropora cervicornis (staghorn coral)
Isophyllia sinuosa (cactus coral)
Montastrea annularis (common star coral)

Siderastrea radians (round starlet coral)
Siderastrea siderea (starlet coral)
Diploria strigosa (brain coral, box 29)
Diploria labyrinthiformis (depressed brain coral)
Favia fragum (star coral)
Agaricia agarites (foliose coral)
Manicina areolata (common rose coral)

Soft corals

Gorgonia flabellum (Venus sea fan)
Gorgonia ventalina (common sea fan, box 30)
Plexaurella grisea (split pore sea whip)
Pseudoplexaura sp. (sea rods)
Pseudopterogorgia americana (ostrich plume)
Eunicea spp. (knobby candelabra coral)

Other common invertebrates

Condylactis gigantea (purple anemone)
Stoichactis helianthus (sun anemone)
Zoanthus sociatus (green colonial anemone)
Zoanthus ocellaris (eyeball anemone)
Panulirus argus (spiny Caribbean lobster)
Echinometra lucunter (common urchin)
Diadema antillarum (black spiny urchin)
Lytechinus variegatus (green sea urchin)
Tripneustes esculentus (white urchin)
Haliclona rubens (red sponge)
Chondrilla nucula (brown sponge)
Hermodice carunculata (fire worm)
Ophiothrix angulata (brittle star)
Eucidaris tribuloides (pencil urchin)
Clypeaster rosaceus (heart urchin)
Meoma ventricosa (large heart urchin)
Mellita lata (sand dollar)
Chiton tuberculatus (West Indian chiton)
Atrina seminuda (spiny pen shell)
Pinna carnea (amber pen shell)
Cyphoma gibbosum (flamingo-tongue snail)
Ophiocoma echinata (large hairy brittle star)
Sabellastarte magnifica (magnificent feather duster fan banded worm)
Sabella melanostigma (feather duster worm)
Mithrax sculptus (small green crab)
Microthele parvula (small sea cucumber)
Holothuria mexicana (donkey dung sea cucumber)
Octopus briareus (reef octopus)
Crangon formosus (snapping shrimp)
Stenopus hispidus (barber shrimp)
Gonodactylus oerstedii (green mantis shrimp)
Aplysia protea (sea hare)
å*Aurelia aurita* (moon jelly)
Oreaster reticulatus (West India sea star)
Strombus gigas (queen conch)

Macrobenthic algae

Greens:

Halimeda opuntia (L.) Lamouroux (coralline watercress alga)
Halimeda incrassata (Ellis) Lamouroux (three finger leaf alga)
Caulerpa racemosa (Forsskal) J. Agardh (green grape alga)

Caulerpa sertularioides (S.G. Gmelin) Howe (green feather alga)
Udotea flabellum (Ellis & Solander) Lamouroux (fan alga)
Dictyota divaricata Lamouroux (Y-branched alga)
Dictyosphaeria cavernosa (Forsskal) Boergesen (green bubble alga)
Penicillus capitatus Lamarck (shaving brush alga)
Ulva lactuca L. (lettuce leaf alga)
Valonia ventricosa J. Agardh (sea pearls alga)

Reds:

Wrangelia argus (Montagne) Montagne (pink bush alga)
Spyridia filamentosa (Wulfen) Harvey (red bush alga)
Acanthophora spicifera (Vahl) Boergesen (brittle-branch alga)
Ceramium nitens (C. Agardh) J. Agardh (rose tuft alga)
Amphiroa fragilissima (L.) Lamouroux (fragile-branched coralline alga)
Lithothamnion sp. (coralline shelf alga)

Macrobenthic sea grasses

Thalassia testudinum Konig (turtle grass)
Syringodium filiforme Kuetzing (manatee grass)
Halodule beaudettei (den Hartog) den Hartog (shoal grass)

Common fish

Acanthurus bahianus (surgeon fish)
Holocentrus spp. (squirrel fish)
Scarus vetula (queen parrot fish)
Scarus guacamaia (rainbow parrot fish)
Gobiosoma spp. (gobies)
Thalassoma bifasciatum (bluehead wrasse)
Haemulon flavolineatum (french grunt)
Haemulon sciurus (blue striped grunt)
Pomacanthus arcuatus (gray angelfish)
Holocanthus ciliaris (queen angelfish)
Balistes vetula (queen trigger fish)
Chaetodon straitus (banded butterfly fish)
Chaetodon capistratus (four-eyed butterfly fish)
Anisotremus virginicus (pork fish)
Acanthurus coeruleus (blue tang)
Sphyraena barracuda (barracuda)
Stegastes spp. (damsel fish)
Abudefduf saxatilis (sergeant major)
Gramma loreto (fairy basslet)
Synodus saurus (lizard fish)
Aulostomus maculatus (trumpet fish)
Diodon hystrix (porcupine fish)
Gymothorax funebris (green moray eel)
Diodon holocanthus (puffer fish)
Hypoplectrus spp. (hamlets)
Chaetodipterus faber (spade fish)
Blennies (various genera and species)

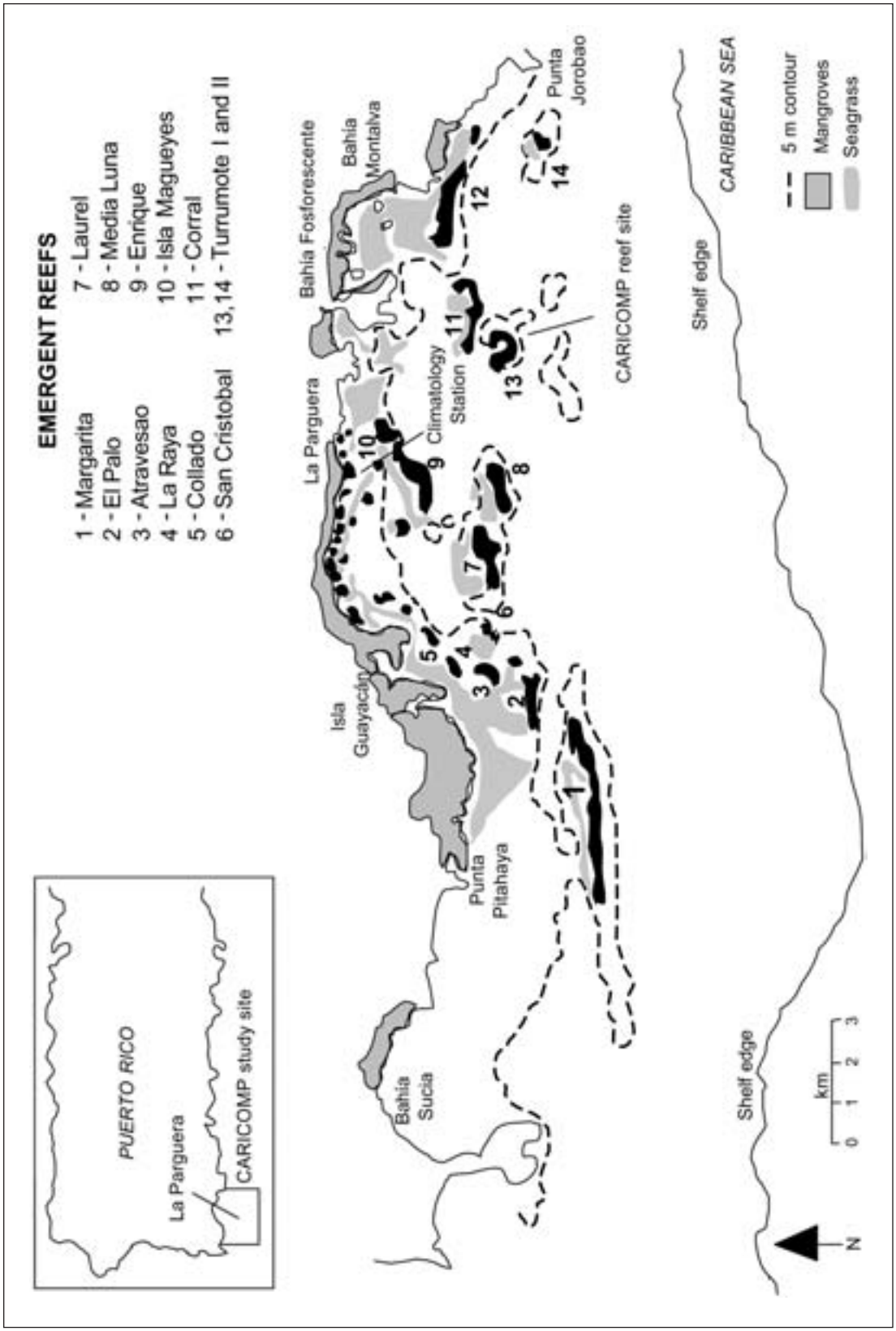


Figure 77—Location map of La Parguera, Puerto Rico and its marine ecosystems.

Box 27. *Porites* spp. (finger corals)

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Porites spp. growing in a shallow water habitat. Notice sea urchins.

There are a variety of stony corals, members of the class Anthozoa, in the shallow coastal waters of Puerto Rico associated with coral reefs. The species which will be profiled in this section all belong to the order Scleractinia. The Scleractinia corals are the master builders of the coral reef because they secrete a hard calcareous skeleton.

Porites and *Acropora* are the two most important genera of hard coral in the world. *Porites* has an estimated 30 species in the Pacific region and three in the Atlantic/Caribbean. *Acropora* has 150 species in the Pacific and three in the Atlantic/Caribbean.

When visiting a reef in Puerto Rico, the most common species of coral likely to be encountered are the finger corals, members of the genus *Porites*. Finger corals are probably the most common species present in the shallow zones of most reefs, lagoons, and nearby seagrass beds. They get their common name because their growth form resembles the fingers of the human hand. Not all *Porites* species are finger-like, as in the case of *P. astreoides*, which is a gibbose (swollen) mass.

***Porites porites* (thick finger coral)**

This is the most common finger coral. This coral forms finger-like clumps of hard coral that may be thick or open, and irregularly shaped. At times, their growth is straight and thick, forming a pavement-like formation that can support the weight of a small adult. It grows in variable water depths from 1 to 49 meters (3 to 160 feet). Branches may be up to 2.5 centimeters (1 inch) in diameter and can approach 25 centimeters (10 inches) in length. Its branches are larger than the other finger corals and tend to have swollen ends. You will often see its gray clear polyps extended during the day giving it a fuzzy look.

***Porites furcata* (thin finger coral)**

This finger coral typically forms dense vertical branching colonies. Branches may be to 1 centimeter (one half inch) in diameter. The tips of the forked

Box 27. continued

branches are not swollen. Some populations of this species can be bright purple. This species frequently produces large areas of coverage in shallow flat areas between reef islands or the rear zones of a reef. Coverage can be hectares (acres) in size, forming a pavement-like appearance. It is associated with all reefs at La Parguera and can grow in nearby seagrass beds. Their dense colonies form habitats for numerous invertebrates such as sea urchins and brittlestars.

***Porites astreoides* (yellow porous coral)**

This species of *Porites* is not finger-like in appearance. This hard coral grows as an expanded mass or as an encrusting mass. It can achieve diameters of 60 centimeters (2 feet) and is common on most back-reef areas of fringing reefs and on patch reefs. It also may be present in seagrass beds and sandy lagoons. It gets its name because its color is sulfur-yellow.

When visiting a reef, hard corals can be a problem for swimmers and snorkelers if they do not have protection for the exposed parts of their body. Many corals have sharp surfaces and will cause skin abrasions. The members of the genus *Porites* are of little threat because their branches are rounded and general surface textures are not very abrasive. They can be handled easily, although it is recommended that no corals be touched if possible.

For more information on these and other coral species, see Almy, Jr. and Carrión Torres 1963, Humann 1996, and Kaplan 1982.

Box 28. *Acropora* spp. (horned corals)

Two species of the genus *Acropora* are very common on the reefs of Puerto Rico. They are normally found on the front side of reefs, although they can appear in lagoons. Their common name is due to the fact that their branched growth forms resemble the horny racks of elk and deer.

***Acropora palmata* (elkhorn coral)**

This large branched coral is the most common coral on the windward side of can also occur in back reef areas and lagoons. This species' growth form exhibits a main stem or trunk, with outward extending flattened colonial branches. The branches actually resemble the horny antlers of a moose rather than an elk. The branches will be rough to the touch owing to protruding cups. When alive it is rusty-brown. Many reefs in Puerto Rico have suffered significant

Box 28. continued

decreases in this species' populations as a result of whiting disease and severe hurricane damage. Some reefs have been turned into virtual coral graveyards as a result of storm damage. This species is known to recover rapidly if storm damage or disease episodes are not frequent. Regeneration occurs via renewed growth of damaged colonies, dislocated fragments, or through new colonies formed from larval sets. Recovery from natural disturbances may take decades. Some human disturbances may prevent recovery owing to the continuation of the disturbance in excess of the coral's tolerance for the stressor, such as chemical pollution or heavy sedimentation.

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Acrophora palmate (elkhorn coral) growing in the fore reef zone.

Under optimal conditions, this species can grow 13 to 15 centimeters (5 to 6 inches) per year. It is one of the main corals in Puerto Rico's fringing reefs and can cover hectares (acres) of surface area. Some colonies may grow to 3.7 meters (12 feet) in length in optimal habitats.

Acropora cervicornis
(staghorn coral)

This species has a more branched growth form and the individual bran-ches do resemble the antlers of a stag deer. Its branches are very rough as a result of the large number of protruding tubular cups, which point toward the branch tip. The individual branches are brown to yellow-brown, cylindrical, and can grow to 2.5 centimeters (1 inch) in diameter. Branched clumps can grow to 2.4 meters (8 feet) in diameter. Under optimum conditions, it can grow 13 to 15 centimeters (5 to 6 inches)

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Acrophora cervicornis (staghorn coral) growing in a lagoon.

Box 28. continued

per year. The branches remain distinct and do not fuse. It is not as common on the windward side of the reef as is elkhorn, and it tends to grow in depths of 3 meters (10 feet) or more. It has been found in depths to 49 meters (160 feet) and is frequently observed in back-reef and lagoon sections of the reef. Lugo et al. (2000) indicate that the zonation and overall morphology of coral reefs are strongly influenced by their exposure to waves and hurricanes. Moderate wave energy favors vertical and rapid growth, while high energy waves favor slow and compact growth. *Acropora palmata* (elkhorn coral) and *Acropora cervicornis* (staghorn coral) are susceptible to breakage and overturn during major storms owing to their branching morphology.

For more information on this species, see Almy, Jr. and Carrión Torres 1963, Humman 1996, and Kaplan 1982.

Box 29. *Diploria* spp. (brain corals)

Some of the most striking corals on the reef are those that strongly resemble the outer surface of the human brain. Colonies form contoured hemispherical domes. Some individuals get to be quite large and can weigh half a ton or more.

G. Miller

Diploria labyrinthiformis (depressed brain coral) growing in the fore reef zone

***Diploria labyrinthiformis* (depressed or grooved brain coral)**

This coral can grow quite large, is hemispherically shaped, and is yellow-brown in color. From a distance this hard coral looks like a large round boulder. When examined closely, it exhibits a hill and valley structure to the alignment of the coral polyps. The outer hills may be up to 2 centimeters (one fourth inch) wide with the valley's depression narrower. This coral is common in rear and side areas, which are protected and may be more than 1 meter (3 feet) in diameter. They are mostly in depths of 4.6 to 15 meters (15 to 50

Box 29. continued

feet) and can be found to 41 meters (135 feet). It can take 20 years for a brain coral to grow to the size of a human head.

***Diploria strigosa* (common brain coral)**

This is a medium-sized, hemispherically shaped, boulder-like coral, green-brown in color. Its ridges and valleys are about the same width (4.5 to 10 millimeters), but are smaller than those of depressed brain coral. This species is common to most reefs and can be found on the lagoon side, as well as in turtle grass beds. They mostly inhabit water 6 to 12 meters (20 to 40 feet) deep, but can be found to depths of 40 meters (130 feet).

For more information on these corals, see Almy Jr. and Carrión Torres 1963, Humman 1996, and Kaplan 1982.

For more information on the animals found in the reefs at La Parguera, see Matthews (1967) and Glynn (1964).

La Parguera is also a major scuba diving port. One of the diving hot spots in the Caribbean is the "wall," which is the transition shelf edge zone to the deeper areas of the insular shelf. The wall is only 10 kilometers (6 miles) from the waterfront. To dive the insular wall requires access to a larger boat with the necessary support facilities, and there are more than 20 dive services operating throughout. The wall runs for approximately 22 miles east toward Ponce and rivals any wall diving in the Caribbean for ease of access and viewing of species diversity. Clarity can be in excess of 30 meters (100 feet). The wall has lots of rowpore sponges, star coral, pillar coral, black coral, yellow crinoids, anemones, and deep water Gorgonians. Water depth ranges from 18 meters (60 feet) to 37 meters (120 feet).

The popularity of the La Parguera area has produced a construction boom in second vacation homes, small hotels, and restaurants in the last decade. This has caused serious deforestation in the area around the village. La Parguera is not only an active tourist destination for its daytime water recreation, but also for its night life. The waterfront from dusk to 1:00 a.m. is heavily plied by tourists seeking boat trips to the nearby phosphorescent bay, as well as the restaurants, bars, and small specialty shops selling handicrafts to visitors. There is little left of the very small, quaint, small-scale local fishing village that La Parguera was through the mid 1970s. Today, well over 100,000 visitors take advantage of La Parguera's tourist and recreation opportunities.

Box 30. *Gorgonians* (sea fans)

Most corals are hard, wave-resistant, and nonflexible. *Gorgonians* or soft corals are just the opposite. They are soft, resilient, and bend or flex when water moves over them. They do not produce the large extensive calcium carbonate structure typical of the hard corals. *Gorgonians* are more abundant in the Caribbean than any other tropical water body. Some *Gorgonians* are typical of deep water, whereas others will be found in shallow waters, such as lagoons, attached to soft sandy bottoms and in other protected back reef zones. Many appear plant-like and have names like fans, plumes, pens, bushy, and candelabra applied to their growth forms. Many are brilliantly colored purple, rust, or yellow. The variable coloration in *Gorgonians* is produced by one or more of the following: pigments in the polyps' tissues, intracellular zooxanthelleae algae in the polyps' tissues, or coloring minerals in the calcareous spicules present in the colony.

They, like their hard coral counterparts, feed on plankton. They are different in that most will extend their tentacles during the day as opposed to the hard corals, which are nocturnal feeders. They are often attacked by the colorful flamingo tongue snails. *Gorgonians* are not considered to be reef builders as hard corals are, but they do add significant amounts of sand in the form of shed calcium carbonate spicules. They are important as resting and feeding sites for many reef animals, and they add textural and spatial richness to the complex reef ecosystem.

***Gorgonia flabellum* (Venus sea fan)**

This is a shallow water species with variable color ranging from yellow to purple or gray. Its common name suggests its fan-like shape. It produces an extensive group of flat interconnected branchlets. They grow to heights and widths in excess of 1 meter (3 feet). *Gorgonia flabellum* prefers clear water and may grow on shallow reef slopes, mostly in water less than 10.7 meters (35 feet) deep. On occasion they will be found to depths of 30 meters (100 feet). They are anchored to substrates by a trunk-like organ. When attached to rocky substrates they are virtually impossible to remove without a large knife or saw. These are the most beautiful of the *Gorgonians* and are normally seen waving gently back and forth as the water moves over and through the large fan-shaped colony.

For more information on these corals, see Humman 1996 and Kaplan 1982.

Of concern to the environmental community in Puerto Rico is the rate of population growth in the area and the extensive use of the marine resources at La Parguera. As a result, La Parguera has been designated a nature reserve by the Department of Natural and Environmental Resources. The Planning Board of Puerto Rico has also designated the village a "zone of special planning" in further recognition of its special marine resource value. However, a special **marine fishery reserve** status has been locally rejected. This is unfortunate because zones of special planning do not appear to protect natural resources in Puerto Rico, and scientific evidence shows that marine reserves conserve biodiversity and replenish fish stocks. According to Lubchenco (2001), population densities average 91 percent higher and species diversity is 23 percent higher in reserves. The reserves work and they work fast. The no-take zones established in the Florida Keys in 1997 are already showing measureable gains in the size of harvestable spiny lobsters and grouper. For a review of the value of marine protected areas see Houde et al. 2001 and Roberts et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems are well documented for the Caribbean (Jackson et al. 2001). Virtually all species of grouper and snapper are commercially extinct in the Caribbean, and 26 grouper species worldwide are being considered for listing as vulnerable to extinction by the International Union for the Conservation of Nature and Natural Resources. Local fishermen now have to take triggerfish and parrotfish, algae grazers that inhibit overgrowth of algae on reefs. Wire mesh fish traps generate less than 10 percent of what they did in the mid to late 1900s (personal comments, La Parguera fishermen 2000).

Puerto Rico's coral reefs represent a valuable source of income and other resources associated with tourism, marine fisheries, shoreline protection, and recreation. A significant number of islanders depend on coral reefs for part of, or their primary source of income. An estimated $140 billion is generated by all Caribbean reef uses (Jameson et al. 1995). Tourism is the fastest growing economic use of coral reefs and is now a significant income producer in Puerto Rico. An estimated 100 million people visit the Caribbean yearly, many of whom engage in scuba diving, which is expected to generate in excess of $1.2 billion by 2005 (Hoegh-Guldberg 1999). Puerto Rico fishermen supply millions of dollars in fish-related income to themselves, food stores, and restaurants throughout the island. These fished species also serve as a healthy source of protein for the local diet. Nearly 33 percent of the world's fish species live in coral reefs. Reefs are no-cost, self-perpetuating natural fish farms, which produce vast quantities of high- quality protein from sea water. Additionally, coral reefs serve as major buffers for storm-

generated waves and flooding. This protection minimizes storm damage to human-made structures throughout the outer coastal fringe. They also help to protect the other two vital marine ecosystems: mangrove swamps and seagrass beds that serve as nursery grounds for the rich assemblage of species that inhabit the shallow waters of the littoral zone. The costs associated with the loss of these essential ecosystems and the services they provide would be enormous. These areas need to be protected more than ever to maintain the present quality of the habitat and promote passive and active restoration in the near future. It is likely that conditions will generally worsen in the future as the human population grows. If maximum protection is not afforded soon, the losses will be even worse and could lead to local and regional species extinctions. In general, the Caribbean is a low-species region, and as Bellwood and Hughes (2001) have indicated, low-diversity regions may be especially vulnerable to damage and destruction because they lack entire families of coral species that might help the reef ecosystem to recover. They also reported that such a scenario, with resultant ecosystem disruption, recently occurred in the Caribbean, where the decline of a guild of herbivorous fish (scarid and acanthurid fishes) owing to overfishing, and a decline in the keystone grazer, the black-spined sea urchins (*Diadema antillarum*) owing to disease, led to widespread algal blooms. Without adequate populations of algal grazers, reefs are likely to be overgrown by algae, such as the genus *Halimeda*. These population shifts produced a **phase shift** in ecosystem structure (fig. 78). For an excellent review of the influences of overfishing and its effect on coastal ecosystems, see Jackson et al. (2001).

Recent research in reef larval connectivity and management strategies indicates that management partnerships could be beneficial among Caribbean states (Roberts 1997). For example, core management partners for Puerto Rico would include the United States and British Virgin Islands, and within the 2-month larval transport area, would include St. Martin, Anguilla, and the Netherlands Antilles. Puerto Rico would be a key partner for the Dominican Republic and Haiti. Each area would need to set up local management protocols that would be designed to work within the overall regional program devised by the international management partners. All cooperators could create no-take reserves optimally spaced both for local benefits and to support populations in other regional reserve systems. As Bellwood and Hughes (2001) have indicated, protection of rich faunas of coral reefs will require a greater understanding of their complexity and diversity. Species diversity variation appears to be best explained by the area of available habitat. This suggests a need for habitat protection at a regional scale, with coordination of reef conservation

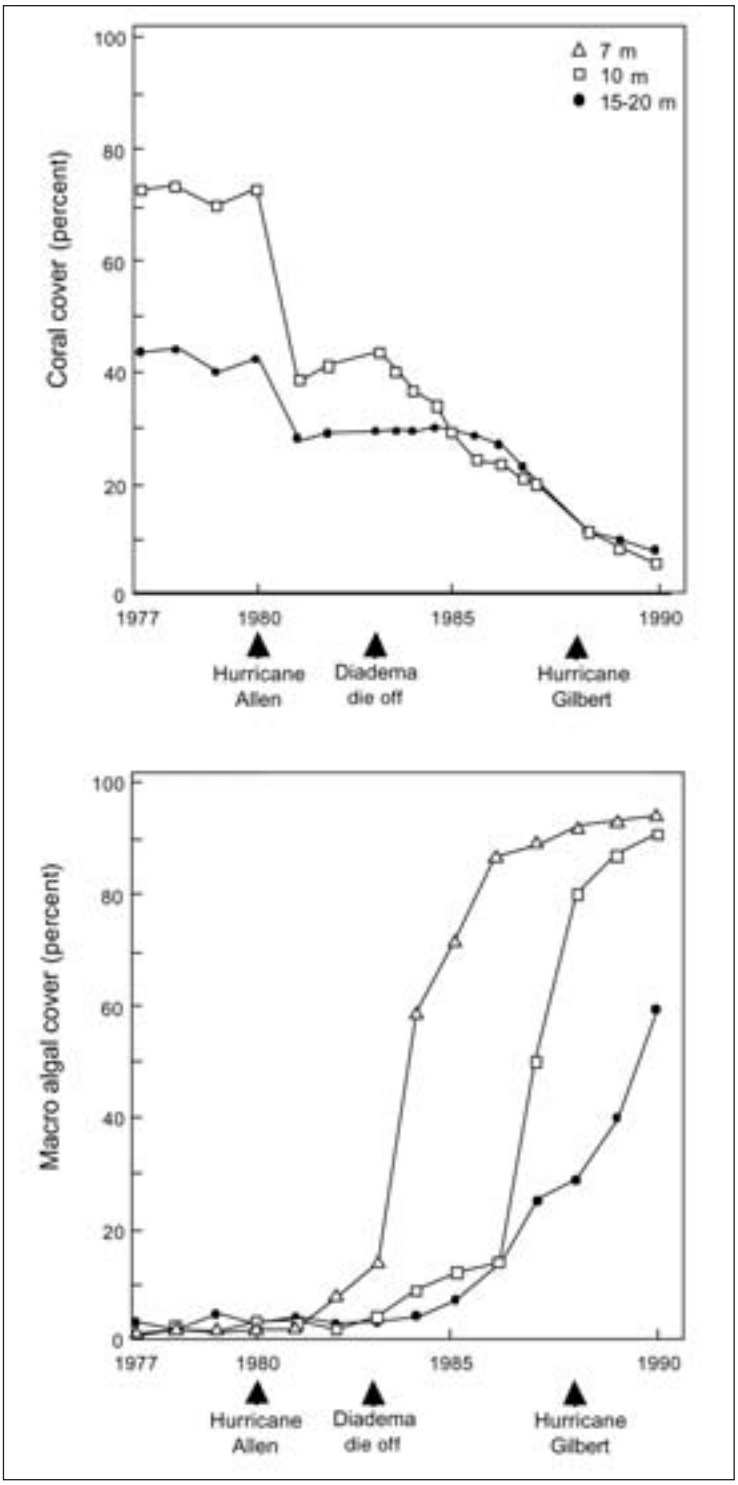


Figure 78—The degradation of coral reefs on the north coast of Jamaica. Two unrelated events, a hurricane in 1980 and the death of the algal grazing black spined sea urchin (*Diadema antillarum*) in 1983 resulted in a collapse in live coral cover (upper) and a population explosion of large algae (lower) because the populations of grazing fishes have been overexploited.

programs international in scope. Bellwood et al. (2004) indicated that Caribbean reef ecosystems are particularly vulnerable to phase shifts owing to lower species richness and composition of important functional groups and that a major scaling-up of management efforts is required in order to avoid further degradation of these ecosystems.

In support of this international effort to preserve the ecological conditions of the Caribbean, the Nature Conservancy has identified as part of their Caribbean Conservation Plan 24 sites representing the greatest opportunities to harbor the Caribbean's biological diversity. These sites have been chosen based on their high biological diversity, salvageability, position in the Caribbean current system that will promote the distribution of larvae downstream, and their ability to receive plankton, eggs, and larvae from upstream sources. In other words, each site, by way of the interconnecting currents, will perform the dual role of being a "**source**," as well as a "**sink**" in the distribution of species. As a source, they will be dispense nurseries, seeding the current with large quantities of urchin, conch, crab, lobster, and fish larvae. As a sink, these sites will receive the larvae from other partner sources (Stolzenburg 1999). In many cases, these sites will have associated sea-grass beds and mangrove swamps. In the case of Puerto Rico, the island is viewed as an important source of organisms for Parque Nacional del Este (sink) in eastern Dominican Republic. Locations of sources in Puerto Rico and in the islands supplying Puerto Rico, the Virgin Islands, and other eastern Lesser Antilles islands need to be determined in the next couple of years.

Healthy ecosystems should be a global concern. All countries and economies depend on natural ecosystems, and these ecosystems are not bound by political lines. Species migrate, air and water pollutants know no boundaries, and fisheries collapse as a result of overfishing. Some experts indicate that we may only have 30 years to remedy our damaged ecosystems to prevent ecosystem failure.

For any group doing marine work in Puerto Rico, a variety of maps that provide the exact locations, sizes, and depths of reefs in the Fajardo and La Parguera areas are available from both federal and commonwealth agencies as indicated in the map section in the appendix.

Symbiosis

Many organisms in nature have developed unique beneficial symbiotic relationships with other organisms. Of significance in these relationships is the lack of similarity in the organisms involved. There are many classic terrestrial examples of this phenomenon, such as ants and plants, protozoans and termites, rhinocerus and

tick birds, wasps and figs, and finches and iguanas. Coral reefs likewise provide excellent examples of symbiosis in the marine environment. We point out that even though these interactions are regularly referred to as symbiosis in the scientific literature, they are technically examples of mutualism. Symbiosis is a term that covers a broad range of organismal interactions, which includes competition, **amensalism**, **neutralism**, **commensalism**, and **mutualism**. Lewis (1985) has a continuum that illustrates these relationships (table 24).

There are two general types of mutualistic symbiotic relationships—internal or endosymbiosis, and external or ectosymbiosis. Both types abound on reefs. As mentioned earlier, the key to the growth and health of coral reefs around the world is the interaction between the coral polyps and their endosymbionts. In this case, the primary algal symbionts are **dinoflagellates** (yellow-brown algae) from the genera *Gymnodinium* and *Amphidinium*. The individuals of both genera are small and spherical and live within the cells of the inner gut tissues of the coral polyps. There may be 1 to 2 million algal cells per square centimeter of coral tissue (Brown and Ogden 1993). They are referred to as **zooxanthellae**. The coral and algae have evolved such close ecological ties that they rarely are found apart. The presence of the algae provide the pigments found in the colors of the many otherwise transparent polyps. Because of the presence of these photosynthetic single-celled algae, corals grow more during daylight hours than at night when the polyps are actively feeding as carnivores on zooplankton. The mutualism involved in this unique relationship relates to the fact that the corals provide dinoflagellate algae with protection, a place to live, adequate access to sunlight for photosynthesis, and metabolic waste products such as carbon dioxide and nitrogen molecules. The association allows algae to obtain compounds scarce in the nutrient-poor waters of the tropics where warm surface waters overlie and lock in cold, nutrient-rich waters, except in zones of upwelling such as in the waters off Perú and Ecuador. The corals benefit by receiving oxygen as a byproduct of photosynthesis, and over 50 percent of the organic molecules from algal food production are used by the polyps as food. These relationships are true of both hard and soft corals.

Probably the classic example of ectosymbiosis on reefs is **cleaning symbiosis**. In this case, cleaner organisms such as shrimp and small fish remove ectoparasites, fungi, and diseased, injured, or dead tissue from larger client animals (hosts). The results are thought to be mutually beneficial in that the host organism is rid of harmful or unwanted matter, while the cleaner is furnished with food and is less susceptible to predation. This relationship is very common among marine fish.

Table 24—Symbiotic continuum in terms of fitness of two associated organisms

Competition -/-
Amensalism -/0
Agonism -/+
Neutralism 0/0
Commensalism 0/+
Mutualism +/+

- Fitness decreased.
0 fitness not affected.
+ fitness increased.
Source: Modified from Lewis 1985.

Interestingly, there are special behaviors that have developed as a form of "communication" between cleaners and hosts based on body movements that serve to initiate the cleaning interactions. Hosts will pose, specifically position themselves, or swim in specific areas where cleaners are located. Other cues may be body coloration. Many fish have variable color forms on reefs. The cleaners respond to these communications by inspecting a host through swimming closely or physically contacting the host's body (tactile communication). The areas where cleaning takes place are referred to as **cleaning stations**.

One of the most interesting cleaning relationships is between shrimp and their fish hosts. Some shrimp will be found in association with anemones, or in a small hole in hard coral, such as the red and white barber shrimp (fig. 79). Fish approach and the shrimp wave their antennae or bodies back and forth. Interested fish then position the part of their body most needing cleaning in proximity to the shrimp. This is usually the head and gills. The shrimp then mounts the body of the host and removes parasites, other growths, and dead or injured tissues with its claws. The fish remain almost motionless. Their gill covers are opened individually for inspection and cleaning. Fish will permit the cleaners to enter their mouth cavities without jeopardy of being eaten. This is even true of top predators such as barracuda. Cleaning stations can often be spotted on a reef because of the "line-up" of fish waiting for their turn to be cleaned. Fish will migrate to known cleaning sites in large numbers. Hundreds of hosts may be cleaned in a day by a single cleaner.

At one time this phenomenon was thought to be an ecological novelty exhibited by just a few organisms, but we now know it represents one of the primary behavior/health relationships on a reef and may be the best example of interspecific cooperation among dissimilar animal groups in nature. There are dozens of fish species that serve as cleaners, at least six species of shrimp, and even crabs. Most

G. Miller

Figure 79—View of beautiful barber shrimp, one of the reef's best examples of cleaning symbiosis.

will have special anatomical adaptations that aid in cleaning. Many will be brightly colored, which may serve as visual communication for identification and location. Some cleaner species only clean in their juvenile phase; virtually all are physically small, and most obtain additional food from other sources. All cleaners gain a high degree of immunity from predatory fish. In fact, this relationship has been copied by some predatory fish, in that they mimic cleaners as a way of attracting hosts, which are then preyed upon. Not only are fish cleaned, but hosts also include rays, marine turtles, marine iguanas, and sea urchins.

The health of many reef organisms is highly dependent on their being cleaned regularly. Without regular cleaning, many fish will exhibit fungal growths, ulcerated sores, frayed fins, and ever-increasing numbers of ectoparasites, and wound healing can be slower. There are implications for humans in this unique relationship in that fish with commercial value are also subject to these infections. It is important that reef ecosystems, with their high diversity and specialized niches, be kept as complete as possible. Knowledge gained from understanding these subtle ecological relationships is now being applied to **mariculture**. Cleaning fish are being introduced into commercial fish farms with the expectation that the health of the commercial fish stocks can be better maintained without continued reliance on chemical pesticides currently being used to control parasites.

Coral Dieback

Coral reefs are some of the oldest marine systems on this planet. Most modern reefs are between 5,000 and 10,000 years old. Unfortunately, coral reefs are now experiencing mass mortalities over a wide geographic range. The frequency of these events and number of species and individuals being affected seem to be rising. Coral reefs throughout the tropical world are now exhibiting a variety of diseases causing dieback. These diseases include coral bleaching, rapid wasting disease, yellow band disease, white pox, black band disease, sea fan disease, and lethal orange disease. There are now at least 13 identified diseases of coral, three of which were newly reported in 1997. The identity of the causative agent is known for only three of these diseases. No one knows whether this relates to decreased host resistance, increased pathogen transmission (Harvell et al. 1999), or improved worldwide monitoring of the reefs.

Coral throughout the Caribbean appears to be sickening at an accelerating rate. Some of the most important of Caribbean coral species (*Acropora*) have been dying at increasing rates, and some reefs are now overgrown with algae. In some instances, the causative agent(s) generating dieback is purely speculative, and explanations for why this is occurring range from pesticide exposure and sewage runoff, to light deprivation. These stressors may be making the coral susceptible to pathogens. It may also be that a synergism is occurring; that is, two or more causative agents may be interacting to produce an effect greater than their individual effects. It has recently been reported that there may also be a relation to events taking place in the mainland of Africa that may be leading to one or more of these dieback events. In sub-Sahara Africa, large clouds of dust are being generated and blown to the western Atlantic and the Caribbean by trade winds. The causes, according to the U.S. Geological Survey, appear to be droughts and overgrazing 3,000 miles (4800 kilometers) away. They estimate that several hundred million metric tons of dust annually are being blown across the Atlantic. Interestingly, the dust contains a nonmarine soil fungus (*Aspergillus*) that has been connected to the decline in sea fans (*Gorgonia flabellum*). Sea fans now exhibit four colors, three related to this illness: (1) dead with totally eroded flesh and only the skeleton remaining, (2) area in dieback zone turning color, (3) deep purple as the coral attempts to fight off the infection, and (4) normal healthy color. Research is now being conducted to see if African dust and *Aspergillus* are present in the hard coral skeletons laid down over the last 50 years on reefs in Puerto Rico and the U.S. Virgin Islands.

The rest of this section will only be concerned with one of the dieback diseases known as "whiting disease or coral bleaching." Coral bleaching was first described by Yonge and Nicholls in 1928 from the Great Barrier Reef (Brown and Ogden 1993). The first coral bleaching in the United States was recorded in the Florida Keys in 1911 and 1914 (Williams and Bunkley-Williams 1989). A series of bleaching events have been recorded in Neotropical Caribbean waters during the last 35 years. Various explanations have been suggested for the cause of bleaching events, including changes in salinity, eutrophication, chemical pollutants, nitrate loading, increased ultraviolet light, turbidity, and disease agents (Brown and Ogden 1993). In the summers of 1987, 1990, and again in 1997–98, Caribbean reefs seemed to turn white because of a higher than normal incidence of coral bleaching. The 1997–98 event was observed worldwide and was the worst on record. The main culprit identified at the time for its cause was increased surface temperature of the ocean. Since then, a number of other bleaching events have occurred elsewhere, and most correlated well with elevated surface sea temperatures. In 1991, the University of Miami (Florida) held a major workshop on temperature relationships to coral and reached that conclusion. Sea temperatures in the tropics have shown nearly a 1 ºC (1.5 ºF) increase in the past century. Another 1 to 2 ºC (1.5 to 3 ºF) increase is projected for this century. Temperatures in excess of 30 ºC (86 ºF) appear to be the threshold temperature that triggers bleaching events. An estimated 25 percent of the world's coral reefs have already been destroyed or severely degraded through problems arising from warming associated with climate change (Roberts et al. 2002). Harvell et al. (2002) reviewed the importance of climate warming and disease risks for marine biota. They indicated that climate warming can increase pathogen development, survival, transmission, and susceptibility. Major *El Niño* events appear to produce extensive bleaching episodes. During these elevated temperature events, reef-building corals appear to be stressed, causing them to expel millions of microscopic zooxanthellic dinoflagellate endosymbiotic algae from their tissues. One explanation for why the algae are expelled relates to possible creation of plant toxins as byproducts from photosynthesis. The algae are vital to the well-being of the coral as they supply 63 percent of nutrients used by the coral (Glynn 1991).

The loss of the algae correspondingly produces a change in the color of corals, as it is algae pigments that are primarily responsible for their host coral's coloration. This loss of color then makes the coral appear whitish or transparent against the white limestone skeleton that surrounds the polyp, thus the terms whiting

disease or coral bleaching. Bleaching can be partial, or severe to the point of being lethal to the coral. Most bleached corals are not dead, but they appear to have reduced viability. If corals do not regain their zooxanthellae, they will then be more vulnerable to other stresses that can reduce growth and ultimately lead to death. Repeated bleaching greatly reduces a reef's general productivity. There have been documented cases where a genus such as *Millepora* (fire coral) has totally disappeared from reef systems (Glynn and de Weerdt 1991). A wide variety of corals and **hydrocorals** are now known to exhibit this response, including the common forms such as *Millepora alcicornis* (branched fire coral), *Acropora palmata* (elkhorn coral), *Montastrea annularis* (common star coral), and *Diploria labyrinthiformis* (depressed brain coral). All are typical of the reefs found throughout Puerto Rico and the Caribbean region. More than 60 species of corals have been affected (Williams and Bunkley-Williams 1989). In 2005, coral reefs were subjected to another major bleaching event precipitated by ocean warming in the range of 3.5 ºC (5 ºF) above normal for a period of 6 to 8 weeks during September and October. Estimates indicated bleaching occurred in at least 80 species. In Culebra, researchers estimated up to 95 percent of small corals were affected, as well as soft corals (extremely rare). This event also affected corals in other areas in the Caribbean as cited by the United States Coral Reef Task Force. According to Edwin Hernández, a University of Puerto Rico marine biologist, a lot of mortality was observed. Staghorn (*Acropora cervicornis*) and elkhorn (*Acropora palmata*) corals were especially hard hit. In some areas, 90 percent of their populations died. This may result in a genetic bottleneck effect owing to their very low population levels prior to the bleaching event. Both species are candidates for endangered species status (Rust 2006).

Bleaching can take a toll on coral reproduction and their ability to recolonize. In some instances, coral recolonization appears to start fairly quickly after a bleaching event, but it may take a long time for complete recovery as a result of interruptions of sperm and egg production. The new points of regrowth, although appearing healthy, when checked for viable sperm and egg production, may exhibit only a 50-percent production of gametes. Warm water appears to work two ways. One is the full bleaching scenario and the second is the damage done to reproductive organs. Even if bleaching does not occur, this double whammy greatly affects the potential of corals to adequately reseed themselves when acceptable water temperatures return.

There is potentially an even more important problem confronting reef recovery: the likelihood of an increase in the frequency of warm water events in the future

associated with global climate change. Without correct temperatures for reproduction and necessary adult populations to produce viable sperm and eggs, the long-term outlook for healthy and diverse coral reefs does not appear good. In addition, once corals are lost, their zones of occupation may be overrun by macrobenthic algae or other encrusting organisms, making recovery even more difficult. As Hoegh-Guldberg (1999) indicated, "unrestrained warming cannot occur without loss of coral reefs on a global scale." He also indicated that based on a series of models run to predict change in the frequency of bleaching events, the frequency of bleaching is set to rise rapidly. The highest rate of bleaching event increase is projected to occur in the Caribbean, and within 30 to 50 years bleaching is likely every year. Table 25 reviews the changes in bleaching events as a function of temperature change.

Although there is good correlation with high water temperatures and coral bleaching, there is still some uncertainty on this issue. Research continues in order to find one or more verifiable cause-and-effect relationships. Some experts feel that many of the degraded reefs and their associated dieback are a function of their proximity to developed or fast-growing sections of the world, such as the keys in Florida or the islands of the Caribbean, and that most remote oceanic reefs do not appear to be imperiled. Those already damaged by anthropogenic impacts and with weak ocean currents, which cannot keep water temperature from reaching the bleaching threshold, have shown the worst bleaching episodes. Recent paleontological evidence shows that Caribbean reefs have been remarkably stable as far as community structure is concerned. The same dominant and rare species of coral have remained relatively constant over the past 220,000 years. However, in the past few decades, species shifts have been observed that suggest an unnatural, nonrandom, possible relationship to human activities (Stokstad 1991).

As a result of all the scrutiny given to zooxanthellic coral, new insight may be emerging with a not-so-grim outlook for bleached corals. Shedding of the symbiotic algae may be a seasonal phenomenon during which approximately 75 percent of the zooxanthellae are expelled without harm. The remaining 25 percent is not enough to give coral its true color, thus it appears white. Later, the algae can be replenished or new algae taken on by the coral. Research underway is looking to assess seasonality, variability in algal species and host specificity, variation in zooxanthellae concentrations, temperature thresholds, and depth and light variations. Hopefully, from this array of current research, conclusive answers regarding the cause of coral bleaching will be forthcoming in the near future.

Table 25—Coral bleaching issues and temperature change

Will coral bleaching increase in the future?	Bleaching events are projected to increase in frequency until they become yearly events by 2050 in most oceans. In some areas (e.g., Southeast Asia and Caribbean), bleaching is expected to occur more rapidly (by 2020). In 20 to 40 years from now, bleaching is projected to be triggered by seasonal changes in water temperature and will no longer depend on *El Niño* events to push corals over the limit. This will become critical as bleaching events exceed the frequency at which corals can recover from bleaching-related mortality and lowered reproductive capacity. Evidence suggests that coral reefs will not be able to sustain this stress, and a phase shift to algal-dominated benthic communities could result.
Why were there few coral bleaching events prior to 1980?	Increases in sea temperatures have become more critical since 1980, when *El Niño* disturbances began to exceed the thermal tolerances of corals and their zooxanthellae. Prior to this, *El Niño* or other disturbances rarely exceeded the thermal limits of corals and zooxanthellae.
Why are corals growing so close to their thermal limit?	Before recent increases in sea temperature, corals and their zooxanthellae lived in water that typically rarely rose above their maximum thermal limits. Owing to the increases in sea surface temperature over the last hundred years (1 ^{o}C [1.5 ^{o}F]), corals may be just below their upper thermal limits. Prior to this warming, corals would have always been a degree or two below these critical levels. Proximity of corals to thermal limits is tacit evidence that they have not been able to acclimate to these increases. There has been little evidence of thermal adaptation (genetic change) of corals in these areas over this period, although there may be signs of species shifting taking place.

Source: Modified from Hoegh-Guldborg 1999.

For further reading see Aaxelrod and Hamilton 1981, Amadon 1967, Atwood et al. 1992, Benchley 2002, Bunkley-Williams et al. 1991, Chaplin 1972, Clifton 1997, Connell 1978, Darwin 1842, Deloach 1993 and 1997, Fagoonee et al. 1999, Foster 1985, Gaski 1988, Goenaga 1990, Goenaga and Cintrón 1979, Goenaga et al. 1989, Goreau et al. 1979, Greenberg 1979 and 1980, Griffith and Williams 1985, Hartman 1973, Hughes 1994, Humman and Delvach 2002, Jaap 1984, Kaplan 1988 and 1998, Kjerfve 1998, Lang 1974, Lehmann 1983, Lieske and Myers 2002, Limbaugh 1961, Littler et al. 1989, Littler and Littler 1995, Losey 1972 and 1974, Losey and Margules 1974, Lugo et al. 2000, McLaughlin and Zahl 1966, Muscatine and Porter 1977, National Aeronautics and Space Administration 2001, Odum 1971, Pennisi 1997, Peters 1997, Pike 1989, Poulin and Grutler 1996,

Ray and Grassle 1991, Rogers 1974, Sale 1991, Sarokin and Schulkin 1992, Sebens 1994, Stryowski and Bonem 1993, Talbot and Wilkinson 2001, U.S Department of the Interior, Geological Survey 1999, Veron 1995 and 2000, and Wilkinson and Beddermeier 1994.

Special underwater references—

There are three references for fish and invertebrates of coral reefs that can be taken with you in a boat or even underwater while diving or snorkeling. Two are plastic 6- by 10-inch sheets, which can be hung around your neck or wrist, that cover fish, corals, and other marine invertebrates common to Caribbean reefs. The other is a complete book printed on plastic paper (65 pages) devoted to fish. All three are useful field guides for students and recreation divers. The *Fishwatcher's Guide* book by Chaplin was cited earlier. See the appendix for the source of color educational wall charts depicting the coral reef ecosystem and the fishes of Puerto Rico.

Chapter 7: Disturbances in Puerto Rico and the Caribbean

Hurricane Effects on Ecosystems

Hurricanes are powerful tropical storms that start as summer depressions in the warm waters off the west coast of Africa. The westerly trade winds push the depression toward the Neotropics north of the equator and as it rides over large expanses of warm water it picks up energy and windspeed (fig. 80). The origin of the English term "hurricane" derives from the Taíno Indian word for hurricane, which was *Juracan*. *Juracan* was used in reference to their god of evil whose anger produced fierce winds. These storms can affect vast areas of marine and terrestrial ecosystems. They constitute one of the most devastating natural disasters and are now costing the United States $5 billion per year (Bengtsson 2001). In 1998, Hurricane Mitch killed at least 10,000 people in Central America. There are five categories of hurricanes based on windspeed (table 26). If the winds associated with the storm reach 120 kilometers per hour (kph) or 75 miles per hour (mph), it is a Class I hurricane (called typhoons or cyclones in Indo-Asian waters). As the storm reaches the Lesser Antilles where water temperatures may be higher, the strength of the storm can build to a Category 2 moderate hurricane, with wind-speeds of 154 to 176 kph (96 to 110 mph), or a Category 3 extensive hurricane (178 to 208 kph or 111 to 130 mph). Any hurricane of Category 3 or higher is considered major. On occasion, hurricanes and tropical storms also spawn in the Caribbean Sea and Gulf of Mexico and can be equally destructive. The years 1995 to 2000 experienced the highest level of North Atlantic hurricane activity in the reliable weather record. The past 6 years have seen a doubling of overall activity and a 2.5-fold increase in major hurricanes. This increase has produced a fivefold increase in hurricanes affecting the Caribbean. This present level of activity is projected to persist for another 10 to 40 years (Goldenberg et al. 2001). The 2005 hurricane season was the greatest on record with 26 named storms, 13 of which were hurricanes. An estimated $125 billion in damage was associated with just four of the hurricanes.

Hurricanes impact the Caribbean area annually with the highest frequency occurring in September. More than 70 hurricanes have passed over Puerto Rico since the early 1700s. For a review of the history of hurricanes in Puerto Rico, see Quiñones (1992).

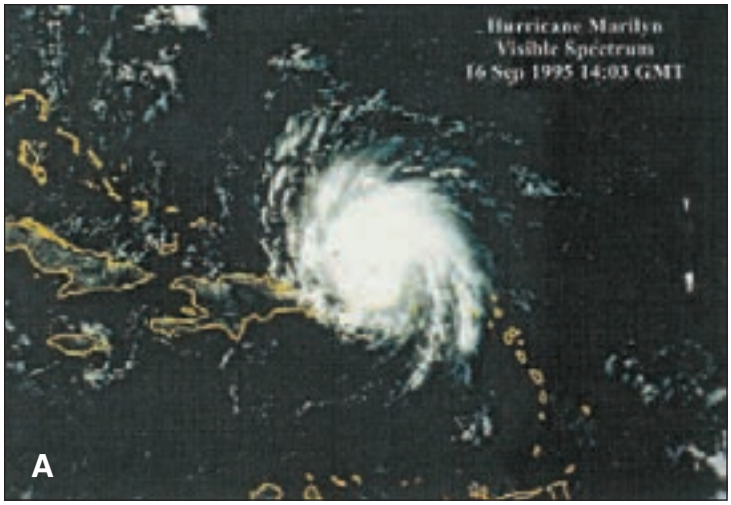
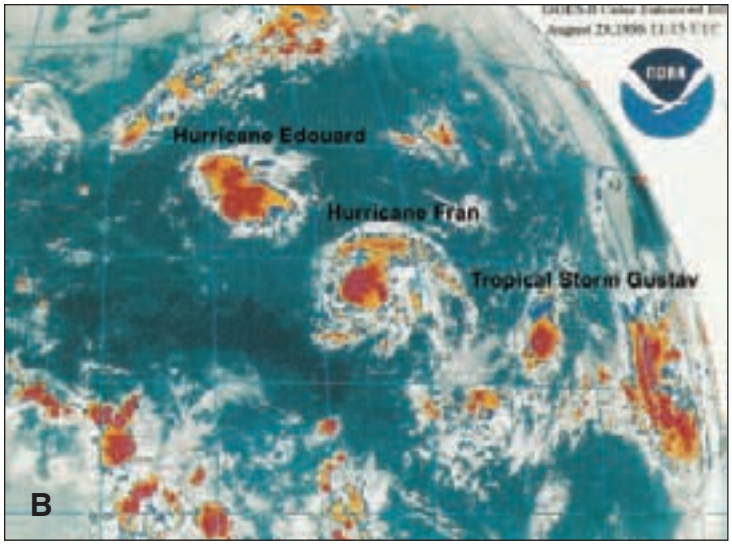


Photo: Courtesy of NOAA

Satellite image of Hurricane Marilyn as it passed over the U.S. Virgin Islands on September 16, 1995.



Courtesy of NOAA

Satellite image of two hurricanes, a tropical storm, and a tropical wave over the Atlantic Ocean. All these systems orginate off the coast of Africa—as illustrated by the tropical wave on the right of the image—and travel in a westerly direction towards the Caribbean or the North American mainland. The Caribbean is on the bottom left of the image shrouded in clouds.

Figure 80—Atlantic hurricane development and trajectory patterns.

Terrestrial Effects

In September 1989, Hurricane Hugo roared into the northeast section of the Caribbean and half a dozen islands received direct hits, including St. Croix in the U.S. Virgin Islands and the east end of Puerto Rico. At times, winds were 224 kph (140 mph - Category 4 hurricane). These violent winds can be devastating to

Table 26—Categories of hurricanes based on windspeed and the Saffir-Simpson Scale

Category	Windspeed	Storm nomenclature	Storm surge (above normal tide)	Possible damage
	kph[a] (mph)[b]			
1	120 to 152 (75 to 95)	Minimal or weak	1.2 to 1.5 (4 to 5)	Mainly to tree branches, mobile homes damaged, power lines down
2	154 to 176 (96 to 110)	Moderate	1.8 to 2.4 (6 to 8)	Tree blowdowns, heavy damage to mobile homes, roofs off buildings, some local and regional flooding
3	178 to 208 (111 to 130)	Extensive or strong	2.7 to 3.7 (9 to 12)	Tree blowdowns, structural damage to buildings, flooding can be widespread
4	210 to 248 (131 to 155)	Killer or very strong	3.9 to 5.5 (13 to 18)	Major vegetation destruction, signs down, major structural damage to buildings, major flooding and beach erosion
5	In excess of 248 (in excess of 155)	Catastrophic or devastating	>5.5 (>18)	Severe damage to buildings of all types, all vegetation types damaged, low-lying buildings can be washed away, severe beach erosion and nearby coastal roads damaged and underwater, heavy damage to phone and electric delivery

[a] Kilometers per hour.
[b] Miles per hour.

forested ecosystems. In addition to extreme wind velocities, vast quantities of rain are associated with these storms adding stress to weight-bearing parts of plants, such as stems and roots. Frequently, stems snap and trees fall as a result. Sections of the El Yunque National Forest received more than 300 millimeters (12 inches) of rain as the storm's eye passed just east of the forest. Hurricane Hugo produced in excess of $9 billion in damage and disrupted the lives of 2 million people along its path through the Caribbean and into the Southeastern United States. Puerto Rico suffered an estimated $2.5 billion in property damage.

Hurricanes are equally destructive to natural ecosystems. Plants, animals, and habitats are stressed, damaged, or destroyed depending upon the intensity and duration of the storm. This is true of both terrestrial and aquatic systems. In many instances, habitats may be permanently altered, whole populations may disappear,

A.E. Lugo

Figure 81—Effects of Hurricane Hugo in the El Yunque National Forest.

and vital food and nesting resources may be lost for an indefinite period. For example, more than 200 landslides were recorded within the El Yunque National Forest as a result of Hurricane Hugo (fig. 81). Evidence indicates that hurricanes may be the most important factor controlling populations and ecosystem dynamics in most, if not all, islands in the Caribbean. In the El Yunque National Forest, and specifically the road to the forest (Route 191), the canopy was opened up as if a can opener had taken the top off the forest. The 12.2-meter (40-foot) leafy branch-covered archway that led up to the high canopy was totally opened to the sky. The road now receives full sunlight, and much of the vegetation still exhibits scars from the severe effects of the storm in 1989. In the hardest hit areas, 60 percent of the trees were downed or damaged, and 27 percent of the endangered Puerto Rican wild parrot population was lost.

In general, human systems may be more subject to damage than those in nature. The big difference is that in 6 months or a year, human systems are rebuilt and no hurricane effects are observable. This is not the case in natural systems. Nature rebuilds much more slowly because it is not buoyed up by vast amounts of cash, energy, and out-of-system resources. Hurricane damage in nature generally causes a crash in stored energy and resources, and will require time for the natural processes to replace them via complex successional and ecosystem development processes.

Hurricanes on average occur four to five times a year in the Caribbean. Puerto Rico is seriously affected about every 21 years, and these storms appear to have direct effect on the size of trees, biomass accumulation, and species diversity. Some experts have described forests in these areas as "hurricane disturbance systems" because of their ability to quickly alter ecosystem processes as the storms drastically alter animal and plant populations. As we are now in a period of global climate change, there are important questions to be answered: With a predicted increase in the frequency and intensity of storm events, will severely damaged systems have enough recovery time to attain prehurricane status before the next storm strikes? Is it conceivable that some areas may remain in some stage of succession indefinitely?

What changes do hurricanes produce? The following is only a partial generic list.

- Complete felling of some trees resulting in vast amounts of biomass being shed and **root balls** forming
- Partial to complete deleafing and debranching resulting in massive litterfall
- Alteration of nutrient cycles
- Elimination of reproduction for some individuals
- Interruption of some phases of growth
- Loss of some of the local animal pollinators or seed vectors
- Vastly altered amounts of light throughout the forest
- Stresses to roots via altered water regime and rocking/twisting of aboveground parts
- Landslides
- Alteration of mortality patterns and species turnover
- Alteration of succession patterns and forest regeneration
- Light-requiring species respond rapidly
- Flood damage associated with streambeds and flood plains related to species presence and coarse woody debris increases
- Reduction in some forest invertebrates
- Altered population structure of vertebrates (some enhanced, others declined, depending on species niches—frog, lizard, and bird responses differ). In general, they exhibit a decrease, but some species may rebound rapidly or actually benefit

For detailed reviews of ecosystem, plant, and animal responses to hurricanes in the Caribbean and long-term responses of Caribbean ecosystems to disturbance, see the special issues of *Biotropica* by Walker et al. 1991 and 1996.

Over a long period, hurricanes may have produced an adaptive ecosystem response in areas where they are frequent. For instance, compared to tropical rain forests in South America, there are no **emergent trees** present in Puerto Rico's forests (fig. 82). Areas with high frequency of hurricanes tend to exhibit flatter wind-sculpted canopies.

The following list identifies other possible adaptive responses.

- Forests exhibit high species dominance.
- Similar numbers of species are present per unit area.
- Low biomass accumulation because they tend to be in a constant state of recovery.
- Species that are present tend to be highly resilient.
- A higher percentage of young individuals and pioneer species are present in forest stands.

It is estimated that possibly 12 million hurricanes have passed over Puerto Rico since plants covered its complex landscape (A.E. Lugo 2001, personal comment). Clearly, hurricanes represent a major selection factor on species and ecosystems. The species combinations found on many Caribbean islands are likely those that are capable of thriving under natural stress in hurricane-mediated disturbance conditions. For additional information on hurricane effects in a period of climate change, see Lugo (2000).

Marine Effects

Hurricanes can play havoc on coastal ecosystems including mangrove swamps, submerged seagrass beds, and coral reefs. The strong winds generate powerful deep waves that can crash into these ecosystems for hours or days. They also produce extensive storm surges. When Hurricane Hugo struck eastern Puerto Rico, waves in the 3.9-meter (13-foot) size class were common. The energy of the waves can physically break apart the species present and alter the normal physical, chemical, and light relationships required for these systems to be maintained. As was the case in the terrestrial ecosystems, vast quantities of freshwater are directly deposited into these systems. Nearby streams that may have been intermittent carry vast quantities of freshwater, sediment, and organic matter into these coastal ecosystems. Alteration of pH, salinity, and turbidity may have drastic effects on the physiology of plants and animals present.

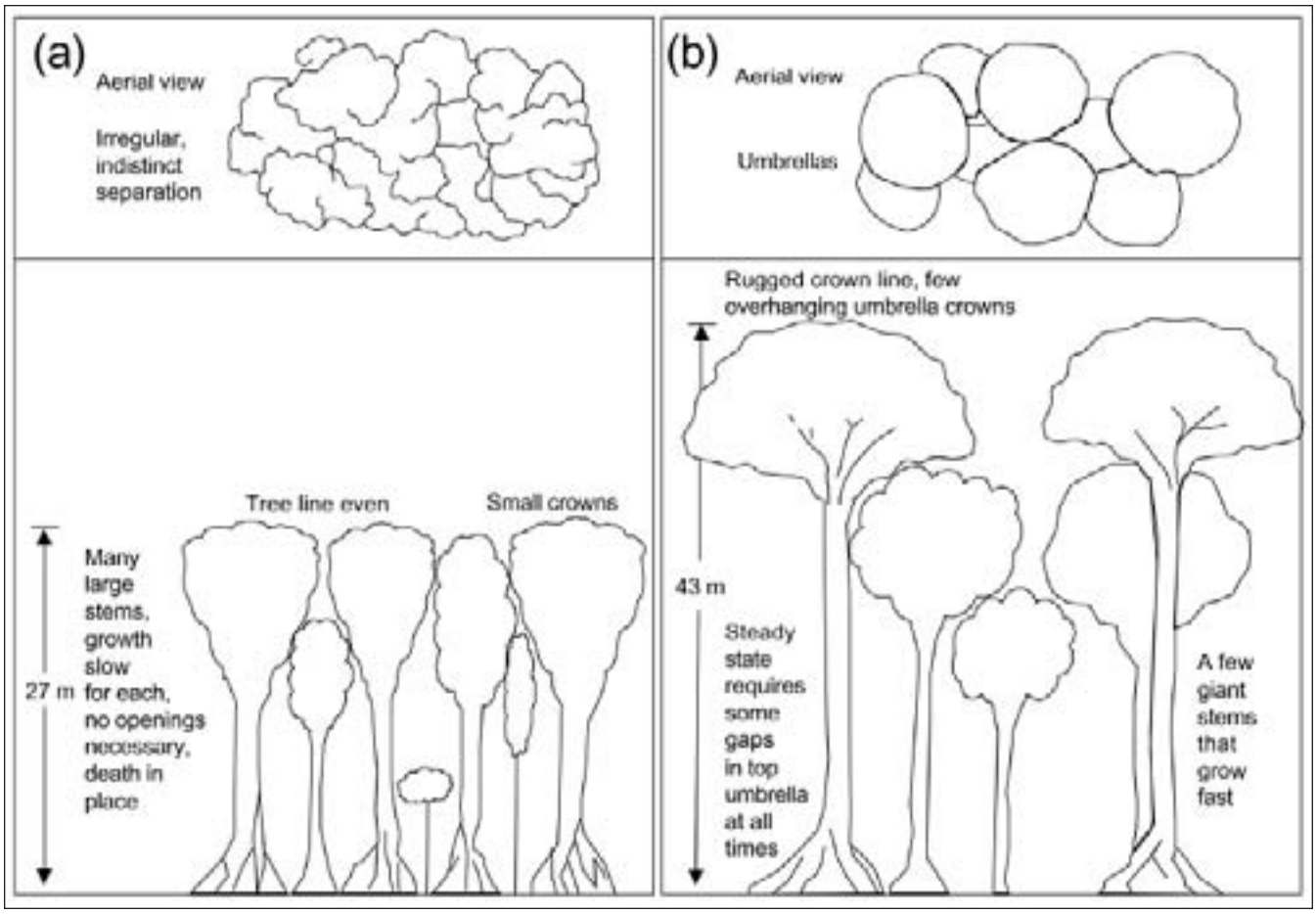


Figure 82—Long-term hurricane effects on canopy design in (a) hurricane-prone vs. (b) non-hurricane areas. Theoretical diagram of forest structure in relation to the hurricane factor showing differences in crown sizes, canopy-stem ratios, boundaries of crowns in aerial views. (a) Hurricane type (Dominica, Puerto Rico), (b) Lowland equatorial type (Costa Rica).

The following is a partial list of the kinds of changes hurricanes can produce in coastal ecosystems.

- pH
- Salinity
- Turbidity
- Physical breakage of live organisms and deposition of debris piles
- Scouring
- Alteration of light regimes
- Deleafing
- Sand blasting
- Leaf chlorosis
- Organic deposition (natural and human)

G. Miller

Figure 83—Hurricane-produced damage on coral reefs in the Caribbean.

- Sedimentation/inundation
- Chemical runoff
- Interruption of food chains
- Temperature change
- Depth increases or decreases
- Oxygen and nutrient changes
- Alteration in dominant species populations or phase shift to algae dominance
- Permanent changes in structure and function if severe and repetitive

Hurricanes usually damage shallow coral reefs most because of the wave damage inflicted on *Acropora palmata*[1] (elkhorn coral) and *Acropora cervicornis* (staghorn coral). Many other corals, such as soft corals, may suffer from sedimentation and burial by coral rubble because they are sedentary. Following Hurricanes Hugo and Georges, the east end of Puerto Rico around Culebra suffered almost total destruction of elkhorn coral. Virtually all colonies over 1 meter (3 feet) were fragmented or overturned (fig. 83). *Porites* spp. (finger coral) and staghorn coral, along with elkhorn coral formed large piles of coral rubble, which covered extensive areas of living coral (USDI Geological Survey 1999). Table 27 summarizes some of the common hurricane effects observed on coral reefs.

[1] See appendix 1 for Common and Latin names.

Table 27—Common hurricane effects observed on Caribbean coral reefs

Feature	Effect
General damage	Highly variable, from little to none, to total destruction over short distances, with shallow water portions of reefs generally experiencing highest damage
Key species of hard coral damaged	Branching corals: *Acropora palmata* (elkhorn), *Acropora cervicornis* (staghorn), *Porites* spp. (finger)
Resistant species	*Montastrea* (boulder star coral) and *Diploria* (brain corals)
Fish	Generally short-term to minor changes, many migrate to less disturbed reefs or protected areas and deeper water; some population decrease likely
Predation	Likely to increase for those species that have lost cover, grottos, caves, etc., or protective background coloration when they spend more time in unprotected open water
Algae	Some lost owing to buildup of coral and sediment overburden; more habitat exposed/created owing to rearrangement of the reef creating new surfaces for colonization
Gorgonians	Burial and abrasion likely, can lead to major loss of colonies, but regeneration can be rapid
Echinoderms	Shallow water residents most affected, those in back reefs and protected lagoons or deeper zones may escape damage or population depressions
Indirect actions	New territories involving coral, algae, and fish may lead to low survival rates of coral or loss of fish if the new habitat conditions do not meet their necessary spatial needs or position on the newly reconstituted reef
Regeneration rates	Dominant branching species likely to regrow rapidly from upright survivors and fragments, creating sizeable populations in 15 to 20 years. Most reef productivity is the result of free-living algae, which are rapid recolonizers of newly exposed hard substrates

Source: Modified from Lugo et al. 2000.

Seagrass beds can suffer from severe scouring produced by waves and currents. Many beds can be buried under vast amounts of sediments dislodged at sea or deposited from rain-induced erosional disturbances on land.

Mangrove swamps can be structurally broken apart, deleafed or blown over, and become susceptible to infections. Some areas will be either inundated with sea or freshwater, both of which can produce major changes in forest composition and altered succession patterns. Early growth after hurricanes is likely to be rapid because of full sunlight and the extra nutrients made available from the decomposing debris produced by the storm. Mangrove swamps exhibit traits of disturbance-prone ecosystems such as environmental tolerance to stress, resilient growth, and early reproduction, all of which should promote rapid recovery. Roth (1997) stated that the even-agedness of many Caribbean mangrove stands, as well as their youth and generally small stature, may be attributable, in part, to posthurricane origins. Mangrove canopies in the Caribbean are about 50 percent shorter than their counterparts in Asia where hurricanes are infrequent.

For further reading see Basnet et al. 1992, Hughes 1994, Kjerfe et al. 1997, Lugo et al. 2000, Odum 1970, Robinson 1997, Weaver 1989 and 1999, Wiley and Wunderle 1993, Woodley et al. 1981.

High Rainfall, Drought, Landslides, and Fire Events

The climate of Puerto Rico is cyclic (fig. 84). Decades of increasing annual rainfall alternate with decades of decreasing rainfall. Because of these dramatic oscillations, mean rainfall values are not useful for the purpose of planning water use or understanding ecosystem and landscape functioning. Rainfall is a main driver of **primary productivity**, **water cycle**, streamflow, **aquifer** recharge, soil oxygen content, sediment transport, **mass wasting**, lowland flooding, water supplies for human consumption, and so forth. Given all these important roles of rainfall, the cyclic swings of annual rainfall have enormous implications for the events that we see unfolding on landscapes. The effects of either too little or too much water are modified by human activity. Human activity can increase the vulnerability of the landscape to too much rain or drought, or can create situations where natural processes occur at greater intensities. We will illustrate this in the discussions below.

One effect of human activity on rainfall events is the long-term global change now picking up speed in the world. Scatena (1998) and others reported evidence of decreasing rainfall in Puerto Rico over the last 100 years. Such reductions in rainfall, coupled with increased urbanization of Puerto Rico and the canalization of rivers would tend to dry up the island and change the islandwide distribution of plant communities. Others suggest that hurricane frequencies will increase in the future. Increased hurricane frequency also impacts vegetation and rainfall in a direction opposite to that of a periodic decrease in rainfall. These changes, if they occur, will fundamentally change the response of the biota to its environment and the welfare of humans on the island. However, we have no idea how global change processes will interact to create the ecosystems of the future. Keep these matters in mind as we describe some examples of excessive rains, drought, fires, and landslides in Puerto Rico and elsewhere in the Caribbean.

Periodically, tropical waves, northern fronts, or hurricanes dump large quantities of water on Puerto Rico. Rainfall events of 25 millimeters (1 inch) per hour lasting for many hours cause floods in the lowlands and landslides in the uplands. These events are common to islanders who suffer the consequences of washed-out roads, flooded homes and highways, interrupted water and power services, and so on. Of interest are the effects of these events on the ecology of Puerto Rico.

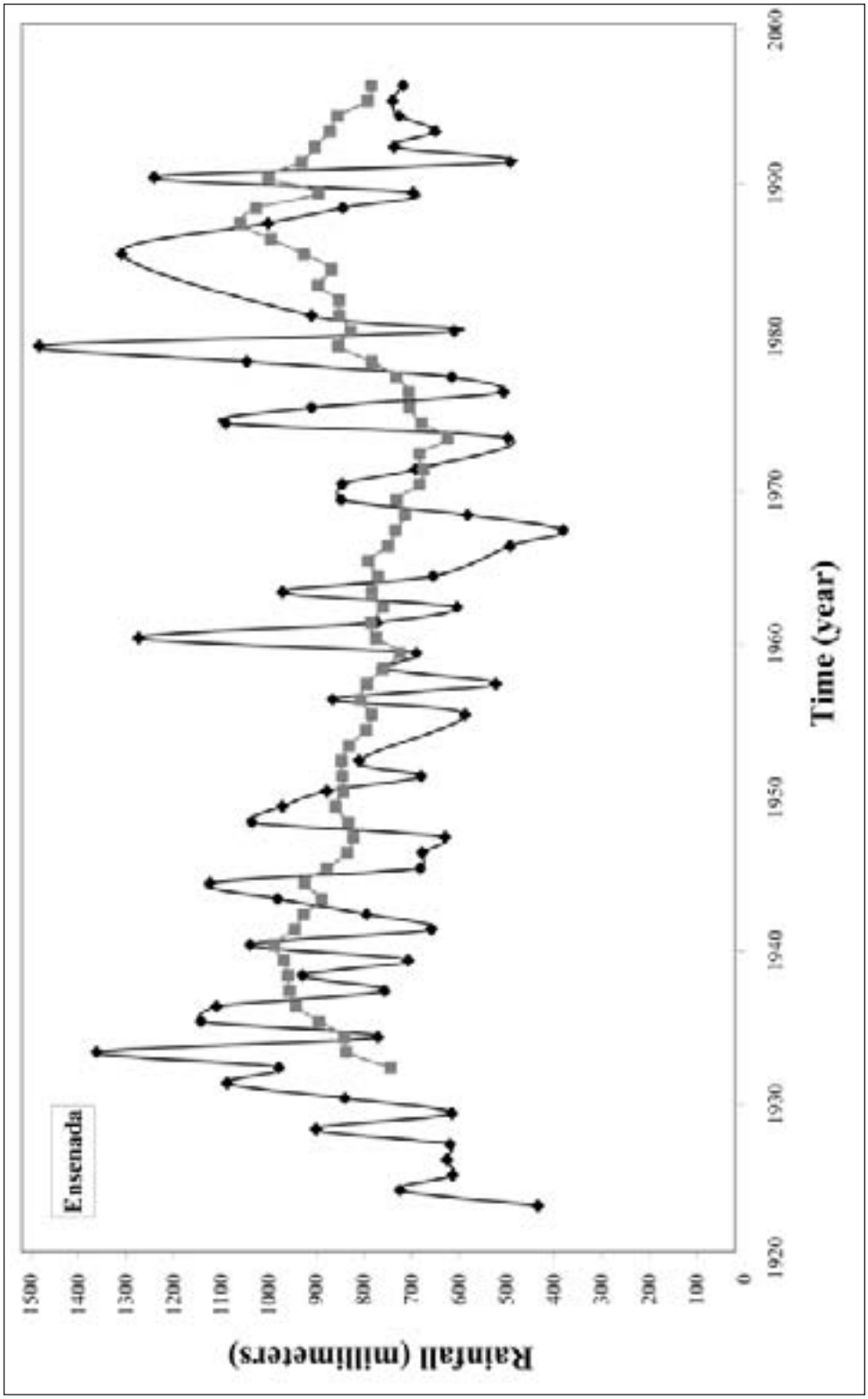


Figure 84—Cyclic climatic rainfall patterns in Puerto Rico.

High rainfall events produce many important functions to the island ecosystems. For example, they recharge soils and aquifers with moisture, thus mitigating and postponing drought. They produce large quantities of sediment, and transport sediments from montane regions to coastal plains. In so doing, high rainfall events help shape the land, river, and stream channels, fertilize flood plains, reduce salinity in estuaries, serve as signals for the reproduction and migration of organisms, and generally rejuvenate the landscape.

Landslides are a product of high rainfall events. If rainfall exceeds 200 millimeters (8 inches) in a day, landslides are triggered. Landslide formation increases with rainfall, poor land use practices, and particular geologic formations that are more prone to sliding than others. In a small watershed, 26.4 square kilometers (10.2 square miles) in Puerto Rico, Larsen and Roman (2001) counted 2,000 landslides since 1820 when forest clearing began. These landslides produced 660,000 cubic meters/square kilometer (23.3 million cubic feet) of sediment or the equivalent of lowering the mean surface level of the watershed by 6.6 centimeters (2.5 inches). These numbers are staggering and represent an extreme case of anthropogenic disturbance in the tropics.

In December 1999, excessive rains fell along the north coast of Venezuela near Caracas, the capital city. Nine hundred and eleven millimeters, or 36 inches, fell over 2 days—about 2 weeks after the region had experienced 200 millimeters or 8 inches of rain in 2 days. The magnitude of the subsequent floods, landslides, mudflows, and avalanches was without known precedent, and over 19,000 people were killed. Boulders weighing 300 to 400 tons were moved to the coast by these events; buildings were covered by debris, and the shape of the coast of Venezuela changed. Such is the force of nature when extreme natural events combine with large human populations.

The formation of landslides has repercussions to vegetation (Walker 1999). Landslides remove all vegetation from the surface of the landscape affected and set succession back to primary succession. Plant succession usually starts in nutrient-poor soils and unfavorable growth conditions such as impermeable surfaces, high light intensity and temperatures, and high rates of runoff. The plants best adapted to these conditions are lower vascular and nonvascular plants, ferns, and grasses. Arrested succession is common on landslides. This means that the orderly change of plant species stops and a particular stage retains dominance over a site. Usually, ferns and grasses dominate these arrested successions. However, on favorable sites, succession proceeds to a forest. Studies in the Luquillo Mountains show that after 60 years, a native forest can occupy the site where landslides occurred previously.

The tropics are usually associated with rain forests and abundance of rainfall. However, about half of the tropical forest area is dry forest where organisms are limited by water. Drought is common in these environments. The subtropical dry forest life zone constitutes the driest conditions in Puerto Rico, and rainfall as low as 300 millimeters (12 inches) per year has been recorded in some locations. When drought occurs, plants wilt, leaves fall, the tops of tree branches die off, and many trees are killed. Events such as these are common in the dry tropics, but they also occur in the wet tropics. In the Luquillo Mountains, for example, severe droughts occur with frequencies that approach one per decade. In 1992, such a drought occurred and scientists could not find any deleterious effects on trees. This suggests that the native flora of Puerto Rico is adapted to periodic drought. It is possible for all of Puerto Rico to be under the influence of recurrent droughts. During this time, water shortages and rationing are common islandwide.

Regardless of the recurrence of drought events, fire is not a natural event in the island. We know of no native plant community subject to fire or adapted to fire. However, in 1999, the Fire Department reported 2,975 wildland fires in Puerto Rico (fig. 85). The cause of nine of the fires was lightning; the others were set by humans. Most of those fires occur near roads and in zones with less than 1500 millimeters (60 inches) of rainfall. Moreover, because of the introduction of many fire-adapted exotic grasses from Africa to Puerto Rico, we now observe the development of new fire-dependent ecosystems in Puerto Rico. These ecosystems are near highways and roads, and are dominated by alien grasses. These ecosystems are expanding at the expense of native ecosystems not able to survive the new fire regime introduced by human activity.

For further reading see Larsen and Santiago Román 2001, Larsen and Torres Sánchez 1998, Larsen et. al 2001, and Myster and Walker 1997.

The Urban Forest Interface

As human activity continues to increase in Puerto Rico, it becomes the major disturbance regime in the island. We end the section on disturbances by focusing on the **urban forest interface** in Puerto Rico.

What is a greenspace or **greenway**? Green open space, green natural area, green travel space, urban trail system, all describe a greenway or greenspace. Greenways may be linear parks that have large irregular perimeters that frequently conform to some special geographic feature such as a river, a steep mountain, or the interface zone of a city. Greenways can effectively serve as corridors for foot and bike traffic, or be specialized recreation corridors for jogging, biking, and bird

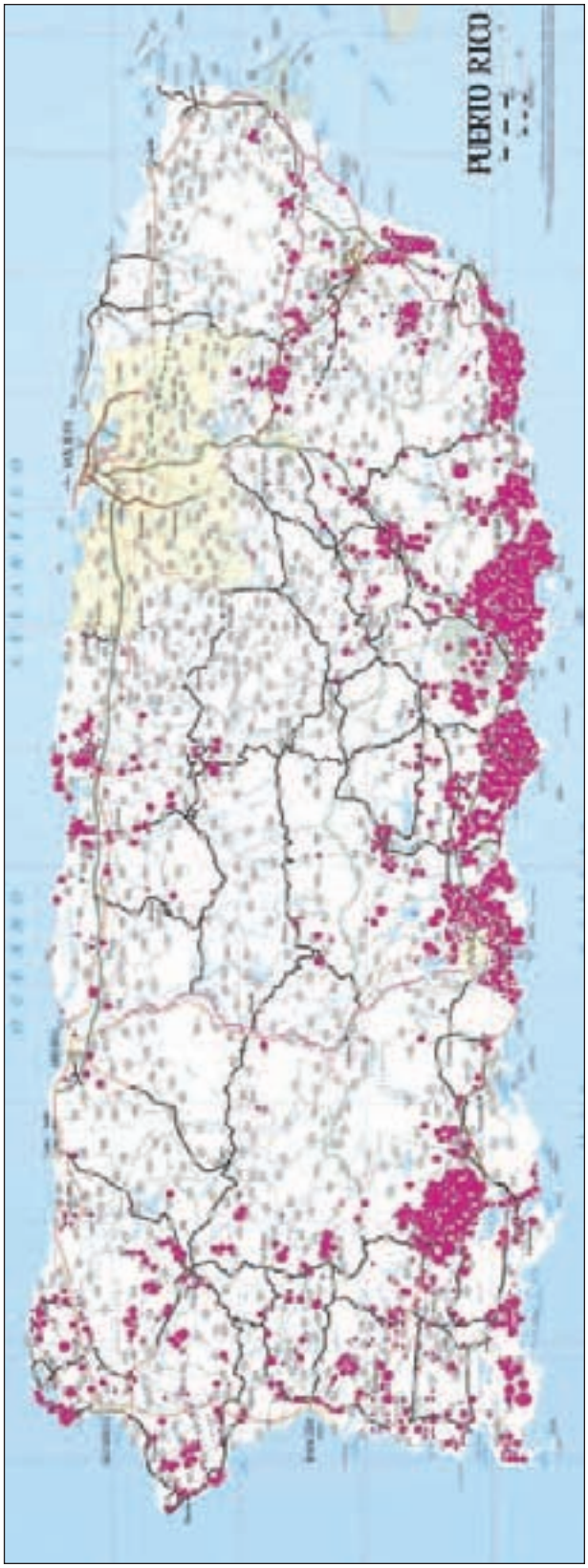


Figure 85—Fires in Puerto Rico.

watching. They frequently connect commercial and residential nodes, tourist attractions, education facilities, and so forth. In many areas, they are used as "soft engineering" approaches to increasing water quality whereby vegetative buffers help to filter out pollutants. They also slow and store floodwaters and help to reduce sediment loss. Greenspaces and greenways are also very important because they serve as urban wildlife refuges and migration corridors thereby ensuring some opportunity for humans to coexist with wild plants and animals. Many serve as focal points for the teaching of environmental biology to children in urban schools. Their presence may also substantially enhance the property values of nearby businesses and residential areas and increase the liveability of an urbanized landscape.

Puerto Rico is currently experiencing rapid rates of urbanization throughout most low-elevation areas of the island. San Juan, as of 2002, has only 16 percent greenspace remaining, and that percentage appears to be declining rapidly (fig. 86). The rate of loss of greenspace is now critical because, at present rates of development, virtually all greenspace will be lost by 2025.

Today, in the municipality of San Juan, there are a couple of significant forest inholdings that represent the last opportunities for permanent greenspace to be set aside. There are about 27 000 hectares (72,700 acres) of undeveloped greenspace in the six municipalities of greater San Juan, with most of it in their southern boundaries. There is currently a proposal being discussed that could link some of these small contiguous urban forest remnants to others in the adjacent municipalities. These areas were all previously deforested, but are currently in various stages of secondary succession and have great value as a wildlife refuge for native species, especially birds, amphibians, and reptiles. There are about 200 hectares (500 acres) controlled by the University of Puerto Rico on the urban campus shared with the Department of Agriculture, the USDA Forest Service, International Institute of Tropical Forestry, and the Botanical Garden in Río Piedras. This space could serve as the locus for development of a major greenspace for that area.

A field trip through this area will allow you to see the urban forest interface and see the many values that greenspaces such as this have, including:

- Wildlife refuge
- Plant refuge
- Protection of headwater streams
- Reduction of noise
- Reduction of flood damage
- Filtering urban water sources
- Education/research

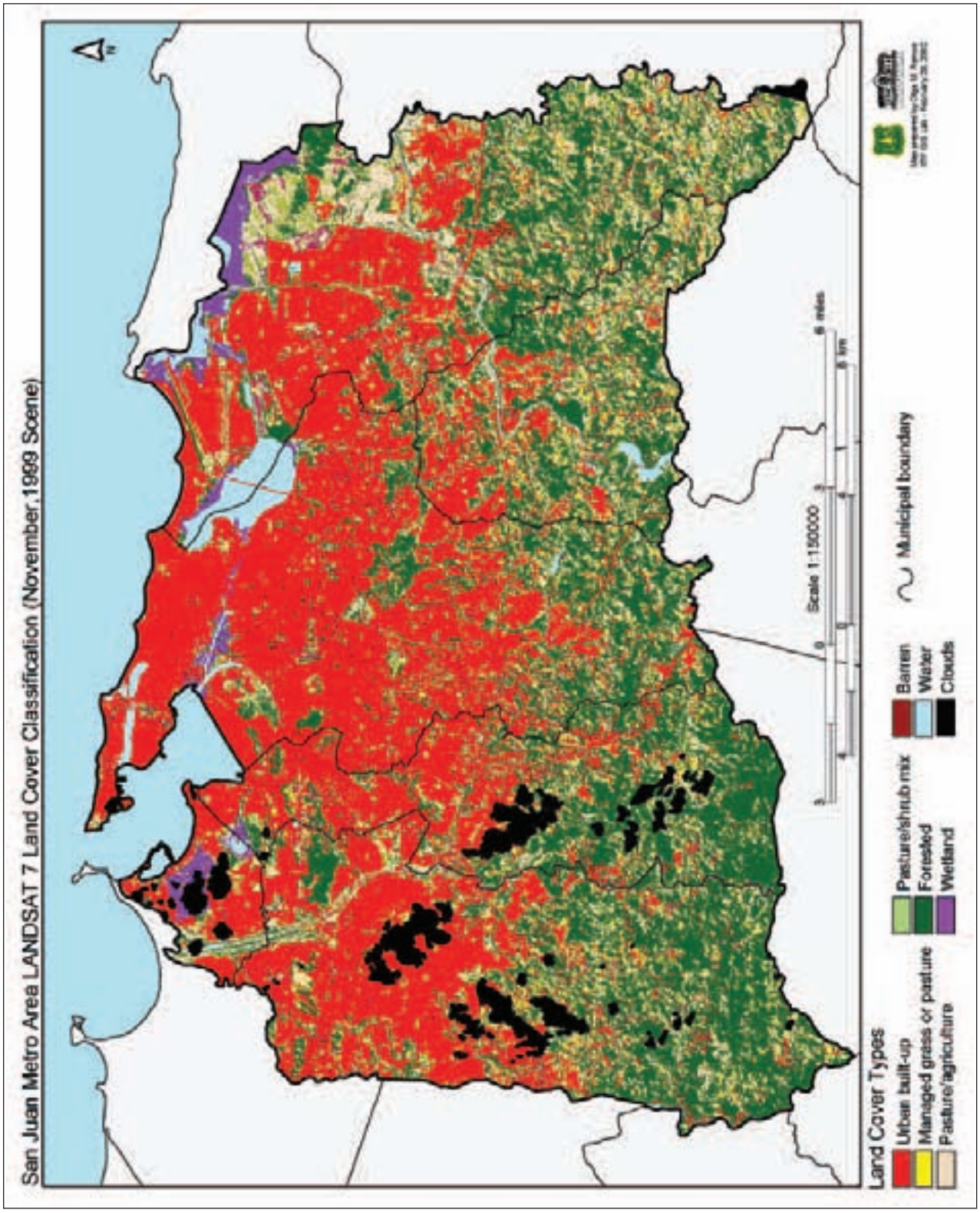


Figure 86—Urban forest map of greater San Juan.

- Bird watching
- Urban greenspace recreation
- Air pollution reduction
- Urban climate modifier

Things to be observed are:

- Various successional species and stages of successional development
- Hilltop-to-flood-plain transect
- Urban/forest interface
- Río Piedras flood plain
- High pollution zone near business district with oil contamination and solid wastes
- Filtered water on natural flood plain
- Flood plain plant zonation
- Lianas
- Low epiphyte presence
- Root balls–hurricane damage
- High light demanding plants–storm gaps and early-succession species with low survival of adults and seedlings
- Nitrogen fixers
- Alien plant species
- Plant adaptations to reduce predation
- Poison plants *Urtica* and "Molinero's"—spiny trunks

Controversies associated with sites like this include:

- University growth–recreation (satellite campus)
- Río Piedras public use zone
- Continued demand for space for economic growth
- Little historical precedent for protecting urban greenspaces in Puerto Rico
- Zonation conflicts
- Mindset toward jobs, growth, and political ambitions (is growth always good?)
- Will greenspace development have enough economic/community value to justify permanent set-asides?
- Few jobs produced
- No products for sale
- Little, to no tax revenues will be generated

Greater San Juan could adopt a "hectare for hectare" (acre for acre) mindset. That is, for every hectare developed, a hectare is set aside and protected or restored. This is the last easy opportunity for the creation of urban greenspace for the many communities involved. In a few years, these green remnants will be paved over. Future generations will have little opportunity to identify with nature, to enjoy the sweet smell of a working forest, or to enjoy the beauty of fish in a stream. This is a small area to set aside compared to the many benefits current and future generations will receive from these greenspaces.

One of the great challenges throughout the world's urban areas is how to make communities more livable. Invariably, one of the most meaningful options is the designation of greenspaces. Many cities are in many ways **urban deserts**, and it is only in greenspaces such as parks, urban forests, and linear riparian zones along rivers that urbanites are provided with opportunities to get some relief from life in the urban jungle.

For further reading see American Forests 2002.

Chapter 8: Environmental Organizations and Environmental Infrastructure

The El Yunque National Forest and the International Institute of Tropical Forestry

There are 155 national forests in the U.S. National Forest System, and the El Yunque National Forest (EYNF) is the only tropical rain forest. The EYNF is among the smallest forest units in a U.S. National Forest System that encompasses over 77 296 641 hectares (191 million acres). It is, however, the largest forest reserve in Puerto Rico. This unique forest, which, until 2007 was called the Caribbean National Forest, is located on the eastern side of Puerto Rico in the *sierra de Luquillo* Mountains. The forest is the only national forest that is also an experimental forest, the Luquillo Experimental Forest. As such, it is dedicated to research, as well as other national forest functions.

Owing to the prevailing trade winds and orographic effects, rainfall is plentiful in the EYNF. Average rainfall throughout the forest is 3000 millimeters (120 inches), but some areas in the forest receive more than 5000 millimeters (200 inches) of rainfall per year. This is equivalent to more than 378 billion liters (100 billion gallons) of water. It is the "rainiest" national forest and consequently it is the only forest with no forest fire problem. Although this forest encompasses only 11 322 hectares (28 000 acres), it is big in terms of biodiversity. The EYNF has more species of trees than are present in all the other 154 national forests together. Some 240 tree species are native to the area. Twenty-six species are endemic to the forest, and another 45 species are found only in Puerto Rico. Its elevation ranges from 100 to 1077 meters (330 to 3,533 feet). There are seven peaks over 930 meters (3,050 feet) high with *El Toro* (the bull) the tallest at 1075 meters (3,526 feet). It constitutes the largest single area of natural managed forest on the island.

The United States inherited this forest when Spain ceded Puerto Rico to the United States as a result of the settlement of the Spanish-American War. The original inholdings of forest were set aside by decree in 1876 by the King of Spain, and as such, this is one of the oldest reserves in the hemisphere and compares with the date of the designation of Yellowstone National Park (1872), the United States' first national park and the world's oldest national park. Its original size was 4920 hectares (12,300 acres) and this royal designation saved it from deforestation, which ultimately produced more than 90 percent loss of forest cover in Puerto Rico by the early 1900s. In 1903, President Theodore Roosevelt designated the area the

Luquillo Forest Reserve, and it was later incorporated into the U.S. National Forest System. In 1946, the Puerto Rican government designated the forest a commonwealth wildlife refuge, because it provides habitat for 120 vertebrate species such as birds, bats, lizards, amphibians, and fish. The forest has 68 bird species, including 9 island or EYNF endemics: The Puerto Rican parrot,[1] Puerto Rican lizard cuckoo, green mango hummingbird, Puerto Rican emerald hummingbird, Puerto Rican tody, Puerto Rican woodpecker, elfin woods warbler, Puerto Rican tanager, and the Puerto Rican bullfinch. It is also home to the Puerto Rican boa, the island's largest native snake species, which is under protected status. Much larger numbers of invertebrates are present, and some are yet to be discovered.

The Forest Service manages the EYNF/Luquillo Experimental Forest under a policy of multiple use that calls for the integration of the various desirable uses of the area for the greatest general good. Both social and economic returns are considered. Areas within the forest are dedicated primarily to what is considered their best uses, but may also be used for other purposes that do not unduly interfere with the primary use.

The principal objective of management is to make these forest lands as productive as possible and to demonstrate the results. About 6070 hectares (15,000 acres) of the forest are capable of timber production. This area is being managed so that the yield will not only be sustained in the future, but will increase through forest improvement. Part of this area is set aside for experimental investigations to determine the best techniques of timber management. Elsewhere, inferior trees are removed and are being replaced by more productive young growth. Trees with poor form are cut or poisoned, and the mature trees of better formed species are marked for sale by forest officers. Sales are made to local operators, and the timber is harvested according to sound forest practices. The trees are cut and the logs are removed in a manner favorable to the growth of future timber crops, as well as the preservation of soil, water, and other values. Twenty-five percent of the revenues from the sale of timber, forest products, and land uses is returned to the local government for roads and schools.

Three-fourths of all the virgin timber that remains in the Puerto Rican forests, which once covered the entire island, is included in the Luquillo Experimental Forest. An area of approximately 809 hectares (2,000 acres), known as the *Baño de Oro* Natural Area, has been permanently set aside by the Chief of the Forest Service to preserve in virgin condition the four types of forest of these mountains.

[1] See appendix 1 for Common Latin names.

Figure 87—Map of the El Yunque National Forest/Luquillo Experimental Forest.

This area is to be used only for scientific studies. No trees are ever cut, nor is the area to be traversed by a road or trail.

Under the program of development followed by the Forest Service in administering the forest, preserving wildlife values is important. The forest has been established as a commonwealth bird refuge to preserve the Puerto Rican parrot and the other birds endemic to the island almost exterminated as a result of uncontrolled hunting and deforestation.

The headwaters of eight major rivers rise in the forest and provide water for domestic purposes and hydroelectric power for the people of eastern Puerto Rico. Mismanagement of the vegetation on steep slopes within the forest might endanger some of the island's best sources of water by causing floods and accelerated soil erosion. Critical areas such as peaks, ridges, and steep slopes, which cover about 1214 hectares (3,000 acres) of the forest, have been closed to timber cutting and other uses so the natural vegetation may continue to protect the soil and retard the runoff of water. The water that flows out of the forest in streams and underground watercourses is relatively free of sediment.

G. Miller

Figure 88—Learning in a natural setting is the basis for ecotourism.

Through the years, more lands were purchased, especially in lower elevations surrounding the original inholdings, and today the forest covers 11 200 hectares (28,000 acres) (fig. 87). Its official name is the El Yunque National Forest/Luquillo Experimental Forest, so designated in 1956 to address research issues. It is the only forest in the Nation with this special designation. In October 1976, the United Nations Educational, Scientific and Cultural Organization (UNESCO) designated it as part of the Man and the Biosphere International Network of Special Reserves. This special designation was given in recognition of its unique species diversity, long history of scientific studies, and its special ecological attributes. The forest is said to have the longest history of study of all tropical forests in the world. Its special protected status assures that it will be there to promote sustainable intergenerational conservation efforts and to provide a standard against which the effect of human impact on the environment can be measured. This forest is an active training site for forest managers and research scientists from around the world. In addition, it is easily accessible by the general public, and today, about half a million visitors from all over the world visit the forest yearly (fig. 88). In recognition of its special role in public education, the USDA Forest Service opened a state-of-the-art forest education center, *El Portal*, in 1997. This "gateway" facility provides a variety of rain forest education exhibits with staff available to answer specific questions, providing forest maps and other literature to the visitor (fig. 89).

G. Miller

Figure 89—View of the entryway to El Portal Visitors Center in the El Yunque National Forest.

There are four distinctive forest types in the EYNF: the tabonuco, sierra palm, palo colorado, and elfin forest. Each of these has been described in detail in the forest zone section of this document, along with tree species profiles and special plant groups typical of the forest types.

One of the special features of this forest is that it is relatively easy to access by the public. It is located within a couple of hours of driving for the island's 3.8 million inhabitants and the countless tourists that visit the island each year. San Juan is only 35 kilometers (25 miles) west of the forest. As part of the USDA

A.E. Lugo

Figure 90—The International Institute of Tropical Forestry located in Río Piedras, Puerto Rico.

Forest Service's mission of providing multiple use, the forest makes available a variety of recreational opportunities. There are 13 trails easily accessed by the public varying in hiking length from 15 minutes to 4 hours or more—one-way. There are four observation towers available for scenic vistas at Yokahú, Mount Britton, El Yunque, and Los Picachos. Primitive camping is available. Most users of the forest are involved with enjoyment of beautiful scenery and waterfalls, its wide variety of unique plants and animals, and the opportunity to enjoy picnic lunches in the cool mountain breezes. Covered pavilions, water, and restroom facilities are available.

The International Institute of Tropical Forestry (institute) is also located in Puerto Rico. In 1928 the U.S. Congress authorized the establishment of a forest experiment station in the tropical possessions of the United States in the West Indies. The experiment station was established in 1939, in Río Piedras, Puerto Rico. Much of their early efforts were centered on repairing damaged watersheds and improving forestry options so that more valuable and useful species would replace inferior timber species on damaged and abandoned lands. Today, the institute is an outgrowth of the original forest experiment station (fig. 90).

The institute now conducts programs in state and private forestry and forestry research and development, and oversees a variety of international cooperative programs. It also provides administrative services to its members. In spite of the

growth in program initiatives and staff, the institute's scientists still conduct inventories, select species for reforestation, and develop silvicultural practices for tropical timber trees. Today, however, many new research avenues are being pursued including economic, social, and environmental benefits of healthy forests, atmospheric pollution, global warming, impacts of tropical deforestation and its effects on global climate, maintaining suitable habitat for various plant and animal species such as the endangered Puerto Rican parrot, hurricane effects, landscape ecology, and disturbance ecology.

The institute is designated an independent region of the USDA Forest Service and reports directly to the Chief. Its Río Piedras facility covers 2 hectares (5 acres) and includes a large headquarters/office building, specialized geographic information systems, geopositioning system and chemistry laboratories, a library, **seed bank**, machine shops, and other support facilities. The institute published the *Caribbean Forester* from 1939 to 1953, and over 1,000 technical papers have been written by its research staff. Its library is purported to house the best tropical forestry collection in the New World. Its technical staff has served throughout the tropical world as research scientists and consultants to dozens of countries and international agencies. The institute has an active training program for tropical foresters, graduate students, and visiting university ecology classes from numerous countries and states in the United States. It maintains the oldest forest research plots in the hemisphere dating back to the 1940s and maintains continuous growth records on over 20,000 trees. In 1988, the National Science Foundation designated the Luquillo Experimental Forest a Long-term Ecological Research Site. In 1990, the institute and the Luquillo Experimental Forest received the USDA Forest Service Stewardship Award for their outstanding contributions to forest conservation.

Administratively, the institute's director is supervised by the Chief of the U.S. Forest Service and the institute operates much like a Forest Service region. Today, the institute has about 65 to 70 employees and an $8 million budget (including grants and contracts). Thirty countries and 80 environmental/governmental/educational organizations have formal agreements with the institute. The institute, in combination with the EYNF, is developing **ecosystem management** initiatives that will allow people in the tropics to use their forests based on sustainable forestry practices that are necessary to maintain healthy, productive, and diverse forests in the new millennium.

For further reading see Lugo and Mastrantonio 1999, Steinkamp et. al 1996, and Weaver 1994.

Puerto Rico's Commonwealth Forests and Nature Reserves

Puerto Rico now has 118 natural areas that include federal reserves, commonwealth forests and refuges, and nongovernment conservation areas. They range in size from the 11 336-hectare (28,000 acre) El Yunque National Forest in the Luquillo Mountains, to the commonwealth protected 2-hectare (4.94-acre) mangrove swamp at Naguabo.

Puerto Rico has 14 commonwealth forests distributed throughout the island (fig. 91). They serve as functioning forests and are operated under the principles of multiple-use resource management. All have trail systems, and some have well-developed bike trails and camping facilities. They are grouped according to their geographic position: karst (K), coastal (C), and mountain upland (U). For a complete description of each forest, its soils, climate, wildlife, unique natural areas, and management issues, see the 1976 *Master Plan for the Commonwealth Forests of Puerto Rico* of the Department of Natural Resources, San Juan, Puerto Rico. All forests are open 7 days a week from 7:00 a.m. to sunset unless posted otherwise. Table 28 provides a description of each forest's location, as well as, size, habitats, and facilities.

Puerto Rico also has regional nature reserves, which serve to protect habitat, and the animals and plants located within and near them. Table 29 provides information about the nature reserves.

As described in the section on environmental organizations in Puerto Rico that follows, there are a variety of nongovernmental organizations (NGO) working at the local and commonwealth level in preservation and conservation of species and critical ecological habitats. The Puerto Rican Conservation Trust is one of the NGOs operating in Puerto Rico. The trust manages 14 high-profile cultural, environmental, and ecologically significant properties encompassing more than 5263 hectares of land (13,000 acres) spread throughout Puerto Rico (fig. 92). Their education programs now reach nearly 150,000 people a year. They offer environmental camps and special education programs in cooperation with the public schools. Their trust properties include:

- **Las Cabezas de San Juan Nature Reserve** (Fajardo) is exceptional for its diversity of marine and terrestrial habitats, with full educational services, programs, and transportation–128 hectares (316 acres).
- **Hacienda Buena Vista** (Ponce) is a fully restored 19th-century farm and coffee plantation with period canal and water-based technology, and functioning coffee and corn mill–218 hectares (496 acres).

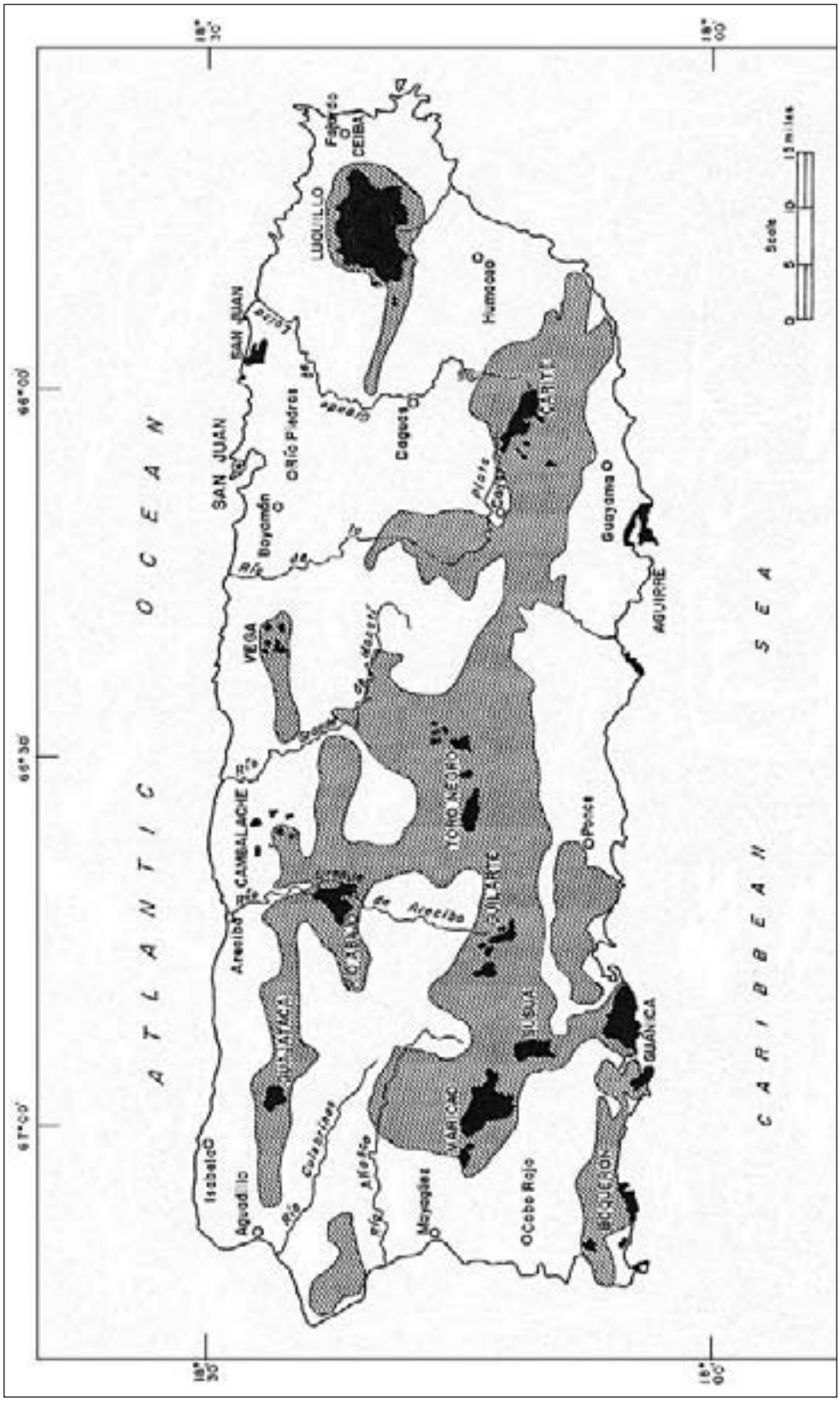


Figure 91—Public forests and forest lands of Puerto Rico. The public forests (solid black) are 14 commonwealth forests (bosques estatales) and the El Yunque National Forest or Luquillo Experimental Forest (federal). Shaded areas are forest lands adjacent to public forests. From Little et al. 1974.

Table 28—Visiting the commonwealth forests of Puerto Rico

Forest name and location	Phone	Size	Habitats
Central office of forest Reserves San Juan, PR	(787) 724-3724	Hectares (acres)	Island-wide coordination of all forest reserves
Piñones[a] (C) Route 187 (behind the San Juan International Airport) along the coast to Loiz[a]	(787) 791-7750	613 (1,513)	Coastal beach (sandy and rocky), mangrove swamps, dry scrub woodland Features newly constructed bike trail throughout the forest's habitats. Lots of sandy beach access, 46 bird species
Ceiba (C) Located between Fajardo and the town of Ceiba along the coast	(787) 852-4440	143 (352)	Coastal beach thicket, salt flats, mangrove swamps, turtle grass beds, manatee habitat
Aguirre (C) Off Route 3 east of Salinas	(787) 864-0105	968 (2,390)	Mangrove swamps, tidal flats, bird rookeries, marine research area, manatee habitat, 60 bird species
Guánica (C) Route 116 to Route 334 and follow signs	(787) 821-5706	3879 (9,582)	Dry forest habitat known for its high bird diversity Beaches, mangroves, and visitor center (center is closed Mondays) Twelve hiking trails are available, maps can be obtained at the education center
Boquerón (C) Forest office west of Boquerón off Route 101	(787) 851-7260	801 (1,979)	Mudflats, salinas, mangrove swamps, and interpretive trails. Very good for coastal birds (50 species) and fish (58 species)
Carite (U) Route 184, southeast of Caguas	(787) 747-4545 (787) 864-8903	2616 (6,460)	Features pine plantation and camping opportunities (16 sites), 30 bird species
Guilarte (U) Located southwest of Adjuntas, south on Route 131 or Route 518	(787) 829-5767 (787) 852-4440	1415 (3,495)	Features a hiking trail to 1204 meter (3,940 feet), Guilarte Peak, and visitors center Five rental cabins are available
Toro Negro (U) Route 143 at km 31.8, east of Route 149	(787) 867-3040 (787) 844-4660	2727 (6,737)	Tallest peaks in Puerto Rico (*Cerro de Punta* and *Cerro La Rosa*), 7 campsites, hiking trails
Susúa (U) Northeast of *Sabana Grande* on Route 368 at km 2.1	(787) 724-3724 (787) 833-3700	1312 (3,241)	Mountain bike trail, good view of carbonate formations, 40 campsites
Maricao (U) North of *Sabana Grande* on Route 120	(787) 724-3724	4151 (10,251)	Observation tower, fish hatchery and hiking trails, 26 bird species (11 endemics)
Vega Alta (K) East of Vega Alta on Route 676 at km 1.5	(787) 833-2240	447 (1,105)	Caves, sinkholes, and highly variable soils

Table 28—Visiting the commonwealth forests of Puerto Rico (continued)

Forest name and location	Phone	Size	Habitats
Guajataca (K) Route 446 south of Route 2	(787) 872-1045 (787) 890-4050	926 (2,286)	Largest hiking trail system in the forest reserves (44 kilometers/26 miles), observation tower, bird watching (45 species) and good view of karst topography. Camping (10 sites) available Forest maps available at the north entrance
Rio Abajo (K) South of Arecibo on Route 10 at km 70.3, then west on 621 to km 4.4	(787) 880-6557 (787) 878-7279	2270 (5,607)	Karst cave systems, hiking trails, large camp sites
Cambalache (K) West of Barceloneta on Route 682 at km 6.6	(787) 881-1004 (787) 878-7279	373 (922)	Camping (12 sites), hiking trails (13 kilometers /8 miles), mountain bike trails, 45 bird species

Note: Camping areas charge $4 per person per night. The cabins at Guilarte Forest rent for $20 per night.

[a] One of the newest additions to the commonwealth forest's recreation system is the recent opening of the $7 million boardwalk and bike trail system added to the Piñones Forest. Not only is this an important local recreation and ecotourist destination, but it guarantees the protection of important coastal wetlands. The new facilities offer opportunities for leisurely coastal walks and up to 7 miles (one way) of biking opportunities. It starts at *Boca de Cangrejos*, just up the beach from the El San Juan Hotel. This area has excellent beach front for swimming. The new path system will include 31 kiosks for bike and auto parking, as well as an information center describing the habitats and recreation opportunities in the area. This boardwalk has produced new opportunities for ecotourist companies to offer bike, nature, and sea kayak trips.

- **Phosphorescent Bay and mangrove swamps** (La Parguera) protects the mangrove swamps surrounding the world-famous bay–327 hectares (807 acres).
- **Sotomayor Nature Reserve** (Caguas) preserves mountain tract of virgin forest at the headwaters of the Turabo River–26 hectares (63 acres).
- **Río Portugues Forest** (Adjuntas) is a conservation easement protecting sierra palm forest on headwaters of the Portugues River–17 hectares (42 acres).
- **San Cristobal Canyon Reserve** (Barranquitas) protects the northern rim of a volcanic rift in the Cordillera Central with ravines over 229 meters (750 feet) deep–405 hectares (1,000 acres).
- **Punta Guaniquilla Reserve** (Cabo Rojo) protects arid promontories overlooking the sea, dry forest areas, two lagoons, caves, mangroves, sculptured limestone rocks, and habitat for the endangered West Indian whistling duck. This is an important wintering and migratory bird sanctuary–157 hectares (388 acres).

Table 29—Nature reserves of Puerto Rico

Reserves name and address	Phone	Habitats
Las Cabezasa[a] de San Juan Nature Reserve Highway 3, then left to Fajardo on Route 194, left at Monte Brisas Shopping Center, then right at next light, left onto Route 987, follow signs to entrance	(787) 722-5882 (787) 860-2560 - (on weekends) Open Friday through Sunday by reservation only. English tours 2:00 p.m Admission = $5/adults; $2/children Group tours available on Wednesdays and Thursdays	128 hectares (316 acres) of coastal headlands, 128 hectares (316 acres) of coastal headlands, mangroves with boardwalk, lighthouse, beaches, cactus populations, bird watching, hiking trails, and new visitor center. Group transportation takes you through the preserve
Humacao Wildlife Refuge Off Route 3 east of Humacao		1215 hectares (3,000 acres) of former cane fields and cattle pasture that is undergoing succession and reclamation
Caja de Muertos Island Nature Reserve Public ferries leave from municipal dock at Ponce on the La Guancha boardwalk early in the morning and return late in the afternoon		Uninhabited island off the coast at Ponce, with hiking trails, lighthouse, dry scrub, and underwater park with good reefs (Take your own shade and water supply)
Boquerón Forest Bird Refuge Route 301 at km 1.1 east of Boqueron	(787) 851-4795	Walking trails and boardwalks through mangrove swamps and lagoon Fishing and hunting are seasonally permitted on this 182-hectare (450-acre) preserve
Lago Lucchetti Wildlife Refuge Near Yauco, Route 128 to refuge entrance at km 12.3	(787) 844-4660	Campsites, recreation area, boat ramp
Lake Tortuguero Reserve East of Manati on Route 2, north on Route 687	(See the wetlands section for details on this preserve)	Freshwater wetlands with a variety of palustrine species and habitats, contains small population of caimans

Other nature reserves are also located at the Lagoon Reserve at Joyuda in Cabo Rojo, Río Espiritu Santo in Río Grande, Wetlands Reserve at *Caño Tiburones* in Arecibo, the Coral Reef Reserve at Guayama.

[a] Las Cabezas de San Juan Reserve has been studied ecologically and taxonomically and a full description of its plant and animal communities has been published in Weaver et al. 1999a, 1999b.

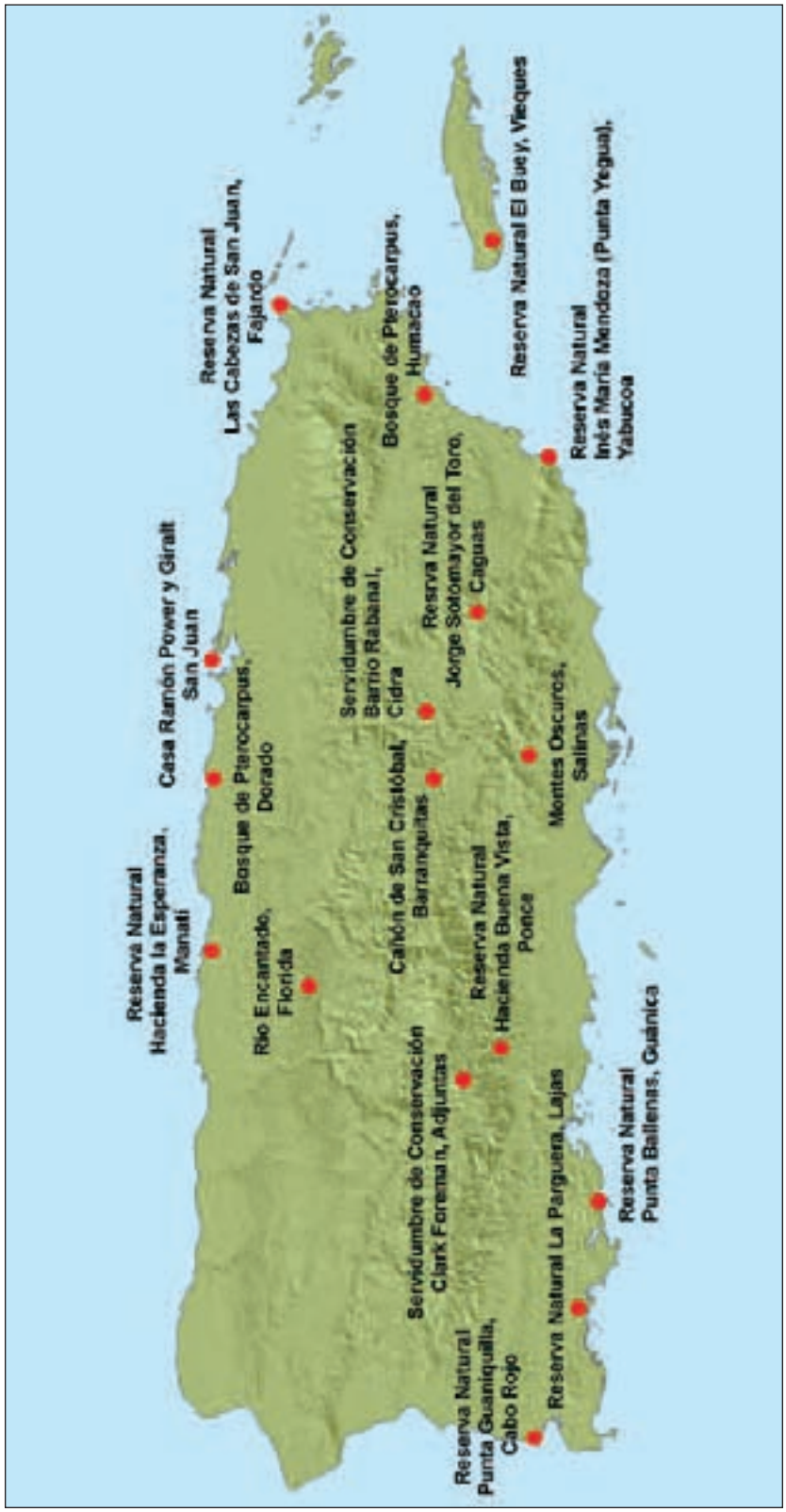


Figure 92—Puerto Rico Conservation Trust properties.

- **Hacienda La Esperanza** (Manatí) protects farmlands on alluvial flood plain bordering the Atlantic Ocean, with coves, karst, and cemented dunes. It also features an old sugar mill and manor house–922 hectares (2,278 acres).
- **Inés María Mendoza Reserve of Muñoz Marín** (Yabucoa) protects scenic tree-lined sandstone cliffs and habitat for the endangered grasshopper sparrow–117 hectares (290 acres).
- **Punta Ballena Reserve** (Guánica) is an extension of the Guánica Forest–68 hectares (167 acres).
- ***Pterocarpus* Forest Reserve** (Humacao and Dorado) protects freshwater marsh and bloodroot swamps–294 hectares (727 acres).
- **Montes Oscuros** (Salinas)—safeguards a large area of rainshadow mountain landscape in cooperation with the National Guard at Camp Santiago–2,834 hectares (7,000 acres).

The conservation trust's headquarters are in the beautifully restored Giralt House in Old San Juan, located at 155 Tetuán Street. There are various trust property exhibits on display, as well as the home that was built in the 1700s. Hours are Tuesday through Saturday, 10:00 a.m. to 4:00 p.m.; (787) 722-5834.

For further reading see Little et. al 1974.

Caribbean Islands National Wildlife Refuge

National wildlife refuges (NWR) in the United States, its territories, and the Commonwealth of Puerto Rico are administered by the U.S. Fish and Wildlife Service (FWS) of the Department of the Interior. There are over 500 refuges in the United States and the Caribbean. Some of the most recently established refuges are the seven refuges in Puerto Rico (4) and the U.S. Virgin Islands (3). These refuges constitute the Caribbean Islands National Wildlife Refuge System (CINWR). They provide visitors with an opportunity to observe a variety of wildlife species, and the plant communities that support them, in addition to archeological sites. Two of Puerto Rico's NWRs are located on the nearby islands of Desecheo and Culebra. The two mainland refuges are in the southwest corner of the island at Cabo Rojo (see app. 2) and Laguna Cartagena (fig. 93). They are located within 7.5 kilometers (4.5 miles) of each other off Puerto Rico Routes 301 and 305. These two refuges are described below. More detailed information describing the other five can be obtained by contacting the CINWR.

The original 237-hectare (587-acre) upland tract was acquired in 1974 and developed into the Cabo Rojo National Wildlife Refuge (CRNWR) in 1978. The

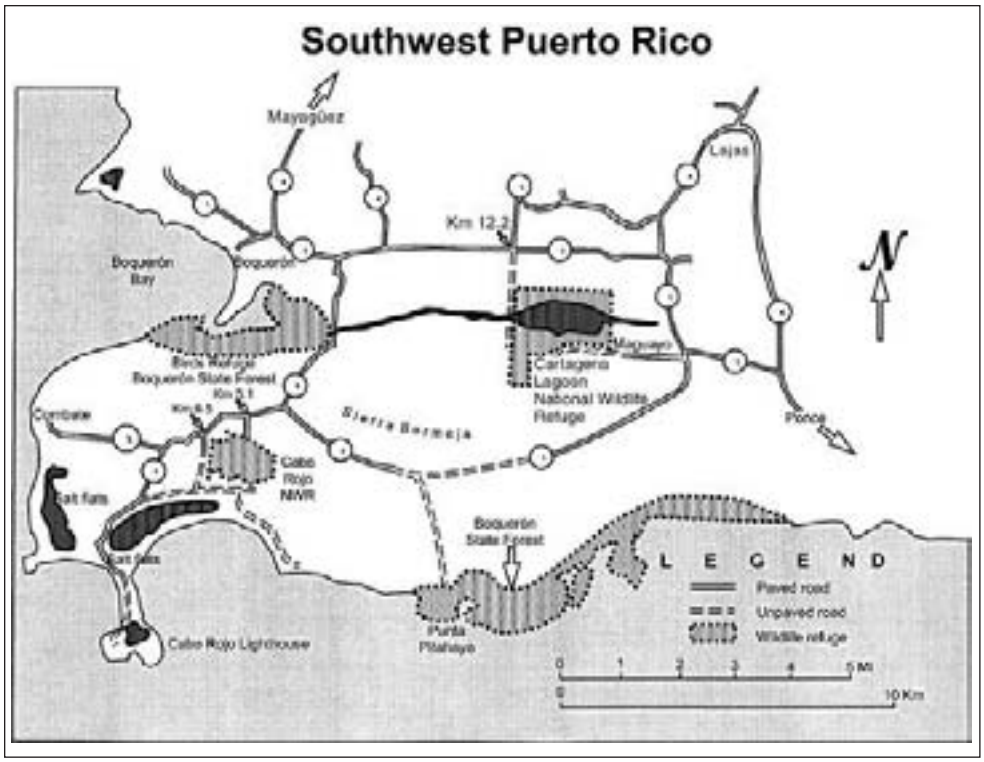


Figure 93—Location of national wildlife refuges in southwest Puerto Rico.

land had been used for nearly 200 years for cattle grazing and agriculture. The refuge lies within the subtropical dry forest life zone but has little of its original vegetation owing to long periods of overgrazing. Much of the vegetation cover today is composed of introduced alien species of grass, forbs, and woody plants. They do not provide optimal nesting habitat or food materials to the animals of the refuge. Restoration management programs are in place to promote regrowth of native herbaceous plant species. Native woody plants are being planted to return much of the refuge land to its original hardwood status typical of the dry forest originally present, including the endangered *Stahlia monosperma* (Tul.) Urban.

The primary wildlife serviced by this refuge are native and migratory Neotropical bird species. This is a habitat used by many species migrating between the North and South America mainlands. Species you can expect to see are:

Winter migrants

- Prairie warbler (*Dendroica discolor*)
- Northern parula warbler (*Parula americana*)

Native species

- Puerto Rican flycatcher (*Myiarchus antillarum*)
- Puerto Rican vireo (*Vireo latimeri*)
- Puerto Rican tody (*Todus mexi canus*)

- Cape May warbler *(Dendroica tigrina*)
- Rock dove (*Columba livia*)
- Adelaide's warbler (*Dendroica adelaidae*)
- Gray kingbird (*Tyrannus dominicensis*)
- Caribbean elaenia (*Elaenia martinica*)
- Yellow-shouldered blackbird (*Agelaius xanthomus*) (endangered species)
- Turkey vulture (*Cathartes aura*)
- Bananaquit (*Coereba flaveola*)

A complete list of refuge bird species is available from the CRNWR.

The only native land mammal species present are bats. Two alien mammals may be seen as you walk the 23 kilometers (14 miles) of trails: Indian mongoose and African patas monkeys. Nearby marine waters of the refuge may contain manatees and whales. Sea turtles may use the beaches for nesting.

The 526-hectare (1,300-acre) Cabo Rojo Salt Flats were purchased from private owners in 1998 through the Trust for Public Lands, The Natural Resources Conservation Service, and the Puerto Rico Conservation Foundation. These lands were incorporated into the refuge. It is a system of saline lagoons, salt flats, and mangrove swamps adjacent to the upland section and constitute the most important stopover site for migratory shorebirds known in the Caribbean region. Species likely to be seen in this estuarine complex are:

- Brown pelican (*Pelicanus occidentalis*)
- Magnificent frigatebird (*Fregata magnificens*)
- Great blue heron (*Ardea herodias*)
- Green-backed heron (*Butorides virescens*
- Cattle egret (*Bublulcus ibis*)
- Snowy egret (*Egretta thula*)
- Ruddy turnstone (*Arenaria interpres*)
- Lesser yellowlegs (*Tringa flavipes*)
- Greater yellowlegs (*Tringa melanoleuca*)
- Least sandpiper (*Calidris minutilla*)
- Semipalmated sandpiper (*Calidris pusilla*)
- Royal tern (*Sterna maxima*)

- Yellow-crowned night heron (*Nyctanassa violacea*)
- Simipalmated plover (*Charadrius semipalmatus*)
- Killdeer (*Charadrius vociferous*)
- Black-necked stilt (*Himantopus mexicanus*)
- Cave swallow (*Petrochelidon fulva*)
- Northern mockingbird (*Mimus polyglottos*)
- Yellow warbler (*Dendroica petechia*)

The Laguna Cartagena National Wildlife Refuge (LCNWR) is 419 hectares (1,036 acres) in the Lajas Valley and is a remnant of a former large lake and associated palustrine wetlands (see app. 2). It is still one of the most important freshwater habitats for migratory waterfowl and wading birds in Puerto Rico and the only significant freshwater marsh in southwestern Puerto Rico. Nearly half of the birds recorded in Puerto Rico have been found in the lagoon and adjacent nearby hills (164 species). Most of this extensive tract was heavily altered by sugarcane growers and cattle farmers. Much of the lagoon is overgrown with *Typha* spp. (cattails), *Eichhornia crassipes* (Mart.) Solms-Laub (water hyacinth), and *Pistia stratiotes* L. (water lettuce). Sediments, fertilizers, and pesticides have run into the lagoon for decades. Water birds have restricted use for feeding and nesting owing to the heavy emergent vegetation. The Puerto Rico Land Administration leased the land in 1989 to the U.S. Fish and Wildlife Service who rehabilitated some of the lagoon for resident and migratory waterfowl. Mitigation activities around the lagoon are converting former grazing and sugarcane lands to forested habitats for resident native species. Birds typical of this habitat are:

- Belted kingfisher (*Ceryle alcyon*)
- Great blue heron (*Ardea herodias*)
- Herons (several species)
- Smooth-billed ani (*Crotophaga ani*)
- Yellow-shouldered blackbird (*Agelaius xanthomus*) (endangered species)
- Bananaquit (*Coereba flaveola*)
- Puerto Rican flycatcher (*Myiarchus antillarum*)
- Caribbean elaenia (*Elaenia martinica*)
- Troupial (*Icterus icterus*)
- Pin-tailed whydah (*Vidua macroura*)
- Common snipe (*Gallinago gallinago*)
- Lesser yellowlegs (*Tringa flavipes*)

For further reading see U.S. Department of the Interior, Fish and Wildlife Service 1997.

Other Environmental Organizations

As was the case throughout much of the world, Puerto Rico had little in the way of publicly organized environmental interests through the mid 1960s. Much of the island had major air and water pollution problems. Solid wastes littered the countryside, and municipal wastes were frequently dumped over beautiful seaside cliffs, set on fire, and burned continuously, resulting in a regional odor that announced the dump's position miles away. Many beaches were littered with beverage containers. The famous Phosphorescent Bay's bottom was a depository for wastes thrown overboard from private boats that would anchor there. Beaches throughout the island were subject to exposure to municipal sewage outfalls via long shore drift because secondary sewerage treatment was basically nonexistent at the time. In light of these problems, on January 30, 1966, a group of 59 professors and intellectuals took out a full-page advertisement in the *San Juan Star* newspaper calling the attention of all Puerto Ricans to the plight of the island's environment.

This was a call to action for environmental cleanup and conservation of natural resources. It marked the beginning of organized environmentalism in Puerto Rico. With the beginning of the environmental movement in the United States and punctuated by the first Earth Day on April 22, 1970, interest in the environment emerged throughout Puerto Rico as well. Today, as in most developed countries, Puerto Rico's environmental issues are front-page news. In the last three decades, numerous commonwealth agencies have been developed to address and control most environmental problems. At the federal level, all of the national agencies have regional offices or personnel specially designated to deal with environmental problems specific to Puerto Rico and the Virgin Islands. For instance the U.S. Environmental Protection Agency (EPA) includes these islands in their New York-New Jersey Region 2.

Although the conservation movement in Puerto Rico started as a general concern of intellectuals over the levels of pollution in soil, air, and water, today, the movement is based on grassroots community action seeking protection from environmental problems that touch their daily lives—for example, water supply,

garbage disposal, or flooding of property. Puerto Rico's growth has been so disorganized and the population density is so high that any proposal for further development projects impacts some sector of society. Because there is a poor tradition of consultation and fair implementation of administrative procedures, new environmental groups develop continuously, each focused on a particular local issue that affects people, habitats, or species. As a result, Puerto Rico's environmental movement is highly fragmented, and the public media contains numerous daily reports of environmental issues that result in confrontation and conflicts among various sectors of society. For a review of critical issues facing environmental organizations and the citizens of Puerto Rico, see Lugo (1994). In August 2003, various environmental and health groups met for the first environmental health summit. Their purpose was to develop methods to support each other and to develop strategies and policies effective locally and globally. One of their main aims was to address the issue of local and global sustainability and to try to reduce the destruction of Puerto Rico's natural resources.

In the 1960s, there were only a handful of NGOs actively involved in pollution control, habitat degradation, recycling, status of native species, environmental education, and so forth. As we entered the new millennium, dozens of groups were dedicated to these issues. Some are watchdog groups that make sure the various governmental agencies are correctly following the law, others are interested in acquiring and conserving valuable habitats and species assemblages, and still others are dedicated to public education and increasing the general public's awareness of the plight of the environment. The following list highlights the key environmental organizations in Puerto Rico. The NGO list identifies groups that are active islandwide. There are numerous other NGOs at work on the local level throughout the island. A complete list of Puerto Rico's NGO's is available from the Puerto Rican Conservation Foundation (2000).

For further reading see López Feliciano 1999, Lugo 1994, Lugo Lugo 1981, and the Puerto Rican Conservation Foundation 2000.

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Metric and English Equivalents

When you know	Multiply by	To find
Millimeters	0.0394	Inches
Centimeters	.3934	Inches
Meters	3.28	Feet
Kilometers	6214	Miles
Square meters	10.76	Square feet
Square kilometers	0.386	Square miles
Hectares	2.47	Acres
Liters	.264	Gallons
Cubic meters	35.3	Cubic feet
Cubic meters	.000811	Acre-feet
Milligrams	.00003527	Ounces
Grams	.03527	Ounces
Kilograms	2.205	Ounces
Metric tons	2204.62	Pounds
Metric tons	1.102	Short tons
Kilocalories	3.968	British thermal units
Celsius degrees	1.8 C+32	Fahrenheit degrees

Inches	25.40	Millimeters
Inches	2.54	Centimeters
Feet	.3048	Meters
Miles	1.609	Kilometers
Nautical miles	1.852	Kilometers
Square feet	.0929	Square meters
Square miles	2.59	Square kilometers
Acres	.405	Hectares
Gallons	3.78	Liters
Cubic feet	.0283	Cubic meters
Acre-feet	1233.6	Cubic meters
Ounces	28.4	Grams
Pounds	.454	Kilograms
Short tons	.907	Metric tons
British thermal units	.252	Kilocalories
Fahrenheit degrees	(F-32)/⅛	Celsius degrees

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Appendix 1: Common and Scientific Names of Plant and Animal Species

Common name	Scientific name
Plants	
African cactus	*Euphorbia lacteal* Haw.
African milkweed tree	*Calotropis procera* (Aiton) W.T. Aiton
African tulip tree	*Spathodea campanulata* Beauv.
Aloe vera	*Sansevieria* spp.
Arana	*Schoepfia arenaria* Britt.
Arrowhead	*Sagittaria lancifolia* L.
Australian pine	*Casuarina equisetifolia* L.
Ausubo	*Manilkara bidentata* (A.DC.) Chev.
Autograph tree (postcard tree)	*Clusia rosea* Jacq.
Avocado	*Persea Americana* Mill.
Ball moss	*Tillandsia recurvata* (L.) L.
Balsa	*Ochroma pyramidale* (Cav.) Urban
Bamboo	*Bambusa vulgaris* (Schrad ex. Wendl.)
Banana	*Musa paradisiaca* L.
Bariaco	*Trichilia triacantha*
Barrio Charcas maiden fern	*Thelypteris verecunda* Proctor
Bayberry	*Myrica cerifera* L.
Baycedar	*Suriana maritima* L.
Beach dropseed	*Sporobolus virginicus* (L.) Kunth.
Beach morning glory	*Ipomoea pes-caprae* (L.) R. Br.
Beach rush	*Scleria microcarpa* Nees
Beach spine	*Anthacanthus spinosus* L.
Begonia	*Begonia* spp.
Bird's nest fern	*Asplenium serratum*
Bird-of-paradise	*Strelitzia reginae* Banks ex Dryand
Black mangrove	*Avicennia germinans* L.
Bladderwort	*Utricularia gibba* L.
	U. obtusa Sw.
Bonzai plant	*Strumpfia maritime* Jacq.
Bougainvillea	*Bougainvillea spectabilis* Willd.
Breadfruit	*Artocarpus altilis* (Parkinson) Fosberg
Broomstraw	*Andropogon gerardii* Vitman

Common name	Scientific name
Plants continued	
Brown strap alga	*Dictyopteris* spp.
Buttonwood mangrove	*Conocarpus erectus* L.
Cachimbo	*Palicourea riparia*
	Psychotria berteriana
Camasey	*Miconia prasina*
Camasey shrub	*Miconia impetiolaris*
Caña Gorda girdlepod	*Mitracarpus polycladus* Urban
Canonball tree	*Couroupita guianensis* Aubl.
Caparosa	*Callicarpa ampla* Schauer
Carrasco	*Comocladia glabra* (Schultes) Spreng.
Cassava	*Manihot esculenta* Crantz
Cat briar	*Smilax coriacea* Spreng.
Cattail	*Typha angustifolia* L.
Century plant	*Agave* spp.
Cerro de Punta Jayuya	*Elaphoglossum serpens* Maxon & Morton ex Maxon
Chase's threeawn	*Aristida chaseae* A.S. Hitchc.
Chicarrón	*Comocladia dodonaea* (L.) Urban
Chickenwood	*Dalbergia ecastaphyllum* (L.) Taubert
Chocolate tree	*Theobroma cacao* L.
Chupacallos	*Pleodendron macranthum* (Baill.) v. Tiegh.
Cinnamon fern	*Osmunda cinnamomea*
Citrus	*Citrus* spp.
Clubmoss	*Lycopodium* spp.
Cobana negra	*Stahlia monosperma* (Tul.) Urban
Coconut palm	*Cocos nucifera* L.
Coco plum	*Chrysobalanus icaco* L.
Coffee	*Coffea arabica* L.
	C. liberica
	C. robusta
Coffee colubrine	*Colubrina arborescens* (Mill.) Sarg.
Coffee leaf rust	*Hemileia vastatrix*
Common bamboo	*Bambusa vulgaris* Schrad. ex J.C. Wendl.
Common coleus	*Coleus blumei*
Common philodendron	*Philodendron oxycardium*

Common name	Scientific name
Plants continued	
Common roadside ferns	*Gleichenia bifida*
	G. pectinata
Coontail	*Ceratophyllum demersum*
Coralline shelf alga	*Lithothamnion* spp.
Coralline watercress alga	*Halimeda opuntia* (L.) Lamouroux
Cordillera maiden fern	*Thelypteris inabonensis* Proctor
Custard apple	*Annona reticulate* L.
Dead man's fingers	*Codium decorticatum*
Dinoflagellates	*Gymnodinium* spp.
	Amphidium spp.
Duckweed	*Lemna perpusilla* Torr.
Eared woodfern	*Thelypteris deltoidea*
Elfin tree fern	*Cyathea dryopteroides* Maxon
Erubia	*Solanum drymophilum* O.E. Schulz
False nettle	*Boehmeria cylindrical* (L.) Swartz
Fiddle-leaf morning glory	*Ipomoea stolonifera* (Cyrillo) Poir.
Figs	*Ficus* spp.
Fire algae	*Pyrodinium bahamense*
Flamboyán	*Delonix regia* (Bojer) Raf.
Florida poison tree	*Metopium toxiferum* (L.) Kang & Urban
Flower fern	*Nephrolepis multiflora*
Fragile-branched coralline alga	*Amphiroa fragilissima*
Frangipani	*Plumeria alba* L.
	P. rubra L.
Giant sedge	*Rhynchospora gigantean* Link
Ginger (wild)	*Alpinia purpurata* (Veill.) Schum.
Ginger (commercial)	*Zingiber officinale* Rosc.
Glassworts	*Salicornia bigelovii* Torrey.
	S. perennis Mill.
	S. virginica L.
Grape alga	*Caulerpa racemosa* (Fors.) J. Agardh
Grapefruit	*Citrus paradise* Maefayden
Grass	*Ichnanthus pallens*
Green bubble alga	*Dictyosphaeria cavernosa* (Forsskal) Boergesen

Common name	Scientific name
Plants continued	
Green feather alga	*Caulerpa sertularioides*
Green filmy fern	*Hymenophyllum rigidum*
Green tube alga	*Enteromorpha* spp.
Guava	*Inga vera*
Guayabota	*Eugenia borinquensis* Britt. Q
Gumbo limbo	*Bursera simaruba* (L.) Sarg.
Gum tree	*Manilkara zapota* (L.) V. Royen
Haircap moss	*Polytrichum* spp.
Hard fan alga	*Udotea flabellum* (Ellis & Solander) Lamouroux
Helecho arbóreo de bosque	*Cyathea dryopteroides*
Heller's cieneguillo	*Daphnopsis helleriana* (Urban)
Hibiscus	*Hibiscus rosa-sinensis* L.
Higo chumbo	*Harrisia portoricensis*
Higuero de sierra	*Crescentia portoricensis*
Higuillo de hoja menuda	*Piper aduncum* L.
Horsetails	*Equisetum* spp.
Insectivorous sundew	*Drosera intermedia* Hayne
Jamaican broom	*Chamaecrista glandulosa* var. *mirabilis* (Pollard) Irwin & Barneby
Jamaica walnut	*Juglans jamaicensis* C. DC.
Jerusalem thorn	*Parkinsonia aculeate* L.
Kapok	*Ceiba pentandra* (L.) Gaertn.
Ladies tresses orchid	*Spiranthes* spp.
Large philodendron	*Philodendron giganteum* Schott
Large pipe cactus	*Cephalocereus royenii* (L.) Byles & Rowley
Laurel magnolia	*Magnolia splendens* Urban
Lemon tree	*Citrus limon* (L.) Burmf. F.
Lettuce leaf alga	*Ulva lactuca* L.
Lignum vitae	*Guaiacum officinale* L.
Lime tree	*Citrus aurantifolia* (Christm.) Swingle
Lipstick tree	*Bixa orellana* L.
Liverworts	*Marchantia* spp.
Lobster claw	*Heliconia caribaea* Lam.
Luquillo Mountain babyboot orchid	*Lepanthes eltoroensis* Stimson

Common name	Scientific name
Plants continued	
Luquillo Mountain stopper	*Eugenia haematocarpa* Alain
Magnolia	*Magnolia splendens* Urban
Maidenhair fern	*Adiantum latifolium* Lam.
Manatee grass	*Syringodium filiforme* Kuetz.
Mango	*Mangifera indica* L.
Mangrove fern	*Acrostichum aureum* L.
Marijuana	*Cannabis sativa* L.
Matabuey	*Goetzea elegans* Wydler
Matchwood	*Didymopanax morototoni* (Aubl.) Dcne. & Planch
Mat fern	*Gleichenia bifida* (Willd.) Spreng.
Maxwell's girdlepod	*Mitracarpus maxwelliae* Britton & P. Wilson
Mermaid's fan alga	*Udotea conglutinata*
Mermaid's wineglass alga	*Acetabularia crenulata* Lam.
Mesquite	*Prosopis juliflora* (Sw.) DC.
Mid-rib seagrass	*Halophila baillonis* Aschers. Ex Dickie
Molasses grass	*Melinis minutifolia* Beauv.
Monte Guilarte hollyfern	*Polystichum calderonense* Proctor
Motillo	*Sloanea berteriana* Choisy ex DC.
Mountain fern	*Dennstaedtia bipinnata* (Cav.) Maxon
Nemoca	*Ocotea spathulata* Mez.
Nigua	*Cornutia obovata* Urban
[No common name]	*Myrica paganii* Krug & Urban
[No common name]	*Vernonia proctorii* L.E. Urbasch
[No common name]	*Tectaria estremerana* Proctor & Evans
Nutmeg	*Myristica fragrans* Houtt.
Orange tree	*Citrus sinensis* (L.) Osbeck
Paddle-blade alga	*Avrainvillea longicaulis* (Kuetzing) Murria & Boodle
Palma de manaca	*Calyptronoma rivales* (O.F. Cook) Bailey
Palo colorado	*Cyrilla racemiflora* L.
	Ternstroemia luquillensis Krug & Urban
Palo de jazmín	*Styrax portoricensis* Krug & Urban
Palo de nigua	*Cornutia obovata* Urban
Palo de ramón	*Banara vanderbiltii* Urban

Common name	Scientific name
Plants continued	
Palo de rosa	*Ottoschulzia rhodoxylon* (Urban) Urban
Papaya	*Carica papaya* L.
Parrotbeak orchid	*Octadesmia montana* (Swartz) Bentham
Peat moss	*Sphagnum*
Pelos del diablo	*Aristida portoricensis* Pilger
Pepper	*Piper aduncum* L.
Philodendron	*Monstera* spp.
Pineapple	*Ananas comosus* (L.) Merr.
Pincho palo de rosa	*Ottoschulzia rhodoxylon* (Urban) Urban
Pink blush alga	*Wrangelia argus*
Pink calcareous alga	*Goniolithon strictum* (Foslie) Setchell & Mason
Pipe organ cactus	*Lemaireocereus hystrix* (Haw.) Britton & Rose
Pitcairn's bromeliad	*Pitcairnia* spp.
Plantain	*Plantago major* L.
Poison carrasco	*Comocladia glabra* (J.A. Schultes) Spreng.
Poison chicarrón	*Comocladia dodonaea* (L.) Urban
Polysiphonia	*Polysiphonia* spp.
Pond apple	*Annona glabra* L.
Pondweed	*Potamogeton nodosus* Poir.
Proctor's staggerbush	*Lyonia truncate* Urban var. *proctorii* Judd
Prickly pear cactus	*Opuntia dillenii* (Ker-Gawl.) Haw.
Puerto Rican century plan	*Furcraea tuberose* (P. Mill.) Ait. f.
Puerto Rican lobelia	*Lobelia portoricensis* (Vatke) Urban
Puerto Rico applecactus	*Harrisia portoricensis* Britt.
Puerto Rico helmet orchid	*Cranichis ricartii* Ackerman
Puerto Rico maidenhair	*Adiantum vivesii* Proctor
Puerto Rico maiden fern	*Thelypteris yaucoensis* Proctor
Puerto Rico manac	*Calyptronoma rivales* (O.F.Cook) Bailey
Red banded alga	*Ceramium* spp.
Red branched alga	*Gracilaria* spp.
Red brittle alga	*Acanthophora spicifera* (Vahl) Boergesen
Red butterfly orchid	*Psychilis kraenzlinii* (Bello) Sauleda
Red coralline alga	*Lithothamnion* spp.
Red filament alga	*Spyridia filamentosa*
Red lace alga	*Dictyurus occidentalis*

Common name	Scientific name
Plants continued	
Red leaf bromeliad	*Vriesea sintenisii* (Baker) L.B. Sm. & Pittendr.
Red mangrove	*Rhizophora mangle* L.
Red tuft alga	*Chondria* spp.
Reed	*Phragmites australis* (Cav.) Trin. ex stend.
Roble de sierra	*Tabebuia rigida* Urban
Rose tuft alga	*Ceramium nitens*
Royal palm	*Roystonea regia*
Salwort	*Batis maritime* L.
Sandspur	*Cenchrus echinatus* L.
Santa María	*Calophyllum brasiliense*
Sargassum	*Sargassum natans*
Sawgrass	*Cladium jamaicense* Crantz
Screw pine	*Pandanus odoratissimus* Parkinson ex Zucc.
Sea bean	*Canavalia maritima* Thouars
Sea fern	*Bryopsis pennata* (Harvey) Collins & Hervey
Sea grapes	*Coccoloba uvifera* (L.) L.
Sea grass	*Spartina patens* (Ait.) Muhl.
Sea ox-eye	*Borrichia arborescens* (L.) DC.
Sea paspalum	*Paspalum vaginatum* (Sw.)
Sea pearls	*Valonia ventricosa* J. Agardh
Sea purselane	*Sesuvium portulacastrum* (L.) L.
Sea rocket	*Cakile lanceolata* (Willd.) O.E. Schultz
Sea vine	*Halophila decipiens* Ostenf.
Sebucan	*Leptocereus grantianus* Britt.
Sensitive plant	*Mimosa pudica* L.
Serpentine manjack	*Cordia bellonis* Urban
Shaving brush alga	*Penicillus capitatus* Lamarck
Shield fern	*Dryopteris* spp.
Shoal grass	*Halodule wrightii* Aschers.
Shortleaf fig	*Ficus citrifolia* P. Mill.
Sierra palm	*Prestoea montana* (Graham) Nichols.
Sintensis' holly	*Ilex sintenisii* (Urban) Britton
Six-leaved seagrass	*Halophila engelmannii* Aschers.
Small spiny tree fern	*Cyathea pubescens sensu* Maxon, non Mett. ex Kuhn

Common name	Scientific name
Plants continued	
Snake plant	*Sansevieria* spp.
Soft fan alga	*Avrainvillea nigricans* Decaisne
Soil fungus	*Aspergillus* spp.
Southern cattail	*Typha domingensis* Pers.
Spanish moss	*Tillandsia usneoides* (L.) L.
Spike moss	*Selaginella* spp.
Spiny tree fern	*Nephelea portoricensis* (Spreng. ex Kuhn) R. Tryon
Staghorn fern	*Platycerium bifurcatum* (Cav.) *C. Christens*.
Stalked lettuce alga	*Halimeda tuna*
Strap alga	*Dictyota divaricata*
Strap fern	*Polypodium crassifolium* L.
St. Thomas prickly ash	*Zanthoxylum thomasianum* (Krug & Urban) Krug & Urban ex P. Wilson
Sugarcane	*Saccharum officinarum* L.
Sundew	*Drosera capillaries* Poir.
Swamp bloodwood	*Pterocarpus officinalis* Jacq.
Swamp water fern	*Blechnum indicum* Burm. f.
Sweet acacia	*Acacia farnesiana* (L.) Willd.
Tabonuco	*Dacryodes excelsa* Vahl
Tank epiphyte	*Guzmania berteroniana* (Schult. & Schult. f.) Mez
Tan petticoat alga	*Padina sanctae-crucis* Boergesen
Te	*Ilex cookii* Britton & P. Wilson
Three finger leaf alga	*Halimeda incrassata* (Ellis) Lamouroux
Thomas' lidflower	*Calyptranthes thomasiana* O. Berg.
Tobacco	*Nicotiana tabacum* L.
Touch-me-nots	*Impatiens sultana* Hook. f.
Tree cactus	*Opuntia rubescens* Salm-Dyck ex DC.
Tree fern	*Cyathea arborea* (L.) Sm.
Tropical lilythorn	*Catesbaea melanocarpa* Krug & Urban
Trumpet tree	*Cecropia schreberiana* Miq.
Turf alga	*Cladophoropsis* spp.
Turk's cap cactus	*Melocactus intortus* (P. Mill.) Urban
Turtlefat	*Auerodendron pauciflorum* Alain

Common name	Scientific name
Plants continued	
Turtle grass	*Thalassia testudinum* Banks & Solana. ex Koenig
Ucar	*Bucida buceras* L.
Uvillo	*Eugenia haematocarpa* Alain
Vahl's box	*Buxus vali* Baill.
Vanderbilt's palo de ramón	*Banara vanderbiltii* Krug & Urban
Vanilla	*Vanilla planifolia* G. Jackson
Vaucheria	*Vaucheria* spp.
Water fern	*Azolla caroliniana* Willd.
Water hyacinth	*Eichhornia crassipes* (Mart.) Solms
Water hydrilla	*Hydrilla verticillata* (L.f.) Royle
Water lettuce	*Pistia stratiotes* L.
Water naiad	*Najas marina* L.
Wet Indian mahogany	*Swietenia mahagoni* (L.) Jacq.
West Indian walnut	*Juglans jamaicensis* C. DC.
Wheeler's peperomia	*Peperomia wheeleri* Britt.
White albizia	*Albizia procera* (Roxb.) Benth.
White cedar	*Tabebuia heterophylla* (DC.) Britt.
White mangrove	*Laguncularia racemosa* (L.) Gaertn. f.
White water lily	*Nymphaea odorata* Ait.
Widgeon grass	*Ruppia maritime* L.
Wild olive	*Buchenavia capitata* Vahl
Wiskfern	*Psilotum nudum* (L.) Beauv.
Woodbury's stopper	*Eugenia woodburyana* Alain
Y-branched alga	*Dictyota divaricata* Lamouroux
Yerba maricao de cueva	*Gesneria pauciflora* Urban
Yew leaf alga	*Caulerpa mexicana* Kuetzing
Animals	
Amphibians	
Bullfrog	*Rana catesbeiana*
Coqui	*Eleutherodactylus coqui*
Golden coqui	*Elecutherodactylus jasperi*
Marine toad	*Bufo marinus*

Amphibians continued	
Puerto Rican crested toad	*Peltophryne lemur*
Puerto Rican rock frog	*Eleutherodactylus cooki*
Anemones	
Eyeball anemone	*Zoanthus ocellaris*
Green colonial anemone	*Zoanthus sociatus*
Purple anemone	*Condylactis gigantea*
Ringed anemone	*Bartholomea annulata*
Sea anemone	*Bartholomea* spp.
Sun anemone	*Stoichactis helianthus*
Birds	
Adelaide's warbler	*Dendroica adelaidae*
American widgeon	*Mareca*
Bananaquit	*Coereba flaveola*
Beaded periwinkle	*Tectarius muricatus*
Belted kingfisher	*Ceryle alcyon*
Black-necked stilt	*Himantopus mexicanus*
Bluejay	*Cyanocitta cristata*
Blue-winged teal	*Anas discors*
Broad-winged hawk	*Buteo platypterus brunnescens*
Brown pelican	*Pelecanus occidentalis*
Cape May warbler	*Dendroica tigrina*
Cardinal	*Richmondena cardinalis*
Caribbean elaenia	*Elaenia martinica*
Cattle egret	*Bubulcus ibis*
Cave swallow	*Petrocchelidon fulva*
Common snipe	*Gallinaza gallinaza*
Elfin woods warbler	*Dendroica angelae*
Gray kingbird	*Tyrannus dominicensis*
Great blue heron	*Ardea herodias*
Greater yellowlegs	*Tringa melanoleuca*
Green-backed heron	*Butorides virescens*
Green mango hummingbird	*Anthracothorax viridus*
Killdeer	*Charadrius vociferous*
Least sandpiper	*Calidris minutilla*
Lesser yellowlegs	*Tringa flavipes*
Magnificent frigate bird	*Fregata magnificens*

Birds continued

Mallard	*Anas platyrhynchos*
Northern mockingbird	*Mimus polyglottos*
Northern parula warbler	*Parula Americana*
Partridge	*Arborophila* spp.
Pearly-eyed thrasher	*Margarops fuscatus*
Peregrine falcon	*Falco peregrinus tundris*
Pintail	*Anas acuta macroura*
Pin-tailed whydah	*Vidua macroura*
Piping plover	*Charadrius melodus*
Prairie warbler	*Dendroica discolor*
Puerto Rican bullfinch	*Loxigilla portoricensi*
Puerto Rican emerald hummingbird	*Chlorostilbon maugaeus*
Puerto Rican hummingbird	*Anthracothorax dominicus*
Puerto Rican flycatcher	*Myiarchus antillarum*
Puerto Rican nightjar or whip-poor-will	*Caprimulgus noctitherus*
Puerto Rican parrot	*Amazona vittata vitatta*
Puerto Rican plain pigeon	*Columba inornata wetmorei*
Puerto Rican tanager	*Nesospingus speculiferus*
Puerto Rican tody	*Todus mexicanus*
Puerto Rican vireo	*Vireo latimeri*
Puerto Rican woodpecker	*Melanerpes portoricensis*
Red-eyed vireo	*Vireo olicaceus*
Robin	*Turdus migratorius*
Rock dove	*Columba livia*
Roseate tern	*Sterna dougallii*
Royal tern	*Sterna maxima*
Ruby-throated hummingbird	*Archilchus colubris*
Ruddy turnstone	*Arenaria interpres*
Semipalmated plover	*Charadrius semipalmatus*
Semipalmated sandpiper	*Calidris pusilla*
Sharp-shinned hawk	*Accipiter striatus venatur*
Slate-colored junco	*Junco hyemalis*
Smooth-billed ani	*Crotophaga ani*
Snowy egret	*Egretta thula*

Birds continued	
Troupial	*Icterus icterus*
Turkey vulture	*Cathartes aura*
White-necked crow	*Corvus leucognaphalus*
Yellow-crowned night heron	*Nyctanassa violacea*
Yellow-shouldered blackbird	*Agelaius xanthomus*
Yellow warbler	*Dendroica petechia*
Corals	
Boulder star coral	*Montastrea annularis*
Brain coral	*Diploria* spp.
Branched fire coral	*Millepora alcicornis*
Cactus coral	*Isophyllia sinuosa*
Common brain coral	*Diploria strigosa*
Common rose coral	*Manicina areolata*
Depressed brain coral	*Diploria labyrinthiformis*
Elkhorn coral	*Acropora palmate*
Finger coral	*Porites* spp.
Flat-topped fire coral	*Millepora complanata*
Foliose coral	*Agaricia agarites*
Fused staghorn coral	*Acropora prolifera*
Horned coral	*Acropora* spp.
Ivory bush coral	*Oculina diffusa*
Knobby candalabra coral	*Eunicea* spp.
Lettuce-leaf coral	*Agaricia agaricites*
Rose coral	*Manicina areolata*
Shallow-water starlet coral	*Siderastrea radians*
Staghorn coral	*Acropora cervicornis*
Star coral	*Favia fragum*
Starlet coral	*Siderastrea siderea*
Stinging fire coral	*Millepora complanata*
Thick finger coral	*Porites porites*
Thin finger coral	*Porites furcata*
Yellow porous coral	*Porites astreoides*
Crustaceans	
Barber shrimp	*Stenopus hispidus*
Barnacle	*Balanus* spp.

Crustaceans continued

Crabs	*Aratus pisonii*
	Goniopsis cruentata
	Grapsus grapsus
Edible land crab	*Cardisoma guanhumi*
Green mantis shrimp	*Gonodactylus oerstedii*
Oyster	*Crassostrea* spp.
Purple-clawed land crab	*Coenobita clypeatus*
Small green crab	*Mithrax sculptus*
Snapping shrimp	*Crangon formosus*
Spiny lobster	*Panulirus argus*
Tiger lucine clam	*Codakia orbicularis*
Wood-boring isopod	*Sphaeroma terebrans*

Fish

Ballyhoo	*Hemiramphus brasiliensis*
Banded butterflyfish	*Chaetodon striatus*
Banded puffer	*Spaeroides spengleri*
Barracuda	*Sphyraena barracuda*
Blueheaded wrasse	*Thalassoma bifasciatum*
Blue striped grunt	*Haemulon sciurus*
Blue tang	*Acanthurus coeruleus*
Caribbean lobsterette	*Metanephrops binghami*
Caribbean snapper	*Lutjanus purpureus*
Catfish	*Ictalurus* spp.
Damsel fish	*Stegastes* spp.
Fairy basslet	*Gramma loreto*
Four-eyed butterfly fish	*Chaetodon capistratus*
French grunt	*Haemulon flavolineatum*
Gobies	*Gobiosoma* spp.
Gray angelfish	*Pomacanthus arcuatus*
Hamlets	*Hypoplectrus* spp.
Large-mouthed bass	*Micropterus salmoides*
Lizardfish	*Synodus saurus*
Parrot fish	*Ablennes hians*
Porcupine fish	*Sparisoma radians*
Pork fish	*Anisotremus virginicus*
Puffer fish	*Diodon holocanthus*
Queen angelfish	*Holocanthus ciliaris*

Fish continued	
Queen parrot fish	*Scarus vetula*
Queen trigger fish	*Balistes vetula*
Rainbow parrot fish	*Scarus guacamaia*
Red hind seabass	*Epinephelus guttatus*
Sergeant major	*Abudefduf saxatilis*
Spade fish	*Chaetodipterus faber*
Squirrel fish	*Holocentrus rufus*
Sunfish	*Lepomis* spp.
Surgeon fish	*Acanthurus chirurgus*
	Acanthurus bahianus
Tarpon	*Megalops atlanticus*
Trout	*Salmo* spp.
Trumpet fish	*Aulostomus maculautus*
Mammals	
Antillean manatee	*Trichechus manatus manatus*
Black rat	*Rattus rattus*
Bulldog fishing bat	*Noctilio leporinus*
Bumblebee bat of Thailand	*Craseonycteris thonglongyai*
Finback whale	*Balaenoptera physalus*
Giant tree shrew	*Solenodon paradoxus*
Humpedback whale	*Megaptera novaeangliae*
Indian mongoose	*Herpestes auropunctatus*
Jamaican fruit bat	*Artibeus jamaicensis*
Puerto Rican hutia	*Isolobodon portoricensis*
Red fruit bat	*Stenoderma rufum*
Rhesus monkey	*Macaca mulatto*
Sei whale	*Balaenoptera borealis*
Sperm whale	*Physeter macrocephalus*
Mollusks	
Amber pen shell	*Pinna carnea*
Atlantic modulus	*Modulus modulus*
Bleeding tooth nerite	*Nerita peloronta*
Checkered nerite	*Nerita tessellate*
Common prickly winkle	*Nodilittorina tuberculata*
Fighting conch	*Strombus pugilis*
Flamingo-tongue snail	*Cyphoma gibbsum*

Mollusks continued

Four-toothed nerite	*Nerita versicolor*
Fuzzy chiton	*Acanthopleura granulate*
Helmet conch	*Cassis tuberose*
Marbled chiton	*Chiton marmoratus*
Queen conch	*Strombus gigas*
Red snail	*Littorina angulifera*
Red octopus	*Octopus briareus*
Reef squid	*Sepioteuthis sepioidea*
Sea hare	*Aplysia dactylomela*
Spiny pen shell	*Atrina seminuda*
West Indian chiton	*Chiton tuberculatus*
West Indian sea egg	*Tripneustes ventricosus*
West Indian sea star	*Oreaster reticulates*
White urchin	*Tripneustes esculentu*s
Zebra periwinkle	*Littorina zigzag*

Reptiles

African python	*Python regius*
American alligator	*Alligator mississippiensis*
American spectacled caiman	*Caiman crocodiles*
Common garter snake	*Thamnophis sirtalis*
Common green iguana	*Iguana iguana*
Culebra giant anole	*Anolis roosevelti*
Eastern painted turtle	*Chrysemys picta*
Gecko	*Hemidactylus* spp.
Green chameleon	*Anolis cristatellus*
Green sea turtle	*Chelonia mydas*
Hawksbill sea turtle	*Eretmochelys imbricate*
Hicotea	*Trachemys stejnegeri*
Leatherback sea turtle	*Dermochelys coriacea*
Loggerhead sea turtle	*Caretta caretta*
Mono ground iguana	*Cyclura stejnegeri*
Mona Island boa	*Epicrates monensis monensis*
Monito gecko	*Sphaerodactylus micropithecus*
Puerto Rican boa	*Epicrates inornatus*
Puerto Rican lizard cuckoo	*Saurothera vieilloti*
Red-eared turtle	*Trachemys scripta*

Reptiles continued	
Spectacled caiman	*Caiman crocodiles*
St. Croix ground lizard	*Ameiva polops*
Virgin Islands tree boa	*Epicrates monensis granti*
West Indian rock iguana	*Cyclura* spp.
Worm snake	*Typhlops* spp.
Sea cucumbers, sea fans, sponges, stars, and worms	
American eel	*Anguilla rostrata*
Breadcrumb sponge	*Haliclona rubens*
Brittle star	*Ophiothrix angulata*
Brown sponge	*Chondrilla nucula*
Common sea fan	*Gorgonia ventalina*
Donkey dung sea cucumber	*Holothuria mexicana*
Feather duster worm	*Sabella melanostigma*
Fire sponge	*Tedania ignis*
Fire worm	*Hermodice carunculata*
Gray sponge	*Ircinia* spp.
Green moray eel	*Gymnothorax funebris*
Large hairy brittle star	*Ophiocoma echinata*
Magnificent feather duster worm	*Fregata magnificens*
Moon jelly	*Aurelia aurita*
Ostrich plume	*Pseudopterogorgia Americana*
Pencil urchin	*Eucidaris tribuloides*
Polychaete worm	*Sabella* spp.
Red sponge	*Haliclona rubens*
Sand dollar	*Mellita lata*
Sea fans	*Gorgonia* spp.
Sea rods	*Pseudoplexaura* spp.
Southern stingray	*Dasyatis Americana*
Small sea cucumber	*Microthele parvula*
Spiny brittle star	*Ophiocoma echinata*
Split pore sea whip	*Plexaurella grisea*
Spotted eagle ray	*Aetobatus narinari*
Upside-down jelly fish	*Cassiopeia frondosa*
Venus sea fan	*Gorgonia flabellum*

Urchins

Black-spined sea urchin	*Diadema antillarum*
Common urchin	*Ehinometra lucunter*
Green sea urchin	*Lytechinus variegates*
Heart urchin	*Clypeaster rosaceus*
Large heart urchin	*Meoma ventricosa*
Red rock urchin	*Echinometra lucunter*

Other animals

Honeybee	*Apis mellifera*
Seahorse	*Hippocampus reidi*
Termite	*Nasutitermes costales*
Tunicate	*Clavelina* spp.

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Appendix 2: Visiting Puerto Rico

For those visitors, instructors, and students who have not been on an extended field trip to a foreign tropical country, following is a list of suggestions you may find helpful.

Definitely take along:

- Flashlight (preferably one that can be used when wet)
- Comfortable shoes (at least two pairs)
  - Field shoes (ankle high preferable)
  - Street shoes (that can double for dress)
- Travelers' checks - any **extra** cash should be in the form of travelers checks. If lost or stolen, they are replaceable; "Don't leave home without them!"
- Sweatshirt, sweater, and/or wind breaker with hood (preferably water repellent)
- Summer-weight sleeping bag or light blanket/sheet. You may be responsible for your own bed clothing and towels in some housing accommodations
- Sunglasses with UV protection
- If you are preparing your own food, take your own eating utensils: knife, fork, spoon, cup, plate, and bowl. It saves having to buy them
- Suntan lotion
- Sun hat (wide brim)
- Small day pack for field trips
- At least two photo IDs are required for airlines. No passport or VISA required for U.S. citizens going to Puerto Rico. If anyone in the group is a foreign national, a passport will be required.

For those groups planning on marine field trips:

- Old sneakers for walking on dead coral, but without holes in the soles. These could double for field shoes above, but wet shoes can be uncomfortable.
- Face plate, snorkel (breathing tube), and flippers (solid heel). You want a good fit (mouth, head, and feet to avoid blisters and cramps). If your group is scuba certified, plan on taking everything you need for the dive. There are dive shops in many communities so you can get access to replacement supplies if equipment breaks. Rentals are available and full-day reef dives are commercially available in the La Parguera and Fajardo areas (see ecotourism section).

- Buoyancy compensator or life vest. You will need some form of buoyancy for trips onto coral reefs, mangrove swamps, and turtle grass beds. Rental boats will provide orange Coast Guard-approved vests.
- Old pair of pants and shirt for diving to protect you from the sun and coral abrasion.
- Gloves for diving, preferably with leather palm. These are vital! Many organisms are sharp and have stinging cells.
- If you plan to take pictures, buy your film in the United States. It will be a little cheaper. Cheap underwater cameras work well in water up to 12 feet deep
- Plastic bag for wet clothes

Things you may find useful:

- Small quantity of insect repellent (rarely needed)
- Small first aid kit (alcohol, band aids, aspirin, matches, needle, bactericide jelly, forceps, and thermometer)
- Binoculars–at least three pairs for the group, depending upon class size
- Extra pair of eyeglasses, if you require prescription glasses
- Knife (Do not carry it on your person or in a carry-on bag–it will be confiscated.)
- Small pocket Spanish-English dictionary
- Shower shoes (flip-flops)
- Know your blood type
- Be in as good physical condition as possible
- Dramamine for motion sickness (mountain roads and small boats)

To be kept in mind:

- Puerto Rico has universal access to potable water, one of the few islands in the tropical world that does. All water coming out of pipes can be assumed to be safe for drinking purposes. Never drink out of rivers, creeks, springs, or catchment basins. There are tropical diseases active there. Check with your local county health department for up-to-date health warnings for diseases like dengue fever. Be sure you are up to date regarding tetanus, diptheria, polio, and so forth, prior to departure.
- There are no poisonous snakes, although there are some scorpions, tarantulas, black widow spiders, and poisonous plants.

- Never swim in coastal brackish or lowland freshwater rivers under 457 meters (1,500 feet) altitude. These are the habitats of a freshwater snail that is the vector for schistosomiasis. It is not present in saltwater or above 457 meters (1,500 feet) altitude owing to cold intolerance.
- Most Puerto Ricans are very friendly toward Americans or other foreign nationals, and the majority of Puerto Ricans are bilingual. Most will be very helpful in providing directions or explaining local customs. There is an English language newspaper (*The San Juan Star*) and an English radio station in San Juan (1030 AM).
- Regarding food, we have **not** had any bad experiences in previous years as to sanitary preparation. Please keep in mind that you will have the opportunity to taste the food and drink of another culture. Hopefully, you will find their dishes more interesting and palatable than hamburgers or typical stateside offerings. Although, if you must, stateside fast food outlets are found everywhere.
- **Do not overpack.** For most field trip groups, there is limited vehicle space and storage in your housing.
- Remember that you are a member of a group; keep your gear organized and respect others' rights and equipment. You'll likely be living in close quarters. Many instances will arise when you will have to make a decision on the basis of majority rule with regard to the schedule, meals, and so forth. Please be open-minded.
- Many units of measure, that is, gasoline purchases, mileages on road signs, will be expressed in metric units. You may find a small wallet-sized conversion chart handy. On the other hand, food is usually sold by the ounce or pound. Air temperatures are usually expressed in Fahrenheit. There is a metric conversion chart included on pages 310–311.
- If you are cooking, do not carry food from the United States. Puerto Rico's food stores offer great variety today, a combination of local and U.S. brands. This is an opportunity to see the variety of locally grown/processed products from Puerto Rico compared to those of the United States. Try as many local products as you can.
- The U.S. Postal Service processes mail in Puerto Rico, and all mail to the continental United States will automatically be airmail and cost the same as when mailed in the United States.
- The legal drinking age in Puerto Rico is 18 years old. This can be a problem for some U.S. students who decide to experiment with alcohol for

the first time. In addition, rum is very cheap because there are no federal taxes applied to Puerto Rican rums consumed on the island.

- Puerto Rico runs on Atlantic Standard Time year round, which is 1 hour ahead of Eastern Standard Time (October-April), but is the same time as Eastern Daylight Savings Time (April-October).
- Sun protection is needed by most visitors to the tropics to block harmful ultraviolet rays. Sunglasses, wide brim hats, and clothing cover for the body work best. For those areas exposed, use a sunblock with at least an SPF of 15 (95 percent protection). An SPF of 30 only increases protection to 97 percent. SUNBURN IS DANGEROUS.
- Phone calls are just like in the United States. Puerto Rico's area codes are 787 and 939. Calls will be charged like any other out-of-state call. You do not have the complications or expense associated with international calls. All local calls are 10 or 11 digit numbers, that is, they all include the area code (most are 787) and, depending upon your location in the island, add 1.
- Puerto Rico uses U.S. currency, so there is no exchange problem. United States traveler's checks are accepted as cash. Be sure to have identification with you. If you are buying something and the price is quoted in pesos, just remember that a peso is equivalent to a U.S. dollar, thus *cinco pesos* is $5.

Purchases:

- Puerto Rico is not a tax-free port as you find in the nearby U.S. Virgin Islands.
- If you do not travel to another foreign country during your visit to Puerto Rico, you will not go through U.S. customs when coming to or departing from Puerto Rico. If you take a side trip to the Dominican Republic, the Virgin Islands, or other islands in the West Indies, you will have to undergo a customs check and declaration.
- If you are 21 or over, you are entitled to return to the United States with 1 gallon (5 fifths) of Puerto Rican rum free of stateside duty and tax, but you will pay commonwealth tax at the time of purchase. Most other purchases are not tax advantaged, other than sales tax.
- You will be subject to a personal luggage check when departing San Juan by the U.S. Department of Agriculture. They will be checking for fresh produce (mangoes, pineapples, oranges, and so forth) and tropical plants and animals that may vector diseases or be potentially damaging alien species if accidentally released into the United States. Any banned organisms will be

confiscated without compensation. You can receive a list of prohibited items when you arrive in the airport by visiting one of the USDA inspection booths located in the departures area of the airport.

U.S. Regulations Regarding Collection and Purchase of Organisms:

- Any collecting of organisms for scientific purposes will require advance permitting from the U.S. government and Puerto Rico's Department of Natural and Environmental Resources. Without permits, they will likely be confiscated, and you may face fines. Some products made from species protected by the Convention on International Trade in Endangered Species (CITES) agreements are still being sold illegally. More than 800 species are banned, and trade in 30,000 items is controlled by CITES and other agreements throughout the world. Their possession can produce big fines.
- Four publications will help you to know what is or is not legal in terms of U.S. Customs, Agriculture Department, and Fish and Wildlife regulations.
- **Department of the U.S. Treasury. 1983.** Know before you go. Washington, DC: U.S. Customs Service.

  For copies, write to: U.S. Customs
  P.O. Box 7407
  Washington, DC 20044
  (202) 566-8195
- **U.S. Department of Agriculture. 1994.** Traveler's tips. Program Aid No. 1083. Animal and Plant Health Inspection Service (APHIS). This brochure is also available at the San Juan airport, departure section.

  For copies, write to: USDA
  APHIS
  Washington, DC 20250
- **U.S. Department of the Interior. 2000.** Facts about federal wildlife laws. Washington, DC: U.S. Fish and Wildlife Service. Also available at the San Juan Airport, departures section.

  For copies, write to: U.S. Department of the Interior
  USFWS
  Office of Law Enforcement
  4401 N Fairfax Drive
  Room 520
  Arlington, VA 22203
  (703) 358-1949

- **World Wildlife Fund. 1997.** Buyer beware.

For copies, write to: World Wildlife Fund
1250 24th St., NW
Washington, DC 20037

Medical problems and prescription drugs:

- If you have any physical limitations, make sure the project leader knows about them prior to your departure. You do not want to get into a crisis situation in the ocean or on top of a mountain.
- If you take prescribed medicine, be sure to have a current prescription with you and the medicine in the original container. Any form of drug consumption that is not legal will jeopardize the entire group and could land you in jail! Penalties can be severe and costs associated with court cases **will** be expensive.

Auto rentals:

- Any person renting an automobile must be at least 25 years old. All major auto rental firms are available at San Juan International Airport or in the major cities on the island.
- Before you leave home, be sure to check with your credit card corporations, personal automobile insurance coverage, and/or your institutional insurance coverage regarding international rentals and any coverage that is extended to you by the above. Insurance coverage will greatly increase rental costs because it is sold on a day-to-day basis. Be sure to have adequate insurance coverage, as it is not uncommon for the party with the "deepest pocket" to be held liable.

The indigenous ceremonial parks near Ponce and Utuado

An interesting field trip for any student or ecotourist group is to visit one of the indigenous ceremonial parks. The easiest park to access is the Tibes Indian ceremonial site, which is 15 minutes north of Ponce on Road 503 at kilometer 2.5. There is a nominal entry fee of $2.00 for adults and $1.00 for children. This park features the pre-Taíno Igneri culture. It has a series of displays, an artifact museum, and outside ***bateyes***, plazas, a burial area, **petroglyphs**, and other stone exhibits.

A second indigenous ceremonial park is located near Utuado. It is accessed by taking Route 10 to Utuado and then Route 111 west to kilometer 12.3. The site is just past the Route 621 intersection. The Caguana Indian Ceremonial Park also has a museum and was used as a major ceremonial area with bateyes and plazas. It was

built in the 1200s. Admission fee is a contribution. Both parks are botanical gardens and have educational staff on site. Descriptive literature is available for self-interpretation, and educational tours can be arranged by appointment.

Phone: Tibes - (787) 840-2255. Open daily except Monday 9:00 a.m. to 4:00 p.m. Caguana - (787) 894-7325. Open daily except Monday 9:00 a.m. to 5:00 p.m.

El Morro and nearby colonial period buildings

El Morro is now a national historic site and part of the U.S. Department of the Interior's National Park Service. Open throughout the year and designated as a world heritage site, it was recently used in the filming of *Amistad*, a movie about an African slave revolt in 1839 on a Spanish merchant ship. *El Morro* means "headland," and it was so named because of its position overlooking the Atlantic Ocean and all of San Juan Bay. There is a nominal entrance fee that includes viewing of a historical video, museum, and self-guided walking tour. Ranger tours are available periodically throughout the day (11:00 a.m. and 3:00 p.m. in English). *El Morro* is located at the tip of Old San Juan. A visit to *El Morro* is worthwhile and up to half a day should be devoted to its full exploration. For those who enjoy period military history, two other forts are located nearby—*San Cristobal* and *San Gerónimo*. If you have time, both are worth visiting. Wear comfortable shoes because you will have a long walk to access *El Morro*, since parking is restricted in the area. It is open daily 9:00 a.m. to 5:00 p.m. The entrance fee is $3.00 for adults (16 to 61) $2.00 for seniors (62 and above), and free for children up to the age of 15 years. Phone: (787) 729-6960. If time permits, visit *La Fortaleza* (Governor's mansion - circa 1630), Casa Blanca (Ponce de Leon's home - 1523), and *Iglesia San José* (among the oldest churches in the New World - 1522). All are within easy walking distance of *El Morro*.

Serpentine outcrops near Maricao

Serpentine outcrops can be easily observed along Route 120 in the Maricao Commonwealth Forest. Route 120 can be accessed off Route 2 at Sabana Grande. There are large road cuts in the areas near Monte del Estado. From the observation deck west of the Monte del Estado Vacation Center is a magnificent view of the entire southern coast from Boquerón Bay to Guánica Commonwealth Forest; including all of the Lajas Valley (take your camera, binoculars, and road map).

The karst landscape with a visit to the Caves at Camuy

One of the best places in the Western Hemisphere to see the various elements of karst topography are the Caves at Camuy. While driving there you pass through

miles of haystack hills. Once there you will be able to tour the largest **solution cave** open to the public in the Caribbean. It has stalactites, stalagmites, an underground river (the Río Camuy), and a large population of bats. In addition, you can also ride a tram and walk via a boardwalk down into two very large sinkholes. This is also an excellent opportunity to see the unique vegetation typical of these areas. This is a commercial operation with a set number of tickets sold each day ($10.00 for adults; $6.00 for children). The admission also includes the tram rides and sinkhole access. To visit the caves, take Route 22 to Arecibo. The park entrance is off Route 129. Driving time is about 2 hours from San Juan.

Buried deep in the karst region of the north coast is one of the great technological marvels of astronomy, the Arecibo Ionospheric Observatory. It is located near the caves. Take Route 635 to 625, and you will find the observatory at the end of 625. See the karst forest section for further description of the observatory. The observatory has an excellent visitor center and public education program.

The Ponce Cement plant

An interesting field trip incorporating mining, manufacturing, fossil collecting, and pollution control can be scheduled with a visit to the large Ponce Cement Company plant in Ponce. This is one of the largest commercial cement operations in the Caribbean and will permit interested educational groups to see surface mining operations, manufacture of both wet and dry cement, and modern pollution control systems mandated by both the U.S. Environmental Protection Agency and Puerto Rico Environmental Quality Board. In addition, a site visit to areas currently being mined for limestone will make it possible to collect large quantities of fossil clams, heart urchins, scallop shells, as well as crinoid stems. The operational mines are ongoing in areas adjacent to the plant just west of Ponce on Route 10. Contact: Puerto Rican Cement at (787) 842-3000.

The University of Puerto Rico's Botanical Garden

An excellent way to gain an introduction to the tropical flora, especially woody species, is to visit the Botanical Garden at the University of Puerto Rico/ Experimental Station campus in Río Piedras. The garden has hundreds of species on display. There are two sections to the garden. The upper section has an outside orchid display. It suffered heavy damage during Hurricane Georges and is being replanted. Many of the plants have identification tags. It is located off the intersection of Route 1, Route 3, and Route 847. The garden is open daily from 9:00 a.m. to 4:30 p.m., and there is no entrance fee. Tell the guard posted at the entrance that you want to visit the gardens. Parking is available adjacent to the *Jardin Botánico*.

Plan at least 2 hours for your self-guided tour. Guided tours for student or organized groups are available by appointment every day except Saturdays, Sundays, and holidays. Special group tours on weekends are available upon request. For tours call (787) 250-0000 or 767-1710. Associated with the Botanical Garden is a herbarium with 36,000 specimens in its collection. The garden is also used extensively for cultural and social programs. Special displays in the garden include palms, aquatics, heliconias, and orchids. A detailed garden map is available from the guard as you enter the grounds. The university has another botanical garden on its Mayagüez campus and it is open from 8:00 a.m. to 4:00 p.m. It is also free of charge. It is located off Post Street. Phone: (787) 831-3435.

Animal observations

For those interested in viewing wildlife, D.W. Nellis' (1999), *Puerto Rico and Virgin Islands Wildlife Viewing Guide* provides maps and descriptions of some of the best wildlife areas to visit with photographs of species likely to be encountered. Cost $9.00.

Should you be interested in viewing tropical animals, Puerto Rico has a recently expanded animal park in Mayagüez. The Puerto Rico Zoo is a 36.5-hectare (90-acre) animal park displaying mostly tropical animals of the Caribbean, South America, and Africa, with emphasis on mammals, birds, and reptiles. Entrance fee is charged according to age. Open Wednesday through Sunday, 9:00 a.m. to 4:00 p.m., at Route 108, Mayagüez, Puerto Rico 00681. Phone: (787) 834-8110.

If you are interested in seeing butterfly art, one of the most interesting displays is to be found in Old San Juan at "The Butterfly People Gallery." It has displays of magnificently colored butterflies in plexiglass boxes for mounting on walls or to display on bookshelves. They range from individual animals in 13- by 13-centimeter (5- by 5-inch) boxes, to flight displays in boxes 3 by 2 meters (10 by 6.5 feet). All displays are for sale. As none are rare species and, according to the company, are artifically reared, they are legal. The gallery is located in an old home known as the birthplace of Muñoz Marín, Puerto Rico's first elected governor, and is at 152 Fortaleza Street, about two blocks from the Governor's residence. Phone: (787) 723-2432.

How to capture a tree frog

Tree frogs are relatively easy to capture by hand. This makes for an interesting evening field trip. Be sure to investigate any nocturnal field site during the day so you do not inadvertently walk yourself or your class off the side of a mountain.

Success in locating frogs is likely from any paved road with dense roadside vegetation or along any forest trail. You are fortunate in that you do not have to worry about poisonous snakes or other dangerous animals while in the rain forest after dusk. Look for frogs in leaf axils of tank epiphytes, under loose tree bark, under folded leaves, and in limb holes. Sometimes, they may just sit on a leaf or branch in full view, or they will be on the ground or a rock. All species are active at night. The only real field trip needs are good flashlights or head lamps. Head lamps have the added advantage of freeing up both hands for the location and capture process. It is best to work in pairs. The study of tree frogs includes important ecological topics such as habitat and resource partitioning, differential expression of vocalization in sexes within a species and among complex species groups, island biogeography, and rapid direct development as an adaptive strategy to cope with a terrestrial life cycle.

Where to bird watch

A free travel map of places to bird watch can be obtained from The Puerto Rico Convention Bureau. It clearly indicates all of the U.S. and commonwealth forests, refuges, and preserves easily accessible for bird watching. See the map reference section in appendix 4 for obtaining copies. See also the three sections on refuges that follow. Phone: 1-800-875-4765.

Neotropical migrants in the Guánica Forest

The Guánica Forest can be accessed via Route 116, just east of the town of Guánica. Take Route 334 to the forest headquarters. An interesting field exercise is to do bird surveys in forested areas in order to determine native residents and Neotropical migrants. The only equipment needed are binoculars and bird guides.

Bats in Camuy Caves

If you want to see a protected cave roost, take a trip to the Caves at Camuy. The caves are located off Route 129 19 kilometers south toward Lares. They sell limited tickets each day and they are open Tuesday through Sunday from 8:00 a.m. to 5:00 p.m. Three levels of tour are available and the ticket prices vary accordingly. Phone: (787) 763-0568. More details are included in the section on moist karst forests.

The Bacardí rum distillery

While in San Juan, you can take a free tour of the Bacardi rum distillery in Cataño. You can drive to it directly or take the Cataño ferry from the ferry depot in Old San

Juan and then take a taxi to the plant. The company store sells many Bacardi products, all emblazoned with the black bat logo. The plant is located on Route 165 at km 2.6. Free tours are available 8:30 a.m. to 4:30 p.m. daily. Phone: (787) 788-8400.

Guánica Forest

To access this unique preserve, take Route 2 west of Ponce to Route 116 west. Route 334 goes to the heart of the forest and the education center. (Phone: (787) 724-3724.) It is open Tuesday through Sunday, 9:00 a.m. to 5:00 p.m. with no entrance fees for individuals or small groups. There are 12 hiking trails and small exhibits at the center. Be sure to have sun protection and your own water supply. This is a warm habitat. A second road (Route 333) runs along the coast where you can observe scenic beaches, seagrass beds, limestone hills, rocky headlands, and fringing red mangrove communities. A trail guide and description of the forest and its species is available from Sr. Miguel Canals, P.O. Box 985, Guánica, Puerto Rico 00653.

To see a variety of coastal species and dry habitats, visit the Las Cabezas Nature Reserve. For the rain forest species and habitats, visit the nearby Caribbean National Forest.

For those individuals or groups who have a limited amount of time for field trips but yet want to see a good cross section of the habitats, species, and ecosystems typical of Puerto Rico and the Caribbean just described, the following visits are recommended. Two reserves, the Caribbean National Forest and the Las Cabezas de San Juan Nature Reserve make the best combination of visits. They are close to San Juan (44 kilometers [27 miles]) and they are only 18 kilometers (12 miles) apart. Both are just off Puerto Rico Route 3 in the northeast corner of the island. We recommend 1 day for each site, which will permit you to take advantage of the education programs, exhibits, hiking trails, and opportunities to discuss the various species and systems being observed. Both areas have good maps and technical literature available for those wanting a detailed description of the habitats to be studied. Both have active public education programs and visitor centers. More information of Las Cabezas is presented in the commonwealth reserves section.

Visiting the karst region of Puerto Rico

Classic karst landscape can be observed in a number of ways. A car trip from Arecibo to Utuado on Route 10 or Route 129 to Lares will take you through karst. The major coastal road, Route 22 from San Juan will take you through a degraded section of haystack hills. Many are disappearing in this area as a result of urbaniza-

tion, road construction, and mining for aggregate. Some of the best karst can be observed in the area around the Arecibo Observatory at the end of Route 625. This trip has the added benefit of offering the opportunity to view the radio telescope.

For more detailed exposure and the opportunity to walk in the karst belt, there are four options. There are three Puerto Rican commonwealth forests at Guajataca, Río Abajo, and Cambalache with miles of maintained paths through the formations. Guajataca Commonwealth Forest is west of Arecibo and Río Abajo is south of Arecibo. Cambalache is east of Arecibo just north of Route 22. For many, the best option is the Río Camuy Cave State Park, south of Arecibo. This 109-hectare (268-acre) ecosystem provides easy access to a large solution cave, extensive sinkholes, and one of the largest underground rivers in the Western Hemisphere. The caves are a reported 45 million years old. One of the sinkholes is accessible via a 205-step staircase to the bottom. It provides an excellent view of sinkhole vegetation. Educational interpretation is a part of the tour. Entrance fees are $10.00 for adults; children, seniors, and groups receive reduced rates. The park is open Tuesday through Sunday at 8:00 a.m. The last tour departs at 3:45 p.m. (707) 763-0568.

Please note, cave exploration in Puerto Rico is dangerous. Many are unexplored and remote, and rescue would be difficult in the event of an accident. Individuals or groups planning cave exploration need to be experienced, with all the necessary safety gear and a full plan on file with someone who can verify the safety of the group. Remember many caves have black hole drops, and a rain event miles away may drastically change the conditions in an underground river in minutes without any warning to the **spelunkers**.

How to access the Arecibo Ionospheric Observatory

The National Astronomy and Ionosphere Center and Arecibo Observatory—the largest radio/radar telescope on earth with an 8.1-hectare (20-acre) radar dish—is located in the heart of the karst region. Driving time is 30 minutes south from Arecibo. Take Routes 22 → 129 → 134 → 635 → 625. The observatory is at the end of Route 625. Visiting hours are 12:00 to 4:00 p.m., Wednesday to Friday; Saturday and Sunday, 9:00 a.m. to 4:00 p.m. Phone: (787) 878-2612. The facility is built in a giant sinkhole, 305 meters (333 yards) in diameter and 172 meters (188 yards) deep and surrounded by haystack hills. The public visitation center has many astronomy and climate educational exhibits and interactive facilities, plus a video that describes its development and operation. Admission fee is $4.00 for adults and $2.00 for students and seniors. It is funded by the National Science Foundation and operated by Cornell University. Its main emphasis is using radar astronomy to determine information about planets, asteroids, comets, and the

moon. The use of radio astronomy allows for the study of energy emitted by galaxies, stars, clouds of gas, pulsars, and quasars. There is great interest in searching for evidence of extra-terrestrial intelligence by detection of their radio signals. The observatory was featured in the film "Contact."

Visiting the rain forest—first start at the gateway (*El Portal*)

Most visitors to the tropics want to see a rain forest. In Puerto Rico your best option is to visit the Caribbean National Forest, the only tropical rain forest in the USDA National Forest System. This 11 200-hectare (28,000-acre) forest has more species of trees than all the other forests in the National Forest System put together. It can be reached from San Juan by taking Route 3 east to Palmer, then Route 191 through the forest. Initially stop at the U.S. Forest Service Education Center, *El Portal* (the Gateway), where you can view many exhibits on tropical plants, animals, products, etc. There is also a movie that introduces you to the forest. It has a bookstore and a concession stand. Entry fees are $3.00 for adults, $1.50 for children and seniors. From there, you can spend the rest of the day driving and hiking the trails in the various sections of the forest. Phone: (787) 888-1810.

If you have an extra day or two, you can drive the Panoramic Route through the heart of the mountains from the east coast to the west coast. This 275-kilometer (165-mile) journey, over a collection of 40 roads, will permit you to see a variety of montane forests and agroforestry systems. This is not a road for those who experience motion sickness.

Visit to *Hacienda Buena Vista*

Hacienda Buena Vista is an old coffee plantation representative of the 19th century. It is a period plantation museum, with excellent examples of 1800s-era processing technology and uses the diverted waters of the Cañas River to supply power for the *Hacienda*. Coffee from the *Hacienda* was exported to the United States and Europe. It also processed corn meal and grew as cash crops a variety of fruits and vegetables, many of which are on display as you walk the trails at the *Hacienda*. *Hacienda Buena Vista* is located 17 kilometers (10 miles) northwest of Ponce on Route 10. The facility is a property of the Conservation Trust of Puerto Rico, which specializes in managing properties of special ecological, historical, or aesthetic value. Entry fees differ for groups and by age. General entrance is $5.00, for adults, and phone reservations are recommended because they limit entry and are open on selected days. To make reservations, call (787) 722-5882. For advanced information or reservations, contact the Conservation Trust at P.O. Box 902355, San Juan, PR 00902-2355.

Visit a large regional produce market

If you have time, you should try to visit a large regional fresh produce market to see the wide variety of tropical fruits and vegetables for sale. If you are in Río Piedras, a large fresh produce/meat/fish/medicinals market is located in the center of town, one block from the bus terminal. There is an underground parking garage and most of the shop managers will be able to provide you local names, common uses, and how to prepare their products. While there, you can taste raw cold coconut milk, *maví* (fermented bark drink of the *maví* tree), and a variety of other local products. Unfortunately, many local markets are disappearing as a result of the rapid expansion of the large food chains now found throughout the island.

Visiting the Tortuguero Lagoon National Reserve, an exceptional wetland complex

Tortuguero Lagoon is one of the best habitats to visit to see a freshwater marsh on the north coast. It is located off Route 2 on Route 687 north. This area is designated the Laguna Tortuguero National Reserve and will be sign-posted on the left. Tortugero Lagoon is 1.6 kilometers (1 mile) from the open coast. The lake depth is up to 3 meters (10 feet) and is fed by underground water from the limestone hills. It is slightly salty owing to salt spray and its connection to the sea. The bottom of the lake is sandy as a result of the decay of limestone and coastal sand accumulation. This is a good habitat to observe *Potamogeton* (pondweed), *Najas* (water naiad), *Utricularia obtusa* Sw. (insectivorus bladderwort), *Nymphaea odorata* Ait. (white water lily), *Typha domingensis* Pers. (cattail), *Cladium jamaicense* Crantz (sawgrass), *Rhynchospora gigantea* Link (giant sedge), *Hibiscus* spp. (hibiscus), *Annona glabra* L. (pond apple), *Blechnum serrulatum* L. (toothed fern), and a wide variety of other wetland species. The area has a series of wetland community types to observe:

- Submergent vegetation
- Open-water marsh—floating leaves
- Emergent marsh
- Marl prairie
- Seasonal swamp thicket
- Evergreen hedge/thicket
- Seasonal swamp woodland
- Wet savanna
- Seasonal semievergreen forest

The area has a clay hardpan under the surficial sands. Coupled with slight increases in soil depth this results in different drainages and plant zonations. There are also marl deposits present with a pH of 8.0, which is very diverse in sedges. Take a shovel and dig a soil pit to expose the clay hardpan. The hardpan impedes water and root penetration, thus species composition of the communities present differ with the changing soil conditions.

Wild populations of the primitive gymnosperm, *Zamia* (cycads), are present. *Drosera intermedia* Hayne (insectivorous sundews) are present in the marl prairie habitat, as is *Sphagnum* (peat moss). There are also ground and arboreal orchids.

This area has *Comocladia* (poison plant) and *Anacardium occidentale* L. (cashew), which is poisonous if the nut is not cooked to denature the toxins in the oils. Both of these are members of the Anacardiaceae (cashew) family.

The lagoon has a variety of fish, turtles, and now an introduced population of *Caiman crocodilus* (American spectacled caiman).

Visit *Las Cabezas* for a good introduction to coastal zone habitats and species

A good place to see the interface of the outer coastal zones and the sea is at *Las Cabezas de San Juan* Nature Reserve in Fajardo. In this one area, the visitor can see coral reefs, seagrass beds, sandy beach, rocky beach, mangrove forest, and dry forest. This is an excellent opportunity to examine a series of interactive systems and learn about the species and the factors that control their distribution. Nearby are examples of areas that were once like the reserve's natural habitats and have now been developed.

Mangrove Field Trips

Mangrove forests are accessible in most sections of the island because many of the forests are part of the growing conservation/**preservation** efforts by both governmental and nongovernmental organizations. The public is now interested in learning about and visiting these unique plants and the complex ecosystem they support. Mangrove areas with easy access are highlighted in table 22. Most have education facilities on site.

Phosphorescent Bay

Puerto Rico has one of the most famous "phosphorescent" bays in the world spurring the growth of a major ecotourist business on the southwest coast in the village of La Parguera. **Bioluminescence** is the emission of light from an organism. Most people identify this process with the common firefly. This phenomenon was first recorded by Robert Boyle in fungi, but a wide range of other organisms such as bacteria, insects, annelids, marine invertebrates, and fish have this ability.

Bioluminescence results from a chemical reaction of luciferin and luciferase, whereby chemical energy is converted to radiant energy at a level close to 100 percent efficiency. This means that little heat is produced and the luminescence is referred to as cold light. There is a technical difference between the processes of bioluminescence and phosphorescence. If organisms emit light stored for some time as electric energy from a previous exposure to light, they are referred to as phosphorescent. So the bay at La Parguera is really a bioluminescent bay.

Why the bay at La Parguera and what organism causes this phenomenon? The small bay in Puerto Rico is approximately 24 hectares (60 acres) and surrounded by mangroves on 90 percent of its shoreline. The mangrove community is dominated by *Rhizophora mangle* (red mangrove). The water of the embayment is protected on the seaward side by two small hills and with a geologic sill at the mouth of the bay. This promotes calm water with a low exchange rate. The benthic zone is composed of the seagrasses *Thalassia testudinum* Konig (turtle grass), *Halophila baillonis* Ascherson (mid-rib seagrass), and up to 50 macrobenthic algae species (Almodovar and Bloomquist 1959). The water of the bay is nutrient rich, which may account for the presence of large populations of the bioluminescent dinoflagellate (fire algae) *Pyrodinium bahamense*. According to Burkholder et al. (1967), there are 17 species of dinoflagellates in the bay, with *Pyrodinium bahamense* the most common. When *P. bahamense* is mechanically stimulated (fish swimming, waves crashing, or motor boat props, and so forth) it bioluminesces. A bucket of sea water from the bay will contain thousands of them. When a person disturbs the water, the water in the bucket "lights" up. At night, motor boat props produce a glow bright enough to read newsprint by and the bay is often called "a sea of fire." The bioluminescent light effect is viewable throughout the year.

What value does bioluminescence have to the species? For some it promotes location of sex partners, for others it promotes capture of food organisms, and for others it promotes escape from predators or disguise. In the case of dinoflagellates, like *Pyrodinium*, there is currently no known value.

In the last 20 years there seems to have been a reduction in the visual intensity of the bioluminescence at La Parguera. This is due to a variety of factors such as the large number of boats visiting the bay in prime time; light from the street lights of the community behind the mangrove fringe; reduction of the mangrove fringe; sky shine from the general growth of La Parguera's expanding houses, businesses, lighted parking lots, and the nearby yacht club; and regional sky shine from the general growth along the southwest coast. The Phosphorescent Bay is truly the

"goose that lays the golden egg" and hopefully will be protected for future generations. It is the economic base of one of the region's major attractions. People from all over the world come to Puerto Rico and La Parguera just to visit *La Bahía Fosforescente*. The red and black mangrove fringe around this bay is of great concern to the Puerto Rican Department of Natural and Environmental Resources because it is being degraded by heavy commercial and recreation boat traffic, houseboats, and general tourist recreation in the bay. However, the department has the power and responsibility of protecting this resource. The fringing forest is now one of the properties being managed by the Conservation Trust of Puerto Rico (fig. 89).

Trips to *La Bahía Fosforescente* are available year round. Each evening, party boats of various sizes make 40-minute trips to the bay. They leave on the hour generally from 8:00 p.m. to midnight. Cost is $5.00 per person. Take a windbreaker as it may be cool. If you have the option, try to time your visit when the moon is less full. Moonlight can reduce the visual effect significantly.

For more information on Phosphorescent Bay see Hastings 1968 and Seliger et al. 1971.

Accessing seagrass beds

One of the best places in Puerto Rico to study seagrass beds is the vicinity of La Parguera. La Parguera in the 1960s was a small fishing village. Today, it is a thriving tourist town largely because of its proximity to the world famous Phosphorescent Bay and the easily accessible coral reefs for snorkeling, scuba diving, and other water sports. There are dozens of islands in the waters of La Parguera, and a large cluster of fringing mangrove swamps line the shoreline. In association with the islands and swamps are large, well-developed seagrass beds. Many beds are to the rear of nearby coral reefs where they occupy the calm waters of the protected lagoons, whereas others occur in the channels and lagoon areas associated with the mangrove swamps on the sublittoral edge.

Access to these seagrass beds is relatively easy. Many sandy beaches will have seagrasses in the shallow water just beyond the wave zone. A good indicator is to examine any beach debris for the presence of seagrass leaves. Many seagrass beds are accessible simply by finding a break in the red mangrove thicket and entering the open water in front. Usually, a turtle grass bed will be present. A more interesting method to access a wide variety of seagrass sites is to rent a boat from one of the boat operators at La Parguera. You do not need to find them; they will have street solicitors wanting to rent you boats as you drive to the seafront. Having a

boat allows you to survey a variety of sites for species composition and variation in growth and development of communities and populations under varying growth conditions such as water depth, clarity, substrate composition, wave/tide action, proximity to predator populations such as black-spined sea urchins, and a variety of human actions such as the shearing effect from motor boat props. All of these features lend themselves to interesting personal observations, and they are worthy of a marine ecology field trip studying a variety of taxonomic characteristics exhibited by each species and observations related to the presence of associated algae. Be sure to look for indications of sexual reproduction and excavate the various vegetative parts of the plants', especially those involved in asexual reproduction.

Accessing the coral reefs of Puerto Rico

Among the most popular areas for sailing and boating are the areas around Puerto Rico's many coral reefs. The areas in and around places like La Parguera and Fajardo, with their generally pleasant weather and beautiful waters make sailing, motor boating, and diving in the area a relaxing experience. However, the coral reefs below the surface of the water must be taken into consideration. Grounding your boat on a coral reef will not only damage the boat but also destroy coral structures that have been thousands of years in the making and are very slow to recover. The following tips will allow people to enjoy their recreation and protect the reef.

"Brown, brown, run aground." Coral reefs grow upward. When they are relatively close to the surface, coral formations will make the water appear brown. Such areas should be avoided. If they are not, a boater will likely run aground or slam the motor prop into coral.

"Green, green, nice and clean." The areas behind and to the sides of a reef are often covered by green seagrasses. The only hazard to a boat is the rather shallow water in some of these areas. Careless motoring through shallow turtle grass beds can tear up the plants, however, and should be avoided because it is very destructive of the habitat and can lead to further erosion.

"Blue, blue, sail on through." Areas where there is deep water, such as on the seaward side of a reef, appear blue. When sailing in blue water, however, remember that coral reefs rise rather abruptly from deep water. Give yourself plenty of room to maneuver. It is best to have a spotter positioned in the bow of the boat to warn the pilot.

Before sailing into any area close to reefs, boaters should thoroughly familiar-

ize themselves with the nautical charts for the area. They should pay particular attention to depth indications. Navigational and Loran charts published by the National Ocean Survey of the National Oceanic and Atmospheric Administration are among the most reliable (see map section in app. 4).

If anchoring in a reef area, **do not anchor on the reef itself**, as anchors can easily destroy coral. Anchor only in sandy areas. The bottom in sandy areas appears white from the boat. Unfortunately, mooring buoys are not common in the waters of Puerto Rico. They would greatly reduce recreation impact on reefs. A few have recently been installed in reefs in the La Parguera area.

The coral reefs of Puerto Rico

There are a variety of ecotourist companies or commercial boat operators in the Fajardo area that specialize in 1 or more days of sailing, scuba diving, and snorkeling on the coral reefs in the waters between Puerto Rico, Culebra, and Vieques. Prices generally start at $60 per person per day. The reefs can also be reached from island beaches. Public ferries are available from Fajardo to both Culebra and Vieques each day. Tickets cost $2.25 to Culebra and $2 to Vieques. For information and reservation, call the Fajardo Ports Authority–(787) 863-0705. *Públicos* (public taxis) will take you to the beach of your choice once you are on the island.

A much more economical way to conduct a field trip with several students is to go to La Parguera on the southwest coast and rent individual boats. Boat rental costs are negotiable, but you should assume that it will cost around $50 per boat, per half day. Each boat can carry five to six people, and the required life jackets are supplied. Each person will have to supply his or her own snorkeling or dive gear. It is best to plan reef activities from 9:00 a.m. to 1:00 p.m. for two reasons. If you go out too early, light conditions will be poor. The other reason relates to winds and waves. By noontime, waves will be larger owing to wind and as a result, water clarity will drop considerably. In addition, most student groups will be tired within 4 hours and be ready to have lunch.

The coral reef and seagrass bed easiest and cheapest to access is at the mangrove island locally called *Isla Gato* (Cat Island). It can be accessed by water taxi from the seafront at one of the boat rentals. They will drop you off and pick you up at a designated time. This island has a Department of Natural and Environmental Resources dock, with a large protected swimming area. There are picnic tables, toilets, and shade. Coral reefs are to the front and sides of the island, and seagrass beds to the rear on the protected side. The island has a red mangrove canopy and provides good views of prop root zonation.

Boat rentals are available from:

Cofresí Boat Rentals—(787) 899-4346

Pepe Boat Company—(787) 899-5025

Torres Boat Service—(787) 899-4281

Free parking is available behind the shops that line the water front. These boat rentals will also be willing to take your group to the Phosphorescent Bay in smaller boats by reservation. They will negotiate a group discount of $1 off the large boat price and generally give you more time in the bay.

Adjacent to the village of La Parguera is Magueyes Island, which is the field station of the Department of Marine Sciences at the University of Puerto Rico at Mayagüez. This is a teaching and research facility that allows their graduate students to live and work at their research sites. Visits to their facilities can be arranged by contacting the department at Mayagüez—(787) 832-4040.

Cabo Rojo National Wildlife Refuge field office

The Cabo Rojo National Wildlife Refuge has a small visitor center with displays and a variety of brochures available to the public. Adjacent to the center is a 3-kilometer (2-mile) interpretive trail and cactus garden. The visitor center is located off Puerto Rico Route 301 at kilometer 5.1. Visiting hours are from 7:30 a.m. to 4:00 p.m. Monday through Friday. Staff biologists and an environmental educator provide a variety of audiovisual lecture programs on topics such as endangered species, sea turtles, and sea mammals. Programs require advance reservations (2 weeks or more), which can be made by contacting:

Environmental Education Office

Boquerón Field Office

P.O. Box 491

Boquerón, PR 00622

Tel: (787) 851-7297 Ext. 29

Fax: (787) 851-7440

The Laguna Cartagena refuge

The refuge has two entrances. Both require a walk to the lagoon. Take Puerto Rico Route 305 at Maguayo or route 306 south of Route 101 near *Hacienda Desengaño*. The refuge is open 8:00 a.m. to 4:00 p.m. Hiking trails are self-guided. There are no educational facilities or staff onsite.

Appendix 3: Ecotourism

Nature, Adventure, and Diving Tours

Tourism is one of Puerto Rico's largest industries (2 million hotel guests in 2002). Globally, tourism has been growing at nearly 4 percent per year. The fastest growing sector of tourism at around a 10-percent growth per year is ecotourism. The ecotourism industry in Puerto Rico has grown rapidly in the last decade since its advent in the early 1990s. Today, there are dozens of companies that offer a variety of activities and destinations to virtually all important environmental areas on the island. Tourism represents a potential threat to natural areas, especially to sensitive sites such as coral reefs and cloud forests. Ecotourism, if properly designed and managed, should permit humans to visit delicate sites and yet avoid or minimize human impact. Ecotourism should always promote conservation, create economic opportunities for local citizens and communities, and be sustainable. A major component of all ecotourism should be educating the visiting public regarding the basic ecology of species and ecosystems visited, and how they are being affected or protected by oversight agencies and the surrounding community. Before making a reservation with any ecotourism company, it is recommended that the following questions be asked. How much of the trip will emphasize education? What are they doing to minimize environmental impact? Do they have a published list of ecotourism principles that they adhere to, such as:

- Provide sustainable benefits for the local community.
- Educate their client travelers.
- Encourage governmental and nongovernmental organization protection of the sites visited.
- Promote local conservation efforts with financial support.
- Adhere to principles of low-impact travel and environmental ethics.
- Work with other ecotourism companies to prevent overexploitation of sensitive species and habitats.
- Help design and build trails, lodges, and other infrastructures compatible with the ecosystem being visited.
- Are they members of the Ecotourism Society, and are they listed in their International Directory [(802) 447-2121]?

For those wanting to see "natural" Puerto Rico without going out on their own, ecotourism companies offer a variety of options that include set programs as short as half-day trips to helping you create your own itinerary from 1 to 7 days. The price typically includes transportation and a guide. Reservations are required.

Entrance fees, overnight housing, air tanks, and so forth may not be included. The following is a list of companies offering services. Please note, these are not endorsed by the authors as we have no experience in using any of their services. Prices differ by length of trip and number in the group. Some of these companies are not full-time operations so you may have to call at different times to have your questions answered. Inquire about contracts, liability, payments, cancellations, and inclusions. Prior to making reservations, "know before you go" regarding all fees, what is supplied, and what happens in the event of a cancellation. Inquire about the size of the tour. Avoid large groups, as much of your time will be spent dealing with large group logistics, and you will have less time to study the habitats and organisms that you are interested in observing.

Company name	**Phone**	**Trip options**
Adven Tours	(787) 530-8311	Mona Island and *El Yunque* trips, bird watching, hiking, camping
Aventuras Tierra Adentro	(787) 766-0470	Various mountain hiking/camping trips, cave exploring, rappelling in sinkholes, and underground river exploration
Alelí Tours	(787) 899-6086	Mangroves, coral reefs, and Guánica dry forest
Attabeira Educative Travel	(787) 767-4023	Education trips to various destinations
Caribbean Reef Divers	(787) 254-4006	Scuba/snorkel reef trips
Copladet Nature & Adventure	(787) 766-0470	Education, nature, and recreation travel trips throughout Puerto Rico
Coral Head Divers	(800) 635-4529	Scuba/snorkel reef trips
Eco Action Tours and Watersports	(787) 723-3113	Various water sports and hiking trips
Eco Xcursión Aquática	(787) 888-2887	Water-based environmental tours
Encantos Ecotours	(787) 272-0005	Various ecotours to multiple destinations, biking, and kayaking in Piñones Forest
Expediciones Montaña Adentro	(787) 898-2723	Mountain treks
Fajardo Tours (catamarans)	(787) 863-2821	Sailing/snorkeling trips

Company name	Phone	Trip options
Hill Billy Tours	(787) 760-5618	"If it's here, they will take you" Nature tours throughout the island
Normandie Tours	(787) 722-6308	Rain forest and Camuy Caves
Paradise Island Ecotours	(787) 832-7933	Trips to commonwealth reserves in western Puerto Rico
Parguera Divers Training Center	(787) 899-4015	Scuba diving training and dive trips
Piñones Ecotours	(787) 253-0005	Biking and hiking trips in Piñones Forest
Sea Ventures (PADI Dive Center)	(787) 863-0199 (800) 739-3483	Diving/snorkeling trips
Sunshine Tours	(787) 810-4545	Rain forest, Camuy Caves, Arecibo Observatory, Phosphorescent Bay

For further reading, see Fennell 1999, Hess 1992, Honey 1999, McLaren 1998, and Whelan 1991.

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Appendix 4: Tools

Educational Wall Charts and Brochures of Ecosystems and Endangered Species

There have been numerous colorful wall charts and brochures developed by several public agencies and nongovernment organizations that depict a variety of ecosystems, processes, and species typical of the Caribbean and Puerto Rico. These documents are excellent visual aids for illustrating the complex nature of some of these ecosystems and the species found there. Others are a pictorial overview of one or more endangered species. Some are diagrammatic in format, whereas others feature actual closeup wildlife photography. All are very useful for educating various public interest groups concerned with the environment. There is not one complete listing for these various products; in fact, the agencies do not have complete listings for their products. The following list brings together some of the best products of each agency and how to access them. Unfortunately, some of the agencies' printing budgets do not allow multiple printings and as the supply runs out, they will not be reprinted unless there is very high demand or new monies are allocated.

Sea Grant Program
Communication Section
University of Puerto Rico
P.O. Box 9011
Mayagüez, PR 00681-9011
(787) 832-3585

Posters:

Mangrove Ecosystem (36 by 25 inches)
Beautifully illustrated with 53 species of plants and animals identified by scientific name in both the aerial and underwater sections of a typical red mangrove ecosystem (in Spanish) - $4.

Coral Reef Ecosystem (36 by 25 inches)
Beautifully illustrated with 105 species of plants and animals typical of a Puerto Rico reef identified by scientific name (in Spanish) - $4.

Seagrass Ecosystem (36 by 25 inches)
Beautifully illustrates the species of plants and animals typical of a Puerto Rico seagrass bed identified by scientific name (in Spanish) - $4.

Give Us a Chance to Live (West Indian manatee) (34 x 24 inches)
Photographic portrayal of survival problems of the endangered manatee. Shows feeding, with young, motorboat strikes, and coastal development issues (in Spanish or English) - $4.

Pelagic Fish Species (22 by 34 inches)
Illustrations of seven species of open water fish found in the waters of Puerto Rico identified by scientific and common names (in Spanish or English) - $3.

Marine Turtles (27 by 34 inches)
Four marine turtles found in the waters of Puerto Rico identified by scientific and common names (in Spanish or English) - $3.

Brochures:

Marine Turtles
This 8-panel bifold (8½ by 14 inches) uses a question/answer format to educate the reader about sea turtles: their natural history, range, feeding habits, why they are endangered, what is being done to protect them, and what individuals can do to help (in Spanish) - Free.

The Manatee
This 8-panel bifold (8½ by 14 inches) uses a question/answer format to educate the reader about the West Indian manatee: their natural history, geographic range (with a map of Puerto Rico), why they are endangered, what is being done to protect them, and what individuals can do to help (in Spanish) - Free.

Coast and Beach Stability in the Lesser Antilles
This brochure explains and illustrates coastal beach erosion on tropical islands and the work being done by the coastal stabilization project sponsored by the United Nations Educational, Science, and Cultural Organization (UNESCO) (in English) - Free.

Fishes of Puerto Rico
This 40-page brochure is a guide to the common fish of the Caribbean. They are pictured and identified by scientific and common names. Various facts are supplied regarding size, weight, and food value (bilingual) - $3.

Commonwealth of Puerto Rico
Department of Natural Resources and Environment
Department 5887
Office of Education and Publications
Muñoz Rivera Avenue, Stop 3
San Juan, PR 00906
(787) 725-8619

Poster titles:

Nature Reserves (17½ by 24 inches)

A photographic collage of 23 nature reserves found throughout Puerto Rico and a short description of the habitats found in each (in Spanish) - Free.

The Marine Turtles of Puerto Rico (8 by 11 inches)

This poster uses closeup photographs to illustrate the protected sea turtles of Puerto Rico and provides information on life histories, beaches used for reproduction, and problems in their survival (in Spanish) - Free.

Brochures:

Marine Mammals of Puerto Rico (8½ by 11)

This brochure documents the whales, dolphins, and porpoises that can be found in the waters in the vicinity of Puerto Rico, issues related to their observation and avoidance, and recommendations for their protection. It provides information on their protection by the 1972 Marine Mammals Protection Act and the 1985 Puerto Rico Department of Natural and Environmental Resources regulations (17 pages in Spanish) - Free.

Please note that many of the posters and brochures described in the Puerto Rico Sea Grant Program and the U.S. Fish and Wildlife Service section were cosponsored by the Department of Natural and Environmental Resources. They may be able to supply copies if the other two agencies cannot.

U.S. Fish and Wildlife Service
Caribbean Field Office
Box 491
Boquerón, PR 00622
(787) 851-7297
(787) 833-5760

Posters:

The Real Puerto Rican Toad (12 by 18 inches)

Describes the background and habitat of the endangered Puerto Rican crested toad and what can be done to protect the species (in Spanish) - Free.

Tiny World Travelers (11 by 17 inches)

Describes the travels of the scarlet tanager, a Neotropical migrant in its summer and winter habitats. Front panel consists of illustrations and back panel provides life history information and teaching activities (in English) - Free.

Give Us a Chance to Live (18 by 24 inches)

Collage of photographs related to various endangered species (plant and animal) and their habitats - Free.

Reward (saving protected sea turtles) (11 by 14 inches)

Describes the issue of illegally killing sea turtles and the financial reward for identification of those who do. (bilingual) - Free.

Endangered Species: The Road to Recovery (26 by 39 inches)

Illustrated collage of various U.S. endangered species (in English) - Free.

Endangered Means There's Still Time (18 by 24 inches)

Collage of photographs of endangered species and habitats (in English).

Brochures:

Various brochures describing the Caribbean Islands National Wildlife Refuge system are available. These describe location, size, habitats, history, and wildlife species typical of each.

This agency also provides a variety of publications describing the problem of endangered species in general and the status of individual species, as well as recovery plans for the individual species.

Species in Danger of Extinction in Puerto Rico and the Virgin Islands.

This 9½- by 12-inches packet of information consists of individual one-page descriptions of many of the endangered species in the U.S. Virgin Islands and Puerto Rico (in Spanish) - Free.

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Publications Office
7600 Sand Point Way NE
Seattle, WA 98115
(206) 526-6107

Poster:

Sea Turtles of the World (36 by 24½ inches)
Illustrated presentation of the world's sea turtles, their scientific and common names, short life history descriptions, and a shell key (in English) - $5.

This agency has many wall charts and brochures describing a variety of habitats, regional species groups, and fisheries research.

U.S. Environmental Protection Agency
Endangered Species Coordinator
Region 2
2890 Woodbridge Avenue
Building 209
Edison, NJ 08837

Poster:

Save Our Species (22 by 25 inches)
Illustrations and descriptions of a variety of U.S. endangered species on the front and a review of the Endangered Species Act and threats to species on the back (in English) - Free.

The Environmental Protection Agency has a variety of other posters and brochures too numerous to cite here. Request their lists for review.

National Wetlands Inventory
U.S. Fish and Wildlife Service
9720 Executive Center Drive
Suite 101, Monroe Building
St. Petersburg, FL 33702
(800) USA-MAPS (872-6277)

Poster:

Wetland Resources of the United States (40 by 66 inches)
Illustrates all the primary wetland areas of the United States and Puerto Rico (in English) - Free.

Numerous other wetlands maps, posters, and brochures are available from:

EPA Wetlands Information Hotline - (800) 832-7828
FAX - (703) 525-0201
e-mail - wetlands-hotline@epamail.epa.gov

Texas Partners in Flight
4200 Smith School Road
Austin, TX 78744
(512) 389-4970

Poster:

Migratory Landbirds of the Southeast: Valuable and Vulnerable (22 by 30 inches) in color, illustrates 25 migratory landbirds, with their names and primary habitats on the front. The back panel describes each species, provides scientific names, and explains why each is vulnerable (in English) - Free.

Ciudadanos del Karso
Urb. Las Cumbres
497 Ave. E Pol, Box 230
San Juan, PR 00926
(787) 760-2100

Posters:

El Karso Norteño

A drawing shows a partial view of the landforms (over and below ground) of the north karst region of Puerto Rico and the human activities negatively affecting it with written information on the same poster. Fifteen topics are discussed to summarize the importance of the karst region and the problems it is facing (in Spanish) – Free.

Los Murciélagos

Photos of all the bat species currently found in Puerto Rico, with a brief description of each. It has a summary in the center explaining the ecological importance of bats (in Spanish) - Free.

Boa

This poster shows the endemic boa species of Puerto Rico, *Epicrates inornatus*, an endangered species, and explains that they are not dangerous to people and are beneficial to agriculture (in Spanish) - Free.

National Geographic Society
1145 17th St., NW
Washington, DC 20036

Poster:

Coral World

A spectacular two-sided poster, with one side a world map depicting the location of all major coral reefs and the other side showing a virtual reefscape. The reefscape uses illustrations and closeup photography to depict coral morphology development, geography, reef types, communities, natural threats, human use and abuse, and reef conservation (in English) – Free.

Video Tapes

A multitude of video tapes are available for loan, rent, or purchase describing many of the tropical ecosystems and the plant and animal species described in this document. The following list contains just a few titles successfully incorporated into a college-level course in tropical ecosystems by the senior author. Should you decide to use films to supplement classroom activities, we suggest the films be previewed for suitability of the intended audience. Most film vendors have a free 2-week preview policy; you just have to request it.

Title/length	Topic	Source
"The Parrots of Luquillo" (28 minutes)	Life history of the endangered Puerto Rican parrot.	Free loan. USDA Forest Service Caribbean National Forest Río Piedras, PR 00928
"The Rain Forest" (60 minutes)	Wonders of tropical rain forests in Central America.	National Geographic Society 1145 17th St., NW Washington, DC 20036
"Tropical Rain Forest" (40 minutes)	General review of rain forests with emphasis on animals and methods of investigation.	Finley-Holiday Film Corporation P.O. Box 619 Whittier, CA 90608 (800) 345-6707

Title/length	Topic	Source
Selva Verde (58 minutes)	Reviews the animals of the tropical rain forests in Costa Rica and Panama with emphasis on survival adaptations and predator-prey relationships.	Nature Series Center for Public Service TV University of North Carolina Chapel Hill, NC (919) 962-8191
"Hope for the Tropics" (58 minutes)	Focuses on efforts to save the tropical rain forests.	National Audubon Society PBS Videos 666 Pennsylvania Ave. Washington, DC (202) 547-9009
"Rain Forests—Proving Their Worth" (28 minutes)	Contrasts the economic values of standing rain forests versus areas cut for timber and pasture.	The Video Project 5332 College Ave., Suite 101 Oakland, CA 94618 (415) 655-6050
"Secret World of Bats" (58 minutes)	Reviews the critical roles that bats play in ecosystems and problems produced by humans in the alteration of ecosystems and bat roosts.	Bat Conservation International P.O. Box 162603 Austin, TX 78716
"Edge of the Sea" (30 minutes)	Very good on animal adaptations and feeding, and as an introduction to mangroves and sea turtles—organisms that live at the edge of the sea.	Time-Life Videos David Attenborough Living Planet Series
"Creatures of the Mangroves" (60 minutes)	Excellent review of mangrove ecosystems and plant and animal adaptations.	National Geographic Society 1145 17th St., NW Washington, DC 20036

Title/length	Topic	Source
"Margins of the " Land (55 minutes)	Good review of the ecology of mangrove swamps.	Time-Life Films Living Planet Series Available from: North Carolina Film Library Audio Visual Branch 1811 Capital Blvd. Raleigh, NC 27635 (919) 733-4376
"Treasures of the Great Barrier Reef" (60 minutes)	Underwater review of the Great Barrier Reef's ecology. A variety of animal species are reviewed and coral reproduction is highlighted.	NOVA WQBH Video P.O. Box 2284 South Burlington, VT 05407 (800) 255-9424
"Cities of Coral" (60 minutes)	Good review of corals and the complexities of coral reefs.	Educational Video Network 1401 19th St. Huntsville, TX 77340 (409) 295-5767
"Perils of Plectropomus" (56 minutes)	Excellent review of the life and death struggles of fish on a coral reef, with special reference to fishing pressures produced by humans.	Bullfrog Films P.O. Box 149 Oley, PA 19547 (800) 543-3764
"Jewels of the Caribbean" (60 minutes)	Review of coral reef species of the Caribbean region.	Teacher's Video Co. P.O. Box 4455 Scottsdale, AZ 85261 (800) 262-8837
"Ecology of the Coral Reef" (23 minutes)	Reviews general ecology and the decline of coral reefs and their inhabitants.	Man and the Biosphere Series–Films for the Humanities and Sciences Box 2053 Princeton, NJ 08543 (800) 257-5126

Sources of Maps and Visitor Guides to Puerto Rico

Individuals or groups planning to spend time in various parts of Puerto Rico will need maps that will help them locate destinations of interest. The following lists sources of free maps and detailed destination guides, as well as sources of maps that must be purchased. Multiple copy requests should be ordered at least 6 weeks in advance. There may be handling and postage charges for group orders. Most of the visitor publications will be available at tourist centers throughout the island, San Juan's international airport, and car rental offices. Detailed street maps are essential for travel in old and new San Juan. When traveling to old San Juan, it is wise to consider using the public bus system (*guaguas or autobus*) because of limited parking. All fares on the regular buses are 75¢. The express bus is $1 between the main bus terminals. You will need quarters because the drivers do not make change. The buses are new, air conditioned, and will drop you at the bus terminal across from the cruise ship docks where you can jump on the free trolley that will take you through Old San Juan. All bus stops have green and white street signs that say *Parada*. Each stop has signposts that indicate which bus numbers stop there. The bus stop going the opposite direction will normally be across the street.

Free Terrestrial Maps and Guides

- "Metropolitan San Juan"—Bus System Map

  Route map to the Metropolitan Autobus System (AMA)
  Department of Transportation and Public Work
  P.O. Box 3909
  San Juan, PR
  Tel: (787) 767-7979

  (These are available at the main terminal buildings.)

- "Puerto Rico Travel Map"—Map illustrates locations of major environmental and recreation sites. This map has good detail, with regional blowup maps.

  Puerto Rico Convention Bureau
  255 Recinto Sur
  Old San Juan, PR 00901
  Tel: (787) 725-2110
  Fax: (787) 725-2133

- Street map of Old San Juan

  Puerto Rico Tourism Company
  Tel: 1-800-866-STAR
  Tel: (787) 721-2400

➢ Official guide to Puerto Rico - ¡*Qué Pasa*!
This magazine is published six times a year. It provides the most complete review of "what is happening" throughout the island. It generally runs over 100 pages in length and includes everything from island history, a 60-day calendar of events, walking tours, location of medical facilities, a variety of maps, shopping, restaurants and hotel, and a breakdown of what to see and do in nine regions of the island.

Puerto Rico Tourism Company
¡*Qué Pasa*! Magazine
P.O. Box 6338
Loíza Street Station
San Juan, PR 00914
Tel: (787) 728-3000
Tel: (787) 268-0135
E-mail:quepasa@casiano.com

➢ "Puerto Rico Travel and Sport Planner"
This is an annual publication that highlights all the main attractions, with special emphasis on ecotourism, sports, and recreation opportunities in various regions of Puerto Rico. It features regional maps, *Paradores* housing locations, and addresses and phone numbers of recreation sites. This is particularly useful for hikers, divers, sea kayakers, beach enthusiasts, and golfers.

Information Center
Puerto Rico Tourism Company
La Casita
P.O. Box 9023960
San Juan, PR 00902-3960
1-800-866-STAR
Tel: (787) 721-2400
Fax: (787) 722-5208

➢ "Places to Go"
This is an annual publication that highlights hotels, restaurants, bars, and regional tourist attractions.

Puerto Rico Tourism Company
(787) 729-9060

Products of the Puerto Rico Tourism Company will be sent to you by contacting their address or phone above. The information center sends out single copies. For multiple copies, requests have to be made to the publishers of the publications, and there may be a charge.

➢ "Puerto Rico Road Map"
The Puerto Rico Department of Transportation and Public Works Authority will provide a detailed roadmap with full coverage of the island, greater San Juan, and the island's other major cities. It has street locators and a distance chart.

Roads Authority
Department of Transportation
P.O. Box 3909
San Juan, PR
Tel: (787) 767-7979

The above map can be obtained commercially from:

Gousha Travel Publications
PO Box 49006
San Jose, CA 95161-9006
Tel: (408) 296-1060

Terrestrial and Marine Maps Available for Purchase

Two additional maps that will prove useful are the USDA Forest Service maps of the Caribbean National Forest.

➢ "Maps of the Caribbean National Forest"
This map has two versions. One is a small pocket-size multifold, the other is a very large wall map. This map includes locations of the trails in the El Yunque recreation area of the forest. They can be purchased at the El Portal Visitor Center as you enter the forest or can be ordered by contacting:
Caribbean National Forest
El Yunque Ranger District
P.O. Box B
Palmer, PR 00721
Tel: (787) 887-2875

Other specialty maps you may find useful are:

- Topographic 7.5 Quandrangle Map
  El Yunque, Puerto Rico
  Sold by: U.S. Geological Survey
  Federal Map Distribution Center
  Box 25286
  Denver, CO 80225
  or:
  Department of Public Works
  San Juan, PR 00910
- Parguera Quadrangle, Puerto Rico
  7.5 minute series (topographic)
  Sold by: U.S. Geological Survey
  Federal Map Distribution Center
  Box 25286
  Denver, CO 80225
  or:
  Department of Public Works
  San Juan, PR 00910
  (Very good for coral reef and mangrove swamp positions and water depths.)
- West Coast of Puerto Rico
  Coastal and Geodetic Survey Map 901
  U.S. Department of Commerce
  National Oceanic and Atmospheric Administration
  Map Distribution Center
  6501 Lafayette Ave.
  Riverdale, MD 20737
  (301) 436-6990
  (Very good for review of terrestrial altitudes and marine depths for the entire west end of Puerto Rico, including Mona and Desecheo Islands; all reefs are shown and depths are expressed in fathoms.)
- East Coast of Puerto Rico—Virgin Passage and Sonda de Vieques
  Coastal and Geodetic Survey Map 904
  U.S. Department of Commerce
  National Oceanic and Atmospheric Administration
  Map Distribution Center

6501 Lafayette Ave.
Riverdale, MD 20737
(301) 436-6990
(Excellent for all of eastern Puerto Rico, Culebra, Vieques, associated small islands and reefs all the way to St. Thomas, Virgin Islands; all depths are expressed in fathoms.)

Governmental Organizations

Commonwealth of Puerto Rico

Department of Natural and Environmental Resources	(787) 724-8774
Marine Resources	(787) 725-8619
Reserve and Refuges	(787) 724-2816
Terrestrial Resources	(787) 722-7517
Las Cabezas de San Juan Nature Reserve–Fajardo	(787) 722-5882
Boquerón Wildlife Refuge–Boquerón	(787) 851-4795
Guánica Forest Education Center–Guánica	(787) 821-5707
Tropical Botanical Garden–Río Piedras	(787) 763-4408
Institute for Tropical Ecosystem Studies	(787) 764-0000 Ext. 2866
Environmental Quality Board	(787) 767-8181
University Sea Grant Program	(787) 832-3585
Puerto Rico Water Resources Authority	(787) 620-2277

U.S. federal

U.S. Department of Agriculture (USDA)	(787) 729-6872
USDA Forest Service	
International Institute of Tropical Forestry	(787) 766-5335
Caribbean National Forest	(787) 888-1880
El Yunque Ranger District	(787) 887-2875
El Portal Education Center	(787) 888-1880
U.S. Environmental Protection Agency	
Caribbean Field Office	(787) 729-6951
San Juan Bay National Estuary Program	(787) 725-8164

U.S. Department of the Interior	
Fish and Wildlife Service	(787) 749-4338
U.S. Geological Survey	(787) 749-4346
Marine Geology Division	(787) 729-6934
Water Resources Division	(787) 749-4346
National Park Service	(787) 729-6777
Cabo Rojo National Wildlife Refuge Environmental Education Office	(787) 851-7297 Ext. 29
Caribbean Islands National Wildlife Refuge	(787) 851-7258
National Oceanic and Atmospheric Administration	(787) 253-4586
Natural Resource Conservation Service	(787) 766-5987
U.S. Army Corps of Engineers	(787) 753-4996 (787) 753-4974

Nongovernmental Organizations

Conservation Trust of Puerto Rico P.O. Box 9023554 San Juan, PR 00902-3554 Tel: (787) 722-5834 Fax: (787) 722-5872 E-mail: fideicomiso@fideicomiso.org	Own and/or manage 14 natural and historic properties on the island
Citizens for the Karst 497 Ave. E Pol Box 230 San Juan, PR 00926-5636 Tel: (787) 760-2100 Fax: (787) 760-2070 E-mail: enlacepr@caribe.net	Specializes in limestone region conservation and research; owns nature reserves in the karst region
Foundation for the Plains Pigeon Project University of Puerto Rico P.O. Box CUH Department of Biology Humacao, PR 00791-4300 Tel: (787) 850-9331 Fax: (787) 850-9417 E-mail: plainpigeon@hotmail.com	Ecology and conservation of endangered Puerto Rican plain pigeon

Guardians of the Mountains P.O. Box 425 Ciales, PR 00638 Tel: (787) 858-9057 E-mail: www.guardianes.org	Promotes nature tours and a new mountain reserve
Herpetological Society of Puerto Rico Metropolitan University P.O. Box 21150 San Juan, PR 00928-1150 Tel: (787) 766-1717 Ext. 6464 Fax: (787) 759-7663 E-mail: um_mortiz@suagm4.suagm.edu	Principal herpetology society, promotes conservation of reptiles and amphibians and their habitats throughout Puerto Rico
Industrial Mission of Puerto Rico* P.O. Box 363728 San Juan PR 00936-3728 Tel: (787) 765-4303 Fax: (787) 754-6462	Very active grassroots environmental action group (*The name does not imply any connection to Puerto Rico's industries.)
Natural History Society of Puerto Rico P.O. Box 361036 San Juan, PR 00936-1036 Tel: (787) 723-8915 Fax: (787) 268-8872 E-mail: f.ferrer@uscac1.usc.clu.edu	One of the older citizen-based environmental awareness groups
Network of Caribbean Marine Mammal Strandings P.O. Box 38030 San Juan, PR 00937-1030 Tel/Fax: (787) 767-8009 E-mail: rcv@caribe.net	Marine mammal conservation and research
Ornithological Society of Puerto Rico P.O. Box 1112 Ciales, PR 00638-1112 E-mail: tody@coqui.net	Main birders group

Speleological Society of Puerto Rico P.O. Box 31074 San Juan, PR 00929-1074 Fax: (787) 783-4566	Offers cave explorations and information about tour companies specializing in cave and sinkhole tours
Puerto Rican Conservation Foundation 382 Ave. San Claudio in PMB 97 San Juan, PR 00926-9910 Tel: (787) 760-2115 Fax: (787) 761-3889 E-mail: fconserv@tld.net	Mainly research; runs an annual environmental Biodiversity Week various areas of the island; publishes the 83-page "Directory of NGO's in Puerto Rico"—$13 (plus handling $5)
Puerto Rican Environmental Alliance 497 Ave. E Pol Box 230 San Juan, PR 00926-5636 Tel: (787) 760-2100 Fax: (787) 760-2070 E-mail: enlacepr@caribe.net	Umbrella group for various environmental and ecology organizations of Puerto Rico
World Wildlife Fund (WWF) Tel: (787) 753-7694	Protection of the world's wildlife
Conserva el Encanto (Keep Puerto Rico Beautiful) Mr. Jaime Pabon Tel: (787) 758-2242	Promotes litter control and island beautification projects
Waterkeepers of Puerto Rico Mr. Ricardo de Soto Tel: (787) 630-7590	Monitor and prosecute violation of environment laws in Puerto Rico's watersheds

Glossary

achene—Dry indehiscent fruit formed from one carpel, with one seed not fused to the fruit wall.

acute—Leaf blade apex ending in a sharp point.

acuminate—Leaf blade apex ending in a tapered point.

adaptation—A feature of structure, physiology, or behavior that promotes the likelihood of an organism's survival and reproduction in a particular environment.

adventitious—Roots having their origin in stem tissue, such as a stilt root.

aerenchyma—Parenchyma tissue with large intercellular spaces for air storage, well developed in aquatic and wetland plants.

aggregate (plant fruit)—Fruit formed from the fusion of multiple pistils in one flower, as in raspberry.

aggregate (mineral)—Any of several hard inert materials (sands, gravel, slag) often used in road construction or manufacturing cement.

agroforestry—Planting of trees and crops together; a system that hosts higher biodiversity than monocultures.

agroecosystem—Mixed system of agriculturally important plants designed to create beneficial habitat for native species and/or migratory species, such as Neotropical migrant birds.

algae—Major division of the plant kingdom consisting of simple nonvascular photosynthetic plants, normally fresh or marine aquatic.

alien (species)—A species accidentally or intentionally introduced into a new territory. May also be referred to as exotic or introduced species.

allochthonous—Material imported into an ecosystem from outside.

alluvial—Deposits of material associated with a stream.

alternate—Arrangement of leaves or branches whereby they occur at different levels on opposite sides.

ambiente—Spanish term for environment.

amensalism—Relationship in which one organism affects another organism, but is not affected in return.

amphibian—A member of the vertebrate class Amphibia, which includes frogs, toads, and salamanders.

amplexus—Male/female locking position for exchange of sperm.

anaerobic—Environmental condition of no oxygen.

angiosperm(ae)—Major group of plants referred to as the flowering plants that produce fruits and seeds.

anthropogenic—Human related, produced, or caused.

apex—Tip of a leaf, stem, or branch.

apical meristem—A group of cells at the growing tip of a shoot or root which, through continuous cell division, forms new plant tissue.

aquifer—Porous rock or permeable unconsolidated material capable of storing or producing water.

aspect—Position facing a particular direction, such as on the side of a mountain.

atoll—A coral reef surrounding a central lagoon resulting from a drowned volcanic cone.

avifauna—A group of birds existing in a particular region.

bagasse—Leftover organic residue resulting from the crushing of sugar cane stems.

bank reef—An offshore reef formed along a wave cut platform in the Caribbean.

barrier reef—An offshore coral reef running parallel to shore and separated by a lagoon from the shore; for example, barrier reef formed in association with a continental land mass such as the Great Barrier Reef of Australia.

bateyes—A section of an indigenous ceremonial park used for games.

bay—Part of an ocean partly enclosed by land, such as the Bay of San Juan.

benthic—Living or growing attached to the bottom of a body of water.

benthos—the bottom of the sea or lake.

bicameral (legislature)—Form of representative government consisting of two houses or legislative chambers.

biodiversity—The genetic, species, and ecological diversity of life in a given area.

bioluminescence (bioluminescent)—Production of light by living organisms.

biomass—Total weight of organisms per unit area.

bleaching—Active loss of endosymbiotic algae from coral tissue resulting in whitening of the polyps and the colony.

bog—A poorly drained wetland area, normally with acidic, spongy ground made of undecomposed organic plant matter.

bole—Another name for tree trunk.

brackish—Water containing salt at levels lower than pure sea water.

buttress(ing)—Arched roots originating in the base of a tree trunk extending away from the base and functioning as support for the tree.

buttress zone—Region of a coral reef dominated by large mounds of boulder coral, generally seaward and deeper than the *Acropora* zone.

bycatch—Incidental capture of nontarget sea organisms, for example, netting of fish while shrimping.

canopy—Top layer of a forest or individual tree.

capsule—A dehiscent fruit with more than two chambers.

Caribs—Fierce Caribbean tribe located in the Lesser Antilles that raided Taíno villages and fought Spanish conquistadores.

carpel—Female part of a plant flower.

cartón—Material produced by termites that makes up their mounds and tunnels.

caste—Functional status of a social insect such as worker or soldier.

catadromous—Organisms that live in fresh water, but migrate to salt water to lay their eggs, such as eels.

cauliflory—Flowers with their origin in the leafless bole of a tree such as cacao.

charismatic species—Attributed to a wild species with a quality of special appeal such as large mammals (bears, elephants, cats, gorillas) that elicits popular support for their survival.

chevron—Body marking looking like a pair of stripes meeting at an angle.

chlorenchyma—Chlorophyll-bearing tissue.

chlorosis—Absence or death of green pigments in plants, for example, produced by salt exposure.

CITES—Convention on International Trade in Endangered Species.

cleaning station—The place where cleaning symbiosis occurs.

cleaning symbiosis—Action whereby two different organisms gain benefit from a cleaning behavior, that is, fish have their ectoparasites removed and cleaner organisms (shrimp, fish) gain access to food.

climax—A stable balanced community, the end of succession.

clone—An individual or group of individuals propagated from an identical progenitor by vegetative means.

cloud forest—Tropical mountain forests that are shrouded in clouds for much of the day, often showing profuse epiphytic growth.

clutch size—The number of eggs laid in a nest.

cnidaria—Animal phylum that includes hydras, jellyfish, sea anemones, and corals.

cnidoblast—A specialized cell giving rise to a nematocyst.

coelenterates—radially symmetrical animals having saclike bodies with only one opening and tentacles with stinging structures; they occur in polyp and medusa.

coelenteron—The body cavity of coelenterates.

commensalism—Relationship between two organisms in which one lives on or in another species that is not harmed or benefited.

community—A defined group of plants and/or animals distinguishable from other assemblages.

compound—A fruit composed of multiple pistils in one flower.

conservation—A resource management ethic that balances proper husbanding of resources and their use for the benefit of people.

convergent evolution—Process whereby natural selection and adaptation cause unrelated organisms to look and act very much alike, for example, cacti and euphorbs.

coppice (coppicing)—A thicket of small trees or the process of harvesting tree and shrub stems for firewood through a series of harvest cuts.

coqui—Generic reference to a genus of frogs (*Eleutherodactylus*) found throughout Puerto Rico.

coral—Colonial marine animals with endosymbiotic algae of the classes Anthozoa and Hydrozoa, grouped as stony or soft coral based on carbonate versus protein exoskeletons.

coralline algae—Algae that precipitate a layer of calcium carbonate, thus making them appear coral-like, for example, *Halimeda* spp.

coral dieback—Death to segments of previously healthy coral colonies related to disease or bleaching events.

coral reef—Complex plant and animal communities forming one of the most productive marine ecosystems in the Earth's tropical zone.

coriaceous—Leathery in appearance.

cotyledons—leaf of the embryo of a seed plant, which upon germination either remains in the seed or emerges, enlarges, and becomes green. Also called seed leaf.

crown—Top layer of a tree.

cutting—Process whereby woody shrub and tree stem growth is harvested by machete or saw for local use.

cuttings—Asexual propagation of plants achieved by cutting sections from a mature plant and planting them.

cyme—An inflorescence in which flowering begins in the middle and progresses toward the periphery.

deciduous—Falling of leaves at end of growing season or onset of drought.

dehiscent—A fruit type that breaks open at maturity.

depauperate—Reduced as in numbers of organisms per unit of area or size of individuals.

detritus—Loose organic material that collects from the disintegration of dead organisms or their wastes.

dicotyledons—The class of angiosperms having an embryo with two cotyledons or seed leaves.

diffusion—Physical process of equalization, for example, movement of gases from high concentration to lower concentration.

dinoflagellates—Members of the division **Pyrrophyta**, mostly marine, single-celled; so called "fire algae" because many are bioluminescent.

dioecious—Having separate sexed male and female flowers on different individuals.

diurnal—Active or opening during the daytime.

domesticated—Animals or plants that have been selected and bred for human use.

dorsolateral—Running down the side.

drop roots—Adventitious roots originating in tree branches.

drupe—Fleshy fruit with one or more seeds, for example, plum or mango.

duff—Accumulated dry organic matter on the top layer of soil.

ecological services—Ecological systems and species provide vast service functions to life systems by performing processes such as cleaning contaminated water and air, pollination, seed vectoring, and decomposition of organic matter.

ecosystem—Biotic community of different species interacting with one another and with the chemical and physical factors making up the abiotic environment.

ecosystem management—The blending of the needs of people and environmental values in a way that will promote a biologically diverse, healthy, productive, and sustainable ecosystem.

ecotone—A transitional area between different habitats or communities.

ecotourism (ecotourist)—Tourism or tourist that emphazes special features of the natural world, for example, wildlife or special habitats.

edaphic—Biologic or ecologic conditions of the soil.

edge effect—A change in species and physical conditions at the boundary between two ecosystems.

effluent—Any substance, such as a liquid industrial waste or sewage, which enters the environment from a point source (pipe).

elfin forest—Short scrubby forest found growing in extreme conditions such as windy rainswept mountain ridges

elliptic—Widest in the middle with equal tapering at both ends of a leaf.

El Niño—Spanish for "Christ Child"; phenomenon that often occurs near Christmas whereby ocean waters off Ecuador and Perú warm. This results in the disappearance of anchovy schools and produces changes in the jet stream resulting in heavy storms and rains over California and the Midwestern United States.

emergent—A wetland plant growing at the edge of a lake, river, or bay where it is constantly moist, such as cattails (*Typha*) in a marsh.

emergent tree—Tall tree growing above the normal canopy of a forest.

endangered species—Wild species with so few survivors that the species could become extinct in most of its range.

endemic—Restricted to a certain geographic area or habitat.

endosymbiotic—A symbiotic relationship where one organism lives inside the cell of another, for example, coral and zooxanthellic algae.

endozoic—Living inside an animal.

Eocene—The second of five epochs in the tertiary period of geologic time approximately 54.9 to 3 million years ago.

epibionts—Organism that lives on the exterior of another, but does not feed on the host; may be plant or animal.

epifauna—Animals that live on the **benthos** or organisms attached to or moving over it.

epiphyte (ephiphytic)—Plants that live on the surface of other plants, but do not derive nourishment from the host.

estuarine—Associated with an estuary where a river enters the intertidal zone of the ocean or the general wetland types that develop there.

eutrophic—A condition in water that is nutrient-rich and supports a high level of biological productivity.

eutrophication—The process by which a body of water acquires a high concentration of nutrients, especially phosphates and nitrates, which can stimulate excessive growth of aquatic plants, especially algae, and this reduces dissolved oxygen.

exotic species—Species that is nonnative, that is, that migrates or is introduced into an ecosystem by humans.

extinction—Disappearance of a species. It can be at the local or regional population level, or the world for the entire species.

facultative—Ability to live under a variety of conditions, for example, may prefer wet habitats, but can live in a upland setting; or may develop a trait occasionally, but not all the time, as in the case of white mangroves producing pneumatophores.

fallow—Land no longer being used for crop production.

family—A group of closely related organisms ranking above genus, designated by the ending "aceae" such as Fabaceae, the legume family.

fauna—All animals present in a given region.

feral—Domesticated animal that has reverted back to the wild, such as dogs or pigs.

field capacity—The maximum amount of water a soil can hold against gravitational forces.

floating-leaved—A wetland plant with floating leaves at the surface, but attached to bottom sediments in a lake, such as water lily (*Nymphaea odorata*).

flora—All plants present in a given region.

follicle—A plant fruit type that opens along one suture, typical of the milkweeds.

Fomento—Called "Operation Bootstrap"; it was an economic development program started in 1950 to promote real estate development, expanded use of ports, and industrial and tourism investment and promotion in Puerto Rico.

food chain—The passage of energy and materials from producers through a sequence of herbivores and/or carnivores.

food web—A group of interrelated food chains.

forbs—Nonwoody plants with broad leaves.

forereef—The slope on the seaward side of a reef that is constantly exposed to waves and currents.

fouling community—Dense growth of organisms on solid surfaces such as boat bottoms and pipes, or red mangrove roots that may interfere with normal operation of either.

fragmentation—Division of habitats into small sections that can produce changes in available territory and reproductive success for sensitive species.

free-floating—A wetland plant floating freely on the water's surface such as duck weed (*Lemna minor*).

fringing forest—Forest located along an ecotone such as mangroves at the intersect between water and land.

fringing reef—A coral reef contiguous with the coast, but lacking a lagoon.

frond—Special term for the leaf of a fern or palm tree; also applied to the leaf-like thallus of marine algae.

frugivore (Frugivorous)—Fruit eater.

fungi—Lower organisms that produce spores, hyphal vegetative structures, and are nonphotosynthetic.

GDP (gross domestic product)—Total market value of goods and services produced within a country during a specific period and which does not include activities of offshore corporations.

genetic bottleneck effect—The result of the loss of genetic diversity when a population experiences a severe reduction in effective population size.

genome—All of the genetic material in one organism.

genus (Genera)—A group of closely related organisms, below family, usually consisting of more than one species. First Latinized word in a scientific name such as *Ceiba pentandra*.

global climate change—Changes in the climate of the Earth. Opinions differ as to the effect of anthropogenic processes such as burning and the release of carbon dioxide (CO_2), methane (CH_4), chlorofluorocarbons, and so forth.

globose—spherical.

gneiss—A foliated or layered metamorphic rock such as granite.

GNP (gross national product)—Total market value of all goods and services produced by a nation's economy during a specific period.

grazer (grazing)—An organism that feeds on live vegetation or animal growth such as cow on grass, or parrot fish on coral.

Greater Antilles—Four largest islands of the West Indies: Cuba, Hispaniola, Jamaica, Puerto Rico.

greenway—A transportation or urban trail corridor area used for recreation that emphasizes natural features associated with a park or river area; it is a soft development zone in an otherwise urban setting.

gymnosperm(ae)—Major group of plants that produce naked seeds borne on seed leaves such as pines.

habitat—The place or environment in which an organism lives, that is, its home.

hair(y)—Any epidermal outgrowth that covers or protects an organism's outer surface.

halophyte (halophytic)—A plant capable of thriving in salt water or saline soils; a shore plant.

hard coral—Those coral species that secrete a hard calcium carbonate skeleton.

haystack hill—Hills that resemble a rounded haystack typical of karst regions.

hepatics—The general term for the class of bryophytes that contains liverworts.

herb(aceous)—Nonwoody seed plant.

herbaceous productivity—Biomass created in a given area by the herb layer of the community.

herbivorous (herbivore)—Animal that feeds on herbaceous plants.

hermatypic coral—Corals involved in reef building such as *Diploria* (brain), *Montastrea* (star) and *Acropora* (horned).

homeostasis—Dynamic equilibrium or steady state in a species or ecosystem.

horticulture—Practice of growing and using plants for human use, such as in gardening and landscape beautification.

host—An organism that supplies nourishment, provides protection, or a place to reside.

hotspot (biodiversity)—An area of unusually high species diversity or endemics.

hurricane—Violent oceanic generated tropical storm with winds greater than 120 kilometers per hour (75 miles per hour).

hydrocoral—Fire coral (*Millepora*); likely to produce skin reactions upon exposure.

hypersaline—Very high salt content.

igneous—The result of extreme heat; silicate minerals formed by the cooling and solidification of magma.

indehiscent—Fruit that does not split open at maturity.

inflorescence—A flowering stem with multiple flowers often branched.

insect—A large class of animal without vertebrae, with three sets of legs and two pairs of wings. Nearly 1 million species are known.

insectivore (Insectivorous)—An organism that preys on insects as a food source.

insular shelf—A shallow underwater ledge or extension of the sublittoral coastline around an island, similar to a continental shelf.

interference competition—When an organism competes with another for space, light, or nutrients and one has an ability to grow under low light or other altered habitat conditions, and as a result outcompetes the other.

interspecific—Between distinct species.

intraspecific—Within a species.

introduced species—Not native, having been brought into a country or introduced into an ecosystem by humans.

invertebrate—Animals without backbones such as insects.

karst—Irregular topography developed by the action of surface and underground water on soluble rock such as limestone and characterized by sinkholes, haystack hills, streamless valleys, underground rivers and caves.

keystone species—Species that play dominant roles in an ecosystem and affect other organisms beyond their own abundance or biomass, for example, bats as pollinators and seed vectors.

lacunae—Large air spaces between cells like those found in aquatic plants.

lacustrine—Related to a lake or wetland associated with a lake.

lagoon—A protected shallow body of water, such as on the leeward side of a coral reef or the inner water section of an atoll.

lanceolate—Shaped like a lance.

lateral root—Moving out sideways away from the center of the plant.

leaching—Washing of ions out of soil, organisms, or plant surfaces.

leaflets—A leaf blade is divided into distinct units, that is, there is not one distinct simple blade.

leeward—Away from the direction the wind is blowing.

legume—Fruit type of the plant family of Fabaceae; fruit that breaks open along two sides such as in *flamboyán*.

lenticel—Air exchange pore in periderm of stems and roots.

Lesser Antilles—A long arc of small islands in the eastern Caribbean Sea extending from Puerto Rico to the north coast of Venezuela.

liana—Woody climbing vine of tropical forests.

limestone—A sedimentary rock composed largely of calcium carbonate ($CaCO_3$), which can be formed by organic or inorganic processes. Many islands in the Caribbean have extensive limestone beds owing to formative activities of marine organisms such as coral and algae.

litter—Partly decomposed plant residues on the surface of soil.

littoral—Growing at or near the seashore; zone between high tide and low tide.

macrobenthic—Macroscopic organisms growing attached in the benthic zone of a water body, seagrasses, for example.

macrophyllous—Having large leaves.

mammal—A class of warmblooded vertebrates that gets its name from the mammary glands used for feeding their young.

mangrove—A generic term applied to many species of tropical plants that can grow with their roots partly or completely submerged in sea water or that make up tidal, riverine, and basin forests in the tropics.

mariculture—The application of the principles of agriculture to the commercial production of marine organisms.

marine—Having to do with oceanic processes, saltwater conditions, or organisms found in marine habitats.

marine fishery reserves—Special areas of the ocean, coral reefs, and estuaries where no or limited use of marine resources is permitted.

marsh—A wetland without trees, dominated by grasses, sedges, rushes, and other herbaceous groups.

mass wasting—Downslope movement of earth materials.

medusa—Free-swimming, bell-shaped stage in a cnidarian life cycle.

meiotic—Reductional division of chromosomes whereby the number is reduced by half.

mesophyllous—Having leaves of moderate size, between microphyllous and macrophyllous.

metabolites—Material produced by metabolism, which is all of the chemical and physical activities necessary to sustain an organism.

metamorphic—Changed rock, that is, any rock that has been changed in texture or composition by heat, pressure, or chemically after its original formation.

microphyllous—Having small leaves.

migratory—Changing habitat according to season, climate, or food supply. For example, movement of Neotropical birds from North America south to the tropical latitudes during the temperate winter.

Miocene—Geologic period between the Oligocene and Pliocene, approximately 7 to 26 million years ago.

mitigation—To create, restore, or preserve other wetlands in exchange for permission to alter preexisting natural wetland associated with a development project, such as a road or building.

monocotyledons—The class of angiosperms having an embryo with only one cotyledon or seed leaf.

monoculture—An agriculture system that grows one crop over an extended area and period.

monoecious—Having the male and female flowers on the same plant.

monogeneric—A plant family composed of only one genus.

monospecific—A taxonomic or ecological unit with one species.

morphology (morphological)—The form or structure of a plant or animal.

multiple fruit—A fleshy fruit formed from several to many separate flowers in a tight inflorescence such as pineapples.

mutualism—A mutually benefical relation between two organisms, in some cases one may not be able to live without the other.

nape—Neck area.

native species—Species that normally live and thrive in a particular location.

naturalized species—An introduced species that over time was able to acclimate to the new conditions and now grows and sexually reproduces like an indigenous species without the aid of people.

nematocyst—A stinging cell of cnidarian coelenterates such as coral and related groups used for protection and obtaining prey.

Neotropical—New World tropics and subtropics roughly corresponding to 25° north and south of the equator.

neutralism—The lack of any effect on either organism in a coexisting relationship.

NGO—Nongovernmental organization.

niche (ecological)—Total way of life or role of a species in an ecosystem including all physical, chemical, and biological conditions a species requires to live and reproduce.

nocturnal—Active or opening during the night time.

node—Place on a stem at which leaves or branches arise.

nut(let)—Dry, indehiscent fruit with a hard woody fruit wall; nutlet is a very small nut-like fruit.

obligate—An organism restricted to a habitat where certain conditions are almost always present.

oblique—Refers to the base of a leaf blade where the two sides do not join at the same position on the petiole; that is, one side is lower.

obtuse—Slightly angled leaf apex.

octocoral—Seafans, and seawhips that exhibit polyps with eight tentacles.

odd-pinnately compound—Plant leaf composed of an odd number of leaflets.

old growth—Pertaining to forests or other ecosystems that have not been cut or altered for centuries.

Oligocene—Geologic period between the Miocene and Eocene, approximately 26 to 38 million years ago.

oligotrophic—Water containing few nutrients resulting in low productivity.

opposite—Leaves or branches are attached at the same level on a stem or node.

orbicular—Round in shape.

orographic rain shadow—Having to do with mountains whereby rain shadows are produced on the downwind side of a mountain after moisture-laden clouds release their water on the windward side.

pallid—Background colors of light brown, cream, or green.

palmately compound—Plant leaf composed of multiple leaflets attached in the form of the human hand.

palustrine—Nontidal wetlands not confined by channels and not marginal to lakes.

panicle—A branched complex raceme inflorescence.

pantropical—Throughout the Earth's tropical zone.

parenchyma—The basic cell type of higher plants, found in tissues such as stem pith, fruit pulp, and leaves and used primarily for storage.

parthenocarpic—The formation and growth of fruit without fertilization and thus without production of viable seeds.

patch reef—A coral boulder complex or clump of corals not attached to a major reef.

peduncle—The main flower-bearing stem of a plant.

pelagic—Living in open water.

periderm—The outer layer of protective tissue of a plant.

persistent—Remaining attached through or after maturation.

petal—Part of the flower that is usually colorful; collectively called the corolla.

petiole—Part of a leaf that attaches a leaf blade to a stem.

petroglyph—A carving on a rock.

phase shift—Changes in one or more species populations produced by predation, disease, or pollution. The organisms that previously were structural dominants in an ecosystem are replaced by different organisms, for example, macro algae replacing coral as a result of overharvesting of herbivorous fish.

pheromone—Chemical substance produced by an individual that can influence the behavior of others of its species, such as mating, feeding, or reaction to danger.

phosphorescence—Release of light caused by prior absorption of energy and continuing release of light energy for a time after the energy source has stopped.

phreatophyte—A plant capable of sending roots deep into the ground to obtain water; sometimes called well plants.

phylum(la)—The major division representing a separate evolutionary line within the animal kingdom.

phytogeography—Study of the geographic distribution of plant species, communities, or ecosystems.

phytoplankton—Single-celled algae from various divisions; characterized by sinkholes, haystack hills, streamless valleys, underground rivers and caves.

pinnately compound—Leaf blade that is divided into leaflets and arranged with the leaflets on each side of a midrib. If there is an even number of leaflets, the condition is referred to as even pinnately compound versus odd pinnately compound.

pliocene—The last of five epochs in the tertiary period of geologic time; 5 to 2 million years ago.

pneumatophores—Aeration roots growing upward from the horizontal roots of black mangroves.

pollen—Microscopic meiotic product of anthers that carry the male sex cell to the female flower part (pistil) prior to fertilization.

pollinator—An organism that provides a vehicle for the transfer of pollen in the process called pollination.

polyculture—Raising of a variety of crops in a small area, whereby the plants are less susceptible to disease and insect pest.

polymorphic—Variable body forms in the life history of an organism.

polyp—One of the individuals making up a colonial animal such as coral; very simple animals lacking organs, possessing tentacles.

population—A group of individuals of a species living in a certain area.

predator—An organism of one species that captures and feeds on parts or all of another organism of a different species (prey).

prescribed fire—A fire that is intentionally set in order to reduce the threat of a wildfire, produce better pasturage, or control unwanted species.

preservation—To protect and keep resources from being destroyed, that is, the keeping of nature for nature's sake regardless of its usefulness.

preserve—An area restricted for the protection and preservation of the natural resources, including plants and animals within its boundaries; frequently defined as a non-use area for extraction purposes.

primary species (forest)—The species or forest typical of an area at its mature or climax stage.

primary productivity—The rate at which energy is stored in an ecosystem via photosynthesis.

productivity—The amount of biological matter or biomass produced in a given area during a given unit of time.

propagate—To increase the number of organisms.

prop roots—Roots with their origin in stem or trunk tissue of a tree like red mangrove that supports the tree in soft, wet, and sometimes anaerobic substrates.

pseudo-bulb—Modified swollen base of a stem used for storing water as in some epiphytic orchids.

pubescence—Hairy covering of plant organs such as leaves and stems.

Pyrrophyta—a division of lower plants comprising unicellular and biflagellate algae that form starchy compounds.

raceme—Inflorescence having a common axis with stalked flowers attached.

rain shadow—Lack of rainfall on the leeward side of mountain ranges.

ramiflory—Flowers with their origin in woody branches.

reclamation—Rehabilitating a degraded or destroyed wetland or other habitat.

recovery plan—A plan for the restoration of protected or endangered species. May include captive breeding, disease control, and/or habitat management.

reef crest—Top of a reef on the ocean-facing side, which may experience air exposure.

reef front—The seaward side of a reef from the edge of the crest to the depth at which coral and coralline algae become rare.

reef slope—Area of increasing water depth on the seaward side of a reef.

reptile—Class of vertebrates including animals such as the snakes, lizards, turtles, and alligators.

reserve—An area that has a special use and is set aside for future use, including its natural resources.

restoration ecology—Seeks to repair or reconstruct habitats and ecosystems damaged by human or natural actions.

rhizome—A thick horizontal stem usually in the soil, which sends out vertical shoots and descending roots at nodes.

riparian—Habitats having to do with riverbanks or corridors.

riverine—Feature or habitat related to rivers; wetlands that fringe rivers or are in channels.

root ball—Large clump of roots and soil exposed as a result of the uprooting of a tree.

rounded—Gently sloping apex of a leaf blade or tree top.

salamander—Small slender predatious amphibians.

saline (salinity)—Water containing salt in solution; sea water has a salinity of 33 to 35 parts per thousand of NaCl.

SAV—Submerged aquatic vegetation, such as seagrass.

savanna—Subtropical or tropical grassland with drought-resistant vegetation and scattered trees; transitional between grasslands and rain forest.

saw timber—Trees that have sufficient length, girth, and proper development from which wood useful for construction or furniture can be sawn.

sclerophyllous (sclerophyllic)—Hard-leaved; leaves resistant to drought because of thick cuticle and reduced air space.

secondary species (forest)—The species or forest typical of an area that has been disturbed (natural or human induced) and is undergoing succession.

sediment (sedimentation, sedimentary)—The material such as released soil particles and organic matter that settles to the bottom of a liquid over long periods (geologic). This can produce rock consisting of various-sized rock fragments and remains of plants and animals, for example, limestone.

seed bank—When seeds are dispersed they may fall and not germinate and get incorporated into the soil in forest, field, and water bodies, only to germinate later when conditions promote their germination.

sepal—Protective parts to a flower bud, usually green and located below the petals; collectively called the calyx.

serpentine (serpentinite)—A green-blue rock that gets its name from its mottled color similar to that of a serpent. A magnesium silicate, low in calcium that produces changes in the usual plant cover of the area.

sessile—Attached to the base of a leaf without a petiole or a flower without a peduncle.

shellfish—Any aquatic invertebrate animal having a shell, such as mollusks and crustaceans.

shrub—A woody plant with more than one main stem, usually less than 5 meters (15 feet) tall.

silviculture—The scientific process of producing and caring for a forest.

sink—An area benefiting from new recruitment of individuals from a distant source.

sinkhole—A depression or hollow place in which drainage collects and which may be open at the bottom leading to an underground channel or river. If solid, some can be farmed.

slash-burn (swidden) agriculture—An ancient farming system in which small patches of tropical forest are cleared and perennial polyculture agriculture is practiced, followed by many years of fallowing the land to restore the health of the soil and the native vegetation.

soft coral—Coral that produces a soft, flexuous, exoskeleton that may take the form of feathers or fans, and show flexibility when water moves over them.

source—Opposite of a sink; an area that serves to export organisms such as immature forms of coral and fish to areas away from their origin.

sound—A long broad inlet of the ocean generally parallel to the coast.

speciation—The evolutionary development of new species.

species diversity—The number of different species and their relative abundance in a given area.

spelunker—A person who investigates caves.

spike—An elongated flower stalk with sessile flowers.

stilt roots—Long, slender, support roots with their origin in stem tissue; red mangrove, for example.

stipules—An appendage at the base of a leaf petiole where it attaches to a stem.

stomata—Openings in leaf and stem surfaces used in gas exchange.

stony coral—Limestone-secreting corals that are reef builders. Members exhibit polyps with six tentacles.

stranglers—Woody plants that begin as epiphytes, later connect to the soil and produce a trunk that eventually kills the structural host tree. *Ficus* and *Clusia*, for example.

stressor—An agent that can change the growth, reproduction, or physiological state of an organism or ecosystem, such as waste heat from a power plant or an oil spill in a mangrove swamp.

sublittoral—Shallow water zone from the low tide point to about 200 meters (650 feet) deep.

submerged seagrass beds—Underwater populations of one or more species of flowering seagrasses, generally located in relatively clear water and soft to firm substrates.

submergent—Wetland plant growing underwater attached to bottom substrates, such as water hydrilla (*Hydrilla verticillata*).

succession (successional)—Process in which communities of plant and animal species in a particular area are replaced over time by a series of different and often more complex communities.

succulent—Plants that grow in warm areas and possess water storage capacity in fleshy stems, for example, cactus.

supralittoral—The seashore zone immediately above the normal tidal submergence zone.

sustainability—Ability of a system to survive for a specified period.

swamp—Wetland type dominated by trees, such as mangrove swamps.

symbiosis (symbiotic)—The intimate living together of members of two different species.

Taínos—Caribbean Indians of the Greater Antilles with a complex social structure. They developed villages and practiced agriculture. Within 100 years of the Spanish conquest, they became extinct.

tannin—Pigments found in the bark of woody plants used in tanning leather and dye pigments.

taxon—A generic term referring to a taxonomic unit of classification such as family, genus, or species.

termites—Social insects of the order Isoptera responsible for degrading vast quantities of plant biomass throughout the tropics; some species are very damaging to human-made wooden structures.

termitophile—Interdependent organisms associated with termite colonies such as beetles, flies, protozoa, fungi, and bacteria.

terrace—A land or reef form that is nearly flat.

thallus—Body of a plant that lacks a true vascular system.

threatened species—A wild species that is still abundant in its natural range, but is declining and could become endangered.

topography—The physical features of the landscape.

trade winds—A tropical wind blowing almost continuously in the same direction, such as the easterly trades on the north side of the equator.

Tragedy of the Commons—The process of degradation of community resources owing to self-interest of individuals who use or destroy more than their fair share, as in, overfishing.

tree—A woody plant with one main stem generally exceeding 5 meters (15 feet) in height.

tubercle—A small rounded protuberance on a plant or animal part.

turbid (turbidity)—A clouded or murky water condition owing to the presence of sediment, effluents, or biological agents that impede the penetration of light.

twice pinnately compound—Leaf condition where each leaflet is compound, that is, there is a double compound condition.

ultramaphic—Igneous rock rich in iron and magnesium and poor in silica.

upland—Elevated land away from the sea, a river or lake, or wetland.

urban desert—A result of the dense clustering of buildings, roads, and parking lots; many urban areas have little dedicated green space, thus they are often desert-like.

urban forest interface—An area where an otherwise natural or wild undeveloped area is adjacent to an urbanized zone.

urbanization—The process of increasing human populations and support infrastructure in an urban area (city; generally considered 20,000 or more people).

vascular tissue—Xylem and/or phloem tissue in plants that permits movement of materials and adds strength.

vector—An agent that moves reproductive bodies such as pollen by bees and fruit or seeds by bats.

vegetative—Growth in plants without reproduction; adds length, width, and biomass.

vertebrate—A subgroup of the chordata distinguished by the presence of a vertebral column, endoskeleton, and nerve cord.

vine—Slender woody plants that do not grow upright on their own, but use other plants or inanimate objects for support.

viviparous (vivipary)—Germinating while still attached to the parent plant, as seeds of red mangroves.

volcanic—Igneous rock composed of materials resulting from volcanism, such as lava.

water cycle—The natural solar-driven cycle of evapotranspiration, condensation, precipitation, and runoff.

well epiphyte—Water-collecting epiphytes frequently found attached to tree trunks in the wet tropics, such as the bromeliad *Guzmania*.

West Indies—Large island group of the Caribbean Sea region including the Greater and Lesser Antilles.

wetland—Ecosystems of several types in which rooted vegetation is found in specific soils that may be saturated with water much of the year such as bogs, swamps, and marshes.

windbreak—Row of trees or shrubs planted to block windflow and reduce soil erosion on cultivated fields and sensitive habitats.

wind shear (training)—Process whereby the drying action of wind can reduce viability of buds on the windy side, causing greater growth on the protected side.

winged—Having slightly expanded surface areas such as along a stem or leaf petiole.

xerophyte—Plant adapted to extremely dry conditions.

zonation—Arrangement of organisms and/or habitats based on biological, physical, and/or chemical features of the environment.

zooplankton—Microscopic animal plankton that float in water.

zooxanthellae—Small endosymbiotic dinoflagellate algae that live inside the inner gut cells of reef-building corals.

Index

(Page numbers in bold signify Literature Cited)

adaptations: 85, 86, 89, 120, 163, 177, 178, 188, 200, 214, 266, 289, **314**, **337**, 394.
adventitious: 106, 115, 183, 197, 198, 199, 220, 404, 408.
aerenchyma: 200, 220, 223, 404.
African tulip tree: see *Spathodea campanulata*.
agroecosystems: 62, 70, 76, 105, 113, 135-137, 145, **329**.
agroforestry: 135, 145, 153, 375, 404.
air plants: 117, 141.
algae: 117, 118, 129, 175, 189, 190, 191, 204, 216, 219-229 passim, 232, 235, 236, 237, 242, 244, 246, 248, 251, 259- 270 passim, 280, 281, **324**, **334**, 347, 378, 380, 404-419 passim, 424.
Pyrodinium bahamense: 347, 378.
Halimeda: 189, 205, 230, 244, 251, 261, 347, 352, 407.
macrobenthic algae: 219, 224, 226, 227, 229, 242, 251, 270, 378.
alien species: 1, 27, 33-34, 36, 45, 48, 51, 52, 55, 56, 71, 84, 232, 346, 305, 366
alluvial: 2, 25, 26, 80, 88, 91, 104, 304, **331**, 404.
Amazona vittata: 42, 55, 56 passim, 60, 72, 125, 355.
amphibian(s): 44, 47, 50, 52, 54, 67, 71, 72, 287, 292, **318**, **337**, **338**, 353, 354, 402, 404, 420
Bufo marinus: 48, 353.
Eleutherodactylus coqui (coquí): 44, 50, 52-54, 72, **337**, **342**, 353.
frogs: 47, 48, 52, 54, 71, 102, 118, 130, **339**, 371-372, 404, 407.
Puerto Rican crested toad (*Peltophryne lemu*): 47, 48, 72, 89, 354, 390.
toads: 47, 48, 404.
tree frogs: 48, 52-55, 118, 130, **337**, 371-372.
Anacardiaceae: 32, 37, 154, 155, **336**, 377.
anthozoa: 233, 244, 254, 407.
anthropogenic: 177, 232, 245, 270, 284, **314**, **315**, 405, 412.
aquatic beds: 168, 169.
Arecibo Ionospheric Observatory: 98, 370, 374.
atolls: 239, 242.
Australian pine: see *Casuarina equisetifolia*.
autograph tree: see *Clusia rosea*.
Avicennia germinans: see mangroves, black.
avocado: 27, 64, 345.
Bacardi rum distillery: 66, 372.

bagasse: 140, 405.
Banana Republics: 148
bananas: 2, 32, 62, 64, 79, 134, 136, 137, 148-151, **313**, **314**, **337**, 345.
bank reef: 242, 405.
barrier reefs: 239, 242, 405.
Great Barrier Reef: 247, 268, 395.
bats: 43, 45, 47, 48, 50, 63-67, 112, 184, 292, 306, **318**, **319**, **326**, **327**, **329**, **330**, **334**, **338**, **339**, **340**, 370, 372, 392, 394, 413, 423.
benthic: 204, 216, 221-232 passim, 271, **333**, 378, 405, 414.
bicameral: 12, 405.
biodiversity hotspot: **314**, **317**, **318**.
bioluminescence: **329**, **338**, 377, 378, 405.
bioluminescent bay: 378.
bleaching: 246, 249, 267, 268, 269, 270, 271, **312**, **313**, **314**, **317**, **319**, **321**, **323**, **328**, 405, 407.
bloodwood: 104, 161-163 passim, 167, 214, **342**, 352.
bog: 127, 157, 165, 172, 173, 405, 424.
Boqueron Bay: 170, 248, 369.
Borínquen: 4, 5.
botanical garden: 33, 125, 156, 287, 369, 370, 371, 400.
breaker zone: 242.
bromeliad (Bromeliaceae): 54, 107, 115-121 passim, 129, 134, 141, **335**, 350, 351, 424.
Vriesea sintenisii (red leaf bromeliad): 121, 134, 351.
Bursera simaruba: 33, 88, 91-92, 180, 193, 348.
buttress: 29, 39-41, 77, 104, 105, 109, 162, 163, 242, 406.
Caribs: 4, 5, 406.
castes: 68.
Cabo Rojo: 20, 57, 75, 86, 138, 143, 238, 301, 302, 306.
Cabo Rojo National Wildlife Refuge: 57, 75, 211, 304, **340**, 382, 401.
Caguana Indian Ceremonial Park: 368.
Caribbean Islands National Wildlife Refuge (CINWR): 304, **340**, 390, 401.
Caribbean National Forest (CNF): 88, 95, 115, 116, 119, 162, 291, **339**, 373, 375, 393, 398, 400.
carton: 69, 70, 406.
Casuarina equisetifolia: 168, 180, 185-186, **335**, 345.
catadromous: 52, 157, 406.

cauliflory: 32, 105, 406.
caves at Camuy: 369, 372.
Cecropia schreberiana: 33, 107, 111-112, 134, **323**, 352.
Ceiba pentandra: 32, 39-40, **324**, 348, 411.
chitons: 44, 188, 190, 191.
chlorosis: 180, 186, 279, 406.
CITES agreement: 367.
citrus: 2, 62, 134, 136, 137, 148, 151-154, 346, 347, 348, 349.
    citrus sinensis: 152, 349.
cleaning symbiosis: 264, 266, **331**, **332**, **336**, 406.
Clusia rosea: 32, 43, 105, 119, 129, 134, 168, **326**, 345.
cnidaria: 44, 233, 235, 237, 407, 415, 416.
cnidocytes: 235.
cobana negra: 73, 75, 346.
Coccoloba uvifera: 32, 177, 180, 184-185, 192, **336**, 351.
coconut palm: see *Cocos nucifera*.
Cocos nucifera: 32, 168, 180, 181-183, 346.
coelenterata: 233.
coelenteron: 235, 407.
Coffea arabica: 1, 2, 7, 8, 9, 19, 32, 58, 59, 62-63, 76, 79, 104, 112, 113, 135-138 passim, 143-148, 346.
    shade-grown coffee: 62, 113, 146.
    sun-grown coffee: 59, 62, 63, 146.
Coffee: see *Coffea arabica*
colonial period: 7-8, 138.
commonwealth: 3, 11-19 passim, 57, 59, 74.
Comocladia glabra: 38, 102.
    dodonaea: 37, 38, 88, 102.
conquistadores: 6, 7, 43.
coppicing: 84.
corals: 44.
    Acropora cervicornis: 231, 250, 256-257, 269, 280, 281, 356.
    Acropora palmate: 190, 191, 250, 255-256, 269, 280, 281, 356.
    Diploria labyrinthiformis: (brain coral) 251, 257-258, 269, 356.
        -*strigosa*: (depressed brain coral) 251, 258, 356.
    bleaching: 246, 267-271 passim, **312**, 313, **314**, 317, **319**, **321**, **323**, **328**, 405.
    finger coral: 231, 250, 254, 280, 356.

grooved brain coral: 257.
hermatypic coral: 236, 412.
horned coral: 255, 356.
Porites spp.: 231, 254-255, 280, 281, 356.
Porites astreoides: 255, 356.
Porites furcata: 356.
Porites porites: 250, 254, 356.
coral reefs: 1, 2, 23, 50, 52, 86, 95.
shallow-water stony corals: 242, 244, 250-251, **311**, **322**.
soft coral: 244, 251, 259, 264, 269, 280, 407, 421.
staghorn corals: 231, 242, 250, 256, 257, 269, 280, 281, 356.
stony corals: 244, 250, 254, 311, **322**.
thick finger coral: 254, 356.
thin finger coral: 254, 356.
Cordillera Central: 8, 19, 20-25 passim, 31-33, 86, 95, 98, 106, 109, 115, 123, 147.
cupey: 43-44.
Cyathea arborea: 106-107, 134.
Cyrilla racemiflora: 31, 125, 127-128, 134.
Dacryodes excelsa: 109-110.
de Leon, Ponce: 6.
Delonix regia: 32, 36, 41-42.
detritus: 188, 203, 216, 221, 237, 408.
Diadema antillarum: 191, 230, 251, 261, 262, 361.
dinoflagellates: 264, 347, 378, 408, 424.
diurnal: 49, 182, 215, 408.
drip-tip leaves: 105.
drought: 119, 130, 209, 213, 216, 267, 282, 284, 285, 408, 420.
dunes: 175-180 passim, 184, 186, 187, 304, **324**, **335**.
ecological life zones: 79, 82.
ecological services: 171, 172, 244, **313**, 408.
ecosystem management: 297, 409.
ecotourism: 3, 4, 57, 65, 213, 245, 248, 249, 294, **326**, **329**, 363, 383, 397, 409.
ecotone: 131, 409, 411.
effluent: 170, 189, 232, 246, 249, 409, 423.
El Morro: 7, 369.
El Niño: 232, 268, 271, **313**, **317**, 409.
El Portal: 119, 294, 295, 375, 398, 400.

El Yunque: 20, 55, 57, 65, 106, 108, 116, 119-121 passim, 124, 133-135 passim, 275, 276, 291-299 passim, 384, 398-400 passim.
emergent vegetation: 167, 307.
endemism: 30, 34-36 passim, **313**.
endosymbiotic: 235, 237, 268, 405, 407, 409, 424.
Epicrates inornatus: 48, 72, 74, 359, 392.
epifauna: 207, 221, 410.
epiphyllous: 118.
epiphyte: 32, 43, 62, 95, 101, 105, 106, 108, 114-122, 124, 125, 129, 133, 134, 141, 163, 200, 225, 289, **322**, **329**, **333**, **337**, 352, 372, 410, 422, 424.
bracket epiphyte: 119.
hemiepiphyte: 119
protoepiphyte: 119.
tank epiphytes: 117, 119, 352, 372.
well epiphyte: 117, 424.
epixylous: 118.
estuarine: 157, 165, 168-170 passim, 195, 216, 306, **323**, 410.
eutrophication: 161, 213, 246, 268, 410.
Fabaceae: 30-32 passim, 35, 410, 414.
facultative: 167, 168, 201, 410.
upland: 168.
wetland: 116, 167.
fauna: 27, 36, 42, 45, 46, 50, 52, 74, 102, 205-207 passim, 216, 221, 223, 226, 244, 261, **317**, **320**, **325**, **335**, 410.
field trip (checklist): Preface, 213, 249, 287, 310, 363, 365, 368, 370-373 passim, 377, 380, 381.
fire: 59, 65, 84, 85, 107, 139, 282, 285, 286, 291, 308, 418.
flamboyan tree: see *Delonix regia*.
floating attached vegetation: 166.
flora: 27, 30, 31, 33, 34, 35, 102, 120, 121, 123, 124, 125, 127, 132, 134, 172, 206, 223, 285, **313**, **315**, **317**, **322**, **329**, **331**, **336**, **341**, 370, 410.
Fomento: 11.
Foraker Act: 9-10.
forereef: 242, 411.
deep: 242.
forest(s)
cloud forest: 121, 128, 131, 133, 157, **321**, **342**, 383, 407.

colorado forest: 115, 125, 127, 128, 133.
Commonwealth: 57, 82, 107.
dry: 23, 26, 36, 58, 80, 83, 84, 85, 86, 118, **334**.
Guánica Forest: 21, 59, 86, 88, 89, 92, 93, 118, 123, 130, 183, 192, 202, 304, **315**, **326**, 369, 372, 373, 400.
moist forest: 26, 38, 44, 82, 94, 95, 102, 104, 108, 220.
rain forest: 20, 21, 26, 59, 65, 80-88 passim, 105, 108, 111-122 passim, 131, 157, 203, 233, 278, 285, 291, 294, **315**, **317**, **318**, **319**, **320**, **322**, **324**, **326**, **334**, **335**, **337**, **338**, 373-375 passim, 385, 393, 394, 420.
subtropical moist forest: 82, 94-105, 108, 220.
fragmentation: 58, 411.
frangipani: see *Plumeria rubra*, 180, 193, 347.
free-floating vegetation: 166.
fronds: 106, 114, 116, 119, 131, 181, 182.
frugivore: 65, 411.
genetic bottleneck: 269, 411.
global climate change: 175, 232, 270, 277, **342**, 412.
Gorgonians: 244, 258, 259, 281, **321**.
Gorgonia flabellum: 251, 259, 267, 360.
sea fans: 233, 244, 259, 267, 360.
Greater Antilles: 5, 16, 18, 27, 30, 35, 46, 47, 76, 123, 162, 174, 412, 422.
greenspace: 285, 287, 289, 290.
gross domestic product: 17, 411.
Guánica: 8, 20, 21, 23, 26, 36, 37, 50, 57, 59, 75, 84, 85, 86, 88, 89, 90, 169, 183, 184, 192, 304, **315**, **326**, 369, 372, 373, 384, 400.
Gumbo limbo: see *Bursera simaruba*
Guzmania berteroniana: 115, 120, 121, 134, 352.
Hacienda Buena Vista: 298, 375.
Halodule wrightii: 169, 223, 225, 226, 252, 351.
beaudettei: 221, 252.
halophytes: 195.
haystack hills: 23, 37, 44, 98, 100, 101, 102, 370, 373, 374, 413, 418.
Holdridge life zone system: 81.
hurricane(s): Preface, 1, 20, 21, 23, 44, 46, 80, 111, 116, 120, 128, 131, 137, 150, 162, 170, 187, 201, 225, 232, 246, 249, 257, 273-282, **312**, **313**, **316**, **318**, **320**, **333**, **338**, **341**, **342**.
effects: 23, 273, 276, 278, 279, 280, 281, 297.

disturbance systems: 277.
Hurricane Hugo: 110, 130, 274, 275, 276, 278, **321**, **322**, **327**, **341**, **342**.
indigenous ceremonial parks: 368.
Inceptisols: 25.
insects: 44, 46, 48, 49, 53, 54, 63, 64, 65, 66, 67, 118, 183, 190, **317**, **320**, **340**, **342**, 377, 413, 422.
termites (*Nasutitermes costalis*): 44, 48, 67-70, 91, 204, 263, **317**, **330**, 361, 406, 422.
interference competition: 224, 413.
International Institute of Tropical Forestry: 59, 80, 107, 287, 291, 296, 310.
invertebrates: 54, 67, 204, 219, 226, 230, 235, 251, 255, 272, 277, 292, **328**, 377.
Jamaican walnut: 31, 76-77.
Jardin Botánico: 370.
Jones Act: 10-11.
Juglans jamaicensis: 73, 76-77, **326**, 348, 353.
kapok: see *Ceiba pentandra*.
karst: 20, 23, 37, 38, 44, 48, 66, 71, 80, 95-102, 120, 124, 143, 188, 298, 301, 304, **316**, **327**, **334**, 369, 370, 372, 373, 374, 392, 401, 412, 413.
La Parguera: 69, 120, 209, 222, 248, 249, 250, 253, 255, 258, 260, 263, 301, **321**, **322**, **325**, **327**, 363, 377-382 passim.
lacunae: 220, 223, 413.
lacustrine: 165, 413.
lagoon: 49, 165, 169, 195, 207, 213, 214, 219, 223, 225, 239, 242, 244, 250, 254, 255, 256, 257, 258, 259, 281, 301, 302, 306, 307, 376, 377, 379, 382, 405, 411, 414.
Laguna Cartagena Refuge: 382.
Laguncularia racemosa: 167, 169, 195, 201, 353.
Lake Tortuguero: 49, 173.
landslides: Preface, 25, 106, 111, 131, 276, 277, 282, 284, **331**, **334**.
Las Cabezas Nature Reserve: 373.
leaves: 28, 29, 37-41 passim, 43, 53, 54, 66, 75, 77, 84-86 passim, 91-93 passim, 101, 102, 105, 106, 109-121 passim, 125, 127-131 passim, 139, 141, 144, 145, 149, 152-156 passim, 156, 162, 167, 177, 178, 181, 182, 184, 186, 196-203 passim, 206, 210, 216, 220-225 passim, 285, 372, 379, 404, 408, 411-420 passim.
Lesser Antilles: 5, 19, 27, 35, 46, 162, 263, 273, **329**, 388, 406, 414, 424.
lianas: 62, 289.

life zones: 79, 80, 82-84 passim, 104, 108, 112, 113, 114, 125, 131, 132, 196, **313**.
limestone: 23-26 passim, 75, 94, 95, 98, 103, 170, 184, 189, 193, 202, 235, 244, 268, 301, 370, 373, 376, 401, 413, 414, 420, 421.
limestone hills: 3, 95, 99, 373, 376.
littoral zone: 199, 261.
long-spined black sea urchins: 191.
lower montane forests: 80.
wet: 125, 128, 131-132.
rain: 82, 132-133.
lower montane life zones: 125.
Luquillo Experimental Forest, Luquillo rain forest, Luquillo Mountains: 20-21, 35-36, 88, 95, 102, 106-110 passim, 114-116 passim, 128-135 passim, 157, 171, 284, 285, 291-294 passim, 297-299 passim, **312**, **315**, **319**, **320**, **321**, **323**, **327**, **332**, **338**, **340**, **341**, **342**.
macroepiphytes: 118, 130.
mammals: 44, 45, 47, 51, 63, 64, 67, 71, 72.
manatee grass: 169, 221, 224, 252, 349.
mangoes: 1, 64, 154-156, 366.
mangroves: 1, 31, 32, 104-105, 169, 170, 201, 203-205 passim, 208-214 passim, 228, 246, 301-302 passim, **312**, **316**, **317**, **318**, **319**, **322**, **324**, **329**, **332**, **333**, **335**, **336**, **337**, **339**, 378, 384, 394, 410, 411.
black mangrove (*Avicennia germinans*): 31, 32, 167, 169, 195, 198-200, 201, 207, **330**, 345, 379, 418.
red mangrove (*Rhizophora mangle*): 32, 69, 128, 167, 169, 195, 196-200, 203-207, passim, 210, 219, **328**, **330**, 351, 373, 378, 379, 381, 387, 411, 424.
white mangrove (*Laguncularia racemosa*): 167, 169, 195, 201, 353, 410.
buttonwood mangrove: 180, 189, 192, 195, 346.
mangrove swamp: 1, 51, 57, 157, 169, 197, 200, 204, 207, 210, 211, 213, 227, 239, 245, 249, 261, 263, 278, 281, 298, 300, 301, 306, **319**, 364, 379, 399, 422.
Maricao: 23, 52, 55, 108, 113, 123, 136, 300, 353, 369.
mariculture: 266, 414.
marine: 1-4 passim, 15, 17, 34, 42, 45, 47, 48, 51, 72, 74, 86, 157, 166, 169, 170, 181, 203, 211, 213-215 passim, 219, 222, 223, 227, 229, 232-300 passim, **311**, **312**, **313**, **314**, **318**, **322**, **325**, **328**, **331**, **335**, **337**, **341**, 353, 363, 377, 380, 399, 404-415 passim.
marine reserves: 260, **316**, **318**.

marl: 23, 376, 377.
marshes: 157, 165, 168-171 passim, 197, 211, 424.
microepiphytes: 118, 130, 154.
microphylly: 85.
migration: 14, 34, 44, 52, 56, 58, 60, 63, 151, 177, 214-216 passim, 284, 287, **317**, **323**.
mitigation: 171, 172, 307, 415.
mogotes: 28, 98, 100.
Mollisols: 25.
mongoose: 47, 51, 53, 57, 306, 358.
Herpestes auropunctatus: 358.
monoculture: 9, 58, 62, 131, 136-138 passim, 145, 162, 196, 198, 404, 415.
mountain oak: 130, 134.
Musa paradisiaca: see bananas.
mutualism: 264-265 passim, **315**, 416.
Myrtaceae: 30, 31, 35.
nematocyst: 407, 416.
Neotropical migrants: 57-63, 145, 372.
niche: 49, 53, 55, 266, 277, 416.
obligate upland: 168.
obligate wetland: 167.
oligotrophic: 249, 416.
Operation Bootstrap: 11, 411.
orchids: 30, 31, 63,71, 73, 74, 102, 107, 114, 117-119 passim, 121-125, 134, 172, **311**, 371, 377, 419.
Organic Act: 9-10.
orographic rain shadow: 19, 20, 27, 86, 417.
palo Colorado: see *Cyrilla racemiflora*, 73, 115, 125, 127, 128, 131-133 passim, 167-168, 295, 349.
palustrine: 161, 165, 168, 172, 302, 307, 417.
palm brake: 115, 116, 128, 131-133 passim.
parrot(s): 57, 171, 276, 292, 293, 297, **339**, 355, 393.
parthenocarpic: 150, 417.
Partners in Flight: 59, 392.
Peltophryne lemur: 47, 48, 89, 354.
petroglyphs: 368, 417.
phase shift: 261, 263, 271, 280, **329**, 417.

phosphorescent bay: 209, 258, 301, 308, 377-379 passim, 382, 385.
phytoplankton: 177, 237, **338**, 418.
pineapple: 32, 79, 104, 137, 141-143, 350, 366, 415.
Plumeria rubra: 32, 88, 92-93.
pneumatophores: 32, 163, 198-199, 200-201 passim, 410, 418.
Poaceae: 31, 32, 137, 221.
poison plants: 155, 289.
pollinators: 64, 118, 120-123 passim, 277, 413, 418.
Polypodiaceae: 30-31 passim.
polyps: 188, 235, 237, 242, 254, 257, 259, 264, 405, 416, 421.
postcard tree: see *Clusia rosea*, 345.
Prestoea montana: 114, 115-116, 128, 131, 134, 167, 168, **327**, **332**, 351.
prop roots: 32, 43, 115, 131, 195-210 passim, 419.
Psilotum nudum: 31, 163, 353.
Pterocarpus officinalis Jacq.: See bloodwood and 104.
Puerto Rican boa: see *Epicratus inornatus*, 292, 359.
Puerto Rican Conservation Trust: 298, 303.
Puerto Rican parrot: see *Amazona vittata*.
rain shadow: 1, 19, 25, 86.
rear zone: 242, 255.
reclamation: 172, 173, 186, 211, 302, 419.
recovery plans: 71, 390.
reef(s): 242, 419.
    reef crest: 242, 419.
    reef flat: 242.
    fringing reefs: 51, 239, 242, 248, 255, 256, 411.
    reef front: 419.
    patch reef: 242, 255, 417.
reptiles: 44-51 passim, 54, 67, 71, 72, 230, 287, **318**, **336**, **337**, **338**, 359-360, 371, 402.
    Caiman crocodiles: 50, 53, 359, 360, 377.
    Caretta caretta: 50, 72, **312**, 359.
    Chelonia mydas: 45, 50, 72, 227, 230, **312**, 359.
    green sea turtle: 50, 72, 222, 227, 230, 359.
    loggerhead turtle: **312**.
    sea turtles: 45, 50 72, 172, 221, 222, 232, 306, 382, 388-391 passim, 394.
    spectacled caiman: 50, 359, 360.

rhizomes: 148, 177, 179.
riparian: 58, 181, 290, 420.
riverine estuary: 213, 217.
roble de sierra: 129, 130, 351.
rocky shorelines: 184, 188.
saline: 88, 198, 219, 306, 412, 420.
salt flats: 169, 171, 300, 306.
sandy beach: 3, 27, 174-188 passim, 248, 249, 300, 377, 379.
scleractinia: 233, 254, **341**.
sea grape: see *Coccoloba uvifera*.
seagrass (beds): 1, 50, 51, 157, 169, 170, 177, 203, 213, 219-232 passim, 237, 242, 245, 249, 254, 255, 261, 263, 278, 281, **313**, **314**, **322**, **325**, **327**, **328**, **329**, **330**, **334**, **335**, **336**, **339**, **341**, 349, 351, 373, 377-381 passim, 387, 414, 420, 422.
sedimentation: 21, 223, 232, 246, 256, 280, 420.
seed bank: 297, 420.
serpentine: 31, 94, 102, 108, **312**, **323**, 351, 369, 420.
shoal grass: 169, 221, 223-226, 252, 351.
sierra palm: see *Prestoea montana*, 114, 115, 116, 128, 131-134 passim, 167, 168, 196, 295, 301, **332**, 351.
sink: 263, 421.
sinkholes: 23, 44, 98, 102, 300, 370, 374, 384, 403, 413, 418, 421.
slope zone: 242.
soils: Preface, 19, 20, 25, 26, 44, 76, 84, 88, 93, 94, 101-109 passim, 116, 129-132 passim, 136, 138, 143, 145, 152, 157, 162, 166-169 passim, 182, 183, 193, 196-199 passim, 207, 210, 211, 267, 282, 284, 292, 293, 298, 300, 308, **320**, **323**, **324**, **333**, 352, 377, 408-410 passim, 412, 414, 420-424 passim.
solution cave: 370, 374.
source: 7, 11, 17, 19, 23, 30, 34, 35, 68, 69, 72, 83, 85, 89, 113, 118, 135, 144, 147, 151, 154, 186, 197.
Spathodea campanulata: 1, 27, 28-29, 33, 36, 134, **326**, 345.
species:
- charismatic: 42, 406.
- endangered: 2, 35, 41, 45, 50, 70-71, 74, 75, 76, 101, 124, 161, 172, 269, 306, 367, 382, 387, 390, 391, 392, 406, 409, 419.
- keystone: 413.
- naturalized species: 34, 36, 123, 183, 416.

threatened species: 245, 423.
Stahlia monosperma: 73, 75, 305, 346.
stranglers: 105, 119, 120, 422.
stressors: 58, 62, 192, 206, 209-211, 232, 267.
submerged aquatic vascular vegetation: 219.
submergent vegetation: 166, 376.
succulents: 85.
sugarcane: 1, 7, 20, 25, 32, 48, 79, 104, 113, 137-141, 143, 144, 149, 162, 170, 307, 352.
supralittoral: 177-179 passim, 190, 422.
sustainability: 3, 309, 422.
swamp bloodwood: see *Pterocarpus officinalis* Jacq., 161, 162-163, 167, 168, 214, 352.
swamps: 1, 3, 51, 57, 125, 157, 162, 165-169 passim, 197, 211, 213, 214, 227, 239, 245, 249, 261, 263, 278, 281, 300-302 passim, 304, 306, **319**, 364, 379, 395, 422, 424.
sweet orange: 151, 153, 154.
Swietenia mahagoni: 36, 93, 353.
symbiosis: 123, 213, 235, 263, 264, 266, **315**, **331**, **332**, **334**, **336**, **406**, **422**.
Syringodium filiforme: 169, 221, 224, 225, 252, 349.
Tabebuia rigida: 129, 130, 134, 351.
tabonuco: see *Dacryodes excelsa*, 65, 107, 108, 115, 125, 132, 134, 295, **327**, **332**, 352.
termitophiles: 67, 68, 423.
Thalassia testudinum: 166-169 passim, 221-225 passim, 252, **325**, 353, 378-380 passim.
tide pools: 190-192.
Tillandsia recurvata: 120, 345.
Trade Winds: 1, 19, 20, 46, 86, 267, 273, 291, 423.
tree ferns: see *Cyathea arborea*, 106, 133, 347, 351, 352.
trumpet tree: see *Cecropia schreberiana*.
turbidity: 219, 223, 236, 249, 268, 278, 279, 423.
turtle grass: See *Thalassia testudinum*.
Ultisols: 25.
urban forest interface: 285, 287, 289, 423.
urbanization: 3, 19, 25, 33, 79, 172, 209, 282, 287, 423,
vector: 27, 43, 64, 77, 112 155, 183, 199, 277, 365, 366, 408, 413, 423.