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Puerto Rican Karst—A Vital Resource

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COVER: *A portion of the karst belt in northwestern Puerto Rico as seen in a Landsat Thematic Mapper image dated 1992 with TM bands 7, 5, 2, in RGB color space. The area extends between the Río Grande de Arecibo and Dos Bocas reservoir in the east and the Río Guajataca and Guajataca reservoir in the west. The Río Camuy river in the center, along with the other rivers, flows through canyons with dramatically steep sides that create visible shadows in the image. Both reservoirs, appearing black in the image, are critical to water resources for the entire island. Representing a portion of the proposed conservation area, the forest appears as a dark green cover that steeply dissects the karst hills. Urban areas, including the coastal city of Arecibo that is visible in the upper right quadrant of the image, are light pink to white in color. Agriculture and pasture lands are bright yellow to light green.*

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Abstract

The limestone region of Puerto Rico covers about 27.5 percent of the island's surface and is subdivided into the northern, southern, and dispersed limestone areas. All limestone areas have **karst**¹ features. The karst belt is that part of the northern limestone with the most spectacular surficial karst landforms. It covers 142,544 ha or 65 percent of the northern limestone. The karst belt is the focus of this publication, although reference is made to all limestone regions. The northern limestone contains Puerto Rico's most extensive freshwater aquifer, largest continuous expanse of mature forest, and largest coastal wetland, **estuary**, and underground **cave systems**. The karst belt is extremely diverse, and its multiple landforms, concentrated in such a small area, make it unique in the world. Puerto Rico's karst forests—whether dry, moist, or wet—share common physiognomic and structural characteristics. Karst forests contain the largest reported number of tree species per unit area in Puerto Rico. Both fauna and flora are rich in taxa; and many rare, threatened, endangered, and migratory species find refuge in the karst belt. Almost all fossil records of Puerto Rico's extinct flora and fauna come from the karst belt.

Twenty-two percent of the island's population uses ground water. The northern limestone supplies 22 percent of the island's public facilities freshwater withdrawals. Seventy-nine percent of the water withdrawn in the northern limestone is ground water, and 340,000 people use this water. Construction in karst is difficult, expensive, and hazardous. Because of its rugged terrain and poor soils for agriculture, the karst belt has a low population density and among the lowest human impacts on the landscape. The karst belt is considered a **wilderness** of ecological and subterranean systems and of karst landforms. Few human dwellings, a continuous forest cover, few or no roads, and no commercial agriculture characterize a portion of the karst belt. In fact, the karst belt of Puerto Rico now represents some of the least disturbed karst habitat remaining in the Caribbean. Nevertheless, the limestone region as a whole is vulnerable to human activities, including cutting vegetation, paving forests, draining and filling wetlands, conversion and transformation of land uses, aquifer overdraft, and contaminating and poisoning ground water. In the northern limestone, rural populations dispose all sewage directly into the natural environment. The karst is vital to Puerto Rico

because its natural resources and environmental conditions provide essential services to the rest of the island, including sustaining quality of life and a prosperous economy. Water, recreation, open space, scenery, biodiversity, wilderness, ecological functions, and abundant natural resources are products and services that the karst terrain offers. The karst needs to be conserved so that the island can continue to receive the full benefits it provides. We propose setting aside 39,064 ha (27 percent) of the karst belt. These lands should be transferred into the public domain to ensure the conservation of a core of natural karst for future generations.

“The North Coast Limestone area, outside of the San Juan area, is one of the few sparsely populated areas in Puerto Rico, and it possesses unique esthetic and geologic qualities in addition to being the last large and undeveloped source of ground water on the island.”

Giusti and Bennett (1976 p ii).

¹ Technical terms shown in **bold** in this report are defined at the end of the document under **Terminology**.

Introduction

Remote sensing images of Puerto Rico show a continuous east-to-west oriented narrow band of closed forest from the northwestern corner of the island almost to San Juan (see cover). This belt of closed forest is only interrupted by the canyons and valleys of several rivers—such as the Río Guajataca, Río Camuy, Río Grande de Arecibo, Río Grande de Manatí, Río Cibuco, and Río de La Plata. These rivers flow northward to the Atlantic Ocean, creating blocks of forest lands that are noteworthy for the scarcity of surface drainage (figure 1) and the prevalence of underground drainage. These lands constitute the karst belt of the northern limestone. As we will show in this publication, the karst belt has been, and continues to be, a critical natural area in Puerto Rico. Its vast natural resources nurtured Puerto Ricans when the island had an agrarian economy. However, the region was deforested. With the abandonment of agricultural activities and a rapid shift in the economy of the island during the second half of the 20th century, forests recovered and the region's water resources powered industrialization. Unfortunately, pollution degraded surface and ground water. Today, Puerto Rico is poised for another economic transformation and the karst belt is available to support the higher level of environ-

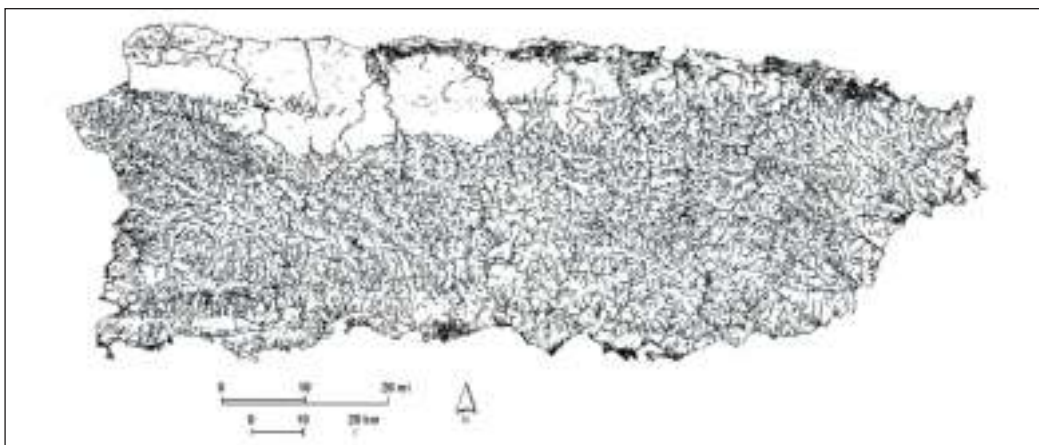


Figure 1. A map of Puerto Rico showing rivers, streams, and channels (U.S. Geological Survey database). The area without an appreciable network of rivers and streams on the northwest coast corresponds to the sector of the karst belt where the dominant drainage pattern is underground. Some of the channels in the northwest are not natural and belong to the Isabela Irrigation District.



Figure 2. Map of Puerto Rico showing the principal physiographic divisions (Monroe 1976). The karst belt is where karst features are most common. Limestones underlie some of the discontinuous coastal plains, such as those on the north coast.

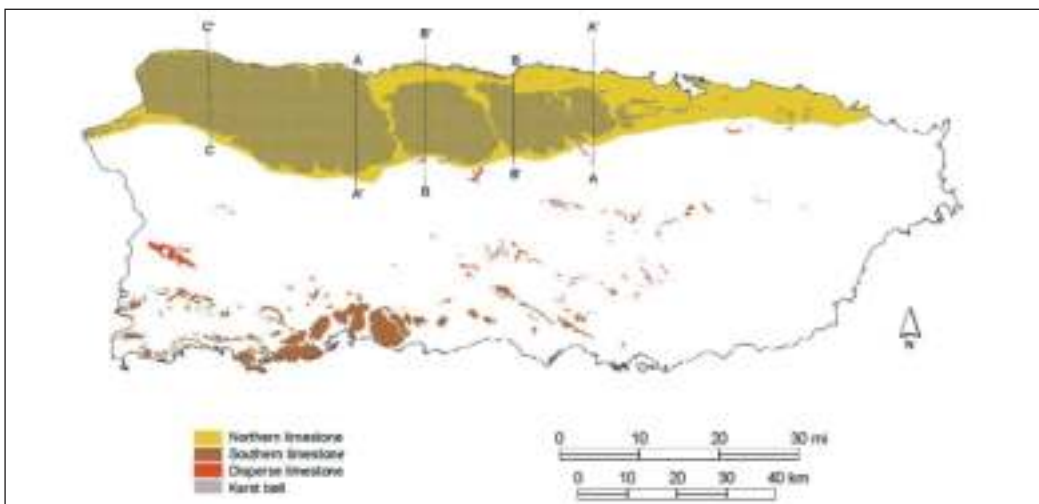


Figure 3. The limestone region of Puerto Rico according to Monroe (1976). The northern limestone includes the karst belt. Vertical lines with letters identify the location of geologic cross sections presented elsewhere in this publication.

mental health and quality of life needed in the 21st century. Our objective is to review the available literature on the karst belt, with the purpose of justifying a conservation ethic for its valuable natural resources and for suggesting that a portion of the karst belt be transferred to the public domain.

Geography of Puerto Rico's Limestone Region

Picó (1950) subdivided Puerto Rico into 11 geographic regions, one of which was the humid northern foothills (table 1). This geographic region included the inland limestone belt and Atalaya Hills, but Picó recognized no other limestone region. Monroe (1976) divided Puerto Rico into three physiographic regions: the karst belt, the mountainous area, and the discontinuous coastal plains (figure 2). Monroe's discontinuous coastal plains included buried karst with no visible solution features. Therefore, the extent of karst in Puerto Rico is much broader than implied by the area of Monroe's karst belt because karst features occur outside the karst belt.

For this review, we digitized Monroe's (1976) map of limestone areas and karst landforms of Puerto Rico. The map did not include adjacent islands—Mona, Monito, Desecheo, Caja de Muertos, and Vieques². Of these, Mona is

Table 1. Area of geographic regions in Puerto Rico. This table was prepared by Fernando Gómez Gómez based on Picó et al. (1975). Totals may not add due to rounding.

Geographic Region	Area (ha)	Percent of Total Area
1. Northern Coastal Plain	119,395	13.3
A. Subhumid western area	33,377	3.7
B. Humid alluvial area	86,018	9.6
2. Humid Valleys of the East Coast	27,800	3.1
A. Fajardo area	9,864	1.1
B. Naguabo-Humacao valleys	11,365	1.3
C. Yabucoa valley	4,939	0.6
D. Maunabo valley	1,632	0.2
3. Caguas Valley	12,868	1.4
4. Valleys of the West Coast	23,208	2.6
A. Culebrinas-Culebras valley	4,217	0.5
B. Córsega area	462	0.1
C. Añasco valley	4,665	0.5
D. Guanajibo valley	13,864	1.6
5. South Coastal Plain	87,779	9.8
A. Ponce-Patillas coastal plain	47,067	5.3
B. Tallaboa valley	2,210	0.2
C. Guayanilla-Guánica area	6,080	0.7
D. Lajas valley	13,763	1.5
E. Southwest mountain belt	18,659	2.1
6. Semiarid Southern Foothills	88,270	9.9
7. Humid Northern Foothills	185,956	20.9
A. Cretaceous northeast area	66,549	7.5
B. Interior limestone belt	95,852	10.7
C. Atalaya hills	23,555	2.6
8. Humid Mountains of the East	133,561	15.0
9. Rainy Mountains of the West	171,168	19.2
10. Sierra de Luquillo	21,331	2.4
11. Vieques, Culebra, and Mona	21,400	2.4
A. Vieques	13,200	1.5
B. Culebra	3,000	0.3
C. Mona	5,420	0.6
Total	892,736	100

the most important in terms of its limestone formation and biodiversity (box 1). Using Monroe's map, we classified various regions of the island (figure 3) and estimated their areas (table 2).

We use the following terminology when referring

to the various limestone areas of Puerto Rico: limestone region refers to all the limestone areas in Puerto Rico including areas where the limestone is buried under alluvial soils or blanket sands. The limestone region is subdivided into three

areas—northern, southern, and dispersed limestone. Northern limestone corresponds to the north coast limestone area including limestones covered by blanket sands and alluvial soils. The northern limestone

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Box 1. Mona Island: The Galápagos of the Caribbean.

Mona is a 5,500 ha tectonically uplifted carbonate island located between the Dominican Republic and Puerto Rico (Aron 1973, Frank et al. 1998a). The island forms a meseta with a gentle tilt to the south, bounded by vertical cliffs on all sides. Cliffs rise from 20 m above the sea on the south to 80 m above sea level on the north. The meseta consists of two Miocene-Pliocene carbonate units: the lower Isla de Mona

Dolomite and the upper Lirio Limestone. Along the southwestern and western side of the island, a 3- to 6-meter-high Pleistocene fossil reef abuts the base of the cliff to form a narrow coastal plain (Frank et al. 1998a). Frank et al. (1998b) considered Mona Island "one of the most cavernous localities on Earth" (p 82). Tarhule-Lips and Ford (1998) suggested that **condensation corrosion**

continue to next page

² Two maps (figures 2 and 16) contain the most important geographic locations mentioned in this publication.

Box 1. continued from previous page

occured at the entrance of some caves in Mona. Karst features include (Frank et al. 1998a):

- A series of flank margin caves developed at the contact between the Lirio Limestone and Isla de Mona Dolomite literally ring the periphery of the island
- A series of large nested sinkholes known as Cuevas del Centro
- A dissolutional valley formed along a fracture known as Los Corrales de los Indios
- Camino de los Cerezos, a pit area containing a large number of vertical shafts, and
- The surface of the meseta which has been etched by dissolution into small-scale pits

Mona is subject to the easterly trade winds year round. However, its westerly position relative to the main island, permits the passage of more cold fronts and this probably accounts for the higher rainfall during winter, compared to Puerto Rico (Calvesbert 1973). The life zone of the island is subtropical dry forest *sensu* Holdridge (1967).

It is believed that Mona never had a connection to other landmasses. For this reason, all nine taxons of Mona's herpetofauna are endemic. They are *Eleutherodactylus monensis*—Mona Tree Frog, *Monachelys monensis*—an extinct turtle, *Sphaerodactylus monensis*—Mona Gekko, *Anolis monensis*—Mona Anole, *Cyclura cornuta stejnegeri*—the endangered Mona Island Iguana, *Ameiva exsul alboguttata*—Siguana de la Mona, *Typhlops monensis*, *Epicrates monensis monensis*—Mona Island Boa, and *Alsophis portoricensis variegatus*. The macroscopic invertebrate fauna of Mona caves includes: 46 nonaccidental species, 25 species known by species name, 2 endemic troglobites, 1 additional troglobite, 3 endemic trogloniles, 34 trogloniles, and 16 guanophile mites (Peck and Kukulova Peck 1981). Mona contains more endemic animal species than all Puerto Rico's other offshore islands combined, including Vieques and Culebra (Raffaele 1973). Birds are also an important component of Mona's ecology. Thousand of seabirds, such as the White-tailed Tropicbird, boobies, and the Magnificent Frigatebird, nest on Mona (Raffaele 1973). Mona Island is a wildlife refuge administered by the Puerto Rico Department of Natural and Environmental Resources.

The vegetation of Mona resembles that of other subtropical dry forests in Puerto Rico and the Dominican Republic (Calvesbert 1973, Woodbury 1973). A short open canopy forest dominated by small trees and shrubs covers most of the island. Despite its dry climate and small size, Mona shows considerable diversity of plant communities. In mapping the vegetation of the island, Cintrón and Rogers (1991) recognized 10 distinct plant associations. Where natural conditions or disturbance are severe, a cactus forest develops. On the deeper soils in sinkholes and depressions, large and high forest trees are present (Cintrón 1979). The best-developed forests in Mona are at the foot of the west-facing cliffs, where moister and deeper soils are protected from wind and salt spray (Rogers 1974). Approximately 11 percent of Mona's flora is either rare or endangered (Woodbury 1973). This vegetation is heavily impacted by the presence of introduced pigs and goats. Most of the damage to vegetation caused by these alien species are by root and bark consumption (Cintrón 1979). Pigs and goats are also having an effect on wildlife, such as the

endangered Mona Island Iguana and the Mona Boa (*Epicrates monensis*) (Ruiz and Chabert 1989).

The caves of Mona are numerous and have been historically used by the Amerindians. A Taino site in Mona was dated to be 360 ± 60 years before present, a date that coincides to the first contact between Taino populations and Europeans (Frank 1998a). The island was exploited for its rich deposits of phosphorite, a granular material derived from bat guano and composed largely of calcium phosphate (Aron 1973). This guano was used as a phosphate fertilizer. For decades, battles were fought for the control of Mona's guano deposits (Arana Soto 1969). The first official concession to extract guano from Mona was made in 1871 to an Englishman named Jackson Hughes (Wadsworth 1973). Guano was extracted from the island until the mid- 1920's, when the Mona Island Phosphate Company sold the franchise to the Chatham Coal & Coke Company of Savannah, Georgia, but this company apparently never extracted guano from Mona (Wadsworth 1973). Today, the history of mining in the island can be reconstructed from relics present in caves (Frank 1998b).

Remoteness and difficult access are the main reason why Mona has survived human pressure. Sandy beaches are very limited and at the present time access to the island is restricted to two beaches: Sardinera and Pájaros. Mona Island does not have any surface water and freshwater resources are limited to a few water wells and rainwater. The island has a freshwater lens that reaches up to 20 m in thickness on the southern end of the island (Richards et al. 1998). Because of differences in hydraulic conductivity, the freshwater lens is not radially symmetrical over the geography of the island. Ground water ranges from sulfide-rich and brackish to oxygenated and brackish (Wicks and Troester 1998). Cintrón et al. (1978) found that an inland mangrove forest in Mona Island was taller than expected because it tapped the freshwater lens below its substrate.

The island is an important nesting site for endangered marine turtles. Leatherback (*Dermochelys coriacea*), Loggerhead (*Caretta caretta*), Hawksbill (*Eretmochelys imbricata*), and Green Turtles (*Chelonia mydas*) commonly nest in the pristine waters of this beautiful island. The nesting beaches of Mona are among the few good sea turtle nesting areas remaining in the world (Wiewand 1973). With the change to American sovereignty in 1898, Mona was publicized in the continental newspapers as follows: "Mona, a fine tropical island of 10,000 acres", "Pearl of the Antilles", "a nesting site of thousands of green turtles, and surrounded by waters teeming with the finest varieties of fish" (Boston Globe on Monday, March 13, 1899, cited in Wadsworth 1973). However, the heavy exploitation of guano resources and the small but constant human settlement on Mona resulted in the introduction of many alien species, which negatively affected wildlife. Goats, cats, pigs, and rats are among the most destructive alien animals on Mona. The Mona Iguana has also been affected by the introduction of alien trees such as Australian pine (*Casuarina equisetifolia*) and mahogany (*Swietenia mahagoni*) (Wiewand 1973). In spite of these obvious human effects, the natural resources of Mona Island are among the best conserved in the Caribbean. Its natural wonders and unique flora and fauna have resulted in many people calling Mona Island "the Galápagos of the Caribbean."

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constitutes a well-defined subterranean aquifer. Southern limestone corresponds to the limestone areas on the south coast as defined by Monroe's map. Dispersed limestone includes all limestone lenses in the central zone of the island and those not included in the northern and southern limestone. The karst belt exhibits surficial karst features and is located within the northern limestone (photo 1).



Photo 1. Aerial view of the karst belt near Arecibo, Puerto Rico. Photo by J. Colón.

Karst landscapes include all landforms produced by the **solution** process—dissolving bedrock by chemical reaction—which dominates the mechanisms of landform sculpturing in karst regions (White 1988). Karst landscapes are classified according to a variety of criteria (box 2). Puerto Rico has examples of most of the types of karst landscapes illustrated in box 2. We recognize that karst features occur outside the karst belt as defined in this publication. In fact, karst features can develop at any time even if the limestone is buried, because of the possibility of subterranean solution on lands where the presence of limestone is not

Table 2. Area (ha) of the limestone region of Puerto Rico, subdivided by geographical, climatic, geoclimatic, land cover, urban cover, and soil suitability. Areas correspond to the maps in figures 3 to 5, 32, and 33. Empty spaces mean that the unit is not found in the particular region. 'Proposal' refers to lands recommended for public domain. For comparison, the area of mainland Puerto Rico is 871,336 ha (table 1).

Units	Karst Belt	Northern Limestone	Southern Limestone	Dispersed Limestone	Limestone Region	Proposal
Total Area	142544	218692	21022	4571	244285	39064
Subtropical Life Zone						
Dry forest			16763	388	17151	
Moist forest	135820	206271	4258	3766	214295	36198
Wet forest	6660	10748		398	11146	2864
Lower montane wet forest				19	19	
Geoclimatic Zone						
Dry alluvial			670	28	698	
Moist alluvial	31233	85174	38	179	85391	1616
Wet alluvial	143	626		1	627	71
Dry limestone			14764		14764	
Moist limestone	102967	107025	2973	163	110161	34371
Wet limestone	6120	6384			6384	2465
Noncarbonate dry forest			66		66	
Noncarbonate moist forest	1254	7462		3	7465	115
Noncarbonate wet forest	228	2034		55	2089	187
Dry extrusive volcanic-clastic			1029	360	1389	
Moist extrusive volcanic-clastic	366	5229	1238	3302	9769	95
Wet extrusive volcanic-clastic	168	1084		337	1421	129
Lower montane wet extrusive volcanic-clastic				19	19	
Dry intrusive			203		203	
Moist intrusive		1381	9	119	1509	
Wet intrusive	1	620		5	625	12
Dry ultramafic			31		31	
Water	64	1673	1		1674	2
Land Cover—1977-78						
Agriculture	11570	29078	525	774	30377	772
Pasture	45662	64313	2650	1455	68418	3819
Highly dense canopy forest	845	1042	12	64	1118	436
Dense canopy forest	59273	63277	12050	1068	76395	31734
Low density canopy forest	98	121	201	7	329	6
Shrub	9337	12880	4037	687	17604	1630
Mangrove	41	2911	58		2969	
Wetlands and salt flats	88	2622	10		2632	3
Rocky areas	55	98	4		102	
Water bodies	480	3030	72	35	3137	171
Development, nonproductive	15095	38773	1403	481	40657	493*
Unclassified		547			547	
Urban Cover—1977-78						
	14556	36085	1362	402	37849	493*
Urban Cover—1994						
	19272	43881	2176	509	46566	597*
Soils						
Suitable for agriculture	39830	65411	1837	390	67638	3038
Unsuitable for agriculture	102714	153281	19185	4181	176647	36026

*These lands are within the proposed area, but would be excluded from acquisition plans.

apparent. Some 50 million km² of land on Earth—20 percent of its surface—is considered karstifiable, and about 15 percent of the contiguous United States have temperate karst (Peck

et al. 1988). In Puerto Rico, the limestone region covers 244,258 ha or 28 percent of the island (table 2).

The main difference between the northern and southern limestone is

climate. Wet and moist life zones (*sensu* Holdridge 1967) characterize northern and much of the dispersed limestone, while dry life zone characterizes southern

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Box 2. Classification of karst landscapes (White 1988).

Common Types

- Doline karst—landscape dotted with sinkholes.
- Cockpit karst—high doline to area ratios but lower depression densities than doline karst.
- Cone and tower karst—a type of karst topography, common in the tropics, characterized by many steep-sided cone-shaped hills surrounded by more or less star-shaped depressions (figure B2-1).
- Fluviokarst—a landscape of deranged drainage, blind valleys, swallow holes, large springs, closed depressions, and caves.
- Pavement karst—areas of bare limestone, usually sculpted into **karren** of various types.
- Polje** karst—a landscape of poljes alternating with intermediate mountain ranges.
- Labyrinth karst—landscape dominated by intersecting solution **corridors** and solution canyons.
- Cave karst—where there are caves and well developed underground drainage with little expression in the form of closed depressions or other karst landforms.

Classification by Cover

- Covered karst—dissolved bedrock surface is covered with some sort of material, soil, or rock.
- Subsoil karst—covered with soil.
- Mantled karst—covered with **allocthonous** rock or sediments. Part of the contemporary landscape and older than its cover.
- Buried karst—covered with allocthonous rock or sediments. Not part of the contemporary landscape and older than its cover.
- Interstratal karst—covered with allocthonous rock or sediments. May or not be part of the contemporary landscape and younger than its cover.
- Subaqueous karst—covered by sea level rise: subfluvial karst, beneath a river; submarine karst, beneath tidal zone.
- Exposed karst—bare rock surface is exposed.
- Naked karst—developed and maintained without any cover or beneath a temporary cover of snow or water.
- Denuded karst—subsoil karst or interstratal karst that has been exposed by erosion of its cover.
- Exhumed karst—mantled karst or buried karst that has been divested of its cover by erosion.
- Relict karst—the topographic or physical remains of a karst that has not been covered and which most of the karsted rock has been removed by subsequent erosion.

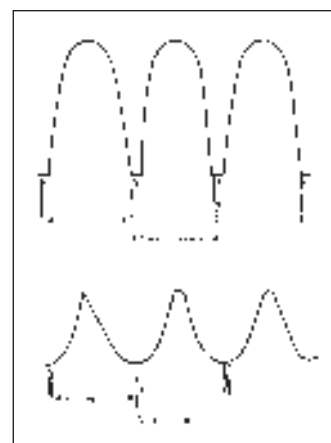


Figure B2-1. An idealized view of the distinction between cone and tower karst and cockpit karst, based on the curvature of the slopes. LF is the spacing between fractures (White 1988).

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limestone (figure 4). We found 4 life zones represented in the limestone region, but 88 percent of the region is in the moist forest life zone (table 2). About 7 percent of the limestone region is in the dry forest life zone, and 4.6 percent is in wet forest life zone. A small area of dispersed limestone is in the lower montane wet forest life zone. Climatic differences lead to different rates of **karstification** (box 3) and thus, to different landscape features. In addition, the nature of the substrate, the depositional environment and **diagenesis** also contribute to differences between northern and southern limestone landscapes. Our focus is on the northern limestone and the karst belt in particular. However, references are made to southern limestone (box 1 and 4) or dispersed limestone where appropriate.

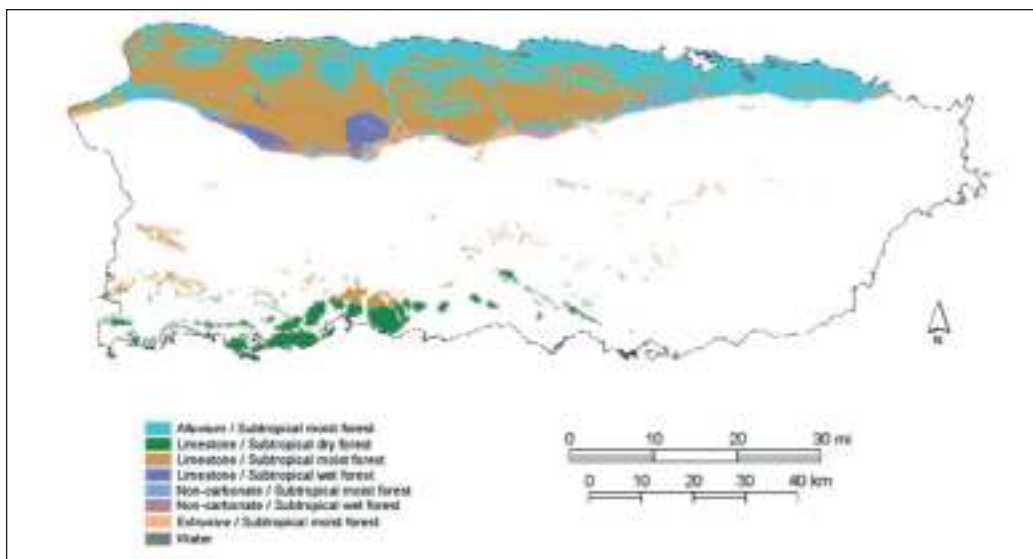
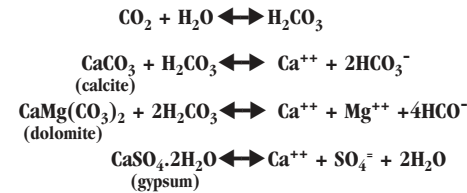


Figure 4. Geoclimatic map of the limestone region of Puerto Rico. The northern limestone is mostly on the moist forest life zone (*sensu* Holdridge 1967) with a small representation of wet forest life zone. The southern limestone is mostly on dry forest life zone with some representation of moist forest life zone.

The northern limestone extends for a distance of 140 km in an east-west direction along the north coast with a maximum width of about 22 km near Arecibo (Monroe 1976). It comprises an area of 218,692 ha or 90 percent of the limestone region (table 2). The total thickness of these limestone formations is about 1,400 m (Giusti 1978). Most of the limestone of the easternmost 25 km of the region is buried under alluvial deposits and only a few outcrops occur, so the karst landscape is most conspicuous west of San Juan and south of the coastal plain (figure 3). The area of the karst belt is about 142,544 ha (table 2), or 65 percent of the northern limestone. The highest elevation in the karst belt is 530 m above sea level and escarpments on the southern edge of the belt commonly reach 400 m in elevation.

Box 3. Karstification of limestone (Monroe 1966, 1976; Román Más and Lee 1987).

Karstification is the process of forming a type of terrain in soluble rocks with surface and subterranean phenomena that are the result of solution. Of the four chemical equations shown here, the one with gypsum is not documented for the karst belt. Giusti (1978) mapped the degree of karst development in the north coast.



This process will dissolve limestone when it shifts to the right and will deposit (precipitate) limestone when it shifts to the left. The equation will shift to:

- The right in the presence of acid water (due to CO₂ or NO₃ or SO₄)—known as **aggressive water**
- The left in the presence of alkaline water
- The left if the temperature increases, causing CO₂ to escape

- The left if the water evaporates, causing CO₂ to escape.

Karstification starts with the dissolution of the original limestone—composed mainly of marine organisms. The original limestone can be replaced by limestone that has been dissolved and reprecipitated by the action of underground water. Reprecipitated limestone into calcite, for example, can fill the shells of organisms and form a cast of their inside and outside after the shells dissolve away. Plant-derived carbon occupies the place of marine derived carbon in altered limestone. After alteration or replacement, karstification proceeds by both solution and reprecipitation.

Solution is most active underground where acidic water comes in contact with and leaches buried limestone. Solution is more prevalent in moist and wet life zones and less in dry life zones, which favor reprecipitation. Surface plant cover accelerates solution processes because they produce acid water due to respiration of organic matter (figure B3-1). Closed depressions appear as products of solution processes. Small closed depressions increase in depth

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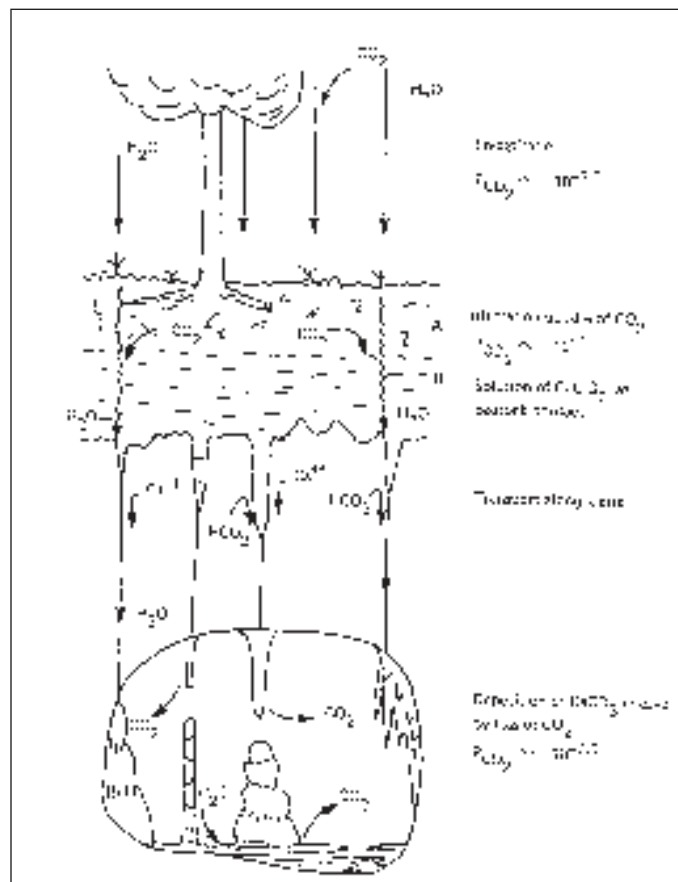


Figure B3-1. Schematic drawing of the physical model for calcite speleothem deposition (White 1988).

Box 3. continued from previous page

as more acids—from root and microbial respiration, humic substances in soil, percolating waters—accelerate the process. White (1988) identified three conditions that guide the development of karst landscapes. First, chemical driving forces—temperature, precipitation, and $p\text{CO}_2$. Second, physical driving forces—precipitation and relief. Third, the hydrogeologic setting including tectonic setting, thickness of soluble rocks, and stratigraphic and lithologic setting.

Jointed limestone is susceptible to increased rates of solution as the joints provide access and passage for acid water. Joints are enlarged by solution, and networks of small solution cavities form above and below the water table. Fractures

in the limestone also lead to enlargement through solution and to the development of drain systems (figure B3-2). Pervasive solution processes lead to underground drainage and few surface streams. Solution also leads to ground surfaces containing many **stream sinks**, or swallow holes; many closed depressions; and a network of minor features, such as low solutional spikes and ridges, on the surfaces of limestone.

Solution of limestone—which is a chemical weathering—is slower than soil erosion. Thus, limestone hills raise in relation to their base valleys covered by constantly eroding blanket deposits. Karstified limestone slopes tend to be nearly vertical.

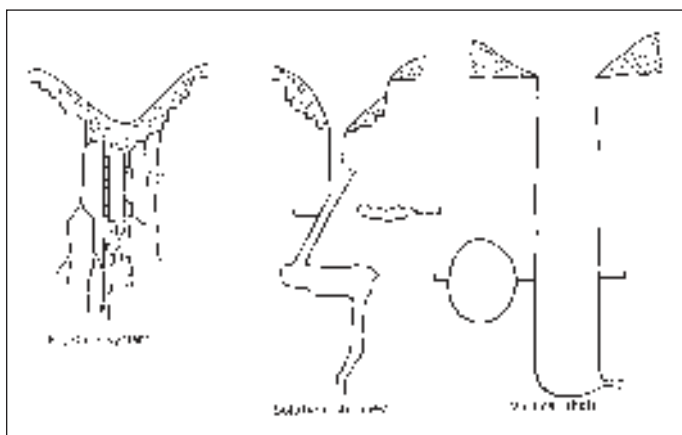


Figure B3-2. Three developments of drain systems for closed depressions: a solutionally widened fracture zone with enough permeability to permit soil transport to the subsurface; a solution chimney, which is essentially a vertical cave developed by selection of one pathway through the fracture system; and a vertical shaft such as the Empalme entrance to the Río Camuy System (White 1988).



Photo 2. Río Grande de Arecibo from Cueva Ventana, Arecibo, Puerto Rico. Photo by L. Miranda Castro.

The Karst Belt Is Spectacular

Puerto Rican karst is spectacular: a wilderness³ with a diversity of landforms, rugged topography, unusual landscapes, and contrasting vistas (photo 2).

Wilderness

“The Atalaya Hills area is one of the least accessible regions of Puerto Rico. Through its area..., not a single road crosses the region, and only a few border it. Its economic activities are very limited. Indeed there are striking contrasts between this undeveloped area and the rich adjacent sections.”

Picó (1950, p. 149).

Puerto Rico is an urban island with an average population density of over 425 people/km². The island has experienced high rates of deforestation. In the 1940’s, it reached a low

forest cover of about 6 percent with a roughly equal area in shade coffee (Birdsey and Weaver 1982, 1987); in 1990, forest cover was about 32 percent (Franco et al. 1997). The karst belt is similar to the rest of the island in terms of the history of forest cover change but with two exceptions. First, people have almost completely abandoned any occupation or use of the rugged karst belt. The density of paved state roads in the karst belt is now negligible compared with the road density of the island as a whole, which is 2.5 km of road/km² (Morales Cardona et al. 1994). Second, as early as 1977 to 1978, forest and shrub cover in the karst belt was 49 percent (table 2), higher than the average value for the island as a whole. Significant portions of the karst belt have 86 percent forest cover or more. For these reasons, this part of Puerto Rico is inaccessible and constitutes wilderness. Its forests have been recovering from past human uses for over five decades and form a continuous canopy over a large area that has very little human influence. Northern karst forests are the largest tract of continuous forest cover in the island. And because of the low human impact on these forest lands, the Puerto Rican karst belt harbors some of the least disturbed karst forests in the Caribbean.

The location of human activity in the northern limestone is almost exclusively limited to the coastal alluvial flatlands

³ The term wilderness is used in its genetic sense and not in the context of the legal definition in the Wilderness Act.

Box 4. The southern limestone (Monroe 1976, 1980).

Deposition of rocks in southern Puerto Rico began earlier and ended earlier than in the north. Rocks in southern Puerto Rico are intensively faulted while those in the north are cut by very few faults. Strata dip in a southerly direction some 10° to 30°. The karstification of limestone in dry life zones is not as common as in wet life zones because the low rainfall inhibits the rate of solution. Moreover, much of the southern limestones are buried under deep alluvial deposits—as deep as 900 m in Santa Isabel.

The Limestone Formations of the southern region are:

- Juana Díaz Formation—Oligocene and Miocene age. Coral reef origin. Basal beds of sand, pebbles, and cobbles overlain by calcareous sandy to silty clay or mudstone. Overlays the volcanic complex of central Puerto Rico. Contains several large caves and closed depressions. **Caliche** is formed on soil surfaces.
- Ponce Limestone—Miocene age. Coral reef origin. Highly fossiliferous. Contains **rock shelter caves** on vertical cliffs, and a few caves. Caliche is formed.
- Guanajibo Formation—Late Miocene, possibly Pliocene. Small outcrops of fossiliferous yellow limestone, mostly weathered to compact silt, sand, and gravel.
- Parguera Limestone—Early Cretaceous.

The Limestone Formations of adjacent islands include:

- Isla de Mona Limestone—middle Tertiary age. Contains many caves.
- Lirio Limestone—Pale and, finely crystalline limestone. Its age is late Miocene to early Pliocene. Maximum thickness of 40 m near Playa Sardinera, Mona Island. Moderately fossiliferous with accumulations of large coral heads and patch reefs near Cueva del Capitan and Cueva Centro. Extensively karstified with caves, karren, sinkholes, pits, and enlarged joints across the plateau surface (Frank et al. 1998a).



Photo 3. Human activity near the karst belt is concentrated on the flat alluvial lands. Photo by J. Colón.

between Loíza and Arecibo and nonalluvial between Arecibo and Aguadilla (photo 3). As a result of land-use patterns, karst lands south of the coastal plain are over 86 percent covered by forests (figure 5). Until the 1980's there was not a single town located on a rugged karst topography from Aguadilla to Toa Alta, a distance of about 100

km. With the exception of the small town of Florida, settlements are just north or south of the karst belt limits. Moreover, many of the inhabitants of towns on the southern limit of the karst belt served as a source of labor for economic activities outside the karst belt (Picó 1950).

The diversity and types of landforms in the karst belt, led Monroe (1976) to declare the region as a “wilderness of karst forms.” This idea was expanded by White (1988) who made the case for caves and underground drainage as wilderness of the same scale as traditional wilderness landscapes. Even in urban areas, caves can be as much wilderness as remote expanses of mountains and forests far from human civilization. The underground landscape, with its total darkness and unusual forms and shapes of rock and mineral deposits, is alien to people in comparison with familiar surface landscapes

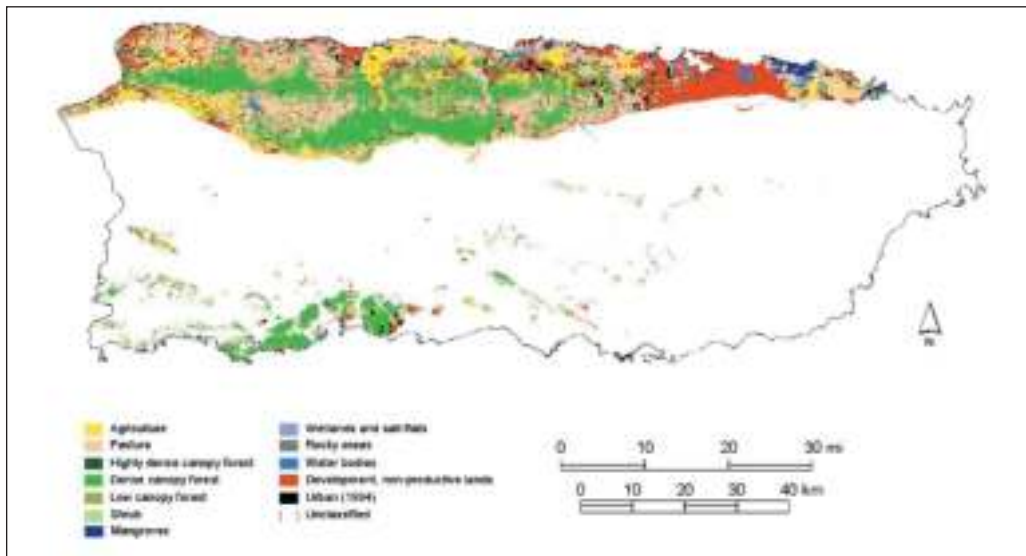


Figure 5. Map of the limestone region showing land cover types for the year 1977 to 1978 (modified from Ramos and Lugo 1994). Notice the high proportion of dense canopy forest in the proposed area of the karst belt and the Guánica area in the southern limestone.



Photo 4. Caving in the karst belt is a unique wilderness experience. These explorers are inside the Río Camuy cave system. Photo by K. Downy.

(photo 4). Caving is a genuine wilderness experience that requires solitude, a leisurely pace, and a sense of absorption in the environment, just as the wilderness experience on a mountain or in a forest (White 1988).

In summary, the karst belt is considered wilderness from three points of view. First, the low level of human influence and vast—for Caribbean island scales—expanse of closed canopy mature forests. Second, it includes karst landforms of such diversity and magnitude that few places in the world match it. Third, it contains a vast expanse of underground rivers, aquifers, and caves of unusual size and beauty.

Diversity of Landforms

“The land forms, developed on the North Coast Limestones of Puerto Rico, constitute one of the finest

examples of tropical karst in the world.”

Giusti and Bennett (1976, p. 4).

Holokarst is a term used to describe landforms with complete karstic drainage and landforms. Such landforms are rare and the few regions in the world with *holokarst* include the Adriatic and the Caribbean (White 1988). If there is mixture of karst landforms and fluvial characteristics, the region is termed *fluviokarst*. The karst belt of Puerto Rico has both types of landforms within short distances of each other.

The variety of landforms in the karst belt is notable and a product of rock type and climate. The moist and wet northern karst belt—for example—is divided into several lenticular bodies of topography corresponding closely to the lithology of the underlying rocks (Monroe 1976). These rocks vary in susceptibility to erosion, and dip generally northward between 1° near the Atlantic Ocean and 5°

Box 5. The Lares Cuesta Scarp as described by Monroe (1976, p 19).

“The most prominent single feature of the [Puerto Rican] karst area is the Lares cuesta scarp, which extends continuously from San Sebastián to Corozal, interrupted only by the alluvial valleys of the major rivers that cross the belt. The scarp is the result primarily of differential erosion of the easily weathered and eroded San Sebastián Formation and volcanic rocks below and to the south and the much more resistant limestone above and to the north; secondarily, it is the result of great landslides which have created a steep cliff by the breaking away of blocks of limestone by diminishing support below as the underlying material is eroded by gullying and sheetwash, and as the clay from the San Sebastián Formation becomes water soaked and forms a gliding surface.

The altitude above sea level of the top of the scarp ranges from a maximum of about 530 m near Caguana between Río Tanamá and the Río Grande de Arecibo to a minimum of about 200 m near Corozal to the east and near Moca and San Sebastián to the west. The relative altitude of the scarp varies, however, with the depth to which a bordering stream has cut its channel. Thus, the steepest and relatively highest part of the scarp is the part just west of Lago Dos Bocas, where the water level of the lake is about 90 m and the top of the scarp is about 430 m, a difference in altitude of 340 m. In contrast, in the area just to the west near Caguana, where the San Sebastián Formation crops out on an only slightly eroded flat at an altitude of about 430 m, the top of the scarp rises to only about 480 m, a difference of only 50 m. The latter represents what might be considered the normal differential erosion, uncomplicated by landsliding induced by nearby rapidly incising streams.”

on their southern border. **Cuestas** are landforms that result from the dipping of the underlying rocks and their differential susceptibility to erosion. They are characterized by a south-facing scarp (box 5) and a long, gently sloping northerly dip slope, commonly obscured and interrupted by a wild array of solution features, such as **closed depressions**—also known as **sinkholes** or **“dolines”** (Monroe 1976).

The Aguada cuesta has the most extensive scarp in the karst belt (Monroe 1976). It extends continuously—with breaks at river valleys—from the western part of San Juan to the west

coast at Aguadilla. Remnants of the scarp can be seen towards the east to Loíza on both sides of Río Grande de Loíza. In the southern part of the Camuy quadrangle, the scarp forms a wall about 50 m high on the upland, both east and west of the valley of Río Camuy.

Río Guajataca contains spectacular ramparts—limestone walls skirting the river canyons—that on the west bank of the river, 3 km from its mouth, reach an altitude of 165 m (figure 6, photo 5). The river flows 155 m below the top of the rampart. The west side of the rampart slopes down to a body of blanket sand 15 to 30 m below its top,



Photo 5. Río Guajataca canyon. Photo by L. Miranda Castro.

making in effect a wall between the generally flat field to the west and the river canyon to the east (Monroe 1976).

Sumidero Tres Pueblos (photo 6) is the largest collapse feature in Puerto Rico (Monroe 1976). It consists of a sheer-walled pit more than 120 m deep and about 140 m in diameter. Río Camuy flows into and out of this depression. Other remarkable geomorphic features of the karst belt—some of which will be described below—include **cockpits**, conical hills or **cone karst**, **dry valleys**, caves and subterranean rivers, rock bridges, **towers** or **mogotes**, **mogote** or **tower karst**, **cuesta karst**, broad valleys, **zanjones**, and many other minor karst features such as karren spikes. Natural windows occur in the southern karst. Southwest of Mayagüez there is an excellent example of tropical pinnacle karren with peak heights of 2 to 3 m. This type of karren is the least understood of the karren forms (White 1988).

Rugged Topography

“The ruggedness of these belts is such that many areas are entirely uninhabited, without even roads or trails crossing them; an exception indeed, for densely peopled Puerto Rico.”

Picó (1950, p. 147).

Karstification in Puerto Rico’s climate and rock types causes slopes to become nearly vertical,



Photo 6. Sumidero de Tres Pueblos. Photo by A. E. Lugo.

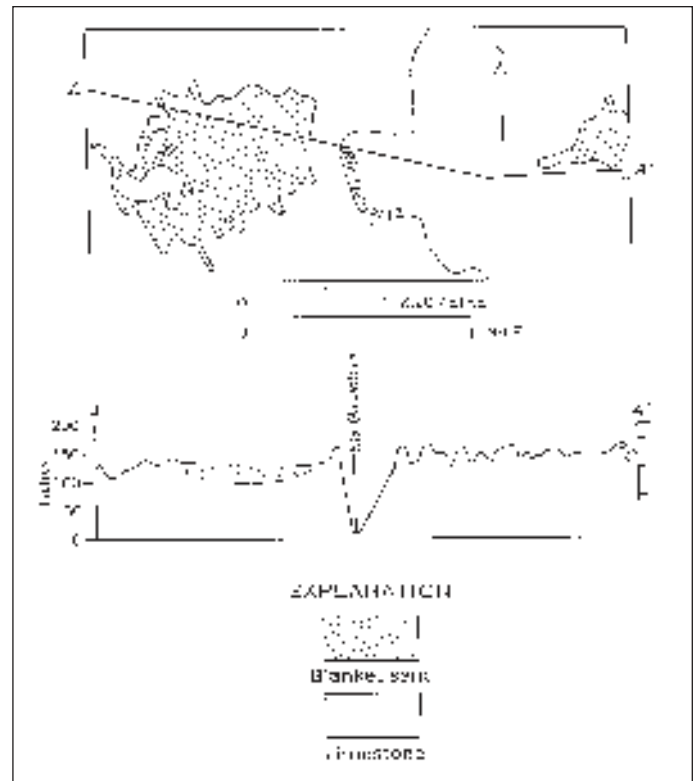


Figure 6. Map and profile showing relation of the Río Guajataca rampart to the canyon and the plain covered by blanket sand (Monroe 1976).

creating a steep topography. The dense concentration of mogotes, cockpits, and cone hills—all characterized by steep slopes—gives the karst landscape the appearance of being a corrugated surface. Traversing the karst is only feasible through valleys between hills, but even these might lead to dead ends. Many times, steep slopes are made of caps of indurated limestone over softer material, which gives way when weight is placed on it, making travel through this terrain very difficult.

The ruggedness of a sector of the karst belt was described by Monroe (1976, p 21):

“North of [the Aguada] scarp, the *cuesta* is an

extremely rugged karst topography characterized by a variety of **karst types**, especially **doline karst** in the Manatí quadrangle and by abundant polje-like valleys and **uvalas** in other areas. In a few areas, the karst is cone karst, much like that formed on the Lares Limestone, but more characteristically the surface is pitted by deep solution dolines separated by rounded ridges, which form a rough irregular slope northward to the broken wall of the Aymamón scarp. The northern part of the area, which is characterized by deep solution and collapse dolines in the Aguada Limestone

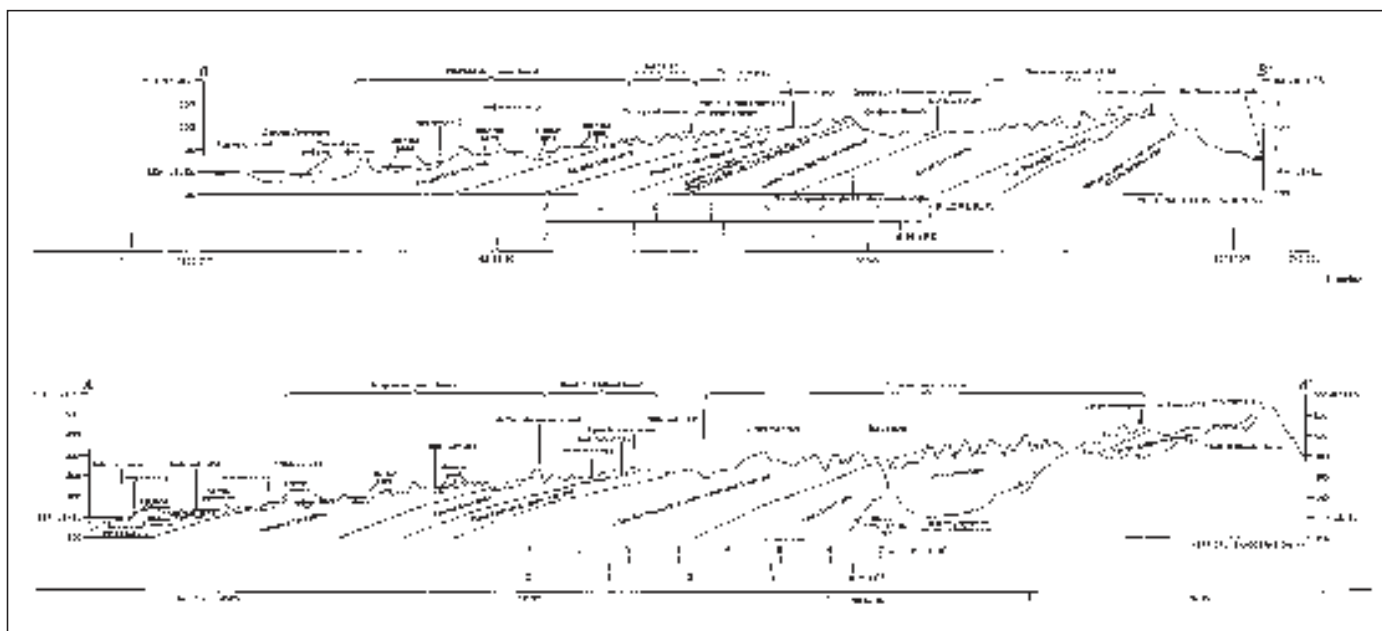


Figure 7. Topographic and geologic north-south sections of the karst belt (Monroe 1976). The sections highlight landscape features—both anthropogenic and natural—supporting geologic formations, and show brackets that classify the overall landscape feature along the sections. The location of the sections is shown in figure 3.

separated by high towers capped by the Aymamón Limestone, is the roughest area in the entire karst belt; in the Quebradillas quadrangle, many of the dolines are more than 70 m deeper than the lowest point in their rims, and the adjacent towers capped by Aymamón Limestone rise some 50 m higher. This area is traversed by sparse horse trails and footpaths, but nearly vertical cliffs make it extremely difficult to pass through. The through highways in the past have followed the larger system valleys, but the Puerto Rican Highway Authority is now beginning to build winding highways through the roughest parts of the karst, generally following the larger horse trails.”

Unusual Landscapes

In Puerto Rico and in a few other places in the world, one finds landscapes such as these formed by cuestras and cone, tower, and doline karst (figure 7). Landscapes dominated by zanjones—groups of parallel long trenches several meters deep—are unique to the karst belt of Puerto Rico (Monroe 1976). The gorges of rivers in the karst belt are spectacular. One example is that of the Río Grande de Arecibo (photo 7), which cuts through the karst with a gorge 800 to 1,200 m wide and nearly vertical walls as high as 200 m (Monroe 1976). This river has deposited over 70 m of alluvial soil over the limestone rock. Río Guajataca has gorges with nearly vertical walls 150 m

high. The coastal plain in the vicinity of Río Grande de Manatí is notable because the meanders of the river are extremely well developed. At the coastline, sea cliffs, sand dunes, and extensive riverine and basin wetlands—some of the largest in the island—dominate the landscape.

Contrasting Vistas

The vistas of the karst belt exemplify why Puerto Rico is an island of contrasts. The region contains an incredible array of topographic features and landforms in a very small area. In less than 1 hour of travel by automobile, an observer can experience an enormous array of contrast in the vistas available for enjoyment.

The observer can focus on the high density of



Photo 7. The gorge of Río Grande de Arecibo. Photo by L. Miranda Castro.



Photo 8. Río Grande de Arecibo delta. Photo by J. Colón.

rugged hills that disappear into the distance or focus on the gigantic river ramparts cutting through the landscape. On the coastline, the observer can enjoy sea cliffs or watch rough seas crash against huge sand dunes. Extensive river valleys, with large expanses of green pasture land and the meandering Río Grande de Manatí or Río Grande de Arecibo, provide an alternative view for enjoyment (photo 8). These rivers lead the

observer to extensive riverine estuaries or to coastal swamps and lagoons. Alternatively, the observer can peek into deep depressions in the ground with disappearing rivers, walk into spectacular caves, or float through one of three known underground rivers. Most of the drainage in this region is subterranean—although thousands of springs and seeps flow out of rock fissures and fall as beautiful waterfalls. Some of the



Photo 9. Cueva Larga. Photo by Fundación de Investigaciones Espeleológicas del Karso Puertorriqueño.

world's most spectacular caves are available for exploration (photo 9). These include the Río Camuy **river cave** system with over 17 km of mapped caves and 16 km of underground river, and the Río Encantado System—the longest continuously traversable underground river in the world (Courbon et al. 1989).

The Karst Belt Has Limestone of Many Ages

Limestone formations in Puerto Rico range in age from the early Cretaceous to the Quaternary—spanning some 146 million years (table 3). The oldest limestone is exposed in the eastern part of the island, west of Caguas through Cidra and Cayey (Monroe 1976). This limestone appears to have originated from fringing coral reefs on the flanks of the volcanic island (photo 10).

Early Cretaceous limestone—Parguera Limestone—is also found on the southwestern coast of the island, particularly between Guánica and the west coast. Limestone in Puerto Rico is of marine origin and has undergone little post-depositional change (Giusti 1978). After emerging above sea level, some of this original marine limestone underwent karstification (box 3) and was transformed to the limestone now on the Earth's surface. The original northern marine limestone has been seen in a core of Lares Limestone taken from 1,129 to 1,136 m below the ground surface between Arecibo and Barceloneta. In the southern limestone, the original marine limestone can be seen in chalk outcrops in the Juana Díaz Formation near Ponce (Monroe 1976).

The limestone region has rock outcrops with small amounts of chalk and dolomite, as well as gravel, sand, and clay derived from volcanic rocks of the mountains (Monroe 1976). The main limestone development in northern Puerto Rico dates from the Oligocene (some 34 to 23.5 Ma—million years ago) and Miocene (some 23.5 to 5.2 Ma) (figure 8). The sequence of limestone formations of late to middle Tertiary age of the north coast limestone (figure 9) is the product of several minor and major regressions and transgressions of the sea that occurred

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Photo 10. Puerto Rican limestone originated from ancient coral reefs, similar to this one in modern day Puerto Rico. Photo by L. Miranda Castro.

Table 3. Phanerozoic geologic timescale (Behrensmeier et al. 1992) with reference to events in Puerto Rico and elsewhere in the world. Million years ago is Ma and represent the estimated time when the Period, Epoch, or Era started. The duration of any period, epoch, or era can be estimated by subtracting the time it started from the time when the next Period, Epoch, or Era started. L = late, M = middle, and E = early.

Era	Period	Ma	Epoch	Ma	Events	
C E N O Z O I C E R A	Q U A T E R N A R Y	Anthropogene	Holocene		Humans (indians) start to populate Puerto Rico/extinction of land mammals. End of last Ice Age. Puerto Rico attains its actual form.	
				0.01		
				Pleistocene	1.64	Extinction of land mammals in Puerto Rico between this epoch and the next. Surficial deposits on the Island-- alluvium, marsh, swamp, erosion, and terraces. Glaciations-- several occur making sea levels rise and fall. Evolution of humans-- from <i>Homo habilis</i> to <i>Homo sapiens sapiens</i> .
	T E R T I A R Y	Neogene	23.5	Pliocene	5.2	Landbridge (Panama Isthmus) completed connecting South and North America. Solution of limestone-- accelerated by corrosion-- from this epoch until the present. Emergence of limestone above sea level. Many different (up to five genera) land mammal species live on the Island. Bipedal primate evolution-- from <i>Australopithecus</i> to <i>Homo habilis</i> .
				Miocene	L	Canary Formation being formed. Rising of Puerto Rico-- fracture occurs on the four sides giving it its actual shape. Beata Ridge deformation allows eastern Caribbean Plate to move separately from Western Plate
		M	Arching along the center of the island landmass, due to neogenic movements in the Caribbean, older tertiary strata emerge and north coast submerges.			
		E	Aymarán Limestone is being formed in the north. Aguada Limestone being formed in the north. Upper members of Cibao Formation being formed in the north. Ponce Limestone being formed in the south. Caribbean plate moves to the west. The landmass that stretched from the Virgin Islands to La Hispaniola is still in place.			
		P a l e o g e n e	23.5	Oligocene	L	Cibao Formation limestone members being formed in the north. Lares Limestone upper part being formed in the north. Jama Diaz formation being formed in the south.
					M	Lares Limestone being formed in the north. Jama Diaz Formation being formed in the south. San Sebastián Formation being deposited in the north. Mountains higher than 3175 m exist allowing growth of tree plant species that exist from cool to temperate climate. Amber from Dominican Republic contains many invertebrates and few vertebrates.
	E				A large island stretches from Virgin Islands to La Hispaniola. <i>Acromecurus</i> -- species of ground sloth-- roamed the landmass. Caribbean Plate starts shift to a more westerly direction.	
	Eocene			55	Rocky Mountains formed. South America isolated from other continents. Intense erosion of mountains of Puerto Rico. High mountains near Utuado and Culex	
			65	Paleocene	65	Palms, cacti, and pines evolve. Andes Mountain range develops. Birds diversify in many sub classes. Cuevas Limestone in the south. Batholith of Utuado and San Lorenzo Caribbean Plate moves west-northwest
M E S O Z O I C E R A	Cretaceous	146	L	Rising of large island from Virgin Islands to La Hispaniola. Caribbean crust actively deforming. Extinction of dinosaurs. San Germán Limestone deposit on the southwest. Volcanic islands in what today is Crecovis and Barranquitas.		
			E	Angiosperms evolve. Caribbean crust is located to the west of South America. Parguera Limestone deposited on the Southwest. Aguas Buenas Limestone deposited on the flanks of the volcanic island. Millions of years of volcanic activity create islands to the east of Puerto Rico (Greater Antilles Foldbelt).		
	Jurassic	208	Older volcanic rocks of Puerto Rico. Caribbean seaway starts to form. Western Laurasia (North America) and Western Gondwana (South America) start to break away			
	Triassic	245	Cycadophyta plants. Pangea continent starts to break away. Dinosauria Infra Class.			

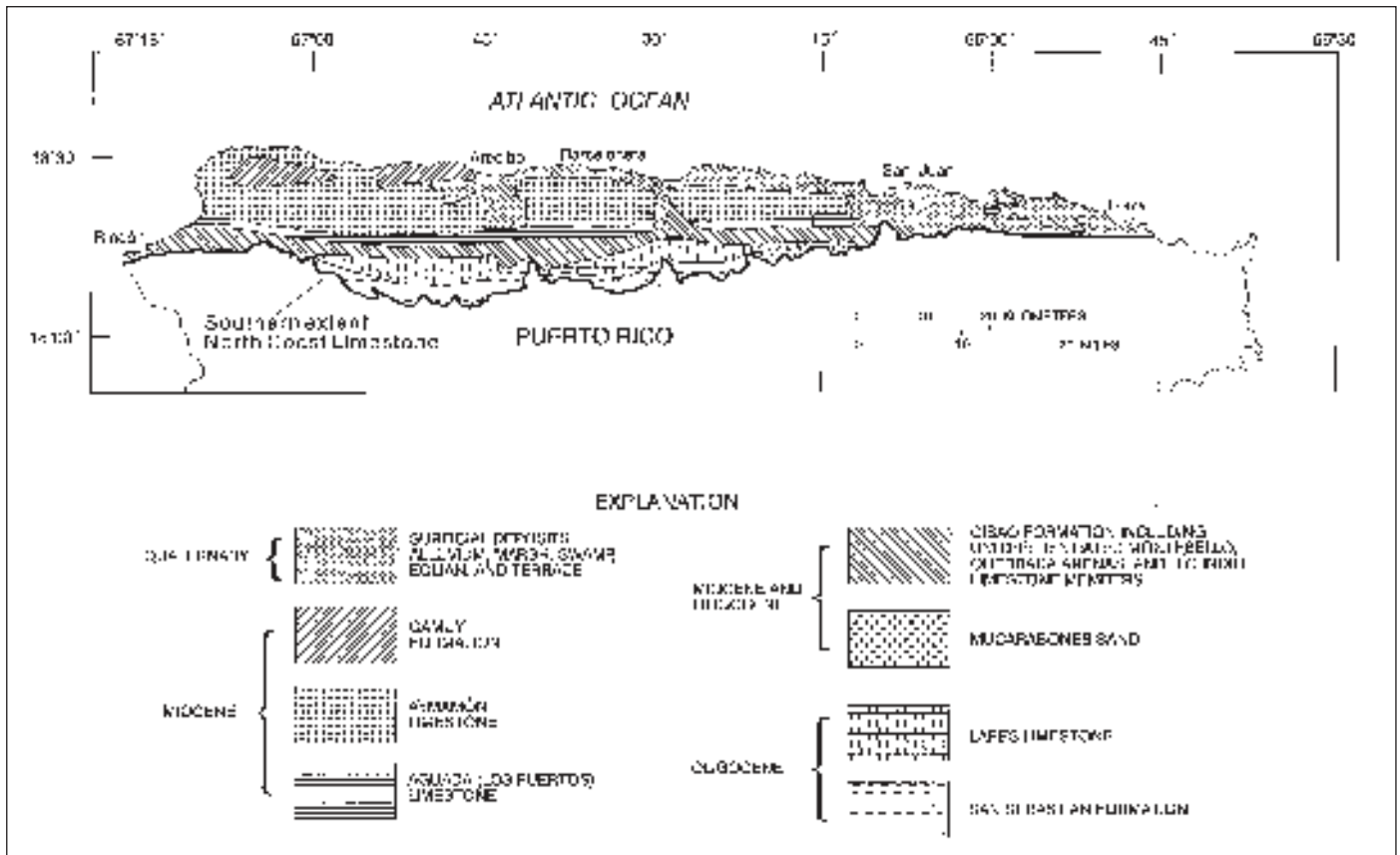


Figure 8. Generalized geologic map of the northern limestone of Puerto Rico (Rodríguez Martínez 1995).

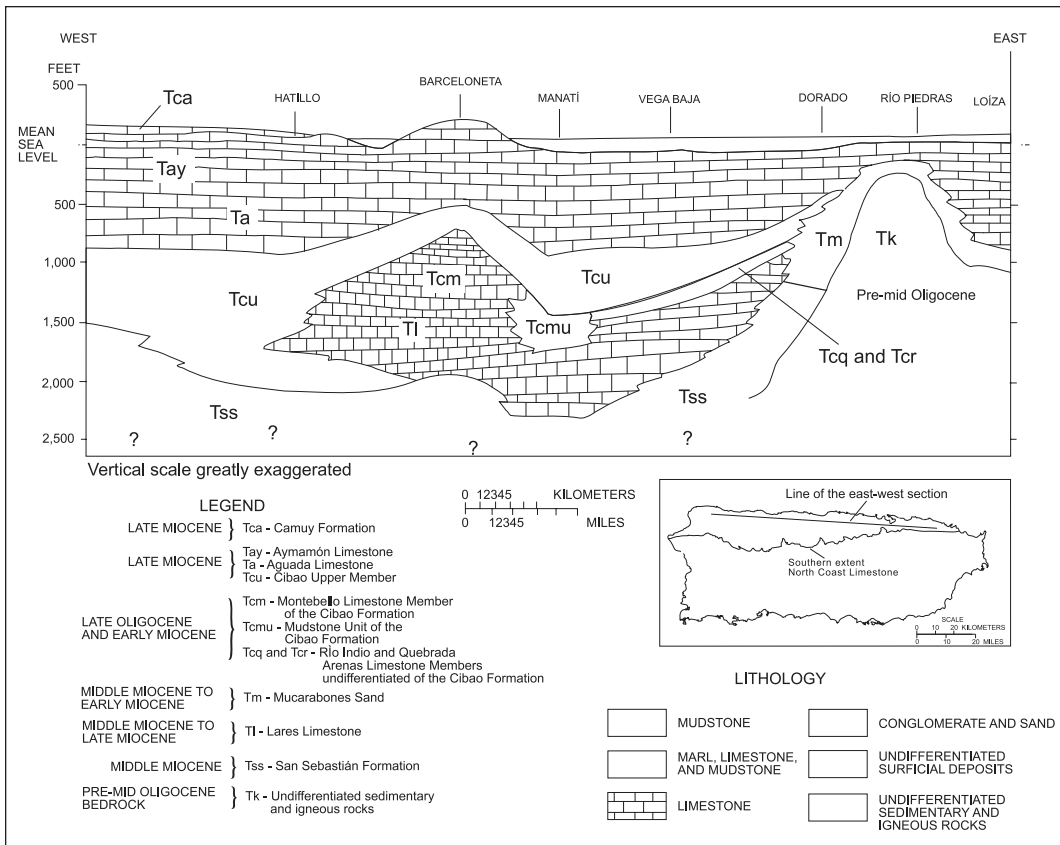


Figure 9. Generalized east-west geologic section sequence of middle Tertiary age on the northern limestone of Puerto Rico (Rodríguez Martínez 1995).

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between Oligocene and Miocene time (Seiglie and Moussa 1984).

Classification of Limestone Strata

The limestones of the north coast appear uniform, and to a nonspecialist it is hard to tell one formation from another. However, they are separated on the basis of paleontological differences (Giusti and Bennett 1976). Each type of limestone interacts with local conditions to produce particular types of karst features in the landscape (box 6). Monroe (1976, 1980) developed the nomenclature for the limestone sequences based on stratigraphy, and Seiglie

and Moussa (1984) modified it with paleontologic and lithologic data collected from two water wells in the Manatí area (Rodríguez Martínez 1995). We use the descriptions of Monroe (table 4) but show the modifications of Seiglie and Moussa (1984) and Rodríguez Martínez (figure 10).

Monroe (1976, 1980) categorized limestone strata into six formations ranging in age from the middle Oligocene to late Miocene (table 4). These formations rest on the San Sebastián Formation, which is not a limestone rock nor does it show karst features, but forms an **impermeable confining bed** below the Lares Limestone and overlies the volcanic base

of the island. In ascending order, the limestone formations are (figure 10) Lares Limestone, Mucarabones Sand, Cibao Formation, Aguada Limestone, Aymamón Limestone, and the Camuy Formation. The Mucarabones sand is not included in table 4. The Mucarabones Sand consists primarily of cross-bedded grayish-orange and yellow fine-to medium-grained sand. Its maximum thickness in the Bayamón quadrangle is 120 m. The total depth of all the strata is about 1,700 m, including more than 300 m of clay, silt, and gravel, mostly at the bottom of the sequence (Monroe 1966).

continue on page 18

Box 6. General pattern of correspondence of karst features with limestone formations of northern Puerto Rico (Monroe 1976). The San Sebastián Formation does not develop karst features.

Lares Limestone	Distinctive cone karst—round pointed cones and, at places, jagged. Sawtooth cones and ridges Large caves	depressions formed by collapse— up to 70 m deep Short caves Natural arches Small polje-like depressions
Cibao Formation	Ridges Cuesta scarps Cliffed cone karst Zanjones Swallow holes Blind valleys	Steep-walled towers connected by knife-edged ridges— when adjacent to Aymamón Limestone.
Aguada Limestone	High south-facing escarpment from San Juan to Aguadilla- up to 100 m Solution dolines— up to 30 m deep— separated by rounded ridge crests Typical tropical cone karst Steeped-walled solution doline	Aymamón Limestone Mogotes Tower karst Cuesta scarp Well-like vertical shafts Few caves Sharp-pointed spikes Solution pans
		Camuy Formation Cylindrical shafts—up to 30 m deep Cuesta scarp Solution holes as wide as 20 cm in diameter in the middle member

EPOCH		MONROE (1981)		SEIGLIE AND MOUSSA (1980)	THIS STUDY
PLIOCENE				QUEBRADILLAS LIMESTONE	
MIOCENE	LATE	CAMUY FORMATION		AYMAMÓN LIMESTONE	CAMUY FORMATION
	MIDDLE				LOS PUERTOS LIMESTONE
	EARLY	AYMAMÓN LIMESTONE		CIBAO LIMESTONE	AYMAMÓN LIMESTONE
		AGUADA LIMESTONE			AGUADA LIMESTONE
OLIGOCENE	LATE	Cibao Formation	UPPER MEMBER	LOWER "MONTEBELLO" EQUIVALENTS IN TIME	UPPER MEMBER
			Montebello Limestone Member		Quebrada Arenas Limestone Member and Río Indio Limestone Members
	MIDDLE	LARES LIMESTONE		LARES LIMESTONE	LARES LIMESTONE
				SAN SEBASTIÁN FORMATION	SAN SEBASTIÁN FORMATION

Figure 10. Stratigraphic nomenclature sequence of middle Tertiary age on the northern limestone of Puerto Rico (Rodríguez Martínez 1995). "This study" refers to the study of Rodriguez Martinez.

Table 4. Strata of middle Tertiary age in northern Puerto Rico (Monroe 1976, 1980). The maximum thickness of strata is in parenthesis (Giusti 1978). Million years ago is Ma.

Miocene—From 23.5 to 5.2 Ma

Camuy Formation—sandstone, limestone and sandy, ferruginous chalk (200 m).
 Unconformity.
 Aymamón Limestone—very pure chalk indurated on surface to hard limestone; slightly ferruginous chalk in upper part, northwestern Puerto Rico (300 m).
 Aguada Limestone—hard stratified limestone grading downward into chalk; locally sandy (90 m).
 Cibao Formation—(230 m)
 Upper member; chalk and soft limestone
 Guajataca member; (in western area only) fossiliferous calcareous clay and limestone containing lenses of sand and gravel as much as 15 m thick.
 Miranda Sand Member; (in eastern area only) sand and gravel, sand and sandy clay.
 Montebello Limestone Member; (in center area only) friable pure calcarenite, indurated on exposure to an erosion-resistant limestone.
 Quebrada Arenas Limestone Member; (in eastern area only) finely crystalline stratified limestone

Oligocene—From 34 to 23.5 Ma

Río Indio Limestone Member; (in eastern area only) compact, chalky yellowish-orange weakly bedded limestone.
 Typical chalk or marl; (in eastern and western areas) sandy and silty clayey chalk.
 Lares Limestone—thin to thick-bedded fairly pure limestone, lower part locally contains grains of quartz and limonite sand, intertongues to west with sand and gravel, mapped with San Sebastián Formation (300 m).
 San Sebastián Formation—mostly thin-bedded sand and clay, some sandy limestone, locally, especially in west, sand and gravel (300 m).
 Unconformity (angular).

Cretaceous to Eocene—From 146 to 34 Ma

Volcanic, sedimentary, and intrusive rocks.

continued from page 16

Origin of the Karst

Karst originates when limestone rock is uplifted and the combined effects of climate and the water table modify its features. Puerto Rican karst was influenced by the tropical climate, including the trade winds, and secondly by the various limestone formations in the island (Monroe 1976). Climate and trade winds function as physical and chemical agents of erosion, solution, redeposition, and reshaping of limestone (box 7). Monroe (1976) summarized the role of climate and winds (p 1):

“The warm humid air of the trade wind belt promotes the rapid and

intense weathering of all intrusive and volcanic rocks, producing thick soils. The torrential rains cause rapid erosion of the soil, and when the soil contains abrasive mineral grains, the erosion rapidly deepens valleys. The rains also lead to the casehardening of limestone, for when the water enters the porous limestone it immediately dissolves the surfaces of the grains and crystals of calcite. As these rains usually last only a short time and are followed by brilliant sunshine, the wet rock is warmed, carbon dioxide is driven off, and calcium carbonate is

reprecipitated essentially in place. The streams containing sand, gravel, and cobbles derived from soil on igneous rocks have eroded deep canyons through the limestone and have greatly enlarged the passages on the river caves of Puerto Rico. The nearly constant wind direction has resulted in asymmetry of many of the limestone hills at places where the hills are sufficiently isolated to allow full play of the wind.”

It follows that the legacy embodied in the karst landscape contains a record of past climatic events, if we could find ways for “reading” the climatic signals. Box 8 shows how scientists are finding and interpreting climatic signals in Puerto Rican caves.

Development of the Karst Topography

Giusti (1978) considered mogote karst as a stage of karst development. First the landscape is pitted by shallow closed depressions. Then, the rugged cockpit karst develops, followed by mogote karst and fluvial drainage over blanket sands. By this scheme, the northeastern karst is older than the northwestern karst. An alternative hypothesis is that the fluvial network—flowing from the interior—

Box 7. Climate facilitates the solution redeposition, recrystallization, and casehardening of limestone (Monroe 1966, 1976).

The climate in Puerto Rico is tropical, but moderated by trade winds that maintain mean annual temperatures within a narrow range—between 21°C at high elevations and 30°C along the south coast lowlands. Measured temperature extremes are 6° and 40°C (Monroe 1976). Trade winds usually blow from the north or southeast. They average 18 km/hr—gusting to 24 km/hr less than 5 percent of the time, and 38 km/hr less than 1 percent of the time—with maxima of 250 km/hr during category 5 hurricanes in the Saffir/Simpson scale. Rainfall is evenly distributed seasonally. Generally, a dry period begins in December and usually ends in March or April. There is a spring rainfall period in April and May, an erratic, semidry period in June and July, and a wet season from August through November. Greatest monthly rainfall is in September (Giusti 1978). There is also year to year variability with distinct wet and dry periods that may last a decade or so but generally with sufficient rain to account for evapotranspiration. Actual evaporation is higher than rainfall in most stations. Rainfall events have sharp boundaries, occur suddenly, and are of short duration (15 to 30 minutes) but intense. Forty of 100 climate stations for Puerto Rico record 30 to 50 days a year with > 12.7 mm of rain. All-day events are rare. Hurricanes can produce up to 400 mm of rainfall in a day.

These climatic characteristics have several effects on the development of the landscape.

- Prevailing temperatures facilitate chemical reactions that dissolve, erode, redeposit, and caseharden limestone.
- Rainfall patterns facilitate solution of limestone and transport of erosive waters.
- Evaporative processes contribute to casehardening and recrystallization.
- Winds shape the landscape by differentially blowing rain into crevices in the rocks on the eastern and northeastern sides of hills, thus soaking those sides more than the western sides.

Climates in dry life zones produce caliche, as evaporating water raises to the surface through capillary action and precipitates pure calcium carbonate.

continues on page 20



Figure B8-1. A selection of stalagmites in Cueva de la Luz, Río Camuy Cave System.



Figure B8-2. A stalagmite sample cut open along its long axis (a), the detailed photo (b) reveals alternate bands of porous, dark colored crystals and dense, light colored crystals.

Box 8. Cave calcites as records of climate. Climate change cannot be detected in all cave calcites but carefully chosen ones can reveal a very detailed history of past climates using some of the methods explained below.

Stalagmites and stalactites in caves are usually made of calcite (CaCO_3), which form where waters drip from the ceiling—the stalactites hanging from the ceiling and the stalagmites sitting on the floor. This water begins as rainfall; it then trickles through the soil, dissolving carbon dioxide gas (CO_2) from the soil organisms, thus becoming dilute carbonic acid (H_2CO_3). This dilute acid then travels through the layers of limestone above the cave dissolving calcite (CaCO_3) from the rock. When the water emerges from a crack in the cave ceiling it contains a lot of dissolved CO_2 and CaCO_3 . When the drip meets the cave air, the CO_2 comes out of the water and diffuses into the cave air. When this happens, the CaCO_3 must also come out of solution and so the drip deposits a tiny layer of CaCO_3 or calcite. Eventually, if the drip remains in the same place for many centuries, the layers of calcite build up to a sizable deposit, some hanging from the ceiling drip point and some growing up from the drip point on the floor (figure B8-1).

These stalagmites and stalactites are of great aesthetic beauty, but they are also of great scientific value because the layers building up over centuries and millennia show variations as climate changed. In some cases the former climate—paleoclimate—can be reconstructed by studying the layers of calcite crystals. This is important because if we understand how and why climate changed in the past, we have a good chance of understanding what is happening to modern climates. In some places, like Puerto Rico, there may be no record of paleoclimate change other than that from the cave calcite—hence their scientific value.

Changing climate is expressed as changing temperature and/or changing humidity. In Puerto Rico, the major changes have been in humidity. Caves are usually quite damp and the calcite builds up slowly layer upon layer by the loss of CO_2 , as explained above. However, if the cave becomes dry the

dripwaters start to evaporate; calcite is then deposited much more quickly and in a more lumpy form. The calcite formed during wet times will show fine, elongate crystals packed in dense compact layers; however, the calcite formed during dry times is often quite porous with holes between crystals, and the crystals are often quite small and chunky in shape. So, the alternation of dense layers with porous layers shows the alternation of wet with dry climates; thus a study of the changing porosity of a stalagmite over time will show changing humidity levels in the cave. Figure B8-2 shows a Puerto Rican stalagmite cut open to reveal porous and dense layers.

Sometimes the different layers may only be apparent at a microscopic scale; for example, some stalagmites from tropical regions with obvious seasonality show a double layer for every single year and the thickness and chemistry of the layers vary with the strength of the El Niño Southern Oscillation. In other examples, the layers are expressed as fluorescent bands that can be detected only with ultra-violet or laser light. Here, the bands usually indicate changing biological activity in the soil above the cave, which is in turn related to changing climate.

Changing climate affects the chemistry in cave calcites. Some common elements, such as oxygen and carbon, exist in two or more different forms—isotopes—where the rare form is slightly heavier than the common form. The balance of the normal, light isotope and the rare, heavy isotope will change under different conditions; for example, the CO_2 from dry tropical grasses has a little more heavy carbon than the CO_2 from wet tropical trees. A vegetation change from grasses to trees causes a shift from more to less of the heavy carbon in the CaCO_3 crystals of the stalagmite. Another example is of the effect of different temperatures on oxygen: if the cave gets colder, the CaCO_3 of the calcite has more heavy oxygen than in warm times.

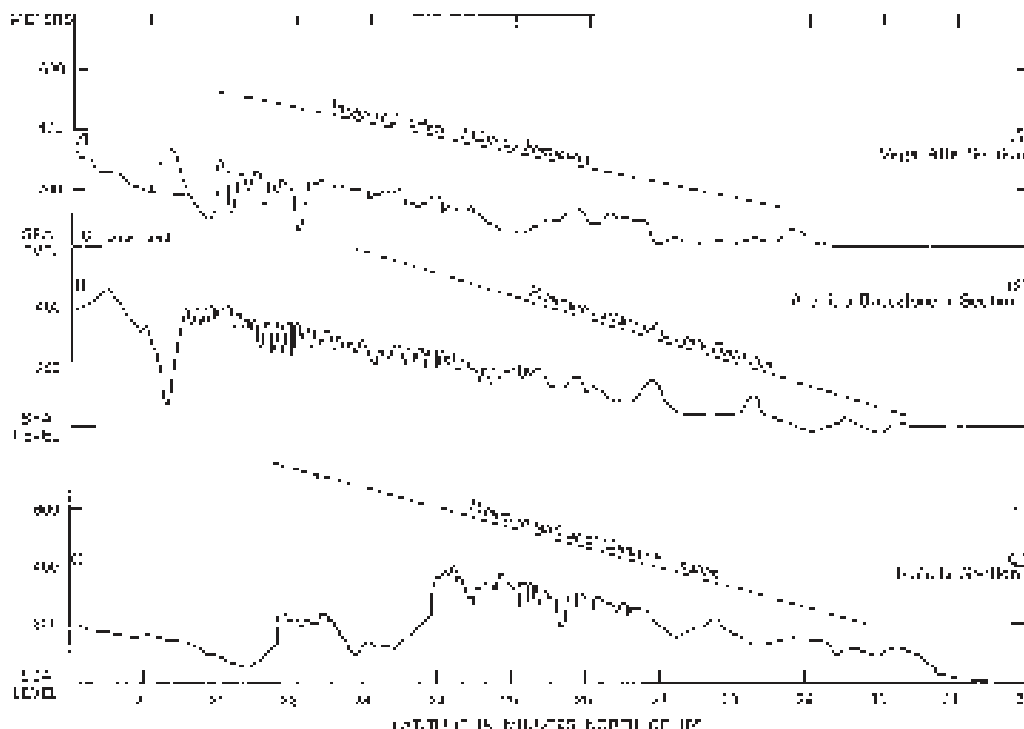


Figure 11. North to south sections through the karst belt with projected original surface of the Camuy Formation (Giusti 1978). The location of sections is shown in figure 3.

developed on the karst surface prior to development of sufficient solutional porosity to divert these streams underground. Depressions and sinkholes then concentrated in the **thalwegs** ultimately disaggregating into the apparently chaotic surface of today. There are still traces of surface channels at the southern fringes of the karst, as well as in some of the larger sinking streams. For example, the Río Tanamá has evidence of caves that formed below the level of now-abandoned surface channels. In this scenario, the largest streams such as Río Grande de Arecibo and Río Grande de Manatí never flowed underground but were always of sufficient size to maintain surface courses to the sea.

Such initial fluvial phases in karst are common in other places such as Belize, Guatemala, and New Guinea (Miller 1987).

Giusti (1978) estimated the rate of **karst denudation** of the karst belt. He reconstructed the original profile of the region (figure 11) and observed that the original surface had a mean altitude of 500 m compared to 230 m today—thus, 320 m of limestone thickness has been dissolved over geologic time. Giusti estimated that the limestone belt emerged from the ocean some 4 Ma. Denudation rates averaged about 0.070 mm/yr—a value that could be 40 percent higher in locations where abrasion was a factor to be considered.

The Karst Belt Is Diverse

The karst features of Puerto Rico have been formed entirely in carbonate rocks and mostly in limestone. The salient aspect of the diversity of the karst belt is the large number of features that result from the modification of limestone. In this section, we discuss the geomorphic, hydrologic, and ecological features of the karst belt and the northern limestone.

Geomorphological Diversity

To describe the geomorphological diversity of the karst belt we follow the order established by Monroe (1976) who

focused on valley and hill features, river and coastal ramparts, zanjones, and caves. Most of the features of the karst belt are illustrated in the two north-south cross sections of the region in figure 7. Box 6 relates the karst features to the particular limestone formation where they are most common.

Valley Features

Dry Valleys—Dry valleys might contain intermittent streams and carry water during heavy rains, but in general they remain dry and are scattered throughout the karst belt. Monroe (1976) described the 10 km-long valley of Quebrada Cimarrona in the southern edge of the Barceloneta quadrangle, which stopped flowing between 1960 and



Figure 12. Topographic map of the northwestern part of Ciales quadrangle, showing entrenched dry valleys having a dendritic pattern. Long dashes show abandoned meanders of Río Grande de Manatí, short dashes trace dry valleys (Monroe 1976).

1965 and since then has been a dry valley. He showed that dry valleys in the Lares Limestone have a dendritic pattern and trend northeastward from the Lares scarp to abandoned meanders of the Río Grande de Manatí (figure 12). Closed depressions drained by **swallow holes** interrupt the valley, so that today's runoff quickly becomes subterranean. It appears that the dry valleys had their course determined by a drainage network eroded on clastic material that once covered the limestone. Continued erosion of the blanket material and capture of the drainage

system by adjacent river channels or underground drainage left the older drainage system exposed in its current dry valley configuration. The hydrological conditions that lead to the dry valleys are illustrated in figure 13. As the process of limestone solution proceeds in a given location, a **hydroperiod** that initially supported superficial drainage evolves into an underground system with a dry valley above the subterranean water flow. Closed Depressions—These form as a result of solution of underlying rocks, collapse of large underground cavities,

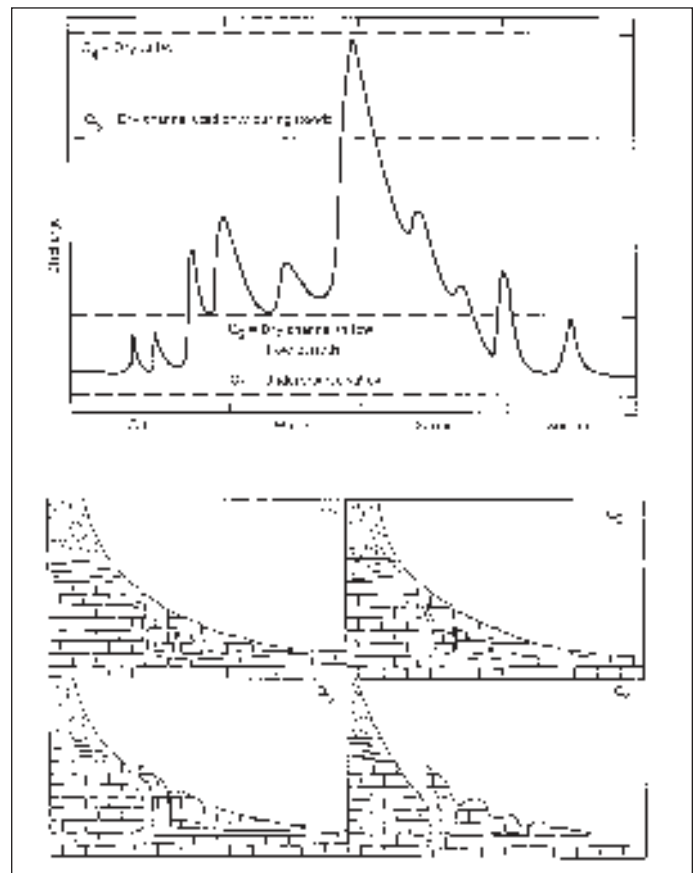


Figure 13. Top—Schematic drawing of annual hydrograph of a surface stream basin. The dashed lines indicate the carrying capacity of the evolving underground drainage system. Bottom—The evolving underground drainage system in a karst region. (Q_1) from an underdrained valley, (Q_2) through a dry channel during low flows with well drained swallow hole, (Q_3) through the development of an incised upstream channel and swallow hole, and (Q_4) to the complete loss of the surface channel with concurrent development of a blind valley upstream and a breakup of the valley profile through the doline development downstream (White 1988). Limestone is represented by blocks and noncarbonate area is stippled.

landslides, or by wind excavation of blanket sands. Closed depressions are also known as dolines or sinkholes. There are thousands of these in the karst belt. Closed depressions can be circular, oval, or irregular, and can be as deep as 120 m. They are a surface expression of one of the stages of karst erosion and can vary widely in their hydrology. The deepest depressions are in the Aguada Limestone, near the exposed contact with the

Aymamón Limestone, and the Lares Limestone near the exposed contact with the Cibao Formation (Monroe 1976). Five of the nine **natural bridges** or short tunnels through which the Río Tanamá flows are collapse features in which the original rock remains. The other four tunnels developed by accretion from the sides due to calcium carbonate from springs that enter at the sides of the canyon.

The most typical doline karst in Puerto Rico is found in the Aguada Limestone in the southern part of the Manatí quadrangle (Monroe 1976). Doline karst merges into mogote karst characteristic of the Aymamón Limestone (photo 11). Giusti (1978) demonstrated that the distribution of dolines on the landscape is random. This suggests that there is no preferential path to the infiltration of water.

The percentage of the area covered by sinkholes is used as an indicator of the degree of development of karst features on a

landscape (Giusti and Bennett 1976). North of the Cibao Formation, the percentage of the land occupied by sinkholes reaches about 50 percent. The percentage of the landscape occupied by sinkholes is related to topographic relief (Giusti and Bennett 1976). There is a fairly wide range of maximum relief figures associated with large-scale sinkhole development. Lower values of relief are associated with early stages of the karst cycle, when sinkholes just start to form, or with late stages when the high areas between sinkholes have been destroyed and sinkholes have been filled.

Comparative analysis of sinkhole frequency—depth distribution (figure 14) shows that tropical karst has greater internal relief than temperate karst, and that Puerto Rico is particularly high in internal relief. Troester et al. (1984) reported that 4,308 sinkholes in Puerto Rico had a density of 5.39/km² with a mean depth of 19 m.



Photo 11. Doline karst. Photo J. Colón.

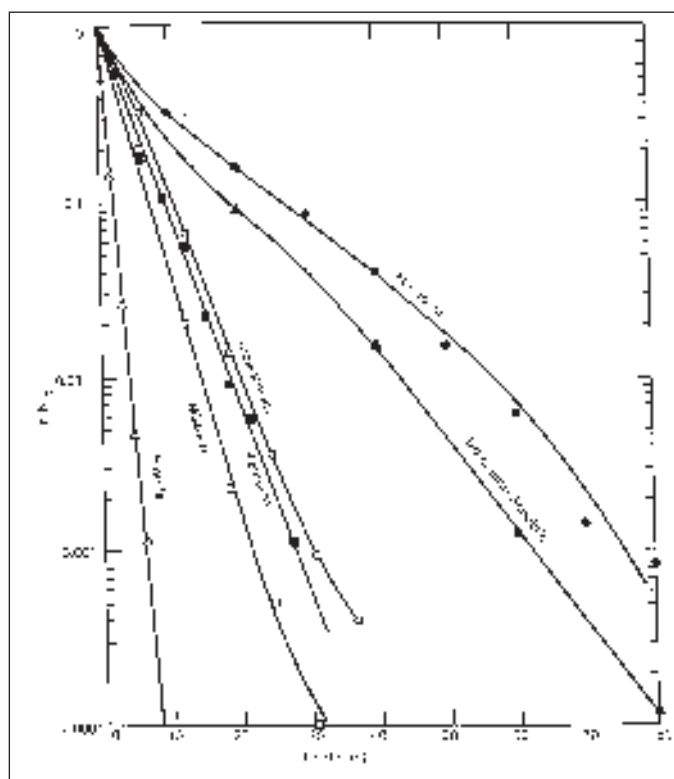


Figure 14. Sinkhole frequency—depth distribution for six karst regions (White 1988). N_0 is the number of sinkholes of zero depth assuming the exponential distribution function is valid over the entire range. n/N_0 is the fraction of sinkholes in the region with the depth shown in the x axis. The slope of the curve indicates the internal relief—from shallow in Florida to a complicated distribution in the Dominican Republic and Puerto Rico.

Filled Sinks—The swallow holes at the bottom of sinkholes or dry valleys can be plugged with clay and as a consequence be filled to the brim with alluvium. These sinkholes are termed filled sinks, and they are abundant in the Manatí quadrangle in the Aguada Limestone and Cibao Formation (Monroe 1976).

Blind Valleys—**Blind valleys** form where a thick mass of marly chalk from the Cibao Formation is overlain by Aguada Limestone and allow intermittent or perennial streams to disappear through swallow holes or caves. They are common in the Vega Alta quadrangle

(Monroe 1976). The caves of blind valleys are sometimes termed quebrada caves because they can fill to capacity by runoff water. For this reason, most of these caves do not harbor any bats or other signs of terrestrial life, although they can contain abundant aquatic life. Waterfowl inhabit the seasonal wetlands that form on the valleys.

Hill Features

Mogote Karst—Mogotes are isolated, steep-sided hills or towers that rise out of the blanket sand deposits of northern Puerto Rico. B. Anthony Stewart, a National Geographic photographer, commented on the mogotes



Photo 12. Mogotes are residual limestone hills. Photo by L. Miranda Castro.



Photo 13. Vertical walls on the side of mogotes. Photo by J. Colón.

of Puerto Rico: “From the air, the mounds reminded me of dyed eggs sitting on end in an Easter Basket” (McDowell 1962, p 783). Most mogotes are about 30 m high, but some reach over 50 m, while others can be as small as a meter or so (Monroe 1976). In parts of the northern coastal area, mogotes may be aligned in ridges along which they form a series of sawteeth. Solution caves are visible on the sides of the mogotes, but they don’t usually pass through the hill. Most mogotes form in the Aymamón Limestone and a few form in Aguada Limestone, with

Aymamón caps. Mogotes are residual limestone hills (photo 12) composed of material that is probably identical to that beneath the blanket sand, except that it has been indurated by precipitation resulting in slight solution of chalky limestone and recementation as water and carbon dioxide are driven out by evaporation (box 9).

Mogotes have a rounded or pointed hard cap, generally 5 to 10 m thick. This cap is formed by repeating soaking by rain followed by almost complete evaporation of the water. The caprock is generally thicker on the eastern side where rain and exposure are more prevalent. On the western side it tends to form a rimrock that overhangs the softer material. Caprock protects the inside of the hill from erosion. This appears paradoxical, given the propensity of limestone to dissolution. Limestone is resistant to erosion while being susceptible to dissolution.

Box 9. Significant features of a mogote described by Monroe (1966) from a road cut along Highway PR 2, km 34.6 between Vega Baja and Vega Alta (figure B9-1).

This mogote is known as Monroe’s Mogote, a popular stop in geology field trips (Troester and Rodríguez Martínez 1990). The salient features are:

- unconsolidated but solution perforated limestone containing molds of mollusks near the northwest end;
- indurations of the same bed at the ends of the cut;
- absence of dripstone in solution perforations in the northwestern two-thirds of the cut, except in the outer rind itself;
- abundance of dripstone in the southeastern third of the cut;
- very steep sides; and
- thick cap of very hard, solution-pitted limestone.

Reprecipitated limestone on slopes tends to form nearly vertical slopes (photo 13). Because these processes occur at differential rates around the mogote—they are

dependent on climatic factors which are not uniform around the hill—the mogote tends to become asymmetric, with a steep slope on the western lee side and a gentler slope

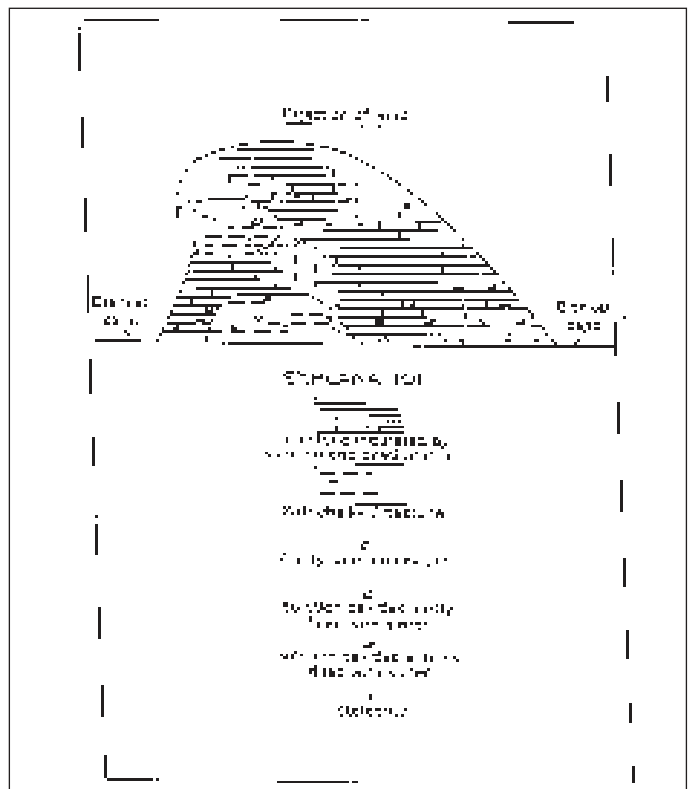


Figure B9-1. Diagram showing the characteristic features of an asymmetric mogote (Monroe 1976)

on the eastern windward side (figure B9-1). The steep slope invariably has an overhanging cap rock or visor of very hard reprecipitated limestone over a weaker, more or less solution-perforated cliff face (Monroe 1976).

Cone Karst—Cone karst is formed by conical hills in the Lares Limestone (figure B2-1). The hills are grouped linearly with intervening sinks. Cone karst occurs also in Cuba, Java, and Jamaica—where it is known as cockpit karst. Its formation, which is still debated, is attributed to solution along joints in the limestone, or to the notion that the cones are residuals after the collapse of caverns of underground rivers. Ciales is a typical area for cone karst. The best developed cone karst in Puerto Rico occurs near the Arecibo Observatory where many of the cones are sharp, pointed, nearly circular or oval, 200 to 300 m in diameter at the base, and rise 50 to 75 m from the bottom of adjacent depressions. In the Florida and Utuado quadrangles, vertical cliffs form towers that cap cones. Monroe (1976) called this “**cliffed cone karst**.”

River and Coastal Ramparts

These are natural walls of limestone at the tops of canyon walls, fault scarps, and around sinks. They form as a result of secondary cementation and differential erosion. They are common along the top of river canyons and at the tops of limestone sea cliffs.

Earlier, we discussed the size of the Río Guajataca canyon’s ramparts (figure 6), which are the best examples in Puerto Rico (photo 14). The formation of this rampart is attributed to casehardening by precipitation of calcite, probably in a joint and on the wall of the canyon (Monroe 1976). Coastal ramparts can be observed at the top of sea cliffs composed of Aymamón Limestone in Quebradillas and Isabela.

Zanjones

Zanjones are parallel trenches resulting from solution of limestone along joints (figure 15). The trenches can be 100 m long or more, with vertical sides ranging in width from a few cm to about 3 m and in depth from about 1 to 4 m. Zanjones are oriented in the same direction with as many as 8 per 100 m (Monroe 1976). First described for Morovis and Florida, the best examples of zanjones are in Lares where individual trenches can be more than 1,800 m long, and 20 m wide, and zanjones are present in a belt 1 km wide. Here, zanjones partially coalesced and formed a particular east-west topography in which individual zanjones cut longitudinal hills (Monroe 1976). Zanjones are an exclusive feature of Puerto Rican karst. The only common feature of the areas of **zanjón karst** is that all are in terrain with strongly stratified limestone in the lower part of the stratigraphic succession of Oligocene limestone (Monroe 1976). Giusti



Photo 14. Ramparts of the Río Grande de Manatí, near Ciales, Puerto Rico. Photo by J. Colón.

(1978) noted that zanjones form where the limestone is thin bedded and brittle.

Caves⁴

The caves of Puerto Rico are primarily developed through solution processes, with additional modification from the abrasion of **clastic**

sediments. They form in areas of alternating beds of hard and soft limestone (Giusti 1978). The major caves of the karst areas are of two basic types—those caves formed by through-flowing rivers of the interior highlands, and those formed by rainfall that has

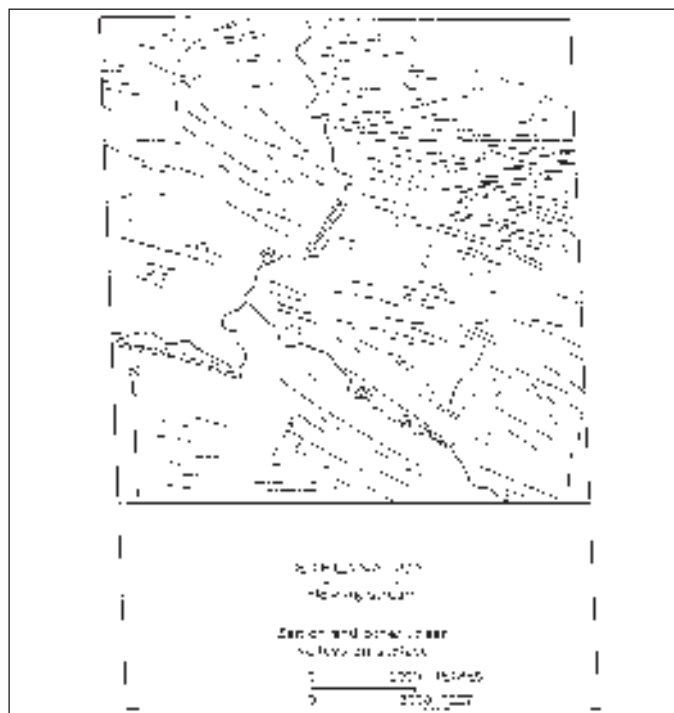


Figure 15. Map of an area north-northwest of Lares showing a landscape dominated by zanjones and the course of Río Guajataca (Monroe 1976).

⁴ Based on Miller 2000

fallen directly on the karst area, then percolated downward through the limestone. Sediment transported through the larger caves by highland rivers is responsible for additional enlargement through abrasion. In addition, there are small “cliff-foot” caves that form in the limestone at the sides of river and stream valleys and “sea caves,” or “littoral caves,” formed through the mechanical action of surf upon rock at the coast. Because of tectonic uplift in the geologic past, some sea-caves now are found tens of meters above their original elevation. Most are generally of small size.

Most of the solutional activity creating and modifying Puerto Rican caves is due to the chemical combination of carbon dioxide—produced in soil—with percolating water. The weak acid that forms can dissolve limestone and carbonate rock over thousands of years. Conversely, percolating water that enters air-filled caves can emit carbon dioxide into the cave atmosphere and subsequently precipitate the mineral calcite—this precipitation produces **speleothem** or formations such as **stalactites**, **stalagmites**, and **travertine** decorations (photo 15) that are often of considerable beauty and attraction (box 8). Because these features exist in a delicate balance with the chemical composition of the percolating ground water, any alteration of the overlying vegetation and soils may dramatically affect their growth due to

disruption of the carbon dioxide produced in the overlying soils.

Caves that form by percolating rainwater of the karst belt are generally less than a few meters in dimension, because this water is generally quickly saturated with the mineral calcite. The water may move downward as diffuse flow through joints and bedding openings, or sometimes as small surface streams that collect in the depressions between mogotes or hills and enter small sinkholes. Eventually, these waters move laterally at the water table surface to emerge as springs in the larger river caves or in the valleys of the through-flowing rivers from the interior highlands.

The caves with the largest known cross sectional dimensions are those formed by streams and rivers that collect on the nonlimestone rocks prior to entering the karst. Typically river caves start off as a network of solution passages. As streams start flowing through the small interconnected solution passages, they introduce such scouring elements as quartz and other hard minerals derived from weathering of the volcanic rocks, and especially the intrusive rocks of the mountains of the island. These grains, and also gravel and silicified siltstone, cut the relatively softer limestone and enlarge stream channels into through-flowing passages, which eventually become large passages. Sand, gravel, and even cobbles of volcanic and intrusive origin



Photo 15. Stalagmites and stalactites in this cave show the results of solution and precipitation processes in caves. Photo by Fundación de Investigaciones Espeleológicas del Karso Puertorriqueño.

have been found in the Camuy system. Not only do the streams and rivers carry abrasive sediment, but their waters are not saturated with respect to the mineral calcite. In addition, their flows are much greater than the many diverse flows that percolate down through the limestone from rainfall. For these reasons, the dimensions of these caves may occasionally exceed 30 m in diameter.

Puerto Rico has some of the world’s largest caves in the Río Camuy and Río Encantado systems. This is due not only to the large sizes of the rivers that form them, but also due to their location in the tropics—tropical caves have never suffered the disruption or physical destruction that may occur at higher latitudes due to glaciation. Some caves are smooth passages without decoration because water flowing through them is so rapid that deposition is not possible.

The caves of Puerto Rico also record the past locations of the water table

surface in the karst. All of the major caves contain more than one level formed either through a combination of tectonic uplift of the karst surface, and/or erosional downcutting by rivers (photo 16). The resulting changes in the surface of the karst aquifers is reflected in the production of several vertically stacked galleries, each a record of the water table’s position



Photo 16. A waterfall in the Río Encantado cave system, an example of a two-level cave. Photo by Fundación de Investigaciones Espeleológicas del Karso Puertorriqueño.

thousands of years ago. Actual ages can be assigned to these levels through radiometric dating of speleothem, or paleomagnetic dating of cave sediments. This is extremely valuable information that can be used to predict locations of ground water resources or earthquake susceptibility by analyzing rates of cave uplift. Unfortunately, careless destruction of cave speleothem or disturbance of sediments can ruin such information before it can be studied.

Narrow **vertical caves** also occur in the karst belt. Their origin is unknown but some may be collapse

features and others are believed to be formed by solution (Monroe 1976). Most are a few meters—up to 10 m—in diameter and as deep as 30 m. Monroe (1976) describes many other types of depressions in northern limestone.

Hydrological Diversity

The karst belt includes several subterranean rivers and streams, aquifers, springs, waterfalls, artificial lakes or reservoirs, lagoons, natural ponds, and wetlands of various kinds (figure 16). These systems are important components of the water

cycle (figure 17). The configuration of the water cycle in the region shows distinct patterns depending on whether the terrain is volcanic, limestone, or coastal limestone wetlands. The presence of limestone results in alternative underground routes for water movement and storage, which are not present in volcanic zones (figure 17). Because of how the aquifer flows in this region, it is apparent that limestone is more effective in routing water to the coastal zone than routing water to rivers and streams during drought conditions (Giusti and Bennett 1976, Giusti 1978).

Rivers and Streams

The eight main through-flowing subaerial rivers of the karst belt are—from west to east—Río Guajataca, Río Camuy, Río Tanamá, Río Grande de Arecibo, Río Grande de Manatí, Río Indio, Río Cibuco, and Río de La Plata. The Aguada Limestone underlies the surficial geology east of Río Cibuco, which is of the mudstone type. Buried limestone occurs from Río Grande de Loíza and covers small reaches of Río de La Plata, Río Hondo, Río Bayamón, and Río Piedras. Río Culebrinas to the west, and Río de La

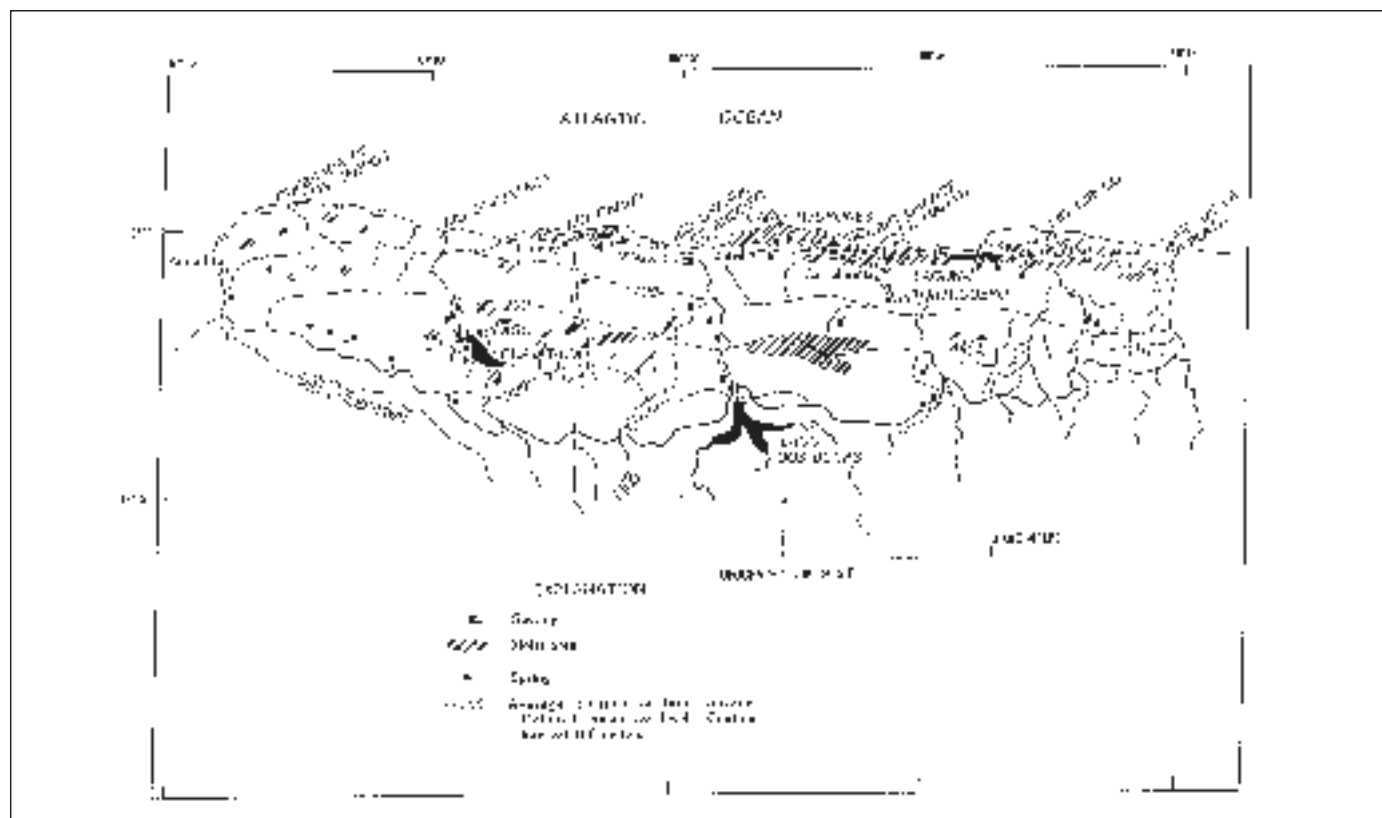


Figure 16. Aquatic systems—principal rivers, springs, artificial lakes, lagoons, and wetlands of Puerto Rico's karst belt. These features are mostly driven by rainfall routing through the underground drainage of the karst belt. Lowland wetlands are directly dependent on rainfall and runoff from the limestone hills. Lago Dos Bocas intercepts runoff from the volcanic zone south of the karst belt (Giusti 1978).

Plata to the east, delimit the karst belt. Numerous dams located mostly in the volcanic sectors of the watersheds influence the frequency and magnitude of discharge⁵ events on these rivers. The result is that low and high flows are reduced with consequences to reducing channel forming events during high-flow periods and lowering the capacity of rivers to support migratory aquatic species during drought periods. Sediment transport is also reduced by the presence of multiple dams in these rivers.

The headwaters of the eight main rivers of the karst belt are over volcanic/plutonic bedrock. For most of them, their surface drainage density is greater over the volcanic/plutonic bedrock than over the limestone substrate

(figure 1). Most of the drainage in the karst belt is subterranean through large or tube-like caves with or without smooth walls, or through a huge network of interconnected passageways only a few centimeters in diameter. Monroe (1976) described this network as a “spongework of interconnected passageways.” Río Grande de Manatí and Río Grande de Arecibo have also incised through the surficial limestone forming three large polygons with areas of 902, 287, and 305 km², from west to east.

Several of the through-flowing rivers have past or present subterranean reaches. These are Río Tanamá, which flows through nine tunnels; Río Camuy, which flows underground through the Lares and Cibao Formations; and Río

Guajataca, which flow through deep narrow gorges that may be deroofed caves (Monroe 1976) or **collapsed sinkholes** (Giusti 1978).

The discharge of some rivers changes as they cross the karst belt (Monroe 1976). Río Camuy increases in flow by a factor of 4.5 when entering the karst belt. Springs and tributaries increase the flow of Río Guajataca as it crosses the karst belt (Monroe 1976). In some instances, flow can decrease if it is captured by subterranean drainage. Giusti and Bennett (1976) observed that the base flow per unit area of watershed in limestone rivers and streams was lower than in volcanic rivers and streams. Thus, the ratio of base flow to total flow is higher in volcanic rivers and streams than those in

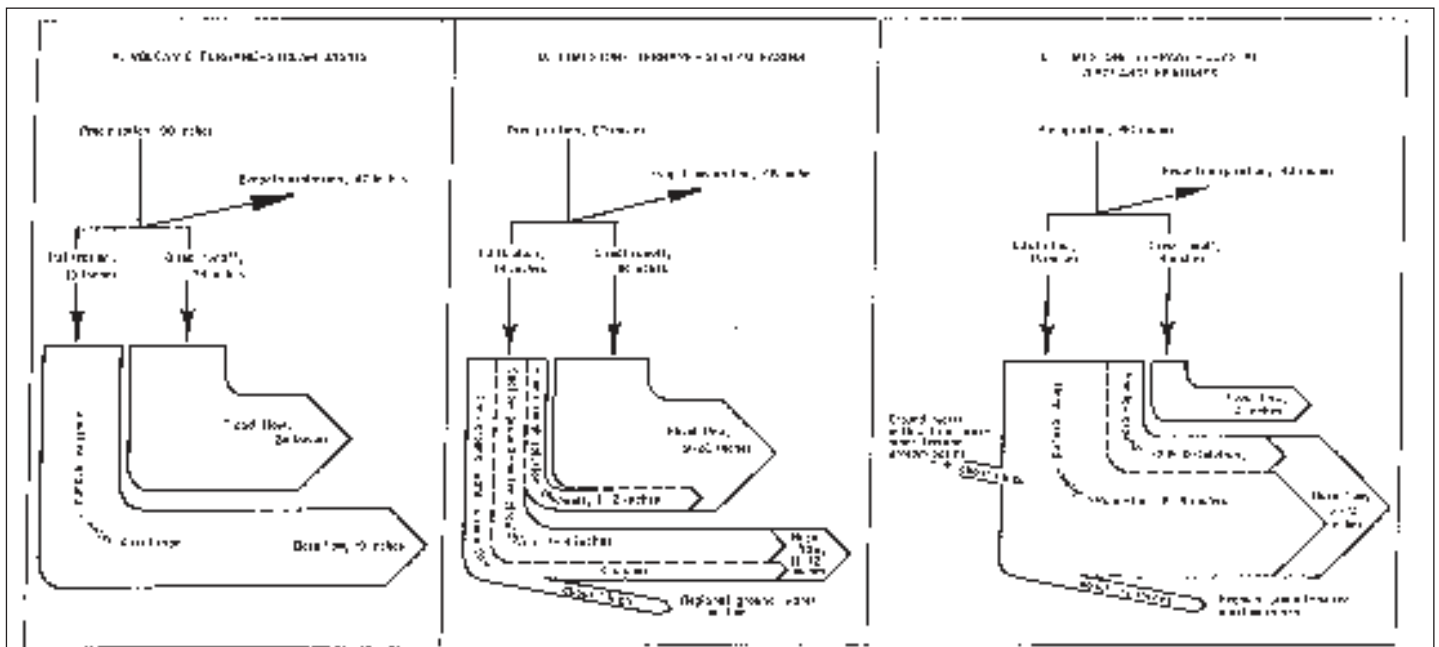


Figure 17. Estimated average annual hydrologic conditions and theoretical flow patterns for stream basins in volcanic and limestone terraces (Giusti and Bennett 1976).

⁵ The term *discharge* is used interchangeably with *flow*.

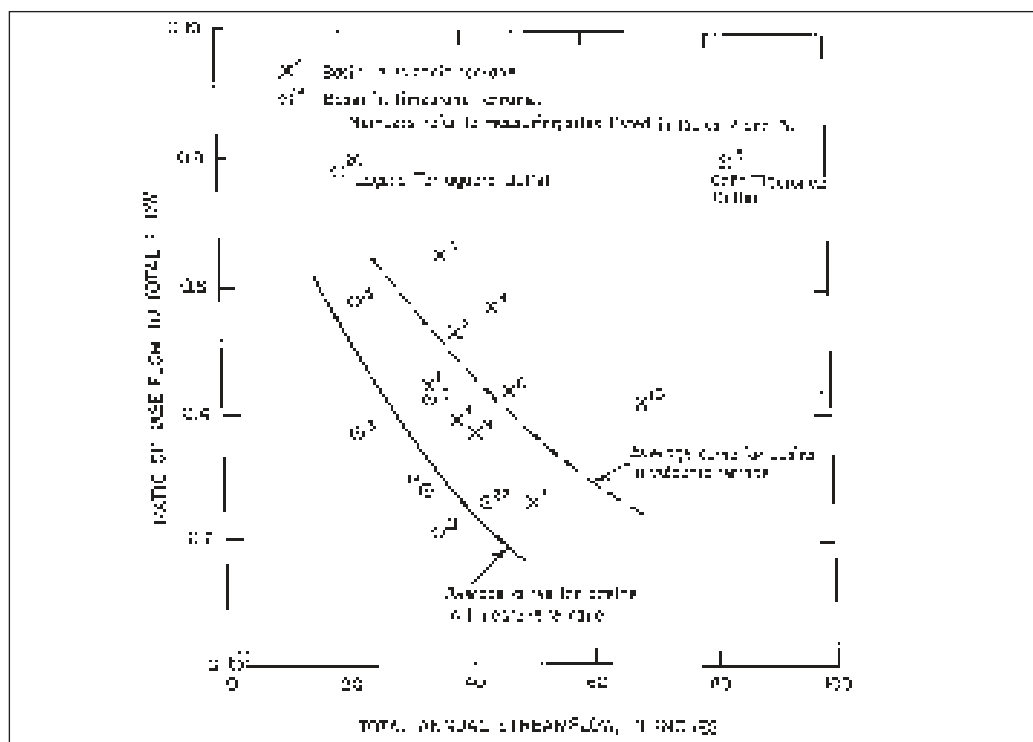


Figure 18. Comparison of the ratio of base flow to total flow against total annual stream flow for basins in volcanic and limestone geology (Giusti and Bennett 1976). To convert to millimeters, multiply inches by 25.4.

limestone (figure 18). This means that flood flow is proportionally higher in limestone than in volcanic basins.

The reason is the contribution of shallow underground water during periods of high rainfall and stream flow (Giusti and Bennett 1976).

Río Culebrinas—This is a highly meandering river approximately 54 km long. Its headwaters originate above 400 m elevation, and the river discharges to the west coast. The urban centers for the municipalities of Aguada, Moca, and San Sebastián are located within the Río Culebrinas watershed. Río Culebrinas flows almost parallel to the limestone-volcanic division, that is, it serves as a south divider for the northern limestone.

All major tributaries draining to Río Culebrinas from the north bring water mostly from the San Sebastián Formation, but also from as far north as the Lares Formation and even the Cibao Formation. In fact, several northern tributaries to Río Culebrinas originate as springs. All tributaries draining to Río Culebrinas from the south bring water from volcanic substrates. The San Sebastián municipality filter plant, operated by the Puerto Rico Aqueduct and Sewer Authority, has two intakes, one over limestone substrate, the other over volcanic substrate. The San Sebastián Formation is characterized by relatively low hydraulic conductivity values and the proportion of surface water contributing to ground

voids is lower compared to watersheds where the limestone is of the Aguada or Aymamón Formations. Río Culebrinas flows at the southern border of the northern limestone and attracts ground water to its watershed from the limestone belt due to ground water level differences.

Río Guajataca—The headwaters of Río Guajataca are over volcanic and plutonic substrates. Its main channel initiates a southern path of approximately 40 km from above 400 m elevation. It flows through all the major limestone formations of the karst belt. Of all the northern rivers, Río Guajataca and Río Camuy present the greatest difficulty for outlining their watersheds. Río Guajataca has over 90 percent of its

watershed over limestone substrate, almost equally divided between Aymamón, Cibao, and Lares Formations with a minor proportion over the Aguada Formation. The municipalities of Lares and Quebradillas are within the Río Guajataca watershed.

Río Camuy—This river originates as three tributaries—Río Piedras, Río Angeles, and Río Criminales—over volcanic substrate and travels approximately 2.7 km to the north from about 600 m elevation. After a short surface reach over limestone, it becomes a subterranean river at the Lares Limestone contact and reappears about 2.8 km downstream—measured in a straight line—at the Cibao Formation, then maintains a northern flow for about 22.3 km to the ocean. The urban centers of the municipalities of Camuy and Hatillo are within its surface watershed.

Río Grande de Arecibo—This river meanders widely within its valley and shows many abandoned channels throughout. According to some, the river is believed to have been a subterranean river flowing into Caño Tiburones. Río Grande de Arecibo has close to one third of its pear-shaped watershed over limestone substrate and travels about 60 km to the Atlantic Ocean from its origin at over 800 m in elevation. Twenty-three km of its length is over limestone and receives the waters from Río Tanamá, which also travels about 19.6 km over limestone.

The urban centers of the municipalities of Adjuntas, Jayuya, Utuado, and Arecibo are within its watershed. The major tributaries to Río Grande de Arecibo, such as Río Tanamá, drain waters from 1,000 m above sea level. Río Grande de Arecibo experiences an abrupt change in substrate from volcanic/plutonic to limestone just downstream from Dos Bocas Reservoir (photo 17).

Río Grande de Arecibo is the main source of water to its alluvial valley (photo 18) (Quiñones Aponte 1986). The valley contains an unconfined aquifer hydraulically connected with the bordering limestone formations so that if water is withdrawn excessively from the river during low flows, aquifer recharge is diminished. The valley is complex hydrologically—Río Tanamá also drains into the valley—and geologically—it is composed of two sub-basins based on underlying geology (Quiñones Aponte 1986). Río Grande de Arecibo and Río Tanamá lose flow to the aquifer during most of the year (Quiñones Aponte 1986). The average loss of water to the alluvium between U.S. Geological Survey (USGS) stations 27750 and 0290 is about 60,560 m³/d (16 mgd [million gallons per day]) plus 43,906 m³/d (11.6 mgd) to the Aguada and Aymamón aquifers.

Río Grande de Manatí—This river has a pear-shaped watershed defined by a high surface drainage

density over volcanic substrate and a low drainage density over limestone substrate. The urban centers of the municipalities of Orocovis, Ciales, Manatí, and Barceloneta are within its watershed. The river originates at 800 m above sea level but receives waters from 1,000 m above sea level, and travels approximately 80 km to the ocean, including approximately 33 km over limestone. Most of its surface path is over volcanic substrate. Over limestone, surface waters concentrate at the main channel and drain to the north over all major limestone formations. The extent of alluvial deposits throughout this river's flood plain, the shape of its watershed, and the distribution of its drainage densities are very similar to Río Grande de Arecibo's.

Río Cibuco—From its origin over volcanic substrates at 700 m elevation, this river travels approximately 36.5 km to the ocean—10 km over limestone. The urban centers of the municipalities of Corozal, Morovis, and Vega Baja are within its watershed, which is over 50 percent limestone. Unconsolidated deposits cover most of the Aguada and Aymamón Formations at the Río Cibuco flood plain. The alluvial deposits within the river's valley reach a maximum depth of 85.3 m. Measured **transmissivity** values reach 7,620 m²/d close to the confluence of Río Indio with Río Cibuco and over 150,000 m²/d at the Río



Photo 17. Dos Bocas Reservoir at the interface between volcanic and limestone areas. Notice the surrounding karst. Photo by A. García Martínó.



Photo 18. Río Grande de Arecibo and its valley confined by limestone hills. Photo by L. Miranda Castro.

Cibuco to Río de La Plata divide, just north of Vega Alta aquifer.

Río de La Plata—The longest river in Puerto Rico—approximately 97.4 km long—and travels through an elevation range of 900 m to the ocean. Less than 25 percent of its watershed is over limestone substrate. The watershed includes the municipalities of Dorado, Toa Baja, Toa Alta, Naranjito, Comerío, Barranquitas, Cidra, Aibonito, and Cayey.

The lower reaches of north coast rivers become estuaries before they reach

the ocean. Sea water penetrates upstream as a saltwater wedge. For example, the saltwater wedge was detected 2.8 km upstream from the mouth of Río Cibuco and 4.8 river km upstream from the mouth of Río de La Plata (Torres González and Díaz 1984). At Río Grande de Manatí, the saltwater wedge can penetrate 10.9 km at zero discharge (Gómez Gómez 1984). The distance of the saltwater wedge's penetration is proportional to sea level and inversely proportional to the freshwater discharge of the rivers.

Aquifers

The northern limestone contains two of the most productive aquifers of the island. The upper aquifer is within the Aymamón and Aguada Limestones and alluvial deposits along the coast. The lower aquifer occurs within various members of the Cibao Formation and the Lares Limestone. The lower aquifer is confined near the coast. The confining unit is locally leaky in the San Juan metropolitan area. The lowest aquifer is thickest and most transmissive in

the northcentral part of the island in the Barceloneta region (figure 19). West of Río Grande de Arecibo, the extent of the lower aquifer is uncertain (Rodríguez Martínez 1995). These two aquifers cover an area of 1,761 km² or 19.7 percent of the area of Puerto Rico, and they represent 64 percent of the total aquifer area of the island (Molina Rivera 1997). The surface to ground water relation of the southern limestone with its alluvial deposits is not as well defined as in the northern limestone.

The north coast aquifer is characterized by large variations of **hydraulic conductivity**, both laterally and vertically (table 5). Values as high as 2,042 m/d and as low as 0.04 m/d have been estimated for the north coast aquifer (Giusti and Bennett 1976). However, the average hydraulic conductivity of the hydrogeologic unit decreases with depth (table 5).

Transmissivity is also highly variable in the karst belt (table 6). An aquifer suitable for water supplies

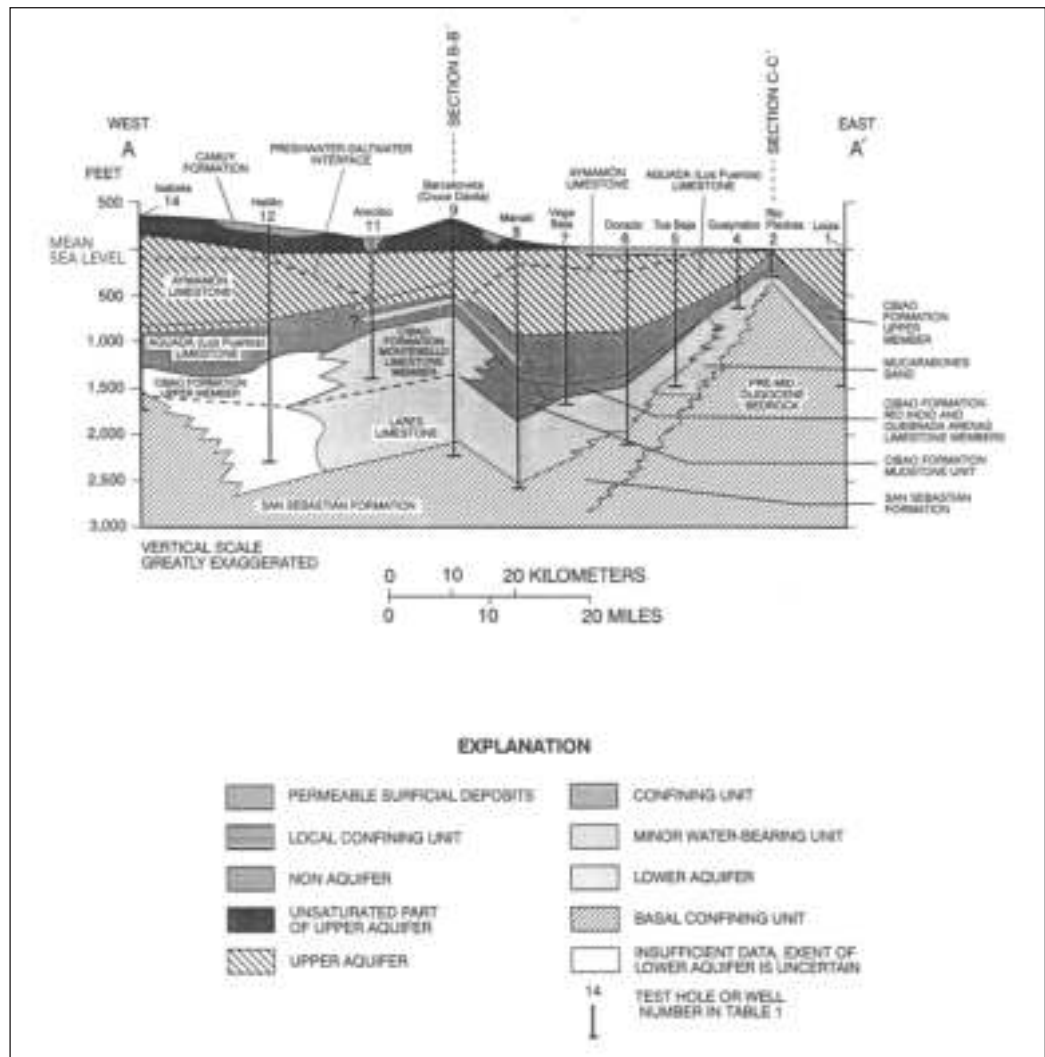


Figure 19. Hydrogeologic section of the north coast aquifer between Isabela and Loíza (Rodríguez Martínez 1995). To convert elevation to meters, multiply feet by 0.3048.

should have a transmissivity of 1,296 m²/d or higher (White 1988). In the Aymamón aquifer, transmissivity values in excess of 185,800 m²/d have been reported where localized cavernous conditions exist (Torres González 1985). Upper aquifer transmissivity values range from 18.6 to over 26,012 m²/d and are generally higher in the area between Río de La Plata and Río Grande de Arecibo, where values have exceeded 9,290 m²/d in six locations (Rodríguez Martínez 1995). Transmissivity estimates for the lower aquifer are highest in northcentral Puerto Rico where the Lares Limestone and the Montebello Limestone Member of the Cibao Formation have values as high as 46.5 and 334 m²/d, respectively (Rodríguez Martínez 1995).

The north coast aquifer is recharged by infiltration from direct precipitation and losing streams. In mogote areas, recharge by direct infiltration through the relatively impermeable blanket sand deposits or the case-hardened limestone surface of the mogotes is very limited. The majority of the recharge is from runoff during large rainfall events (Troester 1999). Runoff from the mogote surface quickly flows into holes and solution channels around the base of the mogote and recharges the aquifer. Runoff from streams in the valleys between mogotes can also

Table 5. Hydraulic conductivity and discharge of north coast limestones (adapted from Giusti and Bennett 1976). Limestone Formations are arranged in increasing stratigraphic depth order. Discharge is reported in million cubic meters per day (Mm³/d) and million gallons per day (mgd).

Aquifer	Width (km)	Hydraulic Conductivity (m/d)	Discharge			
			(Mm ³ /d)	(mgd)	(% of total/km)	(% of total)
Aymamón	12.9	Dorado – Vega Baja	0.073	19.2	18.2	15.5
			82.3			
		Aguada	20.4			
		Cibao	1.2			
Lares	16.1	Vega Baja – Manatí	0.077	20.4	16.3	16.4
			0.4			
		Aymamón	82.3			
		Aguada	4.1			
Cibao	17.7	Caño Tiburones	0.250	66.1	48.0	53.2
			0.2			
		Aymamón	163.1			
		Aguada	26.5			
Lares	12.9	Arecibo – Camuy	0.032	8.4	8.4	6.8
			0.2			
		Aymamón	24.3			
		Aguada	1.6			
Cibao	12.9	Camuy – Guajataca	0.016	4.1	4.1	3.3
			0.2			
		Aymamón	16.5			
		Aguada	1.2			
Lares	19.3	Guajataca - West Coast	0.023	6.0	4.0	4.8
			0.4			
		Aymamón	20.4			
		Aguada	2.0			
Cibao			0.4			
		Total	0.470	124.2	100	100

Table 6. Transmissivity values for selected units of the north coast limestone aquifer (Torres González and Wolansky 1984). The San Sebastián Formation does not form aquifers.

Geologic Units	Associated Aquifers	Transmissivity (m ² /d)
Alluvial deposits	Unconfined	93 to 4645
Camuy Formation	Unconfined	93 to 279
Aymamón Limestone	Unconfined	465 to 4645
Aguada Limestone	Unconfined	186 to 1858
Cibao Formation	Unconfined at outcrop areas, confined at low-dip areas	279
Lares Limestone	Unconfined at outcrop areas, confined at low-dip areas	929
San Sebastián Formation	Not an aquifer	—

flow into sinkholes and recharge the aquifer. Water levels in wells in the mogote region respond immediately to rainfall events (figure 20). Net recharge estimates range from 0 to 495 mm/yr and average about 150 mm/yr across the entire aquifer area (Troester 1999). For mogote areas with internal drainage, these values range from 250 to 495 mm/yr.

The north coast aquifer was subdivided into six main regions defined by the major subaerial rivers. Total ground water flow for the whole north coast aquifer was estimated using hydraulic conductivity values, aquifer thickness, and head gradients through each region (table 5). A discharge of 0.47 Mm³/d [million m³/d] or 124 mgd was estimated. This flow occurs throughout the limestone formations, but particularly through base flow of rivers and streams,

springs, and seepage to the sea or swampy areas. The Caño Tiburones region provides more than 50 percent of the total discharge through the north coast aquifer followed by the Vega Baja–Manatí region. The main condition for the dominance of the Caño Tiburones region is the relatively high average hydraulic conductivity—163 m/d—of its upper Aymamón aquifer. The Dorado–Vega Baja region increases in relative importance when flow values are expressed on the basis of the width of the aquifer (table 5).

Giusti (1978) revised these numbers and lowered the estimate of aquifer discharge to 0.40 Mm³/d or 105 mgd. The reduction was due to the smaller hydraulic conductivity values used compared to those reported in table 5. The average water budget for the karst belt given by

Giusti (1978) was 1,550 mm in rainfall, 1,100 mm in evapotranspiration, and 650 mm in discharge to the ocean. This budget has a 200 mm deficit which is made up by runoff from the uplands. Variation within the region is shown in the three budgets of figure 17. Budget values are best estimates and will change with long-term research. Giusti and Bennett (1976) also compared water budgets for basins with volcanic substrate with those with limestone substrate (table 7). Sites over limestone substrate tended to show greater ground water storage and greater river base flow than sites over volcanic substrates. The apparently anomalous values for Caño Tiburones are due to the artificial modifications to its drainage by reclamation projects. Lowering of the water table to below sea level has forced seawater into the freshwater aquifer.

The least developed sector of the north coast aquifer in terms of pumpage is the western reach between Río Camuy and Aguadilla (Tucci and Martínez 1995). In this region, ground water is deep and water use focuses instead on Lago Guajataca (box 10), an artificial lake. The lower aquifer in the region is fragmented and not highly productive. The upper aquifer is more accessible, although not used extensively. Ground water movement in the region is from the highlands in the south towards the north and west, and locally to streams. A major ground water divide extends from the southeast to the northwest of the region, and separates flow into the karst belt from flow to Río Culebrinas to the southwest.

Within the north coast aquifer is the region—delimited by Río Indio on the west and Río de La

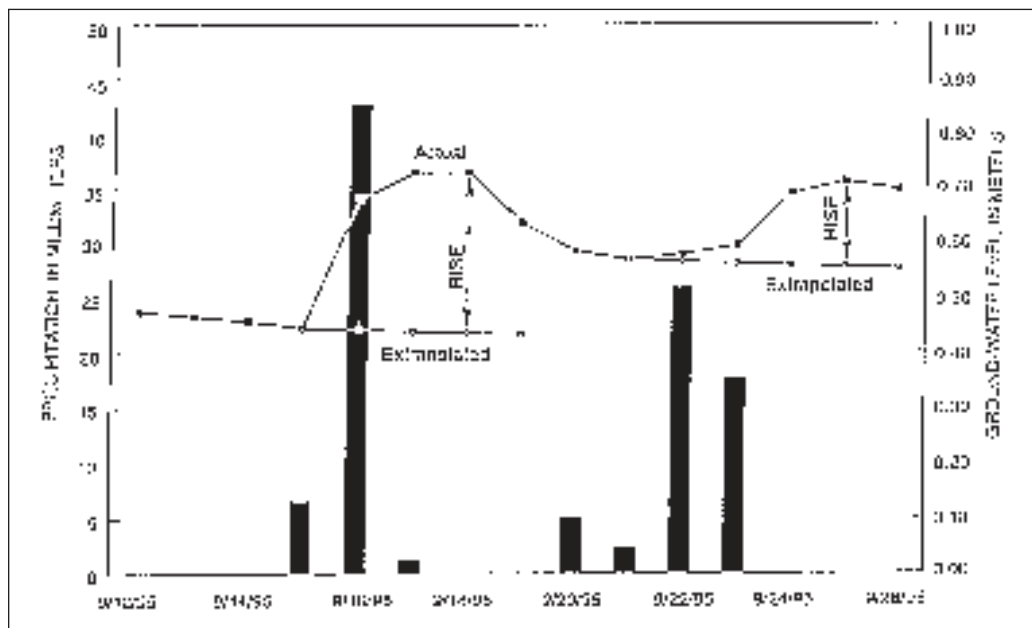


Figure 20. Response of ground water level in the Dorado area to rainfall events (Troester 1999).

Plata on the east (some 13.7 km)—commonly known as the Vega Alta aquifer. Sepúlveda (1999) divided the aquifer into five physiographic regions: the southern karst uplands, the karst upland plateau, the alluvial valleys, the karst valley covered by blanket sand deposits, and the coastal plains. The marsh of Ciénaga Prieta is an integral part of the aquifer and is the main surface water body formed by the Vega Alta aquifer. Approximately 15 m³/s of ground water drained to the marsh before 1930 but the flow in 1995 was 4 m³/s. During the same time interval, the **potentiometric surface** of the coast decreased by about a meter (Gómez Gómez and Torres Sierra 1988). Part of the Vega Alta aquifer—underlying the Vega Alta karst valley—was declared a Superfund site by the U.S. Environmental Protection Agency due to the presence

Table 7. Ground water storage, base flow, and drainage area of stream basins in volcanic and limestone terrain (Giusti and Bennett 1976). Empty cells = no data available.

<i>Stream Basin</i>	<i>Ground water Storage (cm)</i>	<i>Base Flow (m³/s.km²)</i>	<i>Drainage Area (km²)</i>
Volcanic Terrain			
Upper Río Guajataca	10.2	0.012	8.3
Upper Río Camuy	0	0.016	19.7
Río Criminales	-15.2	0.021	11.7
Upper Río Tanamá	5.1	0.019	47.7
Río Grande de Arecibo below Dos Bocas	5.1		429.3
Río Cialitos	12.7	0.012	44.0
Upper Río Grande de Manatí	12.7	0.010	331.5
Río Unibón	-20.3	0.016	13.7
Upper Río Cibuco	12.7	0.012	39.1
Río Mavilla	-45.7	0.023	24.6
Limestone Terrain			
Quebrada Los Cedros	53.3		37.8
Río Guajataca to Lago Guajataca	22.9		78.7
Río Guajataca to ocean	25.4	0.007	76.4
Lower Río Camuy	2.54	0.008	169.9
Lower Río Tanamá	28.0		101.5
Lower Río Grande de Arecibo	63.5		76.1
South Canal (two sites)	22.9	<0.0001	53.4
Caño Tiburones Outlet	-182.9	0.051	46.4
Lower Río Grande de Manatí	-20.3	0.011	173.5
Laguna Tortuguero Outlet	5.1	0.016	43.5
Lower Río Cibuco	-7.6	0.006	170.2
Río Lajas	-22.9	0.008	21.8

of volatile compounds—mainly trichloroethylene, a suspected human carcinogen. Román Más and Lee

(1987) analyzed the geochemical evolution of waters within the north coast limestone aquifer (box 3). Dissolved sulfate

and magnesium, pH, and carbon-13 isotopes generally increased downgradient. Total inorganic carbon and

Box 10. Isabela Irrigation District.

Río Guajataca was dammed in 1928 with an earth dam to form a reservoir—Guajataca Reservoir—a part of the Isabela Irrigation District (figure B10-1). The Guajataca Reservoir, with an original storage capacity of 45.2 million m³, is the only major dam built over limestone substrate and has the lowest loss of storage among island dams due to sedimentation—0.1 percent per year (Morris and Fan 1997). The irrigation district was designed and built to irrigate land used for sugar cane production but it failed due to excessive loss of water by infiltration (see example 1, box 14). Today, the reservoir and its associated channels are used as a supply for drinking water. Water is transferred to six filtration plants with a total filtration capacity of 84,400 m³ per day. However, in 1938, 213,700 m³/d were extracted from the reservoir. Water loss due to infiltration through the porous limestone continues today as it has since its construction. In May 1998, the reservoir reached a critical low level creating water shortages for 250,000 people in the municipalities of San Sebastián, Isabela, Aguadilla, Aguada, Moca, and Rincón.

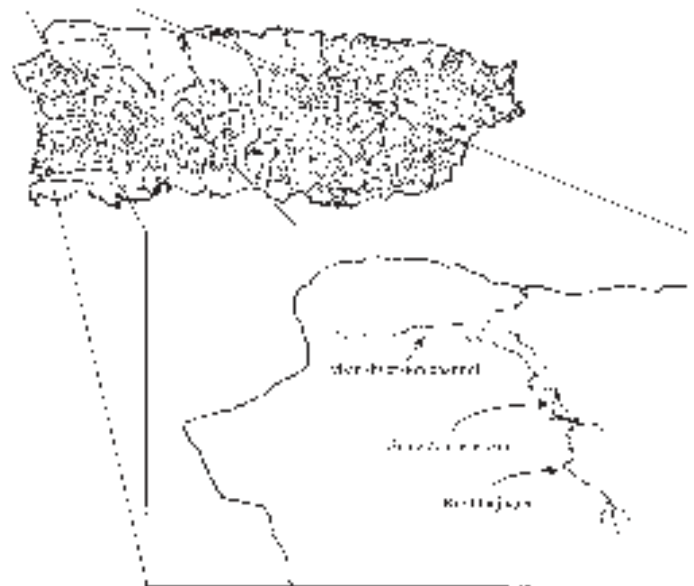


Figure B10- 1. The Isabela Irrigation District constructed over limestone substrate in 1928. See BOX 14 for a narrative of its failure as an irrigation district.

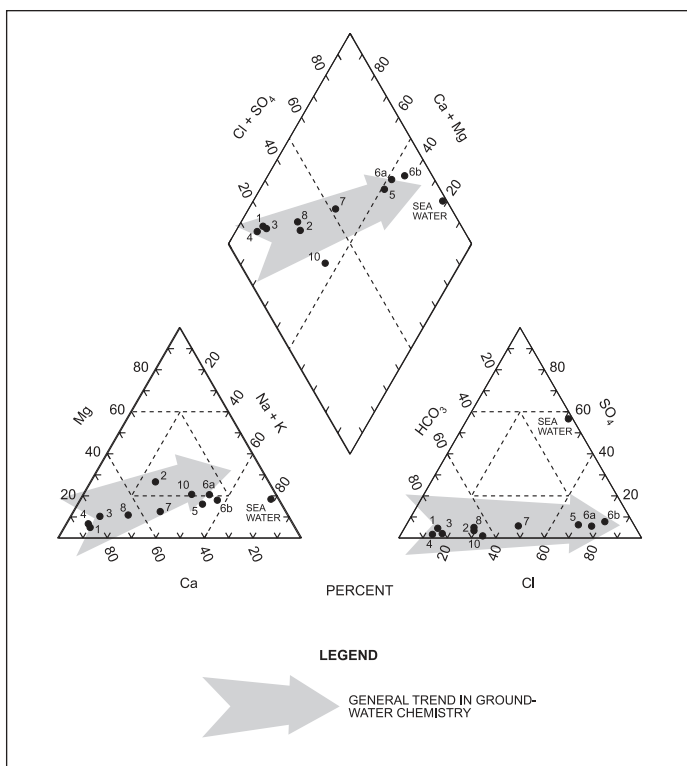


Figure 21. Piper diagram showing general trend in ground water chemistry of sampled water in the Dorado area (Troester 1999).

calcium were lower within the freshwater parts of the aquifer. Carbon dioxide gas dissolves in, and reacts with, water as it infiltrates through soil. This process is followed by calcite dissolution as water recharges the aquifer (figure B3-1). As a result of calcite precipitation and dissolution of gypsum and dolomite, carbon dioxide may degas as the water moves downgradient in the artesian aquifer. In the upper aquifer, continuous recharge of waters rich in carbonic acid maintains the dissolution of the carbonate minerals. Mixing of seawater with fresh ground water dominates the chemistry near the coast.

Water in the lower aquifer is fresh throughout much of its area, but is brackish in some areas

near San Juan and Guaynabo. The quality of water of the two north coast aquifers is fairly similar (Zack et al. 1986). Concentrations of dissolved solids increase along the **hydraulic gradient**. In general, concentrations are below 500 mg/L, but they approach this value in areas of saltwater intrusion, at which point suitability for irrigation and public water supply is affected. The concentrations of nitrate are smaller than the detection limit. Sulfate concentrations are low in comparison to other aquifers in the island. Giusti and Bennett (1976) observed that the quality of river water is similar to that of the aquifer, particularly during base flow conditions.

Piper diagrams show that as ground water flows

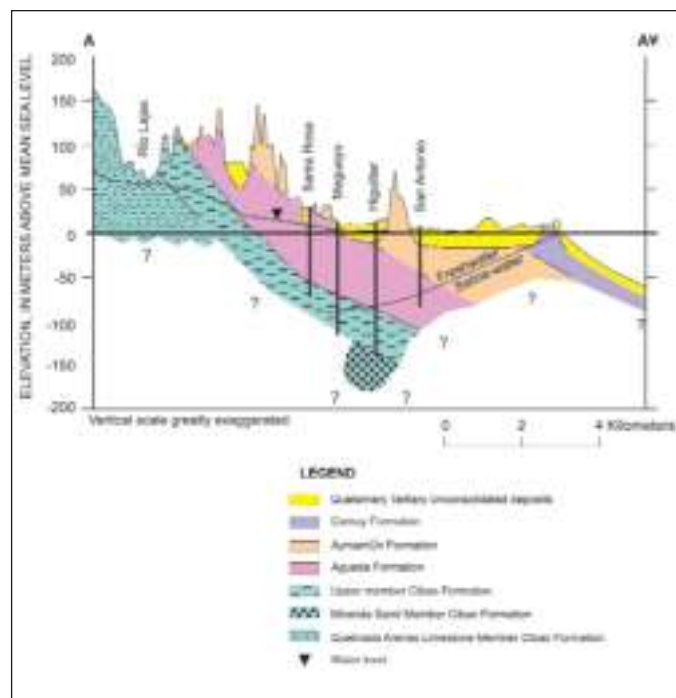


Figure 22. Cross section of the aquifer in the Dorado area highlighting the mixing of salt- and freshwater, as well as the variation in height of the water table as it passes through different limestone strata (Troester 1999).

from the upper aquifer to the Atlantic Ocean, chemical reactions between the water and the minerals in the aquifer change the chemical composition of water. This results in an increase in the concentration of dissolved solids. Ground water in the aquifer changes from a calcium **bicarbonate** solution in the recharge areas to a sodium chloride solution near the coast (figure 21). This is caused by mixing with sea water (figure 22). The changes in the height of the water table along the aquifer cross section in figure 22 reflect the changing hydraulic conductivity of the various limestone elements (Troester 1999). As the hydraulic conductivity changes, the mixing of water with the chemical

components of limestone also changes resulting in changes of its quality.

Artificial Lakes, Lagoons, Natural Ponds, and Wetlands

The northern limestone has many types of artificial lakes, lagoons, ponds, and wetlands (figure 23). They range in size from Caño Tiburones and Lago Guajataca—respectively the largest wetland and artificial lake in the region—to micro wetlands on the bottom of mogotes or small ponds in the valleys between mogotes. These systems also range widely in salinity from saltwater mangroves to mixed seawater and freshwater riverine estuaries, and a freshwater coastal lagoon—Laguna Tortuguero. In the past,



Figure 23. Map of Puerto Rico's wetlands. Modified from del Llano (1988). Heavy lines delimit the area proposed for transfer to public domain.

Caño Tiburones had similar hydrological behavior to Laguna Tortuguero—it was fed by the northern aquifer and discharged freshwater to the ocean (Giusti 1978).

Caño Tiburones is a surface water body delimited in the west by Río Grande de Arecibo and in the east by Río Grande de Manatí. It has an area of approximately 46.6 km² above Aymamón Limestone. Springs are common in its vicinity due to elevations below sea level. The surface deposits are mainly alluvium, which

serve as boundaries for Caño Tiburones. Under natural conditions, Caño Tiburones received runoff water directly from Río Grande de Manatí and Río Grande de Arecibo. Under present conditions, Caño Tiburones loses most of the incoming runoff through diversion channels built as part of an agriculture development plan. The average freshwater volume pumped to the ocean was about 3.15 m³/s. Prior to the artificial drainage of Caño Tiburones, 0.57 m³/s were discharged to the ocean. The water table of

this wetland was lowered below sea level by continuous pumping (photo 19) and the wetland suffered seawater intrusion (Zack and Class Cacho 1984). Saltwater intrusion to Caño Tiburones occurs through four main locations along the north coast and produces zones of salty and saline waters. The four locations are: west of Punta Caracoles, east of Punta Las Tunas, west of Palmas Altas, and east of Palmas Altas (Raúl Díaz 1973).

Laguna Tortuguero (photo 20) has a surface

area of 2.24 km² with a volume of about 2.68 m³ and a mean depth of 1.2 m (Quiñones Márquez and Fusté 1978). Bottom sediments average 2 m deep and their volume is twice the volume of lagoon water. Annual surface and ground water influx to the lagoon is almost six times that of annual rainfall. The lagoon discharges about 20 Mm³/yr. to the ocean. In 1975, water quality was excellent and had low bacterial counts. The lagoon is also known for its excellent fishery.

In addition to Caño Tiburones and Laguna Tortuguero, discharge from the north coast aquifer is



Photo 19. Pump house at Caño Tiburones, Arecibo, Puerto Rico. Photo by J. Colón.



Photo 20. Laguna Tortuguero. Photo by L. Miranda Castro.

responsible for many more of the region's wetlands (photo 21), such as the swampy coastal region between Arecibo and Dorado (Giusti and Bennett 1976). The region's swampy lands include the white sand wetlands around Tortugero Lagoon, which harbor an unusual concentration of endemic wetland plant species—including many rare carnivorous plants. The discharge to these features occurs both as springflow and as seepage. Giusti (1978) estimated that 75 percent of the aquifer discharge occurred inland from the wetlands and from there it flowed to the ocean via Laguna Tortugero and Caño Tiburones. The other 25 percent of the aquifer discharge was direct flow to the ocean floor in a zone a few hundred meters wide. The coastal wetlands themselves are characterized by a particular water budget shown in figure 17c.

Springs and Waterfalls

Springs occur throughout the karst belt (figure 16) in many forms, and many flow over cliffs and rocks as waterfalls (photo 22). These waterfalls are sites of intensive recreation, particularly along roadsides. Springs have been classified as to their origin, rock structure, discharge, temperature, and variability—that is, volcanic, fissure, depression, contact, artesian, tubular, or fracture types (Guzmán Ríos 1983). Puerto Rico has examples of most types. Rodríguez Martínez (1997) classified 67 springs into 2 groups according to their response to rainfall—diffuse type springs, which have little or no response to rainfall and conduit type springs, which exhibit a strong response to rainfall. Ojo de Agua in Vega Baja, Mameyes in Manatí, and Mackovic in Vega Alta, are diffuse springs. Maguayo in Dorado, Ojo de Guillo in Manatí, and San Pedro in Arecibo, are conduit-type springs.

There are no first or second order springs in the karst belt—those with base flows exceeding 2.8320 and 0.2832 m³/s respectively. However, discharges as high as 1.7295 m³/s were measured after rainfall events (Rodríguez Martínez 1997). Rodríguez Martínez (1997) found 10 third order (base flow 0.028 to 0.2832 m³/s), 4 fourth order (0.0062 to 0.0282 m³/s), 14 fifth order (0.0006 to 0.0062 m³/s), 19 sixth order (0.00005 to 0.0006 m³/s), 6 seventh order (0.00001 to 0.00005 m³/s), and 14 eighth order (base flow of a few drops per second) springs. Some of the eighth order springs could be dry and only flow after a rainfall event; otherwise, they stand as nearly circular stagnant pools.

Most of the principal springs in Puerto Rico are in the limestone region. They are associated with all the carbonate units in the middle Tertiary sequence of the karst belt, except the Camuy and San Sebastián Formations (Rodríguez Martínez 1997). Springs

drain the unconfined parts of both the upper and lower aquifers. Springs that drain the unconfined part of the lower aquifer normally issue from the outcrop areas of the Lares Limestone and the Montebello Limestone Member of the Cibao Formation. Those that drain the unconfined part of the upper aquifer issue from both the outcrop and coastal subsurface areas of the Aguada and Aymamón Limestones. No spring is known to issue from the confined part of the lower aquifer (Rodríguez Martínez 1997).

Permeability contrast between successive geologic units appears to be the main factor controlling the occurrence of springs in the karst belt. Ground water flow in the outcrop areas of the upper and lower aquifers appears to be highly controlled by fractures, and consequently most of the springs in these areas appear to be of the conduit type. Ground water flow in the mid valleys and more coastal areas of the upper aquifer



Photo 21. The north coast aquifer discharges through coastal wetlands such as this Toa Baja lagoon at Highway PR 165. Photo by L. Miranda Castro.



Photo 22. A waterfall formed by Sonadora spring, Ciales, Puerto Rico. Photo by L. Miranda Castro.

appear to occur along vertically and laterally discontinuous permeable zones that may be connected by fractures and, as a result, springflow is mostly of the diffuse type (Rodríguez Martínez 1997). The complexity of the underground drainage system that feeds springs is illustrated in figure 24.

Thousands of springs in the northern limestone discharge near the coast. In the western region of the northern limestone—Río

Camuy to Aguadilla—three offshore springs have been reported plus many others that discharge on the coast (Tucci and Martínez 1995). The estimated discharge into the sea is from 0.11 to 1.02 m³/s—a value greater than water use by pumpage (0.08 m³/s) and close to the leakage to streams (1.22 to 1.76 m³/s). The total discharge of some of the principal springs in the karst belt can be as high as 0.08 Mm³/d—20 mgd (Rodríguez Martínez 1997).

Springs discharging into rivers issue from cliffs—sometimes as waterfalls—or emerge through the alluvium, and most discharge on the west side of river valleys, suggesting that the pattern is due to the eastern tilt of the formations (Giusti and Bennett 1976). However, some springs are known to discharge into the east bank of the rivers indicating that the eastern tilt is not the sole factor in determining the discharge

direction of springs on the north coast (Rodríguez Martínez 1997). The explanation is related to the orientation of karst conduits as they pass through various levels of water saturation in the geologic strata. Springs in the Río Grande de Arecibo alluvial plain supplement the water discharge of the river. One of them, San Pedro Spring contributes 32,551 m³/d—8.6 mgd (Quiñones Aponte 1986).

The water quality parameters of spring waters tend to reflect the values observed in underground waters. Rodríguez Martínez (1997) found water quality differences between conduit and diffuse type springs. These differences were related to the hydrological behavior of the springs. Conduit-type springs behave like surface streams in response to rainfall events. As a result, their water quality also exhibits short-term variations. The discharge of diffuse springs changes very little after rainfall events and their water quality reflected that of the aquifers they drained. Water temperature ranges from 22.5 to 28.0 °C. Specific conductance ranges from 289 to 4,000 microsiemens per cm increasing coastward, and pH ranged from 6.9 to 7.8. Calcium, sodium, bicarbonate, and chloride are the main ionic species in spring waters. The main water type is calcium bicarbonate and secondary water types are calcium-bicarbonate-chloride and sodium-bicarbonate-chloride. With the exception

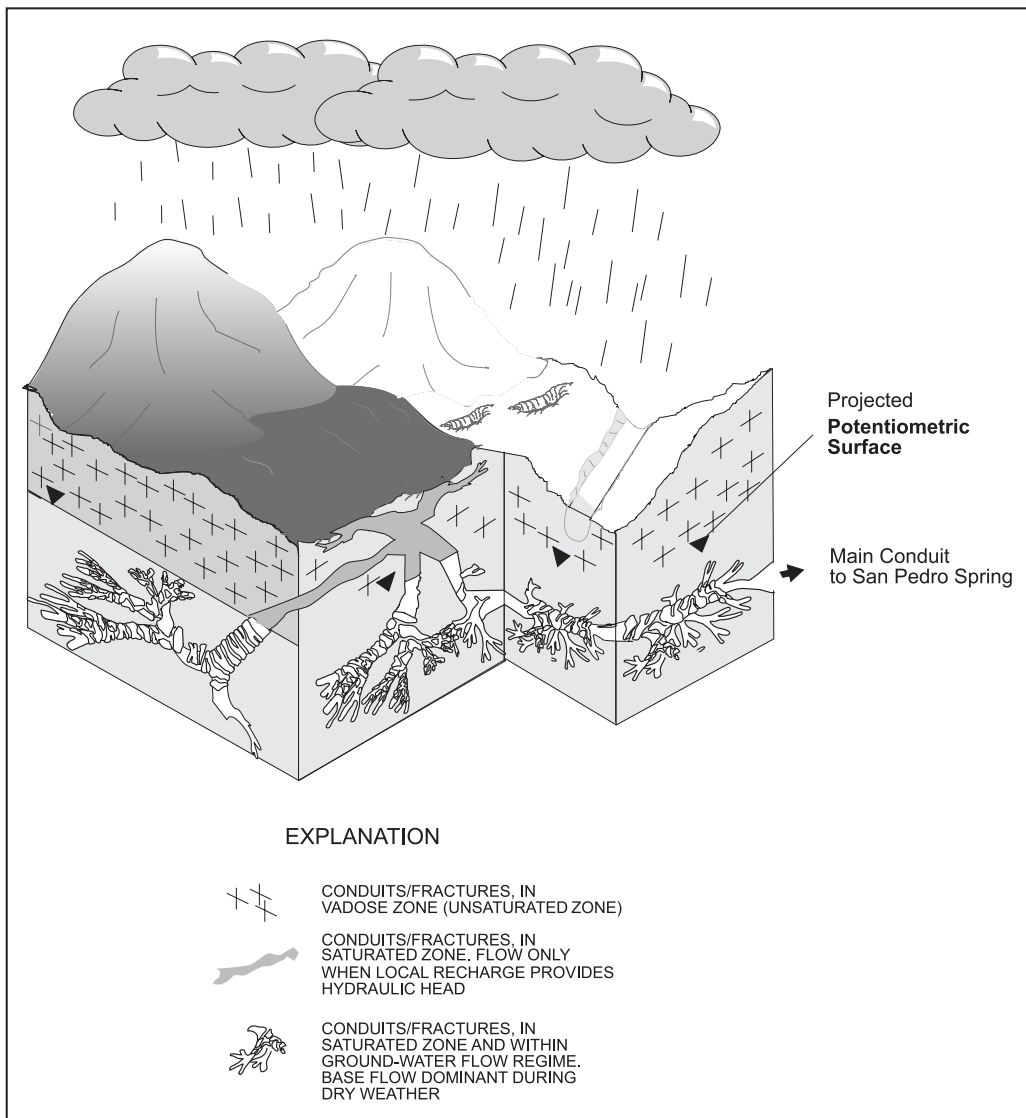


Figure 24. Schematic diagram showing the complexity of the San Pedro spring conduit network (Rodríguez Martínez 1997). This cave system is located in the Río Grande de Arecibo watershed.

of Ojo de Guillo spring, water quality as measured by bacterial counts has remained stationary in the karst belt since 1983. At Luis Pérez in Arecibo, bacterial counts have reached values as high as 35,000 and 27,000 colonies of fecal coliform and fecal streptococci, respectively, per 100 mL (Rodríguez Martínez 1997).

Ecological Diversity

The variety of landforms and hydrologic conditions of the limestone region influences the variety of ecological systems that it contains. Moreover, there are 18 geoclimatic zones represented in the limestone region (figure 4, table 2) that are responsible for the diversity of ecosystems. Ecosystem types range from marine to estuarine, terrestrial, and freshwater systems. A high energy coastline with rocky and sandy beaches, cliffs, marine caves, sand dunes, and coastal marine waters represents the marine coastal environment. Riverine estuaries, low salinity basin mangroves behind sand dunes, and the largest herbaceous wetland in the island—Caño Tiburones, represent the estuarine environment. Freshwater systems include Laguna Tortugero, located a few meters from the ocean; springs, some of which discharge into the ocean; ponds (photo 23); artificial lakes; and small wetlands, some with magnificent royal palms, that appear at the base of

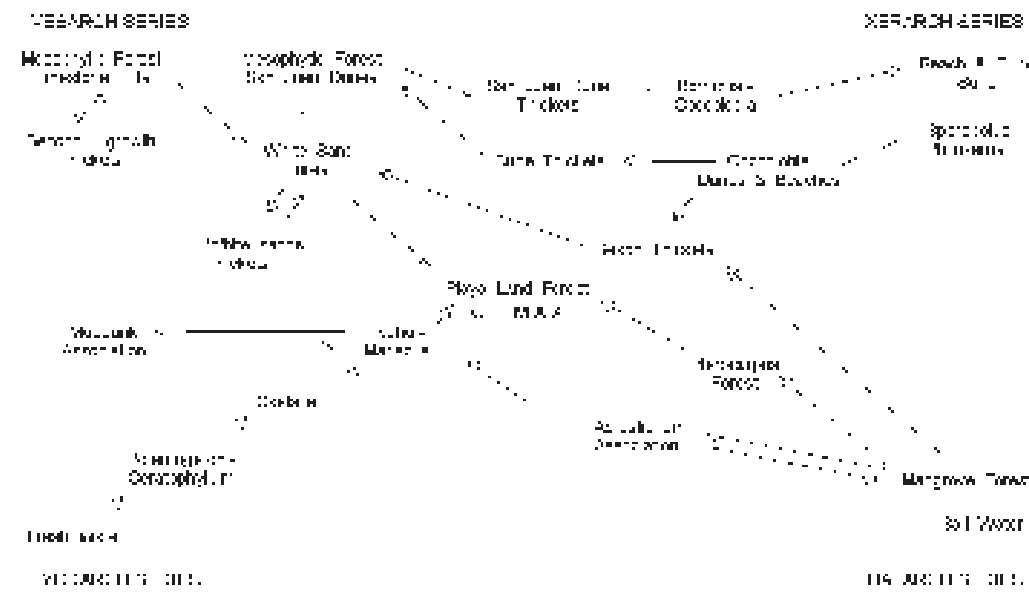


Figure 25. The principal plant associations of the northern coastal plain of Puerto Rico and their assumed successional relations (Gleason and Cook 1926). The diagram is organized as four successional pathways converging on the climax Playa Land Forest in the center. Successions originating in open water are hydrarch, in sea water are halarch, in moist forests are mesarch, and in beach and dune are xerarch.

mogotes and along seeps from the underground aquifer. A diverse vegetation that grows on the white sands of the coast, karst forests with the highest tree diversity in the island, and the ecological systems associated with caves and sinkholes represent the terrestrial component.

Terrestrial Vegetation

Gleason and Cook (1926) constructed a successional scheme for the vegetation of the north coast of Puerto Rico (figure 25). Although the interactions in the scheme have not been demonstrated to occur, the framework remains as a useful overview of the principal vegetation types

of the region. We give greater attention to the hill forests but end this section with a short statement on the other vegetation types identified by Gleason and Cook (1926).

Puerto Rican karst forests, regardless of rainfall conditions, share common characteristics including **physiognomy** and leaf characteristics. Karst forests are characterized by trees of small diameter, high tree density, and leaf scleromorphy. Stands have a tendency to show signs of being exposed to frequent drought conditions. Even in the moist and wet karst belt, forests have a high proportion of deciduous tree species and show a high degree of scleromorphy (Chinaea 1980). This is probably due to the rapid rate of runoff and infiltration of rainwater, low water storage in shallow soils, and high sunlight



Photo 23. Charca Las Tiguas, a wetland near Arecibo, Puerto Rico. Photo by L. Miranda Castro.

and wind acting on vegetation. In the dry southern karst, these tendencies are even more prevalent because rainfall input is lower and more seasonally variable.

Karst forests share many characteristics with other forests in the island. They all have smooth canopies with few emergent trees. This is a response to wind sculpturing and periodic wind storms that prune the canopy and any emergent branches that might develop between events. All of the island's forests also share a high **species dominance** (figure 26).

Usually no more than five tree species dominate stands by accounting for about 50 percent of the stand's basal area and tree density, combined as the **Importance Value** of species. The result is that a few dominant species and a large number of rare species characterize forest stands. Lugo (1991) attributed this high dominance to infrequent and large-scale disturbances such as hurricanes.

The number of species per number of stems (figure 27) and number of species per unit area (figure 28) are also relatively uniform in Puerto Rican forests. For all forest stands studied, 44 tree species are encountered per 1,000 individuals. The relationship between tree species richness and stem density in karst forests is relatively weak ($r^2 = 0.37$) because of the high variability of tree species richness in karst forests. However, the highest count of tree species per

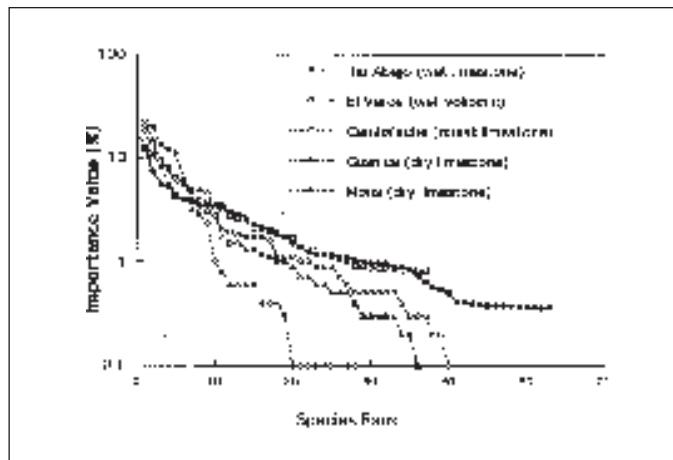


Figure 26. Importance value curves for forest stands in wet volcanic (El Verde), wet and moist karst (Río Abajo, Cambalache), and dry karst (Guánica, Mona) geoclimatic zones of Puerto Rico. Data can be obtained from A.E. Lugo.

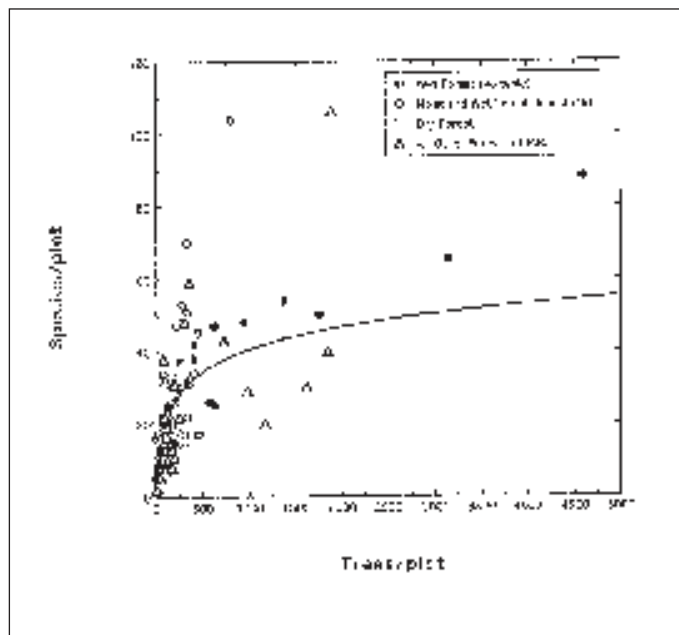


Figure 27. Graph of the number of tree species per plot and the tree density in the plot. Dry forests are from the southern limestone, while moist and wet forests are from the northern limestone. Wet volcanic forests are from the Luquillo Mountains. The relation between number of tree species in a stand (y) and tree density (x) and the number of tree species per thousand individuals (y') is described by, or obtained from, regressions. For wet forests on volcanic rock— $y = -43.78 + 30.89 \cdot \text{LOG}(x)$ with $r^2 = 0.84$, $n = 19$, and $y' = 49$. For moist and wet forests on karst— $y = -13.79 + 20.01 \cdot \text{LOG}(x)$ with $r^2 = 0.37$, $n = 39$, and $y' = 46$. For dry forests on karst— $y = -30.27 + 24.95 \cdot \text{LOG}(x)$ with $r^2 = 0.52$, $n = 26$, and $y' = 45$. For other forests in Puerto Rico— $y = -20.75 + 20.46 \cdot \text{LOG}(x)$ with $r^2 = 0.46$, $n = 40$, and $y' = 41$. For all forests combined— $y = -21.85 + 22.16 \cdot \text{LOG}(x)$ with $r^2 = 0.50$, $n = 124$, and $y' = 44$. The regression line is for all forests. Regression lines for individual forest types have a slightly steeper slope. Data can be obtained from A.E. Lugo.

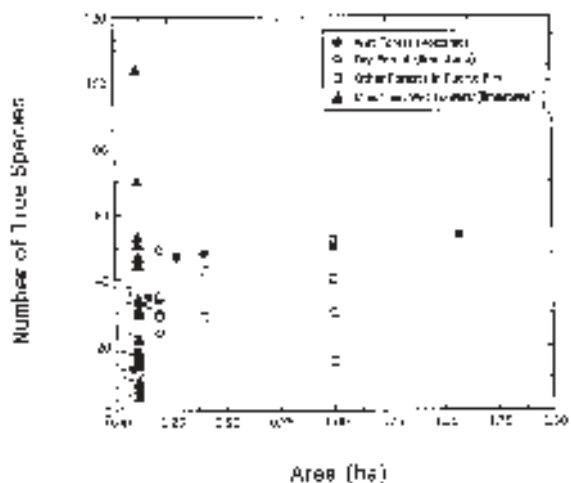


Figure 28. Species-area curve for trees of Puerto Rican forests (Lugo in press).

0.1 ha was on a northern karst forest, while southern karst forests exhibit the same pattern of species-area curve as wet forests on volcanoclastic geology (figure 28).

Karst forests are also characterized by their clumped tree distribution, which is due to the nature of the terrain where they grow. Trees grow best where the soil is deep, but such sites are scarce and abundant rock outcrops limit the locations for adequate tree establishment. In fact, seeds of species like *Plumeria alba*⁶—in the southern limestone—can germinate over rock surfaces, which suggests an extreme adaptation to shallow rocky soil substrates (photo 24). Tree growth in crevices and deep soils provides an advantage during periods of high winds and hurricanes. Well-rooted trees survive strong winds and may only lose their leaves or branches. Few uprooted trees are

observed in karst forests after the passage of a hurricane. The exception is those trees that established over rocks or in shallow soils. Because of soil limitation, trees in karst forests are generally shorter than trees in volcanic forests with the same rainfall but deeper soil.

The most salient characteristic of karst forests is perhaps the most difficult to detect. Karst forests exhibit numerous gradients in vegetation structure, physiognomy, and composition as a result of the many environmental and topographic gradients in the region. Chinaea (1980) described an east-west and north-south rainfall gradient due to the trade winds decreasing rain from east to west—and topography—increasing rain from north to south with elevation. Wind exposure also establishes two gradients within mogotes: greater exposure on the northeast slopes and less on the southwest slopes, and

greater wind on tops compared to bottoms of mogotes. Soil characteristics result in deep fertile soils in valleys and shallow, rocky, and infertile soils on tops of mogotes. Slopes exhibit intermediate edaphic conditions.

Vegetation response to environmental gradients is complex in part because of the effects of past land use, age, elevation, and size of forest stands (Rivera and Aide 1998). However, Chinaea (1980) conducted ordination studies at the level of a single mogote as well as various mogotes while holding some of these variables relatively constant. He found that the basal area of individual species varied according to a normal distribution along humidity gradients from **xeric** to **mesic**. Some species peaked in basal area under mesic conditions while others did under xeric conditions and at any moisture level he

could find a species reaching its optimal basal area. At both single and multiple mogote levels, Chinaea found that as conditions became more mesic, there was a linear reduction in the importance of species with sclerophyllous leaves. Values ranged from over 60 percent of species with **sclerophyllous** leaves in xeric conditions, to almost zero percent under mesic conditions. In contrast, tree height increased along the same gradient from less than 10 m to over 25 m.

Studies of forests in the karst belt have focused on mogotes, where stands have been classified by numerous criteria. For example, Alvarez Ruiz et al. (1997) used age, physiognomy, and land use to classify forest stands. Beard (1949, 1955) used only physiognomy, and Dugger et al. (1979) used topographic position valley, slopes, and tops. The forests of the karst



Photo 24. Trees such as this almácigo (*Bursera simaruba*) can grow in crevices and develop strong root systems that help them survive hurricanes and droughts. Notice how roots penetrate into the crevices. Photo by L. Miranda Castro.

⁶ We maintain the scientific name given in the original sources reviewed.

belt are diverse in species composition and physiognomy. Ordination techniques led Chinaea (1980) to identify three types of forests in the karst belt—mesic forest, dry woodland, and mixed woodland (figure 29). Chinaea also identified cliff forests as a topographic vegetation unit at the edge of cliffs.

The mesic forest is found on the base of mogotes (photo 25). It has a height of 25 to 30 m, a closed canopy, evergreen species with **mesophyll** leaves, a second tree layer with large leaves at 15 to 20 m height, a 5 to 10 m height shrub layer, and a herbaceous and tree seedling layer on the forest floor. Common species in this forest type are *Dendropanax arboreus* (palo de pollo) and *Quararibea turbinata* (garrocho).

The dry woodland occurs on slopes and exposed tops (photos 26 and 27). The canopy of this forest is



Photo 25. A mesophytic forest at the base of a mogote in Ciales, Puerto Rico. Photo by J. Colón.

deciduous and trees reach heights of 16 to 18 m. Leaves are sclerophyllous and range in size from **microphyll** to mesophyll. The forest understory contains shrubs and small trees with evergreen leaves. Leaf size ranges from **nanophyll** to **macrophyll** and most are sclerophyllous. Common species are *Coccoloba diversifolia* (uvilla) and *Bursera simaruba*



Photo 26. Dry woodlands on the slopes of mogotes in Arecibo, Puerto Rico. Photo by J. Colón.

(almácigo). The mixed woodland is a combination of the previous two and is found in intermediate sites between those protected and those exposed. It can occur in lower slopes or on hill tops, depending on the aspect.

The cliff woodland occurs at the edge of cliffs in locations with abrupt changes in elevation. Strangler trees—intolerant of shade and evergreen—dominate this forest type. These trees have specialized

roots that allow them to obtain water and nutrients from long distances. The dominant species are in the genus *Clusia* and include *Clusia rosea* (cupey). This association is conspicuous by the falling root systems on the sides of cliffs and can be seen when driving old roads that pass through the valleys of mogotes. Modern highway construction cuts the mogotes in half and thus this vegetation is no longer visible from expressways.

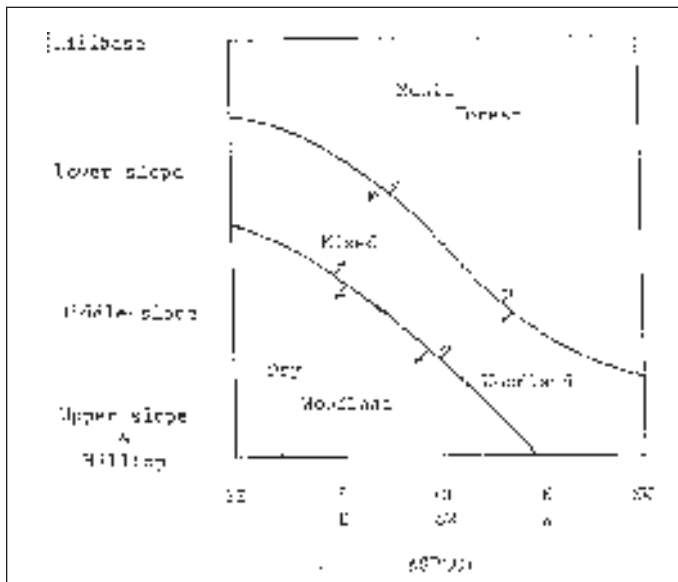


Figure 29. Ordination of main hill forest types in the karst belt (Chinaea 1980).



Photo 27. Dry woodlands on the tops of mogotes and mesophytic forests with an even canopy on the base of the mogotes in Ciales, Puerto Rico. Photo by L. Miranda Castro.

The forests of the flatlands were converted to agricultural uses early in the colonization of Puerto Rico, and it is difficult to reconstruct their original composition and structure. It is believed, however, that forests on the rich alluvial soils of the north coast must have been among the most majestic in the island (photo 28). A forest type that survived in the lowlands is the forest on white sands, initially described by Gleason and Cook (1926). A 1980 study of the stands visited by Gleason and Cook (Figueroa et al. 1984) illustrated the complexity of vegetation structure and composition resulting from past land uses and variations in topography and soil types. Figueroa et al. (1984) studied an area of 39.5 ha and identified six vegetation types based on physiognomy and age (table 8). Of these, the old secondary forest was the stand most closely



Photo 28. Large tree in deep fertile soils in Arecibo, Puerto Rico. Photo by J. Colón.

Table 8. Structure of the vegetation on the moist coastal white sands of Dorado, Puerto Rico (modified from Figueroa et al. 1984). Data are for trees with diameter at breast height > 2.5 cm. The complexity index is calculated for an area of 0.1 ha and is the product of height, basal area, tree density, number of species, and 10⁻³.

Forest Type	Species (no./0.1ha)	Tree Density (no./ha)	Basal Area (m ² /ha)	Height (m)	Complexity Index
Old secondary	32	1880	41.6	19.7	493
Young secondary	19	1833	29.0	19.3	194
<i>Clusia-Zyzygium</i>	11	3200	25.6	20.7	187
<i>Pterocarpus</i>	7	1680	44.6	19.0	100
Disturbed and open	9	1000	21.8	17.0	33
Abandoned palm grove	5	1600	32.6	12.3	32

resembling the original vegetation of the region. Species such as *Manilkara bidentata* (ausubo), *Lonchocarpus latifolius*, and *Pisonia subcordata* (corcho blanco) were present forming stands as tall as 19.7 m with a tree species richness of 32 species/0.1 ha. Two endangered species were observed in 1980: *Cassia mirabilis*—an endemic herbaceous species—and *Ficus stablii* (jaguey)—a tree.

Lugo (in press) found that karst forests had high primary productivity, fast growing trees, and fast regeneration and succession after disturbances. Rivera (1998) studied succession in the karst belt and found that landuse history affected the pattern of regeneration and stand dynamics for many years. Forests in abandoned pastures had a greater woody species diversity in comparison with abandoned coffee sites. They also had a higher tree density but similar basal area (Rivera and Aide 1998). Species composition and dominance was also different in forests

regenerating in abandoned pasture sites compared to those regenerating in abandoned coffee plantations. *Guarea guidonia* was the dominant species in abandoned coffee plantations. This species is used for coffee shade. *Spathodea campanulata*, an alien species, dominated forests regenerating in abandoned pastures. The rate of succession was fast and similar among forest stands. It was accelerated by seed dispersal by bats.

Complex coastal dune/beach vegetation occurs all along the north coast of Puerto Rico (photo 29). This vegetation is controlled by the harsh conditions of the coastal

zone which include sandy soils, low soil moisture levels, constant salt spray, and high frequency of high velocity winds. As a result, the vegetation is generally scleromorphic, of low stature, and wind sculpted. On the most exposed beach sand, the vegetation is prostrate—for example *Philoxerus vermicularis*—or roots high in the beach and creeps towards the ocean as do *Ipomea pescaprae* and *Sporobolus virginicus*. These give way to dune-forming plants such as *Chamaesyce buxifolia*, *Diodia maritima*, and others. Plant thickets develop behind the dune-forming plants. These are dominated by *Coccoloba*



Photo 29. Vegetation of coastal dunes. These dunes show human impact. Photo by J. Colón.

wifera, which can grow to tree size when on the leeward slope of stabilized sand dunes. As the presence of vegetation or the protection of the sand dune itself reduces wind force, plant size increases and eventually forms a closed canopy forest behind the sand dunes.

Wetlands

Freshwater wetlands of the karst belt include marshes at the base of mogotes, forested wetlands in riparian zones including the boils of springs and alluvial valleys, and either forested or nonforested wetlands on valleys between mogotes. The determinant factor on the type of wetland is the **hydroperiod**. A longer hydroperiod favors marshes while shorter ones favor forested wetlands. Ferns and emergent aquatic macrophytes such as *Typha* are the dominant species in the nonforested wetlands. *Pterocarpus officinalis* (palo de pollo), *Roystonea borinquena* (royal palm), *Calophyllum brasiliense* (maría), *Bucida buceras* (úcar), and *Prestoea montana* (sierra palm) predominate in forested wetlands. The endemic epiphytic orchid *Epidendrum kraenzlinii* occurs in the *Pterocarpus* forest as well as the endangered shrub *Sabicea cinerea*.

On upland valleys and at the base of mogotes, springs and seeps dictate the hydroperiod. On the coastal zone, high aquifer discharge is responsible for the formation of wetlands, such as Caño Tiburones

and wetlands surrounding Laguna Tortuguero. In these coastal wetlands, the hydroperiod is generally longer than in the mogote valleys and as a result are dominated by marshes—the largest extensions of such systems in Puerto Rico. Gleason and Cook (1926) listed the aquatic macrophytes that are common in these wetlands including *Typha angustifolia*, *Mariscus jamaicensis*, *Phragmites phragmites*, and many other emergent, floating, and submerged aquatic plants. Because of the abundant number of springs and seeps, the map of the wetlands of the northern karst shows hundreds of small wetlands scattered among mogotes and other hill features, as well as the larger wetland areas of the coastal zone and alluvial valleys of major rivers (figure 23).

Estuaries

Estuaries form in locations where seawater and freshwater mix. Mangrove forests dominated by *Rhizophora mangle* (mangle rojo) follow saltwater wedges that penetrate upstream under freshwater discharge (photo 30). These forests are found on the riparian zone of rivers several kilometers inland, usually as far as the saltwater wedge penetrates the river channel (Lugo and Cintrón 1975). These mangroves, known as riverine mangroves, are among the most productive of all mangroves on the island. In addition to *R. mangle*,

these forests contain other species, more notably *Laguncularia racemosa* (mangle blanco) and *Avicennia germinans* (mangle negro). Abundant freshwater plus nutrients carried by riverine waters contribute to the high productivity of these systems.

Because of the high wave energy of the Atlantic Ocean, mangroves do not grow on the seashore of the north coast as they do on the south coast—that is, fringe mangrove forests do not occur on the north coast nor do overwash mangrove islands. Instead, mangroves grow behind sand dunes at the mixture zone between seawater and freshwater. These mangroves are known as basin mangroves. Unlike basin mangroves in arid coastlines, the basin mangroves of the north coast have low salinity and thus develop a high biomass and tall height structure.

Mangroves behind sand dunes only occur on the north coast of Puerto Rico.



Photo 30. Mangrove forest in Toa Baja, Puerto Rico. Photo by L. Miranda Castro.

All four mangrove species can be found in or near basin mangrove forests—*R. mangle*, *A. germinans*, *L. racemosa*, and *Conocarpus erecta* (mangle botón). In the rear of these forests, the ecological system transitions from estuarine to freshwater. Along the transition one can find thickets of the mangrove fern *Acrostichum aureum* and tree species such as *Annona glabra* (pond apple) and *P. officinalis*. Forested or nonforested wetlands with or without tidal influence develop behind the mangroves in response to hydroperiod.

The Karst Belt Harbors Valuable Natural Resources

Fossil Flora and Fauna

The karst belt provides a bonanza to students of paleontology in Puerto Rico and the Caribbean region. The area has provided significant fossil records since the early 1920's when B. Hubbard (1923) produced a list of fossil plants collected from Río Guajataca near Lares. Charles Arthur Hollick confirmed and added to these reports in his 1924 and 1926 papers. He summed all these, as well as an additional list of Tertiary microfossil plants from the Lares-San Sebastián region, in his volume on Paleobotany of Puerto Rico of the Scientific Survey of Puerto Rico and the Virgin Islands (Hollick 1928). The 88

plant taxa listed for this karst area are recognized as the largest list of macrofossil flora ever produced for the Tertiary of any Neotropical region (Graham 1996). More recent studies on past vegetation of Puerto Rico center on paleopalynology—the study of fossil pollen. Graham (1996) provides a detailed review of both macropaleoflora and micropaleoflora of the region. These data are important for keeping in perspective the evolution of the original flora in the karst, given the significant destruction of vegetation from the early pre-Hispanic period (Domínguez Cristóbal 1989a,b) and the constant human alteration of the region (Torres González and Wolansky 1984, Dopazo and Molina Rivera 1995).

The animal life of modern Puerto Rico is not the same animal community that roamed the many plant communities of Puerto Rico thousands of years ago. Our understanding of this fauna is largely dependent on the fossils recovered from caves or from exposed rocks that abound in the karst belt. When animals die in tropical forests, their bones are quickly destroyed by scavengers and weathering, leaving no fossil evidence of their existence. Fossils of marine animals such as sharks and Dugongs have been preserved in the karst belt. The extinct Great-tooth Shark, *Carcharodon (Carcharocles) megalodon* (Nieves Rivera 1999) that was previously recorded from the Miocene of the Neartic region was

preserved in Isabela and other karst areas. This finding highlights the importance of Puerto Rican karst to understanding the natural history of this species. Sketches on walls have been seen and samples of Dugong (*Caribosirenia tumeri* and *Halitherium antillensis*)—extinct relatives of recent manatees—have been collected in three different sites at the Río Encantado cave system. Collections are deposited at the Smithsonian Institute in Washington, DC. They will probably allow the reconstruction of a complete Dugong skull (Halton 1996).

Fossils of amphibians and reptiles are scarce. Pregill (1981) and Pregill and Olson (1981) discussed the presence and significance of herpetofaunal remains in the Caribbean karst and in particular in Puerto Rico. Most remains found associated with cave deposits are probably the leftovers of either birds, mammals, or natural phenomena. Evidence of the endemic Puerto Rican Crested Toad, *Peltophryne lemur* (photo 31), and of extinct racers of the genus *Leiocephalus* (*L. etheridge* and *L. oartitus*) was found in such karst deposits (Pregill 1981). Fossil material yet to be described has been housed in the U.S. National Museum and in the American Museum (Storrs Olson, personal communication).

Records of many extinct land vertebrates were preserved in caves, where bones are often protected

from the destructive effects of sunlight and rain. Caves can act as natural tombs, which can preserve bones for tens or even hundreds of thousands of years. Animal remains arrive in caves by several processes. Some caves have deep **shafts**, which can act as natural—and very lethal—traps for unwary animals. Other caves may serve as animal dens and preserve their occupants after their deaths. The remains of the endemic dog-sized Ground Sloth (*Acratocnus odontrigonus*, Anthony 1916a) and the Giant Hutía (*Elasmodontomys obliquus*, Anthony 1916a) probably used caves this way.

Fossil remains in caves may be leftovers of food taken into caves by owls; sometimes these owl-pellet deposits may consist of thousands of small bones. Extinct endemic birds preserved in Puerto Rican caves in this way include a woodcock (*Scolopax anthonyi*, Olson 1976), a quail dove (*Geotrygon larva*, Wetmore 1920), a barn owl (*Tyto cavatica*, Wetmore 1920), a swift (*Tachornis uranocetes*, Olson 1982), a

caracara (*Polyborus latebrosus*, Wetmore 1920) a crow (*Corvus pumilis*, Wetmore 1920), and a finch (*Pedinorhis stirpsaricana*, Olson and McKittrick 1981). Small endemic mammals were also eaten by cave-roosting owls (Anthony 1916b); the island-shrew (*Nesophontes edithae*, Anthony 1916a) is the only Puerto Rican representative of the monogeneric family Nesophontidae, currently believed to comprise 11 species (McFarlane 1999a,b). The Puerto Rican Spiny Rats, *Puertoricomys corozalus* (originally called *Proechimys corozalus*, Williams and Koopman 1951) and *Heteropsomys insulans* (which includes *Homopsomys antillensis* as described by Anthony 1917) were also prime owl prey before the arrival of ship rats in the historic era.

Finally, bones in caves may be the remains of human meals. The first evidence of the extinct Flightless Rail (*Nesotrochis debooyi*, Wetmore 1922) and the rabbit-sized Hutía (*Isolobodon portoricencis*, Allen 1916)—which despite its name was apparently



Photo 31. The endemic Puerto Rican Crested Toad. Photo by J. Colón.

brought to Puerto Rico from its native Hispaniola by Amerindians—was recovered from Amerindian cave middens.

The record of Puerto Rico's lost fauna that has been preserved in the karst belt, primarily its caves, is in serious danger of being lost forever. The alteration of caves by mining **guano**, construction of roads, and transformation into tourist attractions has destroyed unique fossil records that were never examined, never protected, never documented. The experience of caves whose visitation rates were excessive and without control over the actions of the visitors can be summarized as destructive: the floors were trampled and eroded, the remains that were easily detected were ransacked, and the potential to recover at least some of these data reduced considerably. Only a small percentage of Puerto Rican caves contain fossils in their natural conditions, untouched by people and still useful for science. Our ability to document the island's past will depend on efforts in securing these deposits for future study by scientists.

Flora

The flora of the karst belt is transitional between the wet forests over volcanic rocks and the dry forests over limestone rocks. Chinaea (1980) found that 80 tree species from the wet volcanic tabonuco forest in the Luquillo Mountains and 27 tree species from the dry

limestone forests also grow in the karst belt. The karst belt has tree species from sites that represent different rock types—volcanic and karst—different life zones—wet, moist, and dry—and different physiographic conditions—coastal and montane zones.

About 25 percent of the tree species in the karst belt are deciduous. Many other species are facultative deciduous and drop their leaves during extreme drought. The most common families are Leguminosae, Myrtaceae, Rubiaceae, Lauraceae, and Euphorbiaceae. The tree species typical of the area are *Aiphanes acanthophylla* (palma de coyor), *Gaussia attenuata* (palma de lluvia), *Coccoloba diversifolia*, *Coccoloba pubescens* (moralón), *Licaria salicifolia* (canelilla), *Zanthoxylum martinicense* (espino rubial), *Bursera simaruba*, *Cedrela odorata* (cedro hembra), *Hyeronima clusioides* (cedro macho), *Sapium laurocerasus* (tabaiba), *Thouinia striata* (ceboruquillo), *Thespesia grandiflora* (maga), *Ochroma pyramidale* (balsa), *Clusia rosea*, *Bucida buceras* (úcar,

photo 32), *Tetrazygia eleagnoides* (verdiseco), *Sideroxylon salicifolia* (sanguinaria), *Sideroxylon foetidissimum* (tortugo amarillo), *Guettarda scabra* (palo cucubano), *Terebraria resinosa* (aquilón), and *Randia aculeata* (tintillo) (Little et al. 1974).

The species richness of the flora of the karst belt is represented in the flora of Río Abajo Commonwealth Forest, which contains species from the moist and wet climates (photo 33) of the region. Initially Little and Wadsworth (1964) and Little et al. (1974) reported the presence of 175 tree species representing 53 families in the 3,000 ha Río Abajo Commonwealth Forest. However, Alvarez Ruiz et al. (1997) later reported that 242 tree species representing 51 families were present in the forest. Only 27 tree species were reported to be deciduous. Of the tree species, 36 were alien, 35 were endemic, and 43 were rare. Woodbury reported 41 endemic tree species (photo 34) and 43 rare tree species in the Río Abajo Commonwealth

Forest (Alvarez et al. 1983). Acevedo Rodríguez and Axelrod (1999) published an annotated checklist for the Río Abajo Commonwealth Forest with 1,030 vascular plant species—878 native, 158 alien, and 88 endemic. Figueroa Colón (1995) estimated that the wet karst belt harbored 23 percent, and the moist karst belt harbored 16 percent of the endemic tree species in Puerto Rico.



Photo 33. Roble (*Tabebuia* sp.). Photo by J. Colon.



Photo 34. The Puerto Rican royal palm (*Roystonea borincana*), an endemic species. Photo by L. Miranda Castro.



Photo 32. Ucar (*Bucida buceras*). Photo by L. Miranda Castro.

Fauna

Different phyla of invertebrate animals form the major portion of the fauna of any area. Our focus is on vertebrates with short statements on aquatic macrofauna and cave invertebrates. There is no comprehensive study of the invertebrates of the limestone region, but we recommend consulting Vélez (1979a, b, c) for a general overview of the island invertebrates. For information on particular animal groups, we recommend the following works: spiders—Petrunkevitch (1929, 1930a, b), insects—Martorell (1945) and Wolcott (1948), terrestrial mollusks—Van der Schalie (1948), aquatic mollusks—Aguayo (1966), decapods—Vélez (1967a), millipedes—Vélez (1967b), centipedes—Santiago de Rohena (1974), scorpions—Santiago Blay (1984), and earthworms—Borges and Moreno (1990, 1992).

Aquatic Macrofauna

Most of the native freshwater macrofauna of Puerto Rico is present in the karst belt, in spite of the low density of subaerial drainage. Compared to continents, the island has a small number of freshwater animal species. The oceanic barrier to dispersal of freshwater species severely limits the number of species in freshwater ecosystems (Covich and McDowell 1996). Most of the freshwater species must migrate between fresh and saltwater systems to complete their life cycles.

We know of over 100 species of **anadromous** and **cathadromous** fish residing in Puerto Rico (Erdman 1972, 1984; Grana Raffucci 1993). River mouths, estuaries, and mangroves are of particular importance for fish survival. While incomplete, tables 9 and 10 lists 99 fish species in 33 families. Most species are marine and/or of commercial value, and 25 are introduced species to freshwater systems, all of commercial or sporting values (table 10). The largest families of naturally occurring fishes in the karst belt are the Gobiidae (eight species), Gerreidae, and Haemulidae (six species each). The families with the most introduced species are Centrarchiidae, Cichlidae, and Poeciliidae (six species each).

Native fish species include Mountain Mullet—locally known as Dajao—American Eel, River Goby, Bigmouth Sleeper, and Sirajo Goby (table 9). These are commonly fished for sport and human consumption. Dajao is a popular freshwater game fish, which can grow up to 30 cm and weight 250 g (Erdman 1967). This species enters the rivers when they are approximately 2.5 cm in length and develop to adulthood. The Dajao has disappeared from many river systems due to the construction of high dams that prevent the species from reaching headwater habitats (Erdman 1967).

We also list 24 species of crustaceans belonging to 8

families. Among these, freshwater shrimp can be more abundant than fish in many rivers (Erdman 1967). There are at least five species that are regularly fished for sport or sale. One of these—*Macrobrachium carcinus*—is reported to weigh up to 0.5 kg and reach 45 cm in length (Erdman 1967, B. Yoshioka personal communication 2000). Some of the largest specimens of this species have come from Río Grande de Arecibo and Río Grande de Manatí. This, and other species, are known to move through underground rivers. Another important crustacean, which inhabits the karst belt, is the Puerto Rican freshwater crab—*Epilobocera sinuatifrons*—locally known as “buruquena.” This species is endemic to Puerto Rico and is heavily harvested by local people as a food item. It can grow over 7.5 cm in width of carapace (Erdman 1967). Their populations are apparently diminishing island-wide. Excessive harvesting, deforestation, and pesticide use near water bodies are among the most important threats to this crab species (Rivera 1994).

While none of the species are listed as threatened or endangered, many native populations of aquatic macrofauna have declined in Puerto Rico due to reservoir construction, other river alterations, excessive water extraction, illegal fishing practices, and water quality problems.

Cave Invertebrates

Peck (1974) studied the cave invertebrate fauna of 14 caves in Puerto Rico and found 78 free-living species. Of these, 52 were known by precise species name. The distribution of these 52 taxa included 23 from the American mainland, 6 West Indian, and 23 endemic to Puerto Rico. Sixteen of the endemics are known from noncave habitats, while the nonendemics are usually associated with caves in other parts of their range. Ninety percent of the total fauna is **troglophilic**, with only two **troglobitic**. Fifty-five percent of the fauna is guano scavengers, **detritivores**, and **herbivores**, while 45 percent were predators. Peck (1974) listed all the 78 taxa that he found and provided details of the location where the specimens were found and of their natural history.

In subsequent trips to Puerto Rico, Peck studied 5 additional caves and added 73 species to the 1974 list (Peck 1981). The additional work added 6 triglobitic species and reported a new total of 151 cave invertebrate species for Puerto Rico. Moreover, Peck found that the cave fauna of the northern limestone had a 43 percent similarity with the cave fauna of the southern limestone. The similarity was mostly due to species requiring moist environments. He highlighted Cueva Los Chorros—15 km south of

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Table 9. Native fish and crustaceans found in waters of the northern limestone of Puerto Rico. Families are presented mainly following the order in García Ríos (1998). Species accounts include personal observations and the literature including Vélez (1967a), Erdman (1967, 1984), Aranda et al. (1979), Nevárez and Villamil (1981), Negrón González (1986), González Azar (1992), Grana Raffucci (1993), and Bunkley Williams and Williams (1994).

FAMILY/ Scientific Name	Common Name (English)	FAMILY/ Scientific Name	Common Name (English)
FISH—OSTEICHTHYES			
ELOPIDAE		Pomadasys corvinaeformis	Grunt
<i>Elops saurus</i>	Ladyfish	<i>Pomadasys croco</i>	Burro Grunt
MEGALOPIDAE		SCIAENIDAE	
<i>Megalops atlantica</i>	Tarpon	<i>Ophioscion adustus</i>	West Indian Croaker
ANGUILLIDAE		<i>Stellifer stellifer</i>	Small Drum
<i>Anguilla rostrata</i>	American Eel	EPHIPPIDAE	
OPHICHTHIDAE		<i>Chaetodipterus faber</i>	Atlantic Spadefish
<i>Aplatophis chauliodus</i>	Toothy Eel	MUGILIDAE	
CLUPEIDAE		<i>Agonostomus monticola</i>	Mountain Mullet
<i>Harengula clupeola</i>	Scaled Sardine	<i>Joturus pichardi</i>	Hognose Mullet
<i>Opisthonema oglinum</i>	Atlantic Thread Herring	<i>Mugil curema</i>	White Mullet
ENGRAULIDAE		<i>Mugil liza</i>	Liza
<i>Anchoa lamprotaenia</i>	Longnose Anchovy	<i>Mugil tricodon</i>	Fantail Mullet
<i>Anchoviella perfasciata</i>	Flat Anchovy	SPHYRAENIDAE	
<i>Centrargaulis edentulus</i>	Whalebone Anchovy	<i>Sphyræna barracuda</i>	Great Barracuda
EXOCOETIDAE		POLYNEMIDAE	
<i>Parexocoetus brachypterus</i>	Shortfin Flyingfish	<i>Polydactylus virginicus</i>	Threadfin
HEMIRAMPHIDAE		ELEOTRIDAE	
<i>Hyporhamphus unifasciatus</i>	Halfbeak	<i>Dormitator maculatus</i>	Fat Sleeper
BELONIDAE		<i>Eleotris pisonis</i>	Spinycheek Sleeper
<i>Belone raphidoma</i>	Houndfish	<i>Gobiomorus dormitor</i>	Bigmouth Sleeper
<i>Strongylura marina</i>	Atlantic Needlefish	GOBIIDAE	
POECILLIDAE		<i>Awaous taiasica</i>	River Goby
<i>vivipara</i>	Top Minnow	<i>Bathygobius soporator</i>	Frillfin Goby
SYNGNATHIDAE		<i>Evorthodus lyricus</i>	Lyre Goby
<i>Cosmocampus brachycephalus</i>	Crested Pipefish	<i>Gobiomorus dormitator</i>	Bigmouth Sleeper
<i>Oostethus brachyurus</i>	Opposum Pipefish	<i>Gobionellus boleosoma</i>	Darter Goby
<i>Syngnathus dunckersi</i>	Pugnose Pipefish	<i>Gobionellus oceanicus</i>	Highfin Goby
CENTROPOMIDAE		<i>Guavina guavina</i>	Goby
<i>Centropomus ensiferus</i>	Swordspine Snook	<i>Lophogobius cyprinoides</i>	Crested Goby
<i>Centropomus parallelus</i>	Little Snook	<i>Sicydium plumieri</i>	Sirajo Goby
<i>Centropomus pectinatus</i>	Tarpon Snook	TRICHIURIDAE	
<i>Centropomus undecimallis</i>	Snook	<i>Trichiurus lepturus</i>	Atlantic Cuttlassfish
SERRANIDAE		BOTHIDAE	
<i>Epinephelus itajara</i>	Jewfish	<i>Citharichthys spilopterus</i>	Bay Whiff
CARANGIDAE		TETRAODONTIDAE	
<i>Caranx latus</i>	Horse-eyed Jack	<i>Canthigaster rostratus</i>	Sharpnose Puffer
<i>Caranx hippos</i>	Crevalle Jack	<i>Sphaeroides greeleyi</i>	Caribbean Puffer
<i>Oligoplites saurus</i>	Leather Jacket	<i>Sphaeroides spengleri</i>	Bandtail Puffer
<i>Trachinotus falcatus</i>	Permit	<i>Sphaeroides testudineus</i>	Checkered Puffer
<i>Trachinotus glaucus</i>	Palometa	SOLEIDAE	
LUTJANIDAE		<i>Achirus lineatus</i>	Lined Sole
<i>Lutjanus apodus</i>	Schoolmaster	<i>Trinectes inscriptus</i>	Scrawled Sole
<i>Lutjanus cyanopterus</i>	Cubera snapper	CRUSTACEANS	
<i>Lutjanus griseus</i>	Gray Snapper	COENOBITIDAE	
<i>Lutjanus jocu</i>	Dog Snapper	<i>Coenobita clypeata</i>	Hermit Crab
<i>Lutjanus synagris</i>	Lane Snapper	ATYIDAE	
GERREIDAE		<i>Atya innocous</i>	Shrimp
<i>Diapterus plumieri</i>	Stripped Mojarra	<i>Atya lanipes</i>	Sinuuous-faced Shrimp
<i>Diapterus rhombeus</i>	Rhomboid Mojarra	<i>Atya scabra</i>	Jonga serrei Shrimp
<i>Eucinostomus gula</i>	Silver Jenny	<i>Micratya poeyi</i>	Compressed-faced Shrimp
<i>Eucinostomus melanopterus</i>	Flagfin Jenny	<i>Xiphocaris elongata</i>	Long-faced Shrimp
<i>Eucinostomus jonesii</i>	Slender Mojarra	PALAEEMONIDAE	
<i>Gerres cinereus</i>	Yellowfin Mojarra	<i>Macrobrachium carcinus</i>	Giant hand Shrimp
HAEMULIDAE		<i>Macrobrachium crenulatum</i>	Pubescent-hand Shrimp
<i>Conodon nobilis</i>	Barred Grunt	<i>Macrobrachium faustinum</i>	Pubescent-hand Shrimp
<i>Haemulon aurolineatum</i>	Tomtate	<i>Macrobrachium heterochirus</i>	Teeth-faced Shrimp
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt		
<i>Haemulon sciurus</i>	Bluestriped Grunt		

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Table 9. continued from page 51

FAMILY/ Scientific Name	Common Name (English)
GRAPSIDAE	
<i>Aratus pisonii</i>	Small Elongated Crab
<i>Goniopsis cruentata</i>	Pentagonal-bodied Crab
<i>Sesarma</i> sp.	Square-bodied Crab
OCYPODIDAE	
<i>Ocyode albicans</i>	Ghost Crab
<i>Ocyode quadrata</i>	Ghost Crab
<i>Uca burgersi</i>	Fiddler Crab
<i>Uca rapax</i>	Fiddler Crab
PORTUNIDAE	
<i>Callinectes danae</i>	Long-spined Blue Crab
<i>Callinectes ornatus</i>	Wide-chested Blue Crab
<i>Callinectes sapidus</i>	Bidentate-faced Blue Crab
GECARCINIDAE	
<i>Cardiosoma guanhumii</i>	Common Land Crab
<i>Ucides cordatus</i>	Land Crab
PSEODOTHELPHUSIDEA	
<i>Epilobocera sinuatifrons</i>	Freshwater Crab/Buruquena

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Arecibo on PR 10—as having a particularly rich faunal community and, thus, deserving special protection, even from biology students and other casual visitors. This cave is small but harbors a troglobitic milliped and cockroach. Guano samples contained cydnid bugs, nitidulid beetles, terrestrial isopods, ants, centipedes, millipedes, 17 species of mites, and abundant fly larvae, ptiliid beetles, and collembola.

The lists of cave invertebrates in Peck (1974, 1981) do not include

organisms from Mona Island (box 1). Peck and Kukalova Peck (1981) published an additional list with 46 species from Mona Island. We summarize some highlights of that list in box 1.

Reptiles and Amphibians

The **herpetofauna** of Puerto Rico consists of at least 70 species of terrestrial amphibians and reptiles, including introduced species. We recorded 51 species (17 families) of amphibians and reptiles for the northern limestone (table 11). Seven families—

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Table 10. Freshwater fish introduced to waters of the northern limestone of Puerto Rico. The list is based on Erdman (1967, 1984), Nevárez and Villamil (1981), González Azar (1992), Grana Raffucci (1993), and Bunkley Williams and Williams (1994). The order of species follows García Ríos (1998).

FAMILY/Scientific name	Common Name	Date Introduced	Geographic Origin
CLUPEIDAE			
<i>Dorasoma petenense</i>	Threadfin Shad	1963	Georgia, U.S.A.
CYPRINIDAE			
<i>Carassius aratus</i>	Goldfish	1900?	China
<i>Pimephales promelas</i>	Fathead Minnow	1957	North America
ICTALURIDAE			
<i>Ameirus catus</i>	White Catfish	1938	North America
<i>Ameirus nebulosus</i>	Brown Bullhead	1916	North America
<i>Ictalurus marmoratus</i>	Marbled Bullhead	1946	North America
<i>Ictalurus punctatus</i>	Channel Catfish	1938	North America
APLOCHEILIDAE			
<i>Rivulus marmoratus</i>	Rivulus	1935	Cuba?
POECILLIDAE			
<i>Gambusia affinis</i>	Mosquitofish	1914	North America
<i>Poecilia reticulata</i>	Guppy	1935?	South America
<i>Xiphophorus helleri</i>	Swordstail	1935	Mexico
<i>Xiphophorus maculatus</i>	Southern Platyfish	1935	Mexico
<i>Xiphophorus variatus</i>	Variable Platyfish		
CENTRARCHIDAE			
<i>Lepomis auritus</i>	Redbreast Sunfish	1957	North America
<i>Lepomis gulosus</i>	Warmouth		
<i>Lepomis macrochirus</i>	Bluegill Sunfish	1916	North America
<i>Lepomis microlopus</i>	Redear Sunfish	1957	North America
<i>Micropterus coosae</i>	Redeye Bass	1958	Southeastern U.S.
<i>Micropterus salmoides</i>	Largemouth Bass	1946	North America
CICHLIDAE			
<i>Astronotus ocellatus</i>	Oscar		
<i>Cichla ocellaris</i>	Peacock Bass		
<i>Tilapia aurea</i>	Golden Tilapia		
<i>Tilapia urolepis</i>	Redeyed Tilapia		
<i>Tilapia mossambica</i>	Tilapia	1958	Mozambique, Africa
<i>Tilapia rendalli</i>	BlueTilapia		

Table 11. List of amphibians and reptiles of the northern and southern limestone areas. Family order is given according to taxonomic closeness. The occurrence of species (O) is (1) if from northern limestone, (2) if from southern limestone, or (3) if from both limestone areas. Frequency descriptions for species in the northern limestone are based on observations by Puente Rolón since 1994. Common = seen or heard in all visits, occasional = could be heard or seen in at least five visits per year, and rare = seen less than five visits per year. For species in the southern limestone, the frequency is based on our general understanding of their status.

FAMILY/Species	O	Common Name	Frequency
AMPHIBIANS			
BUFONIDAE			
<i>Peltophryne lemur</i>	3	Puerto Rican Crested Toad	Rare
<i>Bufo marinus</i>	3	Cane toad, Marine Toad	Common
LEPTODACTYLIDAE			
<i>Leptodactylus albilabris</i>	3	White-lipped Frog	Common
<i>Eleutherodactylus antillensis</i>	3	Field Coqui	Common
<i>Eleutherodactylus brittoni</i>	3	Grass Coqui	Occasional
<i>Eleutherodactylus cochranae</i>	3	Cochran's Coqui	Common
<i>Eleutherodactylus coqui</i>	3	Common Coqui	Common
<i>Eleutherodactylus richmondi</i>	1	Richmond's Coqui	Occasional
<i>Eleutherodactylus wightmanae</i>	1	Melodious Coqui	Rare
HYLIDAE			
<i>Hyla cinerea</i>	1	Green Tree Frog	Occasional
<i>Osteopilus septentrionalis</i>	1	Cuban Tree Frog	Occasional
<i>Scinax rubra</i>	1	Scinax	Rare
RANIDAE			
<i>Rana catesbeiana</i>	1	Bullfrog	Occasional
REPTILES			
EMYDIDAE			
<i>Trachemys stejnegeri</i>	3	Puerto Rican Freshwater Turtle	Occasional
DERMOCHELIDAE			
<i>Dermochelys coriacea</i>	3	Leatherback Turtle	Rare
CHELONIDAE			
<i>Chelonia mydas</i>	3	Green Turtle	Rare
<i>Eretmochelys imbricata</i>	3	Hawksbill Turtle	Rare
CROCODYLIDAE			
<i>Caiman crocodylus</i>	1	North American Cayman	Rare
AMPHISBAENIDAE			
<i>Amphisbaena caeca</i>	3	Common Legless Lizard	Occasional
<i>Amphisbaena schmidti</i>	3	Schmidt's Legless Lizard	Occasional
<i>Amphisbaena xera</i>	2	Xeric Legless Lizard	
ANGUIIDAE			
<i>Diploglossus pleii</i>	3	Puerto Rican Galliwasp	Occasional
GEKKONIDAE			
<i>Hemidactylus haitianus</i>	3	Greater Antillian Gecko	Common
<i>Hemidactylus mabouia</i>	3	African Gecko	Occasional
<i>Phyllodactylus wirshingi</i>	2	Flower-pot Gecko	
<i>Sphaerodactylus klauberi</i>	1	Klauber's Gecko	Common
<i>Sphaerodactylus macrolepis</i>	3	Common Coastal Gecko	Common
<i>Sphaerodactylus nicholsi</i>	3	Nichol's Gecko	Common
<i>Sphaerodactylus roosevelti</i>	2	Roosevelt's Gecko	
<i>Sphaerodactylus townsendi</i>	2	Townsend's Gecko	
IGUANIDAE			
<i>Anolis cooki</i>	2	Dry-forest Anole	
<i>Anolis cristatellus</i>	3	Common Anole	Common
<i>Anolis cowieri</i>	3	Giant Green Anole	Common
<i>Anolis evermanni</i>	3	Small Green Anole	Occasional
<i>Anolis gundlachi</i>	1	Banded Anole	Common
<i>Anolis krugi</i>	3	Orange-dewlap Anole	Occasional
<i>Anolis occultus</i>	1	Dwarf Anole	Occasional

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Table 11. (continued from previous page)

<i>Anolis poncensis</i>	2	Southern Anole	Common
<i>Anolis pulchellus</i>	3	Grass Anole	Common
<i>Anolis stratulus</i>	3	Dark-marked Anole	Common
<i>Iguana iguana</i>	3	Green Iguana	Occasional
SCINCIDAE			
<i>Mabuya mabuya sloani</i>	3	Skink	Rare
TEIIDAE			
<i>Ameiva exsul</i>	3	Common Ground Lizard	Rare
<i>Ameiva wetmorei</i>	2	Blue-tailed Ground Lizard	Rare
BOIDAE			
<i>Epicrates inornatus</i>	3	Puerto Rican Boa	Occasional
COLUBRIDAE			
<i>Alophis portoricensis</i>	3	Puerto Rican Racer	Common
<i>Arrhyton exiguum</i>	3	Puerto Rican Ground Snake	Occasional
TYPHLOPIDAE			
<i>Typhlops granti</i>	2	Southern Blind Snake	
<i>Typhlops hypomethes</i>	1	University's Blind Snake	Occasional
<i>Typhlops richardi</i>	3	Richard's Blind Snake	Occasional
<i>Typhlops rostellatus</i>	3	Common Blind Snake	Occasional

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41 percent—are represented by only 1 species, 4 families—24 percent—are represented by 2 species, two families—12 percent—are represented by 3 species, and 3 families—6 percent each—are represented by 4, 8, and 11 species, respectively. Reptiles are the dominant group with 38 species (67 percent) in 13 families (photo 35). In terms of abundance, 38 percent of the species are considered common, 48 percent as occasional, and

15 percent as rare species.

We found six more species and two more families of amphibians in the northern limestone than in the southern limestone but all those present in the southern limestone were also present in the northern limestone (table 11). Reptilian fauna has one less family (Crocodylidae) in the southern limestone. Four species appear only in the northern limestone, while eight species appear only in the southern limestone. Thirty-two (63 percent) of the herpetofauna we list

appear both in the northern and southern limestone, while four (8 percent) appear only in the southern limestone.

The endemic *Peltophryne lemur* is restricted to the coastal limestone region (U.S. Fish and Wildlife Service 1992b, Rivero 1998) and is the only amphibian species listed as endangered both at Commonwealth and Federal levels. In the north coast, the center of distribution of this species is Quebradillas, while in the south coast it is the Guánica Commonwealth Forest. The breeding site of the southern population is protected by patrolling and kept off limits to the public (Miller 1985, Moreno 1991). The northern population is scattered throughout many locations, mostly private lands (García Díaz 1967, Rivero et al. 1980, Rivero and Seguí Crespo 1992, Hernández Prieto 2001), and is not protected. A 2-year effort to find adults of

the species in and around Quebradillas proved unsuccessful, although singing males were heard twice and bufonid tadpoles were observed on a regular basis (Hernández Prieto 2001). Securing this population is critical since one study suggests that there are sufficient genetic differences between the northern and southern populations to reevaluate their taxonomic status (Goebel 1996).

The distribution of one of the most terrestrial species of *Eleutherodactylus*, the Ground Coquí—*E. richmondi*—includes several municipalities inside the karst belt (Rivero 1998, Joglar 1998). This species has been in decline in the wet volcanic regions of Puerto Rico (Joglar and Burrowes 1996). Our recent survey of amphibians and reptiles led to the discovery of new populations in Arecibo and Ciales (photo 36). The Melodious Coquí—*E. wightmanae*—is a common species in the volcanic region (Rivero 1998) but it is also believed to be declining (Joglar and



Photo 35. *Anolis krugi*. Photo by L. Miranda Castro.



Photo 36. The Ground Coquí (*Eleutherodactylus richmondi*). Photo by A. Puente Rolón.

Burrowes 1996). A population of *E. wightmanae* was found in the Río Abajo Commonwealth Forest and another between Arecibo and Utuado. These represent first records for this species in the karst belt.

One of the rarest species of reptiles in the northern limestone is *Mabuya mabuya sloanei*, which is the only skink known for Puerto Rico (Rivero 1998), and is legally protected at the Commonwealth level. About 10 individuals of this species were observed in Isabela in 1991 (M. González, personal communication). Another species present is the Giant Anole (*Anolis cuvieri*) and it has two color phases. In the most common phase, the body, tail, and extremities are emerald green or yellowish green (photo 37). The less common phase is gray or greenish gray with dark brown mottles and dots (Rivero 1998). Both phases are present in the northern limestone and reproduction between individuals of different phases has been observed. The only



Photo 37. *Anolis cuvieri* in its green phase. Photo by L. Miranda Castro.

endemic turtle, *Trachemys stejnegeri*, was common but has now dwindled in numbers and is considered occasional.

Three sea turtles, the Leatherback (*Dermochelys coriacea*), the Green Turtle (*Chelonia mydas*), and the Hawksbill Turtle (*Eretmochelys imbricata*) nest on a regular basis on karst shores and beaches such as Tortuguero, Arecibo, Quebradillas, Isabela, Aguadilla, Guánica, and Lajas (Rivero 1998). All these species are listed as endangered at both Commonwealth and Federal levels and are protected by international treaties.

The only endemic reptilian species listed as endangered at both Commonwealth and Federal levels is the Puerto Rican Boa (*Epicrates inornatus*) (box 11, Photo 38). Although the species may be found through a wide variety of habitats, from wet montane forests to subtropical dry forests, it can be more easily found in the karst belt (Rivero 1998). The reduction of the boa's population has been attributed predominantly to



Photo 38. Puerto Rican Boa (*Epicrates inornatus*). Photo by L. Miranda Castro.

human impact. The major factors affecting the species are habitat loss, mongoose predation, poaching for its oil, and killing due to fear of snakes created by either religious or cultural prejudices (Reagan and Zucca 1982, U.S. Fish and Wildlife Service 1986).

The Dry-forest Anole (*Anolis cooki*) and the Blue-tailed Ground Lizard (*Ameiva wetmorei*) are two species of concern at Federal and Commonwealth levels but not yet protected by the Endangered Species Act. The reasons for concern are

Box 11. The Puerto Rican Boa.

Boid snakes within the genus *Epicrates* occur in the Neotropics from Costa Rica to Argentina and the West Indies. The Puerto Rican Boa, *Epicrates inornatus*, is the largest native snake of the island. Grant (1933) made the first reference to the apparent scarcity of the boa in Puerto Rico. The secretive habits and cryptic coloration of this species, and the rough terrain with dense canopy forest where the species inhabits, makes it difficult to study individuals for extended periods. For this reason, radiotelemetry was chosen as a technique to study the boa at the Mata de Plátano Reserve.

The reserve is located 7 km southwest of Arecibo, Puerto Rico. Cueva los Culebrones is located within the reserve. Observations of foraging behavior of the boa were performed at the cave entrance beginning 1 hour before sunset until 1 hour after sunrise. Capture hours ranged from 1745 to 0600, but main capture activities were between 1900 and 2400. The average handling time was 12.53 minutes. Radiotelemetry was used to determine the home range, activity, and movement patterns of the boa. Eleven snakes (six females and five males) were fitted with transmitters. The minimum convex polygon method was used to estimate home range areas.

Average home range area for females was 7,800 m², whereas for males it was 5,000 m². The mean area used during nonreproductive period by females was 22,119 m² and 1,326 m² for males. During the reproductive period, all radio-tracked females used a mean area of 16,940 m² and all males used 18,500 m². Ten of the radio-tracked snakes returned at least twice to the cave. Females were active 29 percent of the observations, whereas males were active during 36 percent of the observations. Significant sexual differences in home range were absent from the boa, although a tendency for females to have larger home ranges was observed.

similar. Habitat destruction and apparent competition or displacement in areas where they are sympatric with **congeners**—with *Anolis cristatellus* in the case of *A. cooki* (Hertz 1992; Ortiz 1979, 1985; Ortiz and Janssen 1982), and with *Ameiva exsul* in the case of *A. wetmorei* (Rodríguez Ramírez 1991, 1994).

Birds

We list 223 avian species in 46 families for the northern and southern limestone (table 12). One hundred and ninety-eight species occur in both areas, 17 occur only in the northern limestone, and 8 occur only in the southern limestone.

The northern limestone generally has greater diversity since more data have been recorded in the area and information on introduced and migrant species is available. However, the number of avian species in the southern limestone is close to that of the northern limestone. Six endangered species are found in the northern limestone, while seven are found in the southern limestone. The richest families in number of species are the Scolopacidae (25 species), Parulidae (22 species), and Laridae (18 species). Seventeen families are represented by only one species. Recorded species are almost equally divided between resident (112 species) and migratory (111 species). We include 29 alien species—many with unknown breeding habits—

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Table 12. List of inland and coastal bird species recorded in the northern and southern limestone areas. The occurrence (O) is (1) if from the northern limestone, (2) if from the southern limestone, and (3) if from both limestone areas. The status of the species is described as END = endemic, BR = breeding resident, BM = breeding migrant, NBM = nonbreeding migrant, ES = endangered species (or endemic subspecies), EX = extirpated, and IN = introduced. Uncertainty is indicated with a “?”. The list is arranged according to the American Ornithological Union 1998 check list of North American Birds.

FAMILY/Species	Common Name	O	Status
PODICIPEDIDAE			
<i>Tachybaptus dominicus</i>	Least Grebe	3	BR
<i>Podilymbus podiceps</i>	Pied Billed Grebe	3	BR
PHAETONTIDAE			
<i>Phaeton lepturus</i>	White-tailed Tropicbird	3	BM
SULIDAE			
<i>Sula leucogaster</i>	Brown Booby	3	BR
PELECANIDAE			
<i>Pelecanus occidentalis</i>	Brown Pelican	3	BR
PHALACROCORACIDAE			
<i>Phalacrocorax olivaceus</i>	Double-crested Cormorant	3	NBM
FREGATIDAE			
<i>Fregata magnificens</i>	Magnificent Frigatebird	3	BR
ARDEIDAE			
<i>Ardea alba</i>	Great Egret	3	BR
<i>Ardea herodias</i>	Great Blue Heron	3	NBM
<i>Bubulcus ibis</i>	Cattle Egret	3	BR
<i>Butorides striatus</i>	Green-backed Heron	3	BM
<i>Egretta caerulea</i>	Little Blue Heron	3	BR
<i>Egretta garzetta</i>	Little Egret	3	NBM
<i>Egretta thula</i>	Snowy Egret	3	BR
<i>Egretta tricolor</i>	Tricolored Heron	3	BR
<i>Ixobrychus exilis</i>	Least Bittern	3	BR
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron	3	BR
<i>Nycticorax violaceus</i>	Yellow-crowned Night Heron	3	BR
THRESKIORNITHIDAE			
<i>Plegadis falcinellus</i>	Glossy Ibis	3	NBM
CATHARTIDAE			
<i>Cathartes aura</i>	Turkey Vulture	2	BR, IN
ANATIDAE			
<i>Branta canadensis</i>	Canada Goose	1	NBM
<i>Anas acuta</i>	Northern Pintail	1	NBM
<i>Anas americana</i>	American Wigeon	3	NBM
<i>Anas bahamensis</i>	White-cheeked Pintail	3	BR
<i>Anas discors</i>	Blue-winged Teal	3	NBM
<i>Anas platyrhynchos</i>	Mallard	3	NBM
<i>Anas rubripes</i>	American Black Duck	3	NBM
<i>Anas strepera</i>	Gadwall	1	NBM
<i>Aythia affinis</i>	Lesser Scaup	3	NBM
<i>Aythia collaris</i>	Ring-necked Duck	1	NBM
<i>Aythia valisineria</i>	Canvasback	1	NBM
<i>Dendrocygna arborea</i>	West Indian Whistling Duck	3	BR
<i>Dendrocygna autumnalis</i>	Fulvous Tree Duck	2	BR
<i>Lophodytes cucullatus</i>	Hooded Merganser	2	NBM
<i>Oxyura dominica</i>	Masked Duck	3	BR
<i>Oxyura jamaicensis</i>	Ruddy Duck	3	BR
ACCIPITRIDAE			
<i>Pandion haliaetus</i>	Osprey	3	NBM
<i>Accipiter striatus venator</i>	Puerto Rican Sharp-shinned Hawk	3	BR, ES
<i>Buteo jamaicensis</i>	Red-tailed Hawk	3	BR
<i>Buteo platypterus brunescens</i>	Puerto Rican broad-winged Hawk	3	BR, ES

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FAMILY/Species	Common Name	O	Status
<i>Circus cyaneus</i>	Northern Harrier	1	NBM
FALCONIDAE			
<i>Falco columbarius</i>	Merlin	3	NBM
<i>Falco peregrinus</i>	Peregrine Falcon	3	NBM, ES
<i>Falco sparverius</i>	American Kestrel	3	BR
PHASIANIDAE			
<i>Gallus gallus</i>	Red Junglefowl	3	BR, IN
<i>Numida meleagris</i>	Helmeted Guineafowl	3	BR, IN
RALLIDAE			
<i>Gallinula chloropus</i>	Common Moorhen	3	BR
<i>Fulica americana</i>	American Coot	3	NBM
<i>Fulica caribaea</i>	Caribbean Coot	3	BM
<i>Porphyryla martinica</i>	Purple Gallinule	3	BR
<i>Porzana carolina</i>	Sora Rail	3	BR
<i>Porzana flaviventris</i>	Yellow-breasted Crake	3	NBM
<i>Rallus longirostris</i>	Clapper Rail	3	BR
ARAMIDAE			
<i>Aramus guarana</i>	Limpkin	3	BR, E
CHARADRIIDAE			
<i>Charadrius alexandrinus</i>	Snowy Plover	2	BM
<i>Charadrius melodus</i>	Pipping Plover	3	NBM
<i>Charadrius semipalmatus</i>	Semipalmated Plover	3	NBM
<i>Charadrius vociferus</i>	Killdeer	3	BR
<i>Charadrius wilsonia</i>	Wilson's Plover	3	BR
<i>Pluvialis dominica</i>	American Golden Plover	1	NBM
<i>Pluvialis squatarola</i>	Black-bellied Plover	3	NBM
HAEMATOPODIDAE			
<i>Haematopus palliatus</i>	American Oystercatcher	3	NBM
RECURVIROSTRIDAE			
<i>Hypomatopus mexicanus</i>	Black-necked Stilt	3	BM
SCOLOPACIDAE			
<i>Actitis macularia</i>	Spotted Sandpiper	3	NBM
<i>Arenaria interpres</i>	Ruddy Turnstone	3	NBM
<i>Bartramia longicauda</i>	Upland Sandpiper	3	NBM
<i>Calidris alba</i>	Sanderling	3	NBM
<i>Calidris alpina</i>	Dunlin	3	NBM
<i>Calidris canutus</i>	Red Knot	3	NBM
<i>Calidris ferruginea</i>	Curlew Sandpiper	3	NBM
<i>Calidris fuscicollis</i>	White-rumped Sandpiper	3	NBM
<i>Calidris himantopus</i>	Stilt Sandpiper	1	NBM
<i>Calidris mauri</i>	Western Sandpiper	3	NBM
<i>Calidris melanotos</i>	Pectoral Sandpiper	3	NBM
<i>Calidris minutilla</i>	Least Sandpiper	3	NBM
<i>Calidris pusilla</i>	Semipalmated Sandpiper	3	NBM
<i>Catoptrophorus semipalmatus</i>	Willet	3	NBM
<i>Gallinago gallinago</i>	Wilson's Snipe	3	NBM
<i>Limnodromus griseus</i>	Short-billed Dowitcher	3	NBM
<i>Limosa fedoa</i>	Marbled Godwit	3	NBM
<i>Micropalama himantopus</i>	Stilt Sandpiper	2	NBM
<i>Numenius phaeopus</i>	Ruddy Turnstone	3	NBM
<i>Phalaropus lobatus</i>	Red-necked Phalarope	3	NBM
<i>Phalaropus tricolor</i>	Wilson's Phalarope	3	NBM
<i>Tringa flavipes</i>	Lesser Yellowlegs	3	NBM
<i>Tringa melanoleuca</i>	Greater Yellowlegs	3	NBM
<i>Tringa solitaria</i>	Solitary Sandpiper	3	NBM
<i>Tryngites subruficollis</i>	Buff-breasted Sandpiper	3	NBM
LARIDAE			
<i>Stercorarius pomarinus</i>	Pomarine Jaeger	1	NBM
<i>Anous stolidus</i>	Brown Noddy	3	BM
<i>Chlidonias niger</i>	Black Tern	3	NBM

continued on next page

FAMILY/Species	Common Name	O	Status
<i>Larus argentatus</i>	Herring Gull	3	NBM
<i>Larus atricilla</i>	Laughing Gull	3	NBM
<i>Larus delawarensis</i>	Ring-billed Gull	3	NBM
<i>Larus marinus</i>	Great Black-backed Gull	3	NBM
<i>Larus rudibundus</i>	Common Black-headed Gull	3	NBM
<i>Rhynchops niger</i>	Black Skimmer	3	NBM
<i>Sterna anaethetus</i>	Bridled Tern	3	BR
<i>Sterna antillarum</i>	Least Tern	3	NBM
<i>Sterna caspia</i>	Caspian Tern	3	NBM
<i>Sterna dougallii</i>	Roseate Tern	3	BR
<i>Sterna fuscata</i>	Sooty Tern	3	NBM
<i>Sterna hirundo</i>	Common Tern	3	NBM
<i>Sterna maxima</i>	Royal Tern	3	BR
<i>Sterna nilotica</i>	Gull-billed Tern	3	NBM
<i>Sterna sandwichensis</i>	Sandwich Tern	3	NBM
COLUMBIDAE			
<i>Columba inornata wetmorei</i>	Puerto Rican Plain Pigeon	3	BR, ES
<i>Columba leucocephala</i>	White-crowned Pigeon	3	BR
<i>Columba livia</i>	Rock Dove	3	BR, IN
<i>Columba squamosa</i>	Scaly-naped Pigeon	3	BR
<i>Columbina passerina</i>	Common Ground Dove	3	BR
<i>Zenaida asiatica</i>	White-winged Dove	3	BR
<i>Zenaida aurita</i>	Zenaida Dove	3	BR
<i>Zenaida macroura</i>	Mourning Dove	3	NBM
<i>Streptopelia risoria</i>	Ringed Turtle Dove	3	BR, IN
<i>Geotrygon chrysis</i>	Key West Quail Dove	3	BR
<i>Geotrygon montana</i>	Ruddy Quail Dove	3	BR
<i>Geotrygon mystacea</i>	Bridled Quail Dove	3	BR
PSITTACIDAE			
<i>Amazona amazonica</i>	Orange-winged Parrot	1	BR, IN
<i>Amazona ocreocephala</i>	Yellow-crowned Parrot	1	BR, IN
<i>Amazona vittata</i>	Puerto Rican Parrot	3	BR, END, ES, EX
<i>Amazona ventralis</i>	Hispaniolan Parrot	3	BR, IN
<i>Amazona viridigenalis</i>	Red-crowned Parrot	3	BR, IN
<i>Aratinga canicularis</i>	Orange-fronted Conure	1	BR, IN
<i>Aratinga chloroptera</i>	Hispaniolan Conure	3	BR, IN
<i>Aratinga erythrogenys</i>	Cherry Head Conure	3	BR, IN
<i>Brotogeris versicolorus</i>	White-winged Parakeet	1	BR, IN
<i>Myopsitta monachus</i>	Monk Parakeet	3	BR, IN
<i>Nandayus nenday</i>	Black-hooded Parakeet	3	BR, IN
CUCULIDAE			
<i>Coccyzus americanus</i>	Yellow Billed Cuckoo	3	BR
<i>Coccyzus minor</i>	Mangrove Cuckoo	3	BR
<i>Saurothera vieilloti</i>	Puerto Rican Lizard Cuckoo	3	BR, END
<i>Crotophaga ani</i>	Smooth-billed Ani	3	BR
STRIGIDAE			
<i>Asio flammeus</i>	Short-eared Owl	3	BR
<i>Otus nudipes</i>	Puerto Rican Screech Owl	3	BR, END
CAPRIMULGIDAE			
<i>Chordeiles gundlachi</i>	Antillean Nighthawk	3	BM
<i>Caprimulgus carolinensis</i>	Chuck Will's Widow	3	NBM
<i>Caprimulgus noctitherus</i>	Puerto Rican Nightjar	2	BR, END, ES
APODIDAE			
<i>Cypseloides niger</i>	Black Swift	3	BM
TROCHILIDAE			
<i>Anthracothorax dominicus</i>	Antillean Mango	3	BR
<i>Anthracothorax viridis</i>	Puerto Rican Mango	3	BR, END
<i>Archilochus colubris</i>	Ruby-throated Hummingbird	3	NBM
<i>Chlorostilbon maugaeus</i>	Puerto Rican Mango	3	BR, END
<i>Eulampis holocericeus</i>	Green-throated Carib	3	BR

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FAMILY/Species	Common Name	O	Status
<i>Orthorhynchus cristatus</i>	Antillean Crested Hummingbird	3	BR
ALCEDINIDAE			
<i>Ceryle alcyon</i>	Belted Kingfisher	3	BR
TODIDAE			
<i>Todus mexicanus</i>	Puerto Rican Tody	3	BR, END
PICIDAE			
<i>Melanerpes portoricensis</i>	Puerto Rican Woodpecker	3	BR, END
<i>Spirapicus varius</i>	Yellow-bellied Sapsucker	1	NBM
TYRANNIDAE			
<i>Elaenia martinica</i>	Caribbean Elaenia	3	BR
<i>Contopus portoricensis</i>	Puerto Rican Pewee	3	BR, END
<i>Myiarchus antillarum</i>	Puerto Rican Flycatcher	3	BR, END
<i>Tyrannus caudifasciatus</i>	Loggerhead Kingbird	3	
<i>Tyrannus dominicensis</i>	Grey Kingbird	3	BR
VIREONIDAE			
<i>Vireo altiloquus</i>	Black-whiskered Vireo	3	BM
<i>Vireo flavifrons</i>	Yellow-throated Vireo	3	NBM
<i>Vireo griseus</i>	White-eyed Vireo	3	NBM
<i>Vireo latimeri</i>	Puerto Rican Vireo	3	BR, END
<i>Vireo olivaceus</i>	Red-eyed Vireo	3	NBM
CORVIDAE			
<i>Corvus leucognaphalus</i>	White-necked Crow	3	BR, EX
HIRUNDINIDAE			
<i>Hirundo fulva</i>	Cave Swallow	3	BR
<i>Hirundo rustica</i>	Barn Swallow	3	NBM
<i>Progne dominicensis</i>	Caribbean Martin	3	BM
<i>Progne subis</i>	Purple Martin	3	BM
<i>Riparia riparia</i>	Bank Swallow	3	NBM
TURDIDAE			
<i>Catharus bicknelli</i>	Bicknell's Thrush	3	NBM
<i>Turdus plumbeus</i>	Red-legged Thrush	3	BR
MIMIDAE			
<i>Margarops fuscatus</i>	Pearly-eyed Thrasher	3	BR
<i>Mimus polyglottos</i>	Northern Mockingbird	3	BR
<i>Dumetella carolinensis</i>	Catbird	3	NBM
PARULIDAE			
<i>Dendroica adelaidae</i>	Adelaide's Warbler	3	BR, END
<i>Dendroica caerulescens</i>	Black-throated Blue Warbler	3	NBM
<i>Dendroica coronata</i>	Yellow-rumped Warbler	3	NBM
<i>Dendroica discolor</i>	Prairie Warbler	3	NBM
<i>Dendroica magnolia</i>	Magnolia's Warbler	3	NBM
<i>Dendroica palmarum</i>	Palm Warbler	3	NBM
<i>Dendroica petechia</i>	Yellow Warbler	3	BR
<i>Dendroica striata</i>	Blackpoll Warbler	3	NBM
<i>Dendroica tigrina</i>	Cape May warbler	3	NBM
<i>Dendroica virens</i>	Black-throated Green Warbler	3	NBM
<i>Geothlypis trichas</i>	Common Yellowthroat	3	NBM
<i>Helmitheros vermivorus</i>	Worm-eating Warbler	3	NBM
<i>Mniotilta varia</i>	Black and White Warbler	3	NBM
<i>Oporornis formosus</i>	Kentucky Warbler	3	NBM
<i>Parula americana</i>	Northern Parula	3	NBM
<i>Protonaria citrea</i>	Protonary Warbler	3	NBM
<i>Seiurus aurocapillus</i>	Ovenbird	3	NBM
<i>Seiurus motacilla</i>	Louisiana Waterthrush	3	NBM
<i>Seiurus noveborascensis</i>	Northern Waterthrush	3	NBM
<i>Setophaga ruticilla</i>	American Redstart	3	NBM
<i>Vermivora chrysoptera</i>	Golden-winged Warbler	3	NBM
<i>Wilsonia citrina</i>	Hooded Warbler	3	NBM
COEREBIDAE			
<i>Coereba flaveola</i>	Bananaquit	3	BR

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FAMILY/Species	Common Name	O	Status
<i>Euphonia musica</i>	Blue-hooded Euphonia	3	BR
<i>Spindalis portoricensis</i>	Puerto Rico Stripe-headed Tanager	3	BR, END
<i>Nesospingus speculiferus</i>	Puerto Rican Tanager	3	BR, END
<i>Piranga rubra</i>	Scarlet Tanager	3	NBM
EMBERIZIDAE			
<i>Ammodramus savannarum</i>	Grasshopper Sparrow	3	BR
<i>Sicalis flaveola</i>	Saffron Finch	1	BR, IN
<i>Tiaris bicolor</i>	Black-faced Grassquit	3	BR
<i>Tiaris olivacea</i>	Yellow-faced Grassquit	3	BR
CARDINALIDAE			
<i>Loxigilla portoricensis</i>	Puerto Rican Bullfinch	3	BR, END
<i>Passerina cyanea</i>	Indigo Bunting	3	NBM
ICTERIDAE			
<i>Agelaius xanthomus</i>	Yellow-shouldered Blackbird	3	BR, END, ES
<i>Dolichorhynchus oryzivorus</i>	Bobolink	2	NBM
<i>Molothrus bonariensis</i>	Shiny Cowbird	3	BR, IN?
<i>Quiscalus niger</i>	Greater Antillean Grackle	3	BR
<i>Icterus dominicensis</i>	Black-cowled Oriole	3	BR
<i>Icterus galbula</i>	Northern Oriole	3	NBM
<i>Icterus icterus</i>	Troupial	3	BR, IN
FRINGILLIDAE			
<i>Carduelis cucullata</i>	Red Siskin	3	NBR?, IN
<i>Serinus mozambicus</i>	Yellow-fronted Canary	1	NBR?, IN
PASSERIDAE			
<i>Passer domesticus</i>	House Sparrow	3	BR, IN
PLOCEIDAE			
<i>Euplectes afer</i>	Yellow-crowned Bishop	2	NBR?, IN
<i>Euplectes franciscanus</i>	Red Bishop	3	BR, IN
ESTRIDIDAE			
<i>Amandava amandava</i>	Red Amandavat	1	BR?, IN
<i>Estrilda melpoda</i>	Orange-cheeked Waxbill	3	BR, IN
<i>Estrilda troglodytes</i>	Red-eared Waxbill	3	BR, IN
<i>Lonchura cucullata</i>	Bronze Mannikin	3	BR, IN
<i>Lonchura malabarica</i>	Warbling Silverbill	3	BR, IN
<i>Lonchura malacca</i>	Chestnut Mannikin	3	BR, IN
<i>Lonchura punctulata</i>	Nutmeg Mannikin	3	BR, IN
<i>Vidua macroura</i>	Pin-tailed Widah	3	BR, IN



Photo 40. The Puerto Rican Parrot (*Amazona vittata*). Photo by T. Carlo.

(Snyder et al. 1987). The “José A. Vivaldi Aviary” is located at the Río Abajo Commonwealth Forest within the karst belt and houses about 60 Iguacas. A captive-breeding program for the Puerto Rican Parrots is in progress at this aviary. The species appears to reproduce well in captivity in the conditions of the karst, suggesting that this environment is favorable for the eventual reestablishment of a second wild flock. The conservation of the Puerto Rican Parrot has special importance, since most other *Amazona* species endemic to the West Indies

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mainly estrildid finches (Estrildidae) and parrots and parakeets (Psittacidae).

The karst region harbors 16 of the 17 endemic avian species of Puerto Rico. The only one not recorded in the karst belt is the Elf-woods Warbler (*Dendroica angelae*). This species is restricted to mid to high elevation volcanic and ultramaphic forests in the mountains of Puerto Rico. The most common birds in both northern and southern limestone are native or endemic species. These

include the Puerto Rican Ground Dove, Zenaida Dove, Puerto Rican Tody (*Todus mexicanus*), Grey Kingbird (*Tyrannus dominicensis*), Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican Vireo (*Vireo latimeri*), Bananaquit (photo 39), Black-faced Grassquit (*Tiaris bicolor*), Greater Antillean Grackle (*Quiscalus niger*), and Puerto Rican Bullfinch (*Loxigilla portoricensis*).

Nine endangered species are reported from the karst region, including the Puerto Rican Parrot (photo 40) or Iguaca (*Amazona vittata*) that was extremely abundant in

both northern and southern limestone forests and has been extirpated from both



Photo 39. The Bananaquit (*Coereba flaveola*), a honey creeper. Photo by L. Miranda Castro.

are likewise threatened with extinction (U.S. Fish and Wildlife Service 1999). Whatever is learned from the experience with the Puerto Rican Parrot may be applied to the conservation efforts of other species in the West Indies, the United States, the Neotropics, and worldwide.

The diversity and abundance of wildlife in the karst belt is a result of the diversity of ecosystems, which provide abundant food and shelter—including nesting sites—to bird populations. Karst topography, with its valleys, canyons, hills, sinkholes, caves, and abundant crevices provides a diverse habitat to support wildlife. The abundance of bird species, in turn, accelerates the dispersal and regeneration of trees and shrubs whose flowers, fruits, and seeds constitute part of their diets. This synergy between wildlife and plants accelerated the recovery of forests following the deforestation event that took place in Puerto Rico at the turn of the century (Ricart

Morales 1999, Rivera and Aide 1998).

Raptors belong to a group of prominent birds in the karst belt. They occupy the top of the food web and are thus vulnerable to environmental changes. Two raptor species of the seven inhabiting Puerto Rico are endangered. They are the Puerto Rican Broad-winged Hawk (*Buteo platypterus*) and the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus*) (photo 41). The healthiest population for the Broad-winged Hawk is in the Río Abajo Commonwealth Forest, where 52 individuals have been estimated (Delannoy 1992, 1997; U.S. Fish and Wildlife Service 1997a). Although no nesting sites have been found, individuals of these two species of raptors have been observed at the Río Encantado sector of the karst belt, between Ciales and Florida, east of the Río Abajo Commonwealth Forest. The Sharp-shinned Hawk was once widespread throughout the karst belt (Wetmore 1927). However, habitat alteration—such as

the five nesting sites and more than 80 ha lost to the construction of Highway PR 10—have caused significant reductions of this species. The American Kestrel (*Falco sparverius*) and the Puerto Rican Screech Owl (*Otus nudipes*) are probably the most common raptor species in the karst belt (photo 42). They feed on small reptiles, large insects, and mammals such as mice and bats (Wetmore 1916, 1927).

Migratory raptors such as the Peregrine Falcon (*Falco peregrinus*) occur in the karst between October and April. It is particularly abundant along the coast and along river courses such as the Río Grande de Manatí and Río Grande de Arecibo. Here, extensive open areas allow the falcon to fly unimpeded to capture its prey. Another migratory falcon is the Merlin (*Falco columbarius*) that also visits the island between October and April (Raffaele 1992, Biaggi 1997). While this species is more common on the south coast, it also occurs in the northern limestone.

Besides raptors, the karst belt is visited annually by thousands of Neotropical migrant birds representing well over 40 land bird species and 45 shorebirds and seabirds species (Raffaele 1992, table 12). The majority of the land birds are wood warblers that come from as far as Canada and Alaska through the Atlantic Flyway, but Eurasian migrants have been recorded (photo 43). The diet of these migratory songbirds overlaps considerably with the diet of resident species—mainly insects—but sometimes taking large amounts of fruits and seeds.

Another important group of birds of the karst region is the insectivorous guild, which includes endemic species. For example, the Puerto Rican Nightjar or Whip-poor-will (*Caprimulgus noctitherus*), the Puerto Rican Tody, the Puerto Rican Woodpecker (*Melanerpes portoricensis*), and the Puerto Rican Vireo. Also included in this group are other native species, such as the Grey Kingbird and the



Photo 41. The Sharp-shinned Hawk (*Accipiter striatus*). Photo by C. Delannoy.



Photo 42. The endemic Puerto Rican Screech Owl (*Otus nudipes*). Photo by L. Miranda Castro.



Photo 43. The migratory Northern Parula (*Parula americana*). Photo by J. Colón.



Photo 44. The endemic Puerto Rican Tody (*Todus mexicanus*). Photo by L. Miranda Castro.

Adelaide's Warbler (*Dendroica adelaidae*). These birds are common and well distributed through both northern and southern limestone (Hernández Prieto 1993), preferring dense vegetation in the top of mogotes. The Puerto Rican Tody is one of the most abundant species, particularly in both the arid south and the humid north (photo 44). It is a ground nesting bird, which usually excavates its nesting burrows in riverbanks, landslides, roadcuts, and cave entrances. Of particular interest is the endemic Puerto Rican Nightjar, once distributed in northern and southern limestone and now restricted to patches of dry forest in the southern limestone. The Puerto Rican Woodpecker has a wide distribution. It has an ample diet that includes fruits of several species, invertebrates in dead standing wood and tree branches, and coquí frogs and lizards found inside bromeliads and other epiphytes.

Nectarivorous birds feed on nectar, but depend significantly on other food sources such as arthropods, particularly during the breeding season when the metabolic demand for protein increases. The hummingbird family (Trochilidae) is endemic to North and South America and is an example of this kind of feeding. All five resident species of hummingbirds (including two endemics) occur in the karst belt. The Puerto



Photo 45. The endemic Puerto Rican Emerald (*Chlorostilbon maugaeus*).

Photo by L. Miranda Castro.

Rican Emerald (*Chlorostilbon maugaeus*) is very common, nesting in the forest understory about 2 m aboveground (photo 45). The other endemic hummer, the Green Mango (*Anthracothorax viridis*), is less common than its congener the Antillean Mango (*A. dominicus*). The Antillean Mango is more common in drier areas, and usually nests 7 m aboveground. The Ruby-throated Hummingbird (*Archilocus colubris*) has been observed in Arecibo and Guánica, while a purple-throated hummingbird, possibly the Purple-throated Carib (*Eulampis jugularis*) has been photographed in Guánica and videotaped in Ciales. In 1998, the nectarivorous bird populations starved as a result of the effect Hurricane Georges had on the nectar supply in most forests. However, many forest stands in protected valleys of the karst belt were unaffected by hurricane winds and became refugia for birds.

Frugivores represent another guild in the karst belt. This guild is the most



Photo 46. Fruits of moral (*Cordia sulcata*) are important food source for birds in karst forests.

Photo by L. Miranda Castro.

diverse and abundant and includes pigeons and doves (Columbiformes), parrots (Psittaciformes), and a large diversity of songbirds (Passeriformes). Songbirds include the endemic Puerto Rican Bullfinch, the Puerto Rican Stripe-headed Tanager (*Spindalis portoricensis*), and the Puerto Rican Tanager (*Nesospingus speculariferus*), which constitutes the island's only endemic avian genus. These songbirds feed consistently on fruits and seeds of species such as moral (*Cordia sulcata*) (photo 46), yagrumo macho (*Shefflera morototoni*), yagrumo hembra (*Cecropia schreberiana*), cupey, and guaraguao (*Guarea guidonia*). Some frugivorous birds are highly specialized in their diet. For example, the Antillean Euphonia (*Euphonia musica*) feeds mostly on mistletoes and other parasitic epiphytes (Families Loranthaceae and Viscaceae) that are common in the protected valleys where this species congregated after Hurricane Georges. The Pearly-eyed Thrasher and

the Scaly-naped Pigeon (*Columba squamosa*) were detected more often in karst forests than in those of volcanic rock base (Rivera Milán 1993).

Carlo Joglar (1999) found significant diet preferences among nine common frugivores he studied. Eighty percent of his feeding observations were made on 17.6 percent of the available fruiting species. The size of the bird was associated with diet dissimilarity pattern. Thus, larger birds could take larger fruits and had similar diets. All bird species showed local preferences for a fruiting plant. Karst forests had lower fruit densities than shaded coffee plantations or moist forests outside of the karst belt.

Mammals

Bats are the only remaining native mammals of Puerto Rico (photo 47). They are extremely common in the caves of the karst belt. Fossil records from the karst belt indicate that at least 15 species of bats and 5 terrestrial mammal genera were present in the island. All



Photo 47. Bats are the only remaining native mammals in Puerto Rico and are common in the karst belt. Photo by A. Puente Rolón.

other terrestrial species are now extinct. The 13 extant species of bats in Puerto Rico are distributed in 5 families. About half of the 13 species are West Indian endemics, and 4 genera—*Monophyllus*, *Erophylla*, *Stenoderma*, and *Brachyphylla*—are not found outside the West Indies.

The karst belt is home to all 13 species of bats known to the island, 10 of which use caves as preferred roosting sites (Rodríguez Durán 1998). Among these species are nectar-feeding bats that pollinate flowers at night. Frugivorous bats disperse millions of seeds, some of which are too big to be carried by any other animal in Puerto Rico. The rapid re-establishment of forests on abandoned agricultural lands in the karst belt and throughout Puerto Rico was assisted by the dispersal and pollination function of bats.

One species that captures the imagination is the Fish-eating Bat (*Noctilio leporinus*). This bat does not dive into the water, but picks up fish from just beneath the surface. It is the largest and most majestic of all bat species on the island. However, the greatest effects of bats on ecosystems are probably the result of insect-eating bats. A single colony of these small bats may consume over 20 tons of insects every month (Rodríguez Durán and Lewis 1987). Such rate of insect consumption is beneficial to agriculture and

humans for insect pest control.

Only about one-third of the caves in Puerto Rico harbor bats. Two hypotheses may help explain this observation: either most caves do not meet the biological requirements of bats or roosting associations of mixed species are necessary. The two hypotheses are not mutually exclusive because one advantage of a multispecific assemblage is likely to be a modification of the cave's microclimate. Microclimatic differences at a roost site, due to a variety of microstructures such as stalactites and solutional cavities, may contribute to patterns of association of bats (Rodríguez Durán 1998).

In Puerto Rico, hot caves are used year-round by several species of bats. A single reduced entrance, minimum circulation of air, high density of bats, air temperature ranging from 28 °C to 40 °C, and relative humidity exceeding 90 percent characterize these hot caves. About 11 percent of all caves used by bats are hot caves and these are found mostly in the karst belt.

Antillean bats using hot caves exhibit a high degree of gregariousness and roost fidelity. At least one species—probably two—is known to occur exclusively in these caves and at least five species rely exclusively on hot caves to reproduce. Although up to seven species may occupy a

single cave in Puerto Rico, different species often maintain spatial separation within the roost. It has been suggested that interspecific competition regulates population sizes in these caves. When several species occupy the same cave, they may compete for roosting sites and access to the exit. Narrow cave mouths may physically restrict the flow of bats during periods of activity and limit the number of individuals in the cave. For example, at Cucaracha cave in western Puerto Rico, three species of bats with a total population of 700,000 individuals share a hot cave with a 1.5 m² opening.

Many species of bats inhabiting hot caves are prone to dehydration. These species may roost in large groups because of the benefits derived from a thermoneutral environment—one with an ambient temperature at which energy expenditure is minimal—and reduced dehydration. Also, the development of large colonies may increase both foraging success—by functioning as information centers and reproductive success—by reducing the exposure of newborns to predation and weather. These benefits are opposed by costs associated with permanent use of caves. For example, large numbers of exiting bats attract concentrations of predators to the cave mouth (Rodríguez Durán and Lewis 1985, Rodríguez Durán 1996).

Interspecific differences in diet and foraging patterns result in spacing of peak exit times. Such spacing may allow larger numbers of cave-warming bodies to be present than would be likely in either a single-species colony or a random assemblage of species, in which peak exit times might coincide. Multispecies colonies of cave-dwelling bats present opportunities for studying many patterns of behavior, and the importance of such large assemblages in terms of flux of energy in the ecosystem is likely to be unparalleled. The mythical stories that often are associated with bats have resulted in a poor and unwarranted image. However, ecological research in the karst belt is yielding information that allows us to appreciate the positive role that these magnificent animals play in the functioning of terrestrial ecosystems.

Endemic and Endangered⁷ Species

The degree of endemism for trees in the karst belt is 16 and 23 percent of the total for the island in moist and wet forests, respectively (Figueroa Colon 1995). For bird species, the degree of endemism is 7 percent for the northern and southern limestone areas. The fauna of caves deserves special attention in this section mainly because so little is

⁷Our focus is on species listed through the Federal Endangered Species Act, however, table 13 also shows species listed as endangered by the Commonwealth.

known about it. Culver et al. (1999) assembled a list of obligate cave-dwelling species and subspecies for the contiguous United States and found 927 species, 46 additional subspecies, and 96 families. The list had high endemism with 54 percent of the species known from a single country. Less than 4 percent were formally listed in accordance to the Endangered Species Act. Caves in Puerto Rico have not been studied in any detail and probably harbor many endemic and endangered species that have yet to be catalogued. For invertebrates alone, Peck (1974) reported 29 percent endemism. Box 1 summarizes the degree of species in Mona Island.

The karst region harbors known populations of more than 30 endangered or threatened species (table 13). Most of the endangered species present at the karst belt are plants with a restricted distribution that are vulnerable to habitat alteration and destruction by improper land use practices.

Flora

Chupacallos (*Pleodendron macranthum*) is an endangered tree that only exists in the Luquillo Mountains and in the northern karst forests of Puerto Rico. This is an evergreen aromatic tree that reaches up to 10 m in height and produces a heavy hardwood (Little et al. 1974). The present endangered status of chupacallos is a result of habitat alteration and

Table 13. Plants and animals that inhabit the northern and southern limestone areas and are considered endangered or vulnerable by Commonwealth and Federal agencies. Common names appear if available. Status are endangered (E) or vulnerable (V); levels (L) are Commonwealth (C) or Federal (F).

FAMILY/Species	Common Name	Status (L)
PLANTS		
ADIANTACEAE		
<i>Adiantum vivesii</i>		E (C, F)
ARECACEAE		
<i>Calyptronoma rivaris</i>	palma de manaca	E (C)
ASPLENIACEAE		
<i>Tectaria estremerana</i>		E (C, F)
BORAGINACEAE		
<i>Cordia bellonis</i>	E (C, F)	
BUXACEAE		
<i>Buxus vahlii</i>	diablito de tres cuernos	E (C, F)
CACTACEAE		
<i>Harrisia portoricensis</i>		V(C, F)
CANELLACEAE		
<i>Phloeodendron macranthum</i>	chupacallos	E (C)
FABACEAE		
<i>Cassia mirabilis</i>		E (C, F)
<i>Chamaecrista grandulosa var. mirabilis</i>		E (C, F)
<i>Stahlia monosperma</i>	cóbana negra	E (C)
FLACOURTIACEAE		
<i>Banara vanderbiltii</i>	palo de Ramón	E (C)
ICACINACEAE		
<i>Ottoschulzia rhodoxylon</i>	palo de rosa	E (C, F)
MELIACEAE		
<i>Trichilia triacantha</i>	bariaco	E (C, F)
MYRTACEAE		
<i>Myrcia paganii</i>		E (C)
OLACACEAE		
<i>Schoepfia arenaria</i>		E (C, F)
PIPERACEAE		
<i>Peperomia wheeleri</i>		E (C, F)
RHAMNACEAE		
<i>Auerodendron paucifolium</i>		E (C, F)
RUBIACEAE		
<i>Catesbea melanocarpa</i>		V (C)
RUTACEAE		
<i>Zanthoxylum thomasianum</i>	St. Thomas prickly ash	E (C, F)
SOLANACEAE		
<i>Goetzea elegans</i>	matabuey	E (C)
<i>Solanum drymophyllum</i>		E (C)
THELYPTERIDACEAE		
<i>Thelypteris verecunda</i>		E (C, F)
THYMELAEACEAE		
<i>Daphnopsis helleriana</i>		E (C)
VERBENACEAE		
<i>Cornutia obovata</i>	palo de nigua	E (C)
ANIMALS		
BUFONIDAE		
<i>Peltophryne lemur</i>	Puerto Rican Crested Toad	E (C, F)
DERMOCHELIDAE		
<i>Dermodochelys coriacea</i>	Leatherback Turtle	E (C, F)
CHELONIDAE		
<i>Chelonia mydas</i>	Green Turtle	E (C, F)
<i>Eretmodochelys imbricata</i>	Hawksbill Turtle	E (C, F)
IGUANIDAE		
<i>Anolis cooki</i>	Dry Forest Anole	V (C)
SCINCIDAE		
<i>Mabuya mabuya sloanei</i>	Puerto Rican Skink	V (C)

continue to next page

Table 13. continued from previous page

FAMILY/Species	Common Name	Status (L)
BOIDAE		
<i>Epicrates inornatus</i>	Puerto Rican Boa	E (C, F)
PELECANIDAE		
<i>Pelecanus occidentalis</i>	Brown Pelican	E (C, F)
PODICIPEDIDAE		
<i>Tachybaptus dominicus</i>	Least Grebe	V (C)
ANATIDAE		
<i>Dendrocygna arborea</i>	West Indian Whistling Duck	V (C)
<i>Oxyura dominica</i>	Masked Duck	V (C)
<i>Oxyura jamaicensis</i>	Ruddy Duck	V (C)
ACCIPITRIDAE		
<i>Accipiter striatus venator</i>	Puerto Rican Sharp-shinned Hawk	E (C, F)
<i>Buteo platypterus brunnescens</i>	Puerto Rican Broad-winged Hawk	E (C, F)
RALLIDAE		
<i>Fulica caribaea</i>	Caribbean Coot	V (C)
<i>Porzana flaviventer</i>	Yellow-breasted Crake	V (C)
CHARADRIIDAE		
<i>Charadrius alexandrinus</i>	Snowy Plover	V (C)
<i>Charadrius melodus</i>	Pipping Plover	V (C, F)
LARIDAE		
<i>Sterna antillarum</i>	Least Tern	E (C, F)
<i>Sterna dougallii</i>	Roseate Tern	V (C, F)
COLUMBIDAE		
<i>Columba inornata wetmorei</i>	Puerto Rican Plain Pigeon	E (C, F)
PSITTACIDAE		
<i>Amazona vittata</i>	Puerto Rican Parrot	E (C,
CAPRIMULGIDAE		
<i>Caprimulgus noctitherus</i>	Puerto Rican Nightjar	E (C, F)
CORVIDAE		
<i>Corvus leucognaphalus</i>	White-necked Crow	E (C, F)
ICTERIDAE		
<i>Agelaius xanthomus</i>	Yellow-shouldered Blackbird	E (C, F)
TRICHECHIDAE		
<i>Trichechus manatus manatus</i>	Antillean Manatee	E (C, F)

destruction due to deforestation for urban and agricultural uses and poor forest management (U.S. Fish and Wildlife Service 1997b).

Myrcia paganii and *Auerodendron pauciflorum* are two small evergreen trees that only exist in the moist karst belt. Their status as endangered species is due to their rarity and restricted distribution as a result of rural, urban, and agricultural developments. *Auerodendron pauciflorum* is restricted to a small population of 19 individuals in the limestone cliffs of Isabela. A second

population in the Río Abajo Commonwealth Forest was destroyed as a result of the construction of Highway PR



Photo 48. Mata buey (*Goetzea elegans*), an endangered and endemic species. Photo by E. Santiago.

10 (U.S. Fish and Wildlife Service 1996a).

Beautiful goetzea (*Goetzea elegans*) is a small evergreen tree endemic in the northern karst forest (photo 48). Approximately 50 individuals survive in three different populations. One of the major concerns for this species is the over-collection for scientific and ornamental uses. The largest known populations of this species are in Quebrada Bellaca in Quebradillas. All but one of the known populations in the Guajataca/Quebradillas area has been extirpated since their discovery. The

remaining populations of beautiful goetzea are at risk due to road construction through the karst belt (U.S. Fish and Wildlife Service 1987a).

Chamaecrista glandulosa var. *mirabilis* is a small shrub restricted to the white silica sands in the northern limestone. This species is scattered along the southern shore of Laguna Tortuguero and in one location each in Dorado and Vega Alta. Urban, industrial, and agricultural expansion, as well as sand extraction, may have eliminated other populations. Although few areas of silica sands have not been explored, it is possible that other populations may remain (U.S. Fish and Wildlife Service 1994a). The area encompassing Caño Tiburones is rich in silica sand deposits and has not been searched for this species.

Palma de manaca (*Calyptronoma rivalis*) is listed as threatened (photo 49). Only 3 known populations of this endemic palm, consisting of approximately 275 individuals,



Photo 49. Palma de manaca (*Calyptronoma rivalis*), an endemic species. Photo by A. Puente Rolón.

occur in the northern limestone. These natural populations occur in San Sebastián along the Camuy and Guajataca rivers. Two new populations have been reestablished in the Río Abajo Commonwealth Forest and around Guajataca reservoir. Palma de manaca populations declined due to deforestation for agriculture, grazing, charcoal production, and urbanization. A serious threat to these populations is the elimination of habitat by the extraction of construction material (limestone). A large part of the Camuy river palma de manaca population was destroyed during the construction of a road in the area. Most of the remaining population could be affected by flooding resulting from the deforestation of surrounding areas (U.S. Fish and Wildlife Service 1992a).

Diablito de tres cuernos—Vahl's boxwood (*Buxus vahllei*)—is a small evergreen tree endemic to Puerto Rico. The reasons for its rarity are obscure but attributed to extensive deforestation and urban development in lowland areas of the island. This species is restricted to two populations, one in Rincón and one in Hato Tejas Ward in Bayamón. More systematic searches of the northern limestone may turn up additional populations (U.S. Fish and Wildlife Service 1987b).

Palo de Ramón (*Banara vanderbiltii*) is an endangered evergreen tree

that occurs in the karst belt. The factors limiting the distribution of the species have been deforestation, selective cutting for agriculture, grazing, charcoal production, and cutting for construction materials. Today, the most serious threats are the urban and industrial expansion that encroaches upon the karst—for example, the Río Lajas population west of Bayamón. The cultivation of yams was responsible for the destruction of two mature individuals, an abandoned dump site is located in the area, and power line rights-of-way are located at a short distance from the population (U.S. Fish and Wildlife Service 1991a).

Three endangered ferns occur in the karst belt—*Adiantum vivesii*, *Tectaria estremarana*, and *Thelypteris verecunda*. These ferns are restricted in distribution and vulnerable to habitat destruction and modification. *Thelypteris verecunda* and *A. vivesii* are known from only one population each. A population of *T. estremarana* (23 individuals) is located 200 m south of the Arecibo radio telescope. This species has also been reported for the Río Abajo Commonwealth Forest. Forest management practices and the development of the facilities for a radio telescope could adversely affect the species (U.S. Fish and Wildlife Service 1996b).

Bariaco (*Trichilia triacantha*) is an endangered tree endemic to Puerto

Rico. It is only found in two areas of the southern limestone, where only about 40 individuals exist. The most important factors limiting the distribution of this species have been deforestation, selective cutting for urban and industrial development, agriculture, charcoal production, and cutting wood for fenceposts. Today, residential and industrial developments, as well as poor forest management, threaten this species (U.S. Fish and Wildlife Service 1991b).

Palo de rosa (*Ottoschulzia rhodoxylon*) is an evergreen tree, which may reach up to 15 m in height and 41 cm in diameter. It is endemic to Puerto Rico and Hispaniola, where it is rare. About 191 individuals are known from 13 populations in the island. This species was used intensively for posts and for its valuable reddish colored wood. These factors, together with deforestation, severely reduced the populations of palo de rosa. Studies on the ecology of this species have been ongoing since 1991; as a result, new populations have been discovered in the northern limestone, flowers have been described, and germination studies have been initiated (U.S. Fish and Wildlife Service 1994b).

Fauna

The Puerto Rican Crested Toad is the only bufonid native to Puerto Rico. The species is apparently extinct in Virgin Gorda and the British Virgin Islands, making Puerto Rico the

only place where it still survives. Breeding is sporadic and highly dependent on occasional heavy rains concentrated in a very short period. Toads normally burrow a meter or more in the soil and emerge to breed when soils are saturated after heavy rains that can accumulate at least 5 cm of water in temporary ponds. The destruction or alteration of a particular breeding pond may result in the elimination of a population of this endangered species. Only two ponds are known to function as breeding grounds for the toad in the Guánica Commonwealth Forest. Historically, breeding sites were filled or drained for construction, agriculture, and mosquito control. Overcollection of the species may also have resulted in the elimination of certain populations. The only known populations of this species are located in the southern limestone in the Guánica Commonwealth Forest and in the northern limestone in Quebradillas (U.S. Fish and Wildlife Service 1992b).

The Puerto Rican Boa is Puerto Rico's largest native snake. This species is distributed island-wide but is more common in the karst belt. Historical data suggest a decline in the boa's population numbers, but data on population estimates are scarce.

The Puerto Rican Nightjar (photo 50) is a nocturnal bird, which is mainly restricted to the southern limestone forests (U.S. Fish and Wildlife Service 1984). It also



Photo 50. The Puerto Rican Nighthawk (*Caprimulgus noctitherus*).
Photo by J. Colón.

occurs at the Susúa Commonwealth Forest, which is a moist serpentine (ultramafic) forest where the vegetation is similar in physiognomy to that of the dry limestone forest. In the past, this species was distributed through most karst forests in the island (Wetmore 1916). Although habitat loss is the prime cause of endangerment, the mongoose (*Herpestes auropunctatus*)—an introduced mammal—is regarded as one of the major threats to the Puerto Rican Nighthawk.

The Yellow-shouldered Blackbird (*Agelaius xanthomus*)—is an endangered species endemic to Puerto Rico. There are two recognized subspecies—*A. x. xanthomus* and *A. x. monensis*. The former occurs on the island of Puerto Rico and the later occurs in Mona Island. This species was abundant in the San Juan area (Taylor 1864) and distributed throughout Puerto Rico (Wetmore

1916, U.S. Fish and Wildlife Service 1996c). Its endangered status is due to habitat destruction and alteration, predation by alien mammals, and brood parasitism by the Shiny Cowbird—*Molothrus bonariensis*—(Post and Wiley 1976, U.S. Fish and Wildlife Service 1996c).

The Broad-winged Hawk (*Buteo platypterus brunnescens*) is an endemic raptor subspecies on Puerto Rico. It is highly threatened by fragmentation and disappearance of forested areas. Few individuals remain, mainly in the montane forest reserves of Luquillo, Carite, and Río Abajo in the interior of the island (Pérez Rivera and Cotte Santana 1977, Snyder et al. 1987, Raffaele 1992, Delannoy 1992).

In Puerto Rico, the Broad-winged Hawk coexists with the Red-tailed Hawk (*Buteo jamaicensis*). The Broad-winged Hawk has horizontal black and white bars in the tail, is smaller, and prefers densely

forested habitats (Raffaele 1992). The Red-tailed Hawk is commonly observed flying both in the interior forests of the island, as well as on the coastal plains. Red-tails take advantage of the thermal air currents to maintain flight while searching for prey. The Broad-winged Hawk monitors and waits silently in a branch for its prey. However, it is also possible to observe it flying above the canopy in courtship flights during the breeding season.

The Broad-winged Hawk is considered a rare species in Puerto Rico since the last decades of the 1800's. Different ornithologists who studied the island's avifauna between 1902 and 1935 did not report it, thus, the species was thought to be extinct (Bowditch 1902, 1903; Wetmore 1916, 1927; Struthers 1923; Danford 1931). In 1935, the species was rediscovered in the Luquillo Mountains (Danforth and Smyth 1935). The first nests were found in Luquillo in 1976 (Snyder et al. 1987), where the species was observed mainly in the eastern parts around El Yunque Peak (American Ornithologist's Union 1976, Snyder et al. 1987). Their chicks were fed centipedes, tree frogs, lizards, rats, and birds. The hawk's population in Carite was not reported until 1980 (Hernández Prieto 1980).

The first status survey of the Broad-winged Hawk in the island (Delannoy 1992) revealed that 124 individuals remained in the

three populations (Luquillo, 22; Carite, 50; Río Abajo, 52). Following these findings, a study of the nesting habitat of this species was conducted in Río Abajo from 1993 to 1994. The habitat of nine pairs was described according to conditions around the nest tree and to forest type (plantation and secondary forest) structural characteristics (Tossas 1995). Broad-winged Hawks chose nesting ranges according to the vegetation physiognomy rather than forest type.

Broad-winged Hawk nests were found in trees with an average height of 23 m and a diameter of 55 cm. The surrounding trees in the nesting habitat had an average height of 16 m. The hawks chose nest trees taller than the canopy with a large diameter and crown. These characteristics allow them to improve the monitoring of their territories and have better access to their nests. Broad-winged Hawk nesting areas consisted of valleys delimited by mogotes. Nesting ranges were aggressively defended against other members of its own species, resulting in separated territories with little or no overlap. The territories averaged 41 ha and the mean distance to the nearest neighbor was 714 m (Tossas 1995).

Since October 11, 1994, the U. S. Fish and Wildlife Service included the species in the Endangered Species List. However, the Puerto Rican Broad-winged Hawk still faces serious

problems as its habitat is threatened. The Puerto Rican Broad-winged Hawk population in Río Abajo is presently under development pressure of the forest and adjacent lands in the karst belt. The principal threat is the destruction of its habitat caused by urban development and road construction.

The Puerto Rican Nightjar, the Plain Pigeon (*Columba inornata wetmorei*), and the Puerto Rican Parrot are endangered birds that were common at one time in the karst belt. The Limpkin (*Aramus guarauna*) and the White-necked Crow (*Corvus leucognaphalus*) were also common in the karst but are now considered extirpated. Past land uses are responsible for these events. Today, conditions are different and the karst belt is an ideal habitat to restore these species. In many places, human presence has dwindled and has been substituted by abundant habitat and food resources and low predatory pressure. Throughout the Americas, the primary threat to birds is the destruction and disturbance of habitats on which their existence depends (Wege and Long 1995). The presence of large unfragmented forest reduces the risk of invasion by alien species, thus

reducing interaction of endangered species with alien species. Moreover, the diversity of karst features and topography allow for ample protection against natural catastrophes, such as hurricanes, because—during and in the aftermath of the storms—various protected places are available as refugia for animals with highly specialized diets.

The Karst Belt Is Economically Important

The northern limestone is the site for many types of economic activities, including water supply, mining, agriculture, construction, and manufacturing (box 12). The main industry in the northern limestone is the pharmaceutical industry, which

relies upon the use of the north coast aquifer. In the process of utilizing this water supply, the pharmaceutical industry has contaminated portions of the aquifer. The region is also subject to natural disturbances of economic importance such as landslides, land **subsidence**, floods, droughts, and hurricanes. Water, other

Continued on page 67

Box 12. Industries located on the municipalities of northern limestone. Portions of some of the municipalities may be outside the limestone area.

The northern limestone supports the largest industrial sector of Puerto Rico. As shown in the listing below, more than 200 enterprises are established in this region (Office of Economic Research 1996). Food, textile, agriculture, wood, paper, glass, metal, chemical, and construction industries are the most common manufacturing plants in the region. Among these, the pharmaceutical and technological industries are the most important economic sector. Firms such as Pfizer Pharmaceuticals, Abbot Chemical and Health Products, Bristol-Myers Squibb, Pharmacia & Upjohn, Merck Sharp & Dohme, and Du Pont export their products to supply U.S. markets. Most of these manufacturing companies depend on the high quality water from the north coast aquifer (Cortés Burgos 1990).

Aguadilla

Aguadilla Shoe Corp.
Atlantic Telecom Inc.
Avon Mirabella Inc.
Brewster Hasting Corp.
Café Sanders
Cemi Muebles Inc.
Disposable Safety Wear Inc.
DSC of Puerto Rico Inc.
Elaboración Felo
Erie Scientific Co. of PR
Faulding Puerto Rico Inc.
Flexible Packaging Co.
Fogel Caribbean Corp.
Hewlett-Packard Puerto Rico Co.
Lifestyle Footwear Corp.
Mo-Ka Shoe Co.
Namic Caribe Inc.
PR Safety
Phoenix Cable Ltd. Inc.
Polyagro Plastics Inc.
Productos La Aguadillana Inc.
Tradewings Caribbean Air Services
West Electronic Industry Co.
Western Aviation Services Corp.

Arecibo

Altistra Unimark Inc.
American International Commercial Inc.
American Metal & Electrical Equipment
Arecibo Die Cast Inc.
Arecibo Lingerie Inc.
Battery Recycling Co. Inc. (The)
Best Foods Caribbean Inc.
Candy Rosado Fashion Design
Caribe Carton & Partition Specialties Inc.
Caribe Carton & Partition Specialties Inc.
Caribe General Electric Products Inc.
Cutler-Hammer de PR Inc.
Dulceria Arecibeña Inc.
Dulces Tainos Inc.
Dynacast PR Inc.
Ganaderos Alvarado Inc.
Global Fibers Inc.
Homeline Furniture Mfg. Co.
Jugos Alneed
Kayser Roth Corp.
Las Mesetas Mini Factory
Living Design Furniture Mfg. Inc.
M/A-Com Inc. PR Operation
Merck Sharp & Dohme
Miramar Architectural Products Mfg. Inc.
Pasteleria Los Cidrines
Performance Manufacturing Operations Inc.

Continued on next page

Pharmacia & UpJohn
Resident Mfg. (C.A.R.A.)
Safetech Inc.
Sharelee Mfg. Inc.
Smart Modular Technologies (PR) Inc.
Superior Ind. International P.R. Inc.
Systems bio Industries Inc.
Thermo King of Puerto Rico Inc.

Barceloneta

Abbott Chemicals Inc.
Abbott Health Products Inc.
Agro-Ochoa Inc.
Bristol-Myers Squibb Co.
Frito Lay Snack Caribbean
General Instruments (P.R.) Inc.
Merck Sharp & Dohme
Nycomed P.R. Inc.
Ochoa Poultry Farm Inc.
Pfizer Pharmaceutical Inc.
Playtex Barceloneta Corp.
Technofiber Inc.

Camuy

Ebanistería Rosa
Empresas Cruz Inc.
Hanes Menswear Inc.
Pan-Am Shoe Co. Inc.

Ciales

Artesanía en Muebles La
Cialeña Ciales Div. of Cf. Hathaway
Jack Packaging Inc.
Thermo King Caribbean Inc.
Thermosol de Puerto Rico Inc.

Corozal

Cape Red Textile Inc.
Corozal Industries Inc.
Corozal Meat Processing Inc.
Empacadora La Montaña Inc.
General Fashions Corp.
José Luis Fabrics Inc.
Playtex Corozal Corp.
Proenco Corp.

Dorado

All Steel Manufacturing
Benckiser Puerto Rico Inc.
Best Quality Top Mfg. Inc.
C.P.I. del Caribe Ltd.
Cantera Dorado Inc.
Dorado Carton Co. Inc.
Ecolab Manufacturing Inc.
Emerson Electric Co. Div. #5
Emerson Puerto Rico Inc. Div. #4
Emerson Puerto Rico Inc. Div. #6
Emulex Caribe Inc.
Engineered Parts & Services Inc.
Fortiflex Inc.
Mc Neil Pharmaceuticals Corp.
Metal Machining Co. Inc.
Playtex Dorado Corp.

Ramírez Brothers
San Juan Cement Co.
Tool Makers Inc.

Florida

International Custom Molders of P.R. Inc.
Treesweet of Puerto Rico Inc.

Hatillo

Alicia Plastics Inc.
Borinquen Container Corp.
Emblems Inc.
Empresas Nolla y Amado
Master Mix de P.R. Inc.
Pan-Am Shoe Co. Inc.
Productos Eli
Quality Hardware Mfg. Inc.
Quesos del Reyquito
Tropical Pole Inc.

Isabela

Adriano Aluminum Extrusion
Awning Windows Inc.
Elite Vertical Blinds
Isabela Printing Inc.
Isabela Shoe Corp.
Kent Meters of P.R. Inc.
Master Aggregates Toa Baja Corp.
Outdoor Footwear Co. (The)
Power Electronics Inc.
Terrazos Cofresi Inc.
Tropical Candy

Lares

Aserradero Ramón Vélez
Coach International
Kiddies Manufacturing Inc.
Productos La Torre

Manatí

Cyanamid Agricultural de P.R. Inc.
Davis & Geck Inc.
Du Pont Agrichemicals Caribe Inc.
Du Pont Electronic Materials Inc.
Du Pont Merck Pharma
G.H. Bass Caribbean Inc.
Monte Bello Meat Processing Inc.
N.A.W. Corp.
Ortho Biologics Inc.
Ortho Pharmaceuticals Corp.
Playtex Apparel Corp.
Procter & Gamble Pharmaceuticals P.R. Inc.
Rhone-Poulenc Rorer Puerto Rico
Roche Products Inc.
Safety-Kleen Envirosystems Co. P.R. Inc.
Schering Plough Products Inc.
Tri-Line Co. (The)

Morovis

Air Master Awning Inc.
Eastpak Mfg. Inc.
Grand Master Sales Co. Inc.

Continued on next page

Jardines Bakery
 La Campesina Food Products Inc.
 Laminados Modernos de P.R. Inc.
 Provimi de P.R. Inc.
 Rebmar Inc.
 Rico Chef Food Products Inc.
 Rolon Manufacturing Corp.
 Sweet Fashions Inc.

Quebradillas

Cartonera Quebradillana
 Cooperativa de Empresas Industriales
 De Jesús Millwork
 Empresas del Guajataca Inc.
 Glamourette Fashion Mill Inc.
 Sebastian Designers Mfg. Inc.

San Sebastián

Asociación para un Mundo Mejor
 Avon-Lomalinda Inc.
 Cajas Mayorfes
 Caribe Tropical
 Danzeny Manufacturing Inc.
 Eric's Industries Inc.
 Hanes Menswear Inc.
 La Procesadora Food Corp.
 Manufacturera Ramos Inc.
 Natufruit Conservas Inc.
 New Actino Inc.
 Pepino Concrete Poles
 Productos Doña Yiya
 Torrefacción Café El Coquí Inc.
 Universal Door & Window Manufacture Inc.

Toa Alta

Bayamón Tobacco Corp.
 Caribe Furniture Mfg. Corp.
 Central Carton Corp.
 El Borincano Feed Mills Inc.
 Hygienics Products International Inc.
 J.R. Quality Metals Corp.
 Jasem Inc.
 Muebles Torres
 Ortho-Tain Enterprises
 Plastimex Inc.
 Rockvale Inc.
 T.I.I. Industries Inc.

Toa Baja

Agregados Monteclaro
 Alfa Casting Corp.
 Bayamón Bumpers
 Bayamón Can Inc.
 Bell Air Industries of P.R.
 Boricua Wood Processing Inc.
 Chain Link Fence & Wire Products of P.R.
 Challenger Brass & Cooper Co. Inc.
 Coco Lopez U.S.A Inc.
 Cuttler-Hammer de P.R. Inc.
 Delogar Food Inc.
 Easton Inc.
 Ebanistería Rodríguez
 Empresas La Famosa
 Fuentes Concrete Pile

Gran Master
 Holsum Bakers of P.R.
 Industrial Stainless Corp.
 Jor-Nel Steel Works
 Kane Export Services Inc.
 Legend International Corp.
 Macaribe #2
 Marcus & Alexis Sportwear Inc.
 Master Concrete Corp.
 Master Products Corp.
 Master-Lite Products Inc.
 Metropolitan Marble Corp.
 Mitsubishi Motors Sales of Caribbean Inc.
 Pescadería Atlántica
 Pocholo Machine Shop
 Precision Plastic Products Corp.
 Rico Plastics
 Sand & Gravel Export Corp.
 Scorpio Recycling Inc.
 Seaboard Bakeries Inc.
 Simmons Caribbean Bedding Inc.
 Taini Marble
 Tooling & Stamping Inc.
 Trigo Corp.
 Tropical Fertilizer Corp.

Vega Alta

Able Manufacturing Corp.
 Caribe General Electric Control Inc.
 Caribe General Electric Fabrication Inc.
 El Morro Corrugated Box Corp.
 Inland Paper Corp.
 Margo Farms del Caribe Inc.
 Mark Trece of P.R.
 Olympic Playground Mfg. Co. Inc.
 Owens-Illinois de P.R.
 P.H. Guex Tooling & Fastening Sys. America
 Pharmagraphics Puerto Rico Inc.
 Teledyne Packaging P.R. Inc.
 Terraza Aggregates Inc.
 West Co. De Puerto Rico Inc.

Vega Baja

Aerospace Systems-Power Div.
 Blue Ribbon Tags & Labels of P.R. Inc.
 Caribe General Electric Power Breakers
 Dac Industries Inc.
 Fábrica de Bloques Vega Baja-Div.
 Adoquines
 Fábrica Amionys Rodríguez
 Fábrica de Bloques Vega Baja
 Filete Foods
 Harvey Hubbell Caribe Inc.
 Maxi Prints Co.
 Medtech Plastics Puerto Rico Inc.
 Motorola Electrónica de P.R.
 Muebles La Ponderosa
 Rodríguez y Armaiz Inc.
 Running Manufacturing
 Thomas & Betts Caribe Inc.
 Thomas & Betts P.R. Corp.
 V'Soske Inc.
 Warner-Lambert Inc V.B. Operations

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minerals, agriculture, forestry, and environmental disturbances within the karst belt are discussed next.

Water

The water resources of the karst belt are vast and best described by the water balance for the region (figure 17). The north coast aquifer contains the bulk of the water resources in the karst belt. The rivers that flow through the region carry waters from the northern volcanic formation of the central mountain range. Some of these rivers—Río Guajataca, Río Grande de Arecibo, Río de La Plata, and Río Cibuco—contain dams that are used for water supply or the

generation of electricity. Of the rainfall on the karst belt, some 650 mm or 37 percent flows through rivers and aquifers to the coastal zone and eventually to the ocean. Over 0.37 Mm³/d (100 mgd) of freshwater flows through the north coast aquifer alone and discharges in the coastal zone and the ocean. The region contains the largest water reserves in Puerto Rico and many communities depend on this water for their well being.

Ground water withdrawals by public supply facilities in Puerto Rico increased from 0.28 Mm³/d (75 mgd) to 0.34 Mm³/d (95 mgd) between 1980 and 1995 (figure 30). This is equivalent to 22 percent of the total

freshwater withdrawals to public supply facilities in the island. The pattern of withdrawal shows a steady upward trend except for the period of 1989 to 1990 when the island suffered a severe drought. Ground water withdrawal by public supply facilities in municipalities within the karst belt follows the same trend as island-wide ground water withdrawals. For comparison, ground water withdrawals in 1960 were 0.02 Mm³/d (4 mgd) between San Juan and Cataño, 0.05 Mm³/d (13 mgd) between Bayamón and Arecibo, and 0.02 Mm³/d (6 mgd) between Arecibo and Aguadilla (McGuiness 1963).

Total ground water withdrawals for domestic, commercial, industrial,

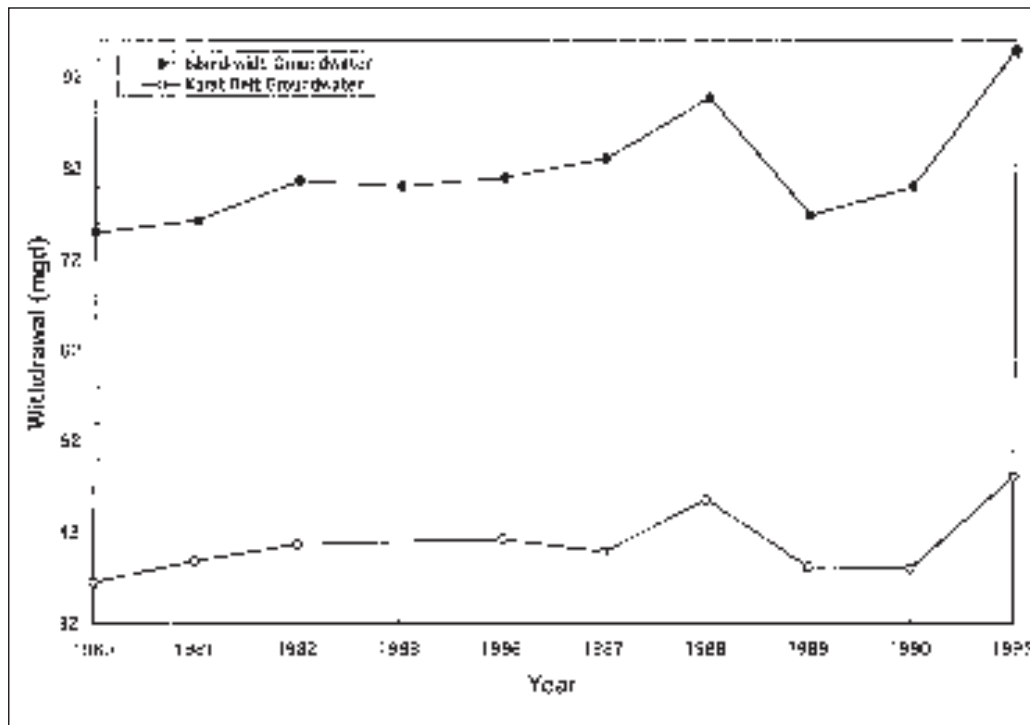


Figure 30. Trends in annual ground water withdrawals by public supply facilities in Puerto Rico and in 13 municipalities in the karst belt. Municipalities are listed in table 14. Data are from Gómez Gómez et al. (1984), Torres Sierra and Avilés (1986), Dopazo and Molina Rivera (1995), Molina Rivera and Dopazo (1995), and Molina Rivera (1997, 1998).

mining, thermoelectric power, livestock, and irrigation averaged in Puerto Rico 0.55 Mm³/d (146 mgd) during 1995 (Molina Rivera 1998). This was 25.8 percent of the total freshwater withdrawals for that year. For the United States in that same year, the corresponding proportion was 19.3 percent (Solley et al. 1998). Ground water is a more important water supply source in Puerto Rico than it is in the United States (photo 51).



Photo 51. The Puerto Rico Water Company's ground water pumps in Dorado, Puerto Rico. Photo by L. Miranda Castro.

Of the ground water aquifers in Puerto Rico, the north coast limestone aquifer is the most important, followed by the alluvial aquifer on the south coast. The north coast limestone aquifer accounts for 33 to 35 percent of all ground water withdrawals in Puerto Rico. Pharmaceutical and electronic industries in the island use water from the

north coast limestone aquifer. For 1990, the total use of north coast aquifer water was 0.20 Mm³/d (52 mgd) (Molina Rivera 1997). This use was distributed as follows: 0.14 Mm³/d (38 mgd) for public supply—the largest among all island aquifers; 0.03 Mm³/d (9 mgd) for domestic and industrial use—61 percent of the island use in this

category; 0.010 Mm³/d (2 mgd) for mining and thermoelectric use—40 percent of the use for this purpose in the island; and 0.011 Mm³/d (3 mgd) for irrigation and livestock—5 percent of the island use for this purpose.

We summarized ground water withdrawals by public supply facilities (table 14) and ground

water use (table 15) for 13 municipalities in the karst belt that used ground water in 1995 (Molina Rivera 1998). The data show that 79 percent of the water withdrawals in these municipalities is ground water as opposed to a 22-percent island-wide average. Some 340,000 people—9.6 percent of the island population—in these municipalities depend on ground water, equivalent to 41 percent of the island-wide population that depends on ground water for their water supply—a total of 827,000 people.

Self-supplied ground water in these municipalities totaled 0.05 Mm³/d (12.5 mgd) or 61 percent of the island-wide total in this category of ground water use. The use of self-supplied ground water in the industrial sector was particularly high in the karst belt—81 percent of the island-wide total.

Table 14. Ground water withdrawals by public supply facilities and people served by ground water in municipalities of the karst belt. We did not include Aguadilla, Isabela, and Toa Alta because they only withdraw surface water. Data are from Molina Rivera (1998) and correspond to 1995. To convert million gallons per day to m³/d, multiply by 3,785.

<i>Municipality</i>	<i>Ground Water</i>	<i>Surface Water (million gallons per day)</i>	<i>Total</i>	<i>Ground Water (% of total)</i>	<i>People Served</i>
Aguada	0.15	0.00	0.15	100	1640
Arecibo	13.76	2.28	16.04	86	76710
Barceloneta	2.94	0.00	2.94	100	22000
Camuy	0.57	1.03	1.60	36	13990
Dorado	8.18	0.00	8.18	100	32120
Florida	1.60	0.00	1.60	100	8740
Hatillo	1.15	3.76	4.91	23	12190
Manatí	7.92	0.00	7.92	100	39460
Moca	0.49	0.36	0.85	58	4500
Quebradillas	0.36	3.14	3.50	10	3090
Toa Baja	3.63	0.00	3.63	100	91140
Vega Alta	1.78	0.15	1.93	92	30220
Vega Baja	5.52	1.84	7.36	75	3340
Total Karst Belt	48.05	12.56	60.61	79	339140
Total Island Wide	95.08	335.78	430.86	22	827000

Table 15. Public supply delivers (surface and ground water), self-supplied ground water, ground water use by livestock, and wastewater treatment by public facilities for the municipalities of the karst belt. We did not include Aguadilla, Isabela, and Toa Alta because they only withdraw surface water. All data are in million gallons per day (mgd) (Molina Rivera 1998) and correspond to 1995. To convert mgd to m³/s, multiply by 3,785. Empty cells = no data.

Municipality	Public Supply Deliveries			Self-supplied Ground Water			Animals*	No. Animals	Wastewater Treatment
	Domestic	Commercial	Industrial	Domestic	Industrial	Mining			
Aguada	2.42	0.22	0.04	0.01	0.00	0.00	0.01	5873	3.53
Arecibo	4.72	1.69	0.10	0.38	1.16	0.00	0.69	235811	6.66
Barceloneta	1.02	0.36	0.01	0.44	3.02	0.00	0.05	2567	4.85
Camuy	1.35	0.37	0.02	0.06	0.00	0.00	0.37	23217	1.22
Dorado	1.70	0.33	0.33	0.00	0.00	0.00	0.00	1.35	
Florida	0.41	0.07	0.01	0.00	0.00	0.00	0.03	2355	0**
Hatillo	1.39	0.39	0.04	0.19	0.00	0.00	0.92	71064	0
Manatí	2.07	1.09	0.08	0.06	1.49	0.67	0.18	10714	0
Moca	1.08	0.18	0.01	0.00	0.00	0.00	0.00	3891	0
Quebradillas	1.11	0.24	0.01	0.03	0.00	0.00	0.15	9735	0
Toa Baja	4.82	0.68	0.21	0.00	0.00	0.18	0.06	3270	0
Vega Alta	1.90	0.39	0.25	0.08	0.00	0.03	0.01	2087	0.94
Vega Baja	2.86	0.56	0.06	1.51	0.00	0.68	0.09	7949	1.84
Total Karst Belt	26.85	6.57	1.17	2.76	5.67	1.75*	2.56	378533	20.39
Total Island Wide	171.19	60.91	14.09	6.37	6.89	2.82	4.45	12042485	184.75

+ Ground water used for livestock, includes dairy cows, cattle, poultry, hogs, pigs, sheep, and goats. Excludes horses and rabbits.
 * Includes 0.19 mgd for Isabela.
 ** Municipalities with “0” are connected regionally.



Photo 52. Cordillera potable water treatment plant in Ciales, Puerto Rico. Photo by L. Miranda Castro.

The treatment of wastewater in these municipalities was 11 percent of the island-wide total—a disproportionate low quantity for the overall water use and population density (photo 52). The rural population is not connected to waste treatment facilities. Therefore, considerable amounts of wastewater are flowing into aquifers and surface waters of the karst belt, relying on natural

systems to absorb and dilute the nutrient loads.

Other Minerals

The main mineral resources of the karst belt are dolomite, calcite dolomite, rock dolomite, siliceous sands, and sands with magnetite (Picó et al. 1975). Lead, zinc, silver, and lignite have been found at the southern ecotone with the volcanic rocks. Limestone rock and

marble—southern limestone—are also used commercially in the region. Monroe (1967, 1971) discussed the economic and engineering geology of the karst. The calcium carbonate in limestone can be used as agricultural limestone—from quarries in the Lares Limestone—as

raw material for cement, as a source of manufactured sand, and as “marble” for terrazzo chips. Portland cement is manufactured from quarries in the Aguada, Aymamón, and Juana Díaz Limestones (photo 53). Silica and alumina deficiencies in limestone are made up



Photo 53. A limestone quarry in Ciales, Puerto Rico. Photo by L. Miranda Castro.

during the manufacturing process with addition of volcanic rocks to the limestone (Monroe 1980). Limestone is also quarried for use as fill material. Large quantities of this material are available in the Aymamón and Aguada Limestones. The purity of parts of the Aymamón Limestone is sufficient for chemical grade limestone. Calcitic dolomite, recognizable by its sugary texture, is present in the Aymamón Limestone near the coast at 18.5-percent MgO. Caves in Mona Island were exploited commercially for guano.

S.S. Goldich identified the mineral boehmite ($\gamma\text{AlO}(\text{OH})$)—one of the group of minerals that constitute bauxite, the principal ore of aluminum—in several soil samples collected from sinkholes in the Lares Formation (Nelson and Monroe 1966). The presence of bauxitic clay in the karst belt was of possible great economic importance, because of the comparison with the bauxite deposits in the karst areas of Jamaica and Hispaniola (Hill and Ostojic 1982, Lafalaise 1980, Hernández 1978). In 1998, Jamaica produced more than 12 million Mg of bauxite and ranked third in the world in bauxite production. Hildebrand (1960) confirmed the presence of boehmite and published eight chemical analyses of the bohemite bearing clays indicating contents of up to 40-percent Al_2O_3 . These favorable results lead to

extensive commercial drilling, however, without finding economic bauxite deposits (Nelson and Monroe 1966).

The soils with bauxitic clays were identified south of Florida (Hildebrand 1960, Cruzado Torres 1996). In this area the bauxitic clays are apparently limited to the soils occurring in depressions within the outcrop area of the Lares Limestone. The soils collected in the zone north of Florida and the Cibao Formation outcrop zone, contained kaolinite and/or hallosite ($\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$) as dominant constituents (Hildebrand 1960, Cruzado Torres 1996). The bauxite deposits in Jamaica occurred in depressions in the Tertiary White Limestone. Because this limestone is remarkably pure, a residual origin is considered unlikely. The bauxite occurrence is explained as having been derived, through intense weathering and leaching, from volcanic detritus washed into the depressions from the older Cretaceous and Eocene volcanic rocks (Zans 1959, Chubb 1963) or from ash blown from Central American volcanoes (Comer 1974).

The bauxitic clay deposits occurring in depressions in the Lares Limestone most probably formed by intense weathering and leaching of the blanket sand deposits (Briggs 1966). In the Lares Limestone outcrop zone the conditions for intense leaching, removal of SiO_2 , were met, whereas in the zones more to the north

kaolinite and hallosite remained stable and were not altered to bauxitic clays.

The dunes on the north coast can provide a small quantity of calcite beach sand, suitable for concrete. Silica sands are extracted from shallow pits in part of the Manatí quadrangle and used in the manufacture of glass. Sand and gravel are also available in the Guajataca member of the Cibao Formation in Quebradillas. Structures recommended for testing for oil and natural gas occur in the Quebradillas quadrangle, north of Quebradillas. These sequences occur at 1,200 to 1,850 m in sedimentary rocks in the north—between Quebradillas and Isabela and west of Vega Baja—and the south—between Ponce and the mouth of Río Tallaboa—of Puerto Rico (Monroe 1980).

Agriculture

“The steep, rocky, unproductive haystack hills are certainly best

utilized by growing timber adapted to their shallow soils than by trying to cultivate them and thus ruin the thin soils.”

Picó (1950, p. 148).

The agricultural uses of the northern limestone are well documented (Picó 1950). Topography is a controlling factor of agricultural activity in this part of Puerto Rico (photo 54). Only 28 percent of the area is suitable for agricultural activity in the limestone region (table 2). Economically important uses are limited to the alluvial soils (Picó 1950). In the past, however, even the rocky limestone soils on the Lares Cuesta and in the bottoms of sinkholes received agricultural attention. Tobacco, sugar cane, coffee, and other crops were planted in these locations with some success at the subsistence level. Pool and Morris (1979) described this traditional agricultural



Photo 54. Pineapple field in Vega Baja, Puerto Rico. Photo by L. Miranda Castro

setting: “Citrus crops, bananas, plantains, avocados, and tobacco are cultivated. The family labor force (father and two sons) does all clearing, weeding, planting, and harvesting by hand. Horses are used to carry the produce to the road (approximately 1.5 km). Livestock, raised mostly for domestic consumption, includes 8 cows, 3 pigs, 25 laying hens, 3 horses, and 10 fighting cocks.”

The alluvial soils that blanket the limestones of the northern limestone constitute some of the finest soils of Puerto Rico (Abuña et al. 1977). They provide prime agricultural land, which is that agricultural land best suited to producing food, feed, forage, fiber, and oil seed crops. Prime agricultural land has the soil quality, growing season, and moisture supply needed to economically produce a sustained high yield of crops when treated and managed using acceptable measures. Slope is 0 to 12 percent and is not excessively erodible or saturated with water during the growing season (Acevedo 1982). In the Arecibo area, 16 percent of the land—some 162,786 ha between Camuy and Vega Alta—is prime agricultural land. The Río Grande de Arecibo has been intensively used for agriculture—for example, sugar cane, improved pastures for dairy and beef cattle, and rice—and was once proposed for increased rice production (Quiñones Aponte 1986).



Photo 55. Pineapple harvest. Photo by L. Miranda-Castro.



Photo 56. Agricultural products from alluvial valleys are for export. Photo by J. Saliva.

In Barceloneta, Manatí, and Vega Baja, large acreage is dedicated to pineapple cultivation (Conde Costas and Gómez Gómez 1999) (photo 55). Other traditional agricultural uses of alluvial soils include plantains, grapefruits—half of the island’s production—sweet potatoes, tanners, sea-island cotton, coconuts, and vegetables (Picó 1950, Acevedo 1982). Many of these crops were produced for export to U.S. winter markets (photo 56).

Subsistence food crops included root crops such as yams and manioc, bananas, plantains, beans, and others.

The nonprime agricultural soils and nonalluvial soils include blanket sands that originate outside of the limestone region, but are transported to the limestone region and cover limestone deposits. These blanket sands were grouped into four types (box 13). Other soils—nonblanket sands and nonsalluvial soils—

Box 13. Blanket sands of the northern limestone (Monroe 1976, based on Roberts 1942).

Blanket sands that cover limestone and fill the spaces between mogotes and the ridges are not derived from limestone. They do not contain calcareous material, have their origin outside the karst belt in the volcanic interior, and were transported by rivers to the coast and subsequently raised above sea level by tectonic forces. After deposition, this material—which is also interspersed with partially karstified surfaces—was weathered to lateritic earth. These sands represent the deposits of the first rivers when the island had recently risen from the ocean. The presence of these sands influences the process of karstification of limestone because they represent a source of acidified water that acts on the underlining limestone. They are also aquifer recharge areas (Giusti 1978). Roberts (1942) subdivided the soils of the karst belt into four groups:

1. Compact—generally clay soil, medium depth, red or yellow, resting on limestone. Acid soil, 90 percent clay.
2. Friable—clay and loamy soil, medium to deep depth, red or yellow, resting on limestone. Acid soil, 74 to 93 percent clay.
3. Very friable—loamy sand and sand, medium deep to depth, red or yellow, resting on limestone. Acid soil, 76 to 92 percent sand.
4. Loose—medium depth, light-colored sand. Acid.

belong to four main soils series on the north coast: Coto, Bayamón, Soller, and Tanamá; and one in the southern limestone—Aguilita (Picó et al. 1975). The Coto series occurs in the Quebradillas lowlands while the Bayamón series occurs east of these lowlands. Soller soils are shallow, black soils with high organic matter and high clay content. Tanamá soils occur on mogotes. The Aguilita soils are analogous to Tanamá in the southern limestone hills.

Outside the alluvial soils, agricultural activity was limited by rugged topography, shallow soils with low capacity for moisture retention, and low fertility (Ríos Lavienna 1933, Picó 1950). Soils unsuitable for agriculture predominate on the limestone hills of

the karst belt. They add up to 78,750 ha and are described in table 16. Shallow soils on mogote hillsides are generally too steep and rocky to cultivate or even graze livestock (Pool and Morris 1979). Cultivation was possible on the sinkholes



Photo 57. Subsistence agriculture on valleys between the mogotes. Photo by J. Colón.

Table 16. Soil types in the region proposed for designation as public lands. All are classified as not suitable for agricultural use (Gierbolini 1975, Acevido 1982). Pockets of soils can be farmed by hand. Approximate area (ha) of this soil in the karst belt is given in parenthesis. The total area of these unsuitable soils for agriculture is 78,750 ha between Aguadilla and Vega Baja.

RsF—Rock outcrop- San Germán complex. Twenty to 60-percent slopes, exposed limestone bedrock, and shallow well-drained soils on hills. Used for pastures (1,087).

Ro—Rock outcrop limestone. Steep to very steep hills where exposed limestone covers 95 percent of the surface (225).

RtF—Tanamá rock outcrop (22,698).

SmF—San Sebastián gravelly clay. Twenty- to 60-percent slopes. Soil is deep, steep to very steep, and well drained. Hilltops and hillsides are well suited for pasture plants and forestry (9,098).

San Sebastián limestone outcrop and limestone rock—limestone outcrops and moderately deep, steep and very steep, porous, gravelly, and clay soils. Soils characterized by many outcrops and by rocks, cobblestones, and gravel on the surface (21,949).

SrF—Soller rock outcrop complex. Five- to 60-percent slopes. Sloping to very steep, well-drained soils, and areas of exposed limestone bedrock (18,410).

Colinas Association—Sloping to steep soils on low rolling and steep hills that have rounded tops. Shallow and moderately deep, porous, loamy and clay soils, and numerous limestone outcrops (5,283).

and solution valleys between mogotes (photo 57). In these regions, pockets of deep fertile soils occur, but their extension is limited. On the mogotes themselves, soil

occurs in small pockets that are very difficult to cultivate, and it has to be done with hand tools and on very small areas. In spite of the limitations, sugar cane, coffee, tobacco, and food crops—for example, manioc, cassava, yams, beans, oranges, corn, sweet potatoes, and bananas—were cultivated for local consumption at one time or another (Ríos Lavienna 1933). Local consumption of food crops was always high, and in 1938 a plan to establish a corn mill in Isabela was canceled when it was realized that local corn consumption was so high that insufficient corn was left for processing at the mill (Picó 1950).

Hurricanes and changing economic conditions in the island led to the demise of agricultural activity in the northern limestone region. The hurricane of 1928—San Felipe—was responsible for the demise of coffee production on marginal soils. Increased attention to sugar cane also contributed to the demise of coffee and tobacco. The shift to an industrial economy after the 1940's eventually eliminated the cultivation of sugar cane. The expansion of rice production suffered by the lack of freshwater, because saline intrusion in the saltwater wedges of river estuaries limited the volume of fresh water available for rice cultivation near the coast. The abandonment of agricultural activity lead to fundamental changes in land cover as discussed in the section on land-use change.

Forestry

The most extensive use of the hilly areas of the karst belt was brush and forest. Mogotes furnished most of the wood for charcoal used for fuel throughout the island. They also produced other forest products, such as fence posts and handles for broom sticks. Coffee was grown under the shade of timber tree species, which themselves were useful as a local source of lumber and other forest products (photo 58). Leaves of the yarey palm—sombbrero (*Sabal causiarum*)—were harvested for the production of brooms, hats, baskets, and roofs for huts. By 1936, the local industry based on this



Photo 58. Wood and other forest products used in a local furniture factory—Muebles Villalobos, Ciales, Puerto Rico. Photo by L. Miranda Castro.

palm tree produced a gross annual income of \$38,000, a significant fraction of the area's economy (Picó 1950).

Woods from karst forests made life possible for the Taino and early settlers. These forests accumulated and held the soil adequate for subsistence agriculture that supported inhabitants of the region for centuries. Many of Puerto Rico's most important plants come from karst forests. Examples are the woods of maga, satinwood or aceitillo—*Zanthoxylum flavum*, and moralón; medicinal plants such as gumbo-limbo or almácigo; and palms, such as coyor, lluvia, and sombrero.

Today, karst forest lands harbor some of the best tree plantations on the island (Francis 1995). Of an estimated 3,992 ha of timber tree plantations in Puerto Rico, Commonwealth forests in the karst belt account for 1,210 ha or 30 percent of

the total. The largest extension of timber tree plantations in the karst belt occurs in the Guajataca Commonwealth Forest with 627 ha. Mahogany—*Swietenia macrophylla* and *S. mahagoni*, mahoe—*Hibiscus elatus*, maría, and teak—*Tectona grandis*, are among the tree species most commonly planted for timber production in the karst belt (photo 59).

Large portions of the karst belt are over 85 percent forested (table 2). These forests hold a key for the future environmental quality of the region. Sound forest stewardship will be required to assure their ecological functions in the new millennium.

Environmental Disturbances

Drought and hurricanes are the climatic extremes in the limestone region and in Puerto Rico as a whole. While a drought or



Photo 59. Wood production from a tree plantation in the Rio Abajo Commonwealth Forest, Arecibo, Puerto Rico. Photo by J. Colón.

a hurricane can occur at anytime, short-duration droughts usually occur in the first 4 months of the year while hurricanes peak in the months of August to October. Also, long-term records of rainfall show a decadal pattern of alternating years with above and below average rainfall (Lugo and García Martínó 1996). Low rainfall intensities of 76 mm/d have a recurrence interval of 1 year while high rainfall intensities of >305 mm/d are possible during hurricane conditions or when low-pressure systems become stationary. These events have a recurrence interval of 100 years (Gómez Gómez 1984).

Hurricanes are instrumental in ending marginal land uses such as agricultural activities in sectors of the karst belt. For example, the termination of coffee production in this region was attributed to

hurricanes that destroyed plantings in shallow soils. A hurricane or other natural catastrophe can also tilt the economic balance against certain crops that are marginally profitable in the karst belt (Picó 1950). Hurricanes are usually accompanied by flooding events and also cause large-scale landslides. Both floods and landslides are costly to the infrastructure, human life, and property. Forests and other natural ecosystems of the limestone region recover quickly from hurricanes and storms (Wadsworth and Englerth 1959, Lugo in press). Moreover, these events transport vast amounts of freshwater to the island and trigger many ecologically beneficial functions such as the reproduction of karst forest plants and animals.

In Puerto Rico, as in the United States, increased investments in structural flood control measures—canalization and dikes—have led to increasing losses and damages due to floods (Lugo and García Martínó 1996). These structures protect for events of certain magnitude and frequency and create the false sense of security that they protect against all possible events. Consequently, construction in flood areas increases. These constructions result in even higher flood levels due to increased runoff. When the meteorological event exceeds the design capacity of the structure, huge areas are flooded and damages can be considerable. As an example, recent flood events

associated with Hurricane Hortense caused severe flooding and large property damages in reaches of Río Bayamón that were canalized to protect from such floods.

The deposition of alluvium and renewal of soils on the coastal plains during floods is a geologic process vital for the maintenance of the fertility and stability of the coastal zone. Moreover, the process cleanses floodwaters and marine coastal systems are protected. Canalization prevents this process. It increases the loss of terrain on the coast and stress marine systems by discharging large sediment loads directly into marine waters. Moreover, structural solutions to floods accelerate the loss of freshwater to the ocean—therefore aggravating the severity of droughts.

Droughts are reflected in low river and stream flows. Seven-day minimum flow values are used as planning criteria for prolonged drought conditions. A minimum amount of water is required in the stream to maintain aquifer recharge, prevent **salinization**, assimilate domestic and industrial waste, maintain aquatic life, and provide water supplies for human and industrial consumption.

Landslides and Subsidence

Landslides occur in the canyons of the Río Guajataca and in Corozal, where large masses of Aguada Limestone have slipped downslope on the

clay top of the Cibao Formation. In the Río Grande de Manatí and Río Indio, landslides consist mainly of blocks of Aguada Limestone that have broken from cliffs and have slid downhill on clay of the upper member of the Cibao Formation. Landslides have partic-

ularly affected modern roads. For example, Highway PR 111 between Lares and San Sebastián and Highway PR 10 in the vicinity of Utuado have been closed for long time periods as a result of recurrent landslides (box 14). In these examples, the landslides

Box 14. Humans take risks by underestimating the challenge of karst, and the public must pay for the consequences.

Example 1. In 1928, the government decided to improve agricultural productivity and irrigate the Aguadilla-Isabela region using gravity water flow from the Guajataca reservoir. The investment was \$4 million and the objective was to irrigate 5,909 ha. The reservoir was built in the Cibao depression just as the Río Guajataca enters the Aymamón Limestone, 8 km south-southwest of Quebradillas. From that point, the water diversion canal passed 3.2 km west of the Río Guajataca channel and about 4.8 km to the receiving lands, which had sandy soils. At its peak of effectiveness, the system irrigated 2,364 ha, but usually it irrigated about 788 ha. The contribution of farmers never exceeded \$30 to \$40 thousand in annual payments for water, when the expectation was \$100,000 per year. The government had to subsidize the operation and levy a tax on the whole island to finance the subsidy.

Example 2. The realignment and expansion of Highway PR 10 through the rugged karst belt resulted in the most expensive road—per kilometer—ever constructed in Puerto Rico. The road was first proposed in 1972, projected to cost about \$10 million, and expected to be ready for operation within a decade. However, just the 4 kilometers through the Río Abajo Commonwealth Forest cost \$10 million per kilometer. Because of the technical challenge of construction in karst, a color video was produced—titled “Defying nature”—highlighting the technical challenges and proposed solutions using engineering technology imported from Europe. More than 20 years later and behind the expected schedule, the road was opened to traffic with great fanfare. However, a few months later it had to be closed due to landslides. Every time rainfall exceeds a certain limit, landslides occur along Highway PR 10 and crews constantly maintain the road from chronic sliding. With the arrival of the new millennium, crews still work full time on Highway PR 10. The cost after construction to stabilize landslides and address other geologic and hydrologic problems has inflated the cost of the road to over \$30 million—and counting. One engineering journal highlighted a sector of the project as among the most expensive road kilometers in the world. All costs are borne by taxpayers. These include unaccounted losses such as habitat destruction and fragmentation of karst forests, effects on flora and fauna, reduced availability of freshwater and contamination of the aquifer, and population sprawl along the road corridor. Developments include increased reliance on septic tanks that further contribute to aquifer contamination.

are not due to karst processes but to the instability of the San Sebastián Formation and poor highway alignment.

Subsidence processes result in the formation of collapse sinkholes in the northern limestone (Soto and Morales 1984). These generally occur on blanket sands during or shortly after heavy rains. Percolating rainwater enlarges the network of drainage passages in the underlying limestone. Blanket sands sag on the surface when underground passages are of small diameter and nearby sands are drawn into them. Over time, a cavity begins to form above the bedrock contact. As drainage passages increase in diameter and more water percolates through them, the cavity increases in size because more sand is removed from above the contact zone. Collapse of the blanket sand layer results in the formation of a collapse sinkhole. The water table, which is usually deep in these blanket sands, does not appear to have an effect on the formation of collapse sinkholes. Analysis of air photography suggests that the region where collapse sinkholes form has been fairly stable since 1936 and appears to be under structural control—most sinkholes form on a northeast orientation (Soto and Morales 1984). Collapsed sinkholes can be dry or filled with water. It all depends on whether the drainage passages in the limestone are open or

plugged with debris. Because subsidence events occur suddenly, they can cause devastating loss of property (discussed in box 16, p. 83).

Floods, Hurricanes, and Drought

As recurrent phenomena in Puerto Rico, the effects of floods, hurricanes, and drought are noticeable in both human dominated and natural ecosystems. River discharge, aquifer recharge, and water supply availability are all proportional to rainfall intensity in the limestone region. The behavior and state of the region's hydraulic systems are all highly sensitive to rainfall intensity. However, rainfall intensity varies in magnitude and depending on the seasonal recurrence interval of phenomena, such as hurricanes, storms, low depressions, and droughts. In this section, we focus attention on the frequency, magnitude, and seasonal patterns of rainfall events associated with Hurricane Hortense (September 9-10, 1996) and Hurricane Georges 2 years later, as well as the 1994 low rainfall year and the historic records of river flow from the northern limestone.

Río Culebrinas—The normal minimum monthly average discharge of this river occurs in March, while the normal maximum average monthly discharge occurs in October. The maximum and minimum historic monthly mean discharge occurred during May 1996 and April 1970,

respectively. Using the 32 years of record for USGS station 1478, we estimated a mean annual discharge of 11.3 m³/s near its mouth. The highest instantaneous discharge was 1953 m³/s in September 16, 1975. Hurricane Georges caused the highest mean daily discharge of 481 m³/s for September 22, 1998. Hurricane Georges' discharge was of sufficient quantity to be equivalent to filling Loiza Reservoir 1.5 times that day. This flow was greater than the 1-percent **exceedence probability** discharge by 594 percent based on a flow duration analysis through 1994 (Atkins et al. 1999).

Río Guajataca—The annual mean discharge of this river, above the Guajataca Reservoir, is 0.19 m³/s and the highest historic daily mean discharge of 14.3 m³/s occurred on September 22, 1998, due to Hurricane Georges. Historic maximum and minimum monthly flow averages occur during October and March, respectively.

Río Camuy—At USGS station 0148, this river has a mean annual flow of 3 m³/s. Historic maximum and minimum monthly average flows occur during September and March, respectively. Hurricane Georges produced a historic instantaneous peak flow and historic daily mean flow of 328 and 225 m³/s, respectively.

Río Grande de Arecibo—This river has the highest mean annual discharge of any river in Puerto Rico:

14.2 m³/s based on a 23 year record (USGS station 0290). Maximum and minimum monthly streamflow averages occur during October and February, respectively. During September of 1998, the daily mean flow was higher than the 10-percent exceedence probability flow for 21 days. Rainfall in two watershed stations (Jayuya and Orocovis) during Hurricane Georges was 559 and 592 mm, respectively, over a 24-hour period, and the daily mean flow above the confluence with Río Tanamá (USGS station 27750) was greater than the 1-percent exceedence probability flow. Río Tanamá has an annual mean flow of 2.5 m³/s. During Hurricane Georges, instantaneous peak flows at Río Tanamá USGS station 0284 and Río Grande de Arecibo USGS station 0290 below the confluence with the Tanamá were at an historic high. However, Río Grande de Arecibo upstream from the confluence with Río Tanamá was not at its historic peak flow. This shows the influence of Río Tanamá over the Río Grande de Arecibo floodplain.

The Río Grande de Arecibo experienced a flood in 1899 when the peak discharge was estimated at 6,853 m³/s (Quiñones Aponte 1986). As of 1986, the largest discharge of this river, since it has been regulated, was in October 13, 1954, when 1,473 m³/s were measured below Dos Bocas dam. The historic peak discharge for

USGS station 27750 occurred in May 1985 when 1,297 m³/s was measured. The lower alluvial valley floods completely to an average depth of 1.2 m, which can occur every 7 years when the discharge reaches 481 m³/s.

During Hurricane Hortense, Río Tanamá reached its highest daily mean discharge of 38.5 m³/s (USGS station 0284)—a value higher than the 1-percent exceedence probability flow. During Hurricane Georges, this same station had a daily mean discharge of 181 m³/s. At Río Grande de Arecibo (USGS station 27750), a daily mean discharge of 348.2 m³/s was reached during Hurricane Hortense, higher than the 206.4 m³/s during Hurricane Georges. Río Grande de Arecibo transported historic high maximum daily average sediment loads of 85 Mg during Hurricane Georges.

During 1994, the daily mean discharge at Río Grande de Arecibo, upstream from its confluence with Río Tanamá (USGS station 27750), reached a historic low of 0.45 m³/s. Eleven historic monthly minimum average discharges occurred between May 1994 and April 1995. At Río Tanamá (USGS station 0284), mean daily discharges reached values of 0.57 m³/s, far above the historic lows of 0.12 m³/s of May 1989. The 7-day, 10-year minimum flows for this station was estimated at 0.75 m³/s (Quiñones Aponte 1986).

Río Grande de Manatí—This river has a mean

annual flow of 329 million m³ or 10.4 m³/s (Gómez Gómez 1984). It overflows its banks every 2 years and major floods can occur once every 7 years. The whole alluvial valley is subject to flooding to at least 1.8 m deep during peak events. The dramatic extent of these floods is apparent from the map by Hickenlooper (1967). At the bridge on Highway PR 2, the main channel of the river was observed in 1928 at 10.06 m above mean sea level. At this stage, the level of the main channel of the river is above the bridge. This event has a return frequency of 39 years. Instantaneous peak stage at USGS station 0381 during Hurricane Hortense was a historic high—11.1 m—but the flow could not be estimated. Hurricane Georges produced a historic high daily mean discharge of 2,276 m³/s, 2,365 percent above the 1-percent exceedence probability flow. Río Grande de Manatí has minimum historic flows—based on a 9-year record—of 1.44 m³/s (Gómez Gómez 1984). The 7-day minimum flows occur in July. The river had historic low flows for 6 months in 1994. Daily mean flow at USGS station 0381 was 0.91 m³/s down from a mean of 10.5 m³/s. Maximum and minimum average discharges occur during October and March, respectively.

Río Cibuco and Río Indio—Flooding is severe and occurs frequently for Río Cibuco (Torres González and Díaz 1984). Large tracts of land (>46.6 km²) are inundated by this

river and Río de La Plata to average depths of 1.8 to 2.4 m. A peak discharge of 793 m³/s in 1965 for Río Cibuco had a recurrence interval of 25 years. Daily mean streamflow reached 100.8 m³/s at USGS station 0395 during Hurricane Georges. The discharge was 312.6 m³/s lower than the historic maximum. Historic monthly averages of daily streamflow values show maximum peaks during the month of May and November, and minimum peaks during March and July. Flows as low as 0.18 m³/s have been reported for Río Cibuco (Torres González and Díaz 1984). During the 1994 drought, Río Cibuco was at historic low flows for 5 months. Base flow downstream from the confluence with Río Indio, was below ground water and the river was discharging the aquifer (Sepúlveda 1999).

The U.S. Army Corps of Engineers described in detail the flooding problems of Río Cibuco and Río Indio—major floods in 1915, 1965, 1966, and 1973—as part of their justification for improving land-use planning (COE 1973). They anticipated flooding to become increasingly more severe due to developments in the floodplains of these rivers. The Corps of Engineers report can be consulted for dramatic photographs of predicted flood levels relative to structures now in place throughout the region.

Río de La Plata—A peak discharge of 3,398 m³/s for Río de La Plata in 1928 was considered the second

largest flood in the river's history. The 1899 flood was probably larger. A discharge of 2,705 m³/s in 1960 had a recurrence interval of 32 years (Torres González and Díaz 1984). Hurricane Georges did not produce historic discharges at USGS station 0460 (at PR 2). However, Hurricane Hortense produced a historic instant peak stage of 8.3 m at the same station, but the flow could not be estimated, and an historic daily mean flow of 1,928 m³/s. This flow was much higher than the 1-percent exceedence probability event of 80.7 m³/s based on a flow duration analysis through 1994 (Atkins et al. 1999). Discharges of 0.21 m³/s are typical minimum flows (Torres González and Díaz 1984). Maximum and minimum average monthly discharges occur in October and March, respectively. Because Río de La Plata is regulated by reservoirs upstream, its low flows have been reduced by 60 percent.

The Karst Belt Has a History of Intensive Use

The land uses of the limestone region of Puerto Rico were dominated by agricultural activities during the first half of the 20th century. Fundamental and rapid changes in land use and land cover occurred after the decline of agricultural activities began in the 1950's. The Río Abajo Commonwealth Forest is a case study for

the karst belt as a whole (table 17). In 1936, the area of deforested and agricultural land was at its peak extension; it declined dramatically by 1950 and 1963 and almost disappeared by 1983. Simultaneously, the area of secondary and dense canopy cover forest have increased rapidly. Tree plantations were established for timber production between 1936 and 1950 and recreation areas have increased since the 1950's. Throughout this period, the wetlands area have remained constant.

Land cover for the whole limestone region is shown for 1977 to 1978 in figure 5. At the time, the overall landscape of Puerto Rico was in transition from a predominant agricultural cover to mixed land uses including pastures, forests, and urban uses (Ramos and Lugo 1994). Even when pastures were the dominant cover types in the island, the limestone region had a predominance of forest cover (table 2). Dense forest cover was 31 percent on the limestone region. Southern limestone had 57 percent dense forest coverage and the karst belt had 42 percent dense forest cover. If all shrub and forest cover are combined, their coverage in the limestone region, karst belt, and southern limestone was, respectively, 40, 49, and 78 percent (table 2). For the island as a whole, forest cover approached 30 percent in the 1980's (Birdsey and Weaver 1982).

Table 17. Land cover—in ha—between 1936 and 1983 in the Río Abajo Commonwealth Forest (Modified from Alvarez Ruiz et al. 1997). Columns may not add up due to rounding.

<i>Land Cover</i>	<i>1936</i>	<i>1950</i>	<i>1963</i>	<i>1983</i>
Deforested/agriculture	1130	692	151	12
Wetlands	59	59	59	59
Young secondary forest	902	1196	1360	1335
Dense crown forest	127	322	692	855
Recreation areas	0	6	13	34
Plantations	0	811	662	692
Total	2219	3087	2936	2988

Developed land covered about 16 percent in the limestone region in 1977 and 1978 and was as low as 6.7 percent in the southern limestone and 11 percent in the karst belt (table 2).

Urban land cover in 1994 in the limestone region was 19 percent (photo 60), 13.5 percent in the karst belt, and 10.4 percent in southern limestone (table 2). For comparison, by 1994 the area of urban land had increased islandwide by 27.4 percent from a 1977 value of 11.3 percent (984 km²) to a 1994 value of 14.4 percent—1252 km²—(López et al. 2001). The increase in urban land cover was faster islandwide than in the limestone region. However, a larger fraction of the limestone region was urban. This is due to the presence of the San Juan metropolitan area and other urban centers on the north coast. The urban cover on the southern limestone region increased at a faster rate than the urban land cover islandwide. The karst belt had the lowest growth rate in urban cover. Most urban cover in the karst belt and southern limestone correspond to coastal lowlands.



Photo 60. Urban sprawl in the coastal zone of the northern limestone.

Photo by J. Colón.

The Karst Belt Is Vulnerable to Human Activity

“All solutions to foundation engineering problems in karst are expensive.”

“Those [reservoirs] constructed in karst terrain have exhibited a distressing inability to hold water.”

White (1988, p. 362, 369).

Limestone rock presents at least three problems to construction projects: differential compaction due to the irregular bedrock surface, soil piping, and collapse of subterranean



Photo 61. Maintenance activities in Highway PR 10. The road had already been officially opened when this picture was taken. Continuous landslides make it unlikely that this level of maintenance will ever abate in this road segment. Photo by L. Miranda Castro.



Photo 62. The transformation of the karst belt by the construction of Highway PR 10 through the Río Abajo Commonwealth Forest. The section of road in the foreground is considered among the most expensive road constructions—per kilometer—in the world. Photo by J. Colón.



Photo 63. Wetland under restoration in the northern limestone. Photo by L. Miranda Castro.

cavities. As a result, the engineering requirements for construction and maintenance of structures in the karst belt are expensive (photo 61). Nevertheless, human activity in the karst belt has always changed its ecosystems and character, but not as fundamentally as at the present. The region is now vulnerable to irreversible damage caused by the dramatic changes in the way people use the karst landscape. The functions and services of the karst belt are endangered by human action, thus the sustainability of human activity is placed in jeopardy. As an example, the USGS identified land use as the main cause for the degradation of ground water quality (Zack et al. 1986). Specifically, they identified industrial waste disposal and accidental spills, municipal landfills, agricultural pesticide application, large ground water withdrawals for urban centers and

irrigation, and barnyard waste or septic drainage. If the quality of ground water is allowed to deteriorate, the island stands to lose over 20 percent of its freshwater supply. For illustrative purposes, we contrast the nature and intensity of anthropogenically induced past and present changes in the karst belt.

Cutting vs. Paving Over Forests

Traditional forest uses require cutting trees for lumber, charcoal, posts, and many other purposes. Sometimes, forest lands are even transformed to other uses, such as for agricultural or built-up land. These conversions have been documented and described in the previous section for the karst belt. Fortunately, forests are able to return on abandoned agricultural and low-intensity, built-up land, either naturally or through planting (Alvarez Ruiz et al. 1997, Rivera 1998, Rivera

and Aide 1998). Today, however, powerful machines not only remove forests but the substrate on which trees grow as well (photo 62). Humans are rapidly transforming the karst landscape by removing mogotes, filling sinkholes and caves, filling wetlands, and generally paving over surfaces to facilitate very intensive uses of the land. Under these conditions, the rehabilitation of forest lands or of the original topography is extremely expensive and difficult, perhaps impossible.

Draining vs. Filling Wetlands

In the past, wetlands were drained for agricultural use—for example, the drainage of Caño Tiburones (Zack and Class Cacho 1984). These drainage projects were reversible because the hydrologic conditions

could be reversed (photo 63). Both Caño Tiburones—northern limestone—and Laguna de Guánica—southern limestone—were drained for agricultural use and are now being restored for conservation purposes. Today, however, wetlands are simply filled with material from mogotes. This eliminates the wetland and makes it very difficult to restore them. Filled mangroves in the Camuy region have led to bankruptcies when the judicial courts ordered the fill removed. In spite of court orders, the mangroves remain buried by several meters of material.

Conversion vs. Transformation of Land Uses

Humans have always converted the landscape to suit their needs. Forests are converted to agricultural



Photo 64. Machines operating near Highway PR 22 km 39.2 destroy two caves. Photo by L. Miranda Castro.

and pasture lands, pastures and agricultural lands are converted to urban or built-up lands, and so on. In the karst belt, the challenges of the unique geological formations initially restricted human transformation activities to the flat areas and the through valleys of the rugged cone, tower, and doline karst. Today, however, geology and topography are no match for modern machines and the karst belt is being transformed (photo 64). Modern machinery allows for the extirpation of mogotes so that terrain can be leveled and wetlands filled. Highways are designed to traverse the region in straight lines as opposed to the wavy roads of the past (box 14). Sinkholes and caves are filled with concrete or fill obtained from mogotes. Meandering rivers are encased in straight concrete channels or converted into lakes by damming. At Caño Tiburones, the water table was lowered several meters by continuous pumping to the ocean and building structures to contain water (Zack and Class Cacho 1984).

Pumping vs. Overdraft of Aquifers

Historically in the northern limestone, pumping allowed people to use the vast aquifer resource. Today, however, pumps are so powerful and used so indiscriminately that the result is overdraft of aquifers—their potentiometric surface is reduced to lower and lower levels. Between 1970 and 1989, heads in the artesian aquifer declined as much as 49 m near the coast where industrial withdrawals are concentrated and an average of 23 m in the unconfined aquifer inland of the industrial complex (Gómez Gómez 1991). Aquifer overdraft results in salinization of coastal aquifers. Saltwater intrusion into the aquifer has been a concern in Puerto Rico as early as 1947 (McGuinness 1963).

Salinization makes the aquifer useless for humans. The USGS documented the salinization of the north coast upper aquifer (Zack et al. 1986). The outcome of this salinization is that the interface between

seawater and freshwater has moved landward, affecting the water quality of the public water supply wells near the coast. During periods of heavy pumping, these wells draw saltwater and become unusable.

Numerous studies show the vulnerability of north coast limestone to salinization as a result of excessive pumping of wells (Gómez Gómez 1984, Gómez Gómez and Torres Sierra 1988, Quiñones Aponte 1986, Torres González 1985, Torres González and Díaz 1984). At Río Grande de Manatí, saline water can be found anywhere in the valley, which limits future water development to the south of Highway PR 2 (Gómez Gómez 1984). Wells in the Vega Baja to Sabana Seca area experienced water level declines of about 2.1 m over a period of 8 years (Torres González and Díaz 1984). Torres González and Díaz (1984) attributed this decline to excessive pumpage. Expanding urbanization, which covers ground water recharge areas with fill or cement, reduces freshwater recharge of the aquifer thus exacerbating the situation. There are known procedures for preventing the salinization of the aquifer; for example, Torres González (1985) estimated the maximum pumping rate at which salinization could be avoided in the Barceloneta area. The wells could produce a maximum of 6 mgd (0.263 m³/s) and pumping at any higher rate would reduce the water level and promote salinization.

Contaminating vs. Poisoning Ground Water

Because of its high permeability, the north coast aquifer is vulnerable to pollution. Its high permeability is good for extracting water from wells; however, it favors the lateral spread of pollutants that might enter the system (Giusti and Bennett 1976). Humans contaminated surface and ground water in the past, but human activity in the region was of low intensity. Any use of water adds substances and reduces the volume of water, the net result is chemical contamination. Traditionally, runoff from agricultural and urban systems contaminated water with such pollutants as organic matter, nutrients, and sediments. This type of pollution continues in the limestone region. An example is nitrate pollution from agriculture runoff, illegal and legal dump sites (photo 65), livestock facilities, and septic tank discharges in the Manatí -

Vega Baja area are the contributing factors (Conde Costas and Gómez Gómez 1999). The nitrate concentration of upper aquifer waters in the Laguna Tortuguero region exceeds the safe limits of 10 mg/L established by the Puerto Rico Health Department. Several wells used for public water supply have been closed as a result of this pollution. These closures represent a loss of water production in the order of 5,800 m³/d.

Today, powerful and hazardous chemicals are being used in homes and industry and must be added to the traditional pollutants when evaluating water quality. As these new chemicals find their way into surface and ground water, the pollution level is raised from contamination to poisoning. These chemicals originate with pesticides used in agriculture and exotic chemicals used in pharmaceutical and other manufacturing processes. Although their injection is now prohibited, examples of materials that have been injected into waste

disposal wells in both north coast aquifers are sewage, oil, neutralized acid, organic compounds, dyes, pickling liquors, pineapple cannery wastes, and brewery wastes. The USGS documented the presence of these poisons in the north coast aquifer. Guzmán Ríos and Quiñones Márquez (1985) found widespread ground water contamination with volatile, synthetic organic chemicals that impairs the suitability of the water supplies for human consumption. By 1986, the U.S. Environmental Protection Agency had permitted 362 generators of hazardous waste: 8 had been included in the National Priorities List of Hazardous Waste Sites designated as Superfund Sites (Zack et al. 1986). These sites occur in the municipalities of San Juan, Arecibo, and Manatí in the northern karst and Guayanilla and Tallaboa in the southern karst.

The long-term aspects of recovering aquifers from contamination by hazardous materials were described in a study of the Vega Alta water table aquifer that was contaminated with volatile organic compounds (Sepúlveda 1999). The aquifer was first detected as contaminated in 1983 when 17 of 90 wells surveyed in Puerto Rico were found to have methylene chloride extractable organic compounds (Guzmán Ríos and Quiñones Márquez 1985). A well in Vega Alta was particularly high in its concentration of



Photo 65. The Arecibo garbage dump. Notice how close it is from the coastal wetlands. Photo by J. Colón.

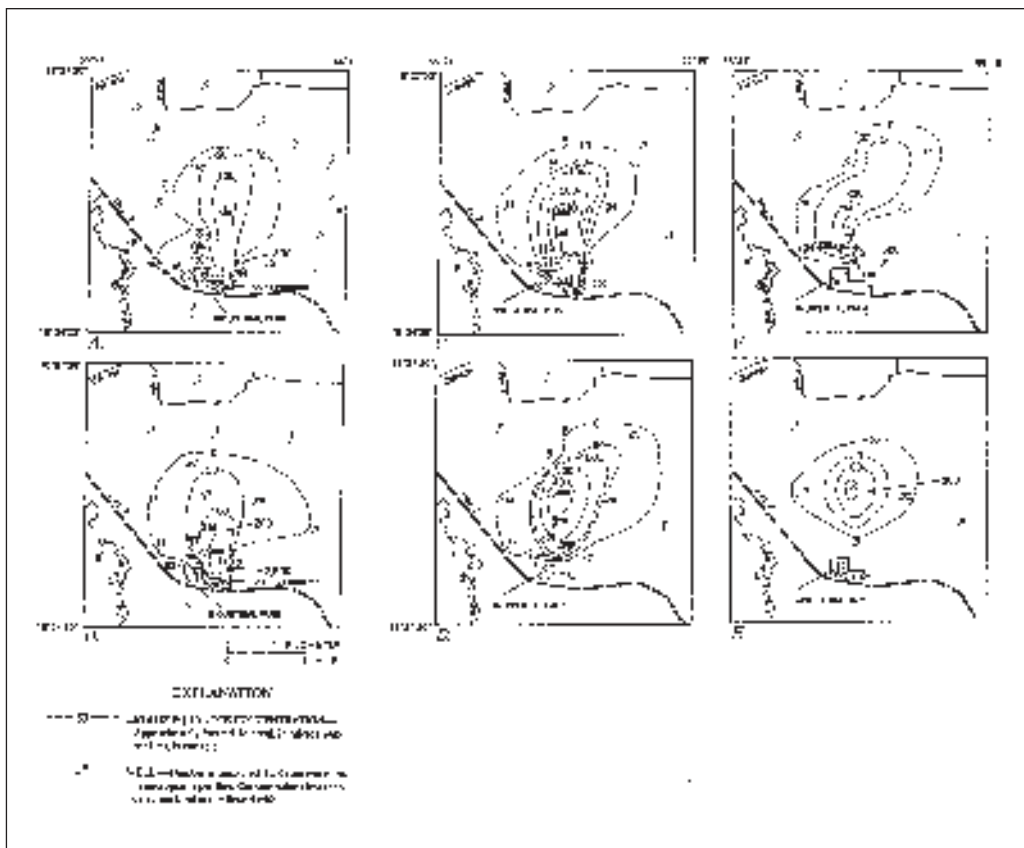


Figure 31. Approximate extent of the plume of trichloroethylene (TCE) in the water table aquifer of Vega Baja. Plumes are shown for elevations of (a) -3.0 m, (b) -3 to -22.9 m, (c) -22.9 to -38.1 m, (d) -38.1 to -53.2 m, (e) -53.2 to -68.6 m, and (f) -68.6 to -86.0 m in the aquifer. The lines represent equal concentration of TCE (Sepúlveda 1999).

trichloroethylene and tetrachloroethylene—two halogenated volatiles used as degreasing solvents in the metal and electronic industries and as solvents in the dry cleaning industry. The Vega Alta landfill and an industrial park were considered potential sources of these contaminants. In 1990 and 1992, the aquifer was estimated to contain 5.9 Mg and 5.8 Mg, respectively, of trichloroethylene (figure 31). Solute influx into the aquifer was estimated at 10 kg/yr under long-term net recharge

rates. Simulation of various remedial actions resulted in an estimated 1.7 to 2.6 Mg—depending on the remedial action—still remaining in the aquifer by the year 2022. Remedial actions were less effective in the deeper layers of the aquifer where hydraulic gradients were smaller than at shallower layers.

Surface Water Pollution

The dearth of sewage treatment, coupled with discharges of point and nonpoint pollutants to

surface waters, causes water pollution problems throughout Puerto Rico. For the karst, this can be illustrated by counts of fecal coliforms and fecal streptococcal bacteria in the waters of Río Grande de Arecibo and Río Tanamá (Quiñones Aponte 1986). Values exceed the U.S. Environmental Protection Agency standards and tend to increase during high runoff events, particularly in May. Waters of Río Cibuco, Río de La Plata, and Río Grande de Manatí experience the same water

quality trends (Torres González and Díaz 1984, Gómez Gómez 1984). As many as 200,000 fecal coliform colonies per 100 mL have been recorded at Río Grande de Manatí. Regulation of river flow by reservoirs has probably decreased the amount of suspended sediments in these rivers (Torres González and Díaz 1984).

The Karst Belt Is Vital to Puerto Rico and Needs To Be Conserved

“As landscapes to be modified and adapted to human purposes, karstlands present formidable challenges. As landscapes offering an intensely satisfying human experience, karstlands are valuable. The unsolved problem...is to balance the essentially economic focus of land use and land development against the essentially noneconomic focus of the wilderness experience.”

White (1988, p 379).

Importance of the Karst Belt

The karst belt of Puerto Rico is not only a significant portion of the total land area of the island, but it is a particularly important area in terms of its environmental assets (box 15). The karst belt is spectacular in terms of its landscapes and environmental contrasts. It contains a large variety of both

subterranean and subaerial landforms. The ecological systems of the karst belt are diverse, reflecting a range of climate conditions: dry to wet forests; physiographic settings—coastal estuarine to terrestrial montane; as well as varied physiognomic conditions—forests, wetlands, aquatic systems, and human-dominated systems. The hydrological systems of the karst belt are dominated by a gigantic ground water aquifer system that discharges millions of gallons of water into the coastal zone daily.

The northern limestone of Puerto Rico also contains valuable natural resources. The aquifer contains one of the largest freshwater supplies of the island. The sand dunes of the coast have supplied enormous amounts of sand for the construction industry in Puerto Rico. Riverine estuaries sustained the populations of marine and estuarine fisheries, as well as crustaceans. In rivers such as Río Grande de Manatí and Río Grande de Arecibo, the incredible *seti* runs are commemorated in public festivals. These runs are composed of millions of postlarvae of the gobiid fish *Sicydium plumieri* that migrate from the ocean upstream between July and January and feed humans and wild animals (Erdman 1961). Limestone deposits constitute a major source of fill material in construction and agricultural activities. Numerous quarries in the region take advantage of siliceous sands, and other chemical-grade products of limestone formations.

Box 15. Environmental assets of the karst region.

Sixty-four percent of the aquifer area of Puerto Rico extends through the northern limestone region. The aquifer discharges some 0.45 Mm³/d (120 mgd of which 0.20 Mm³/d (52 mgd) are consumed. The karst belt also contains:

- The longest river—the Río de La Plata
- The only river that forms a delta—the Río Grande de Arecibo
- The largest riverine discharge—the Río Grande de Arecibo
- The lowest surface drainage density
- The largest riverine estuaries
- The largest coastal wetlands
- The only underground rivers of the island
- The largest caves and cave systems
- The largest sand dunes
- A globally unique landform—the zanjones
- The highest tree species richness per unit land area
- Over 220 species of birds
- Sixteen of 17 endemic island birds
- Thirty-four endangered species—10 avian species, 1 reptile, 1 frog, 22 plants
- Two plant and nine bird species listed as vulnerable
- The only populations of the endangered Crested Toad and of two vulnerable reptiles
- Breeding beaches for three endangered sea turtles
- Over 110 migratory bird species—at least 11 of them breeding here
- Over 90 species of fish associated with the area’s bodies of water
- The most important fossil middens for both Paleobotany and paleofauna
- The only paleontological deposits in the island
- Spectacular landscapes
- A true wilderness

Biologically, the karst belt is rich in species of plants and animals. Almost all fossil records of extinct flora and fauna come from this region. Rare and endemic species occur throughout the region. Federally endangered species find refuge in the karst belt. Restoration of endangered populations appear feasible in this region, which provides unusually large areas of wilderness in an island

known for the predominance of urban and built-up land conditions. The protection of such an important habitat, in many cases the only habitat, in the karst belt for 34 known threatened and endangered species, could potentially represent the down-listing and eventual removal of many of these species from the Federal endangered species list. The region provides high-quality open space for recreation and

Box 16. Karst happenings. This is a collection of curious events or facts from the karst region.

Monroe (1976) reports that during Hurricane San Felipe in 1928, there were so many floating logs down the Camuy River that a gigantic log jam was formed at the entrance of Blue Hole, blocking the flow of the river and causing water to back up for a kilometer and overflow onto Highway PR 129—today PR 134. Even today, logs from this event still can be found in the caves of the Camuy River, and the entrance to Blue Hole is still jammed with logs preventing its use as an entry.

Subsidence can occur in regions with deep karst overlain by noncalcareous material—coastal deposits, alluvial deposits, or blanket deposits—that nevertheless can leach acid waters that dissolve the limestone and cause subsidence.

Alluvial deposits can cover limestones under thick blankets of alluvium. Coalescing valleys can cover most of the limestone, and limestone formations below are only evidenced by isolated hills. Large caves can also fill with alluvium.

Much of the beach sand in Puerto Rico contains many shell fragments. The sand is cemented into beach rock, which is a coarse calcarenite. Cementation may be related to precipitation of calcium carbonate when shells are exposed to acid waters.

Quebrada de los Cedros in Moca contains a concrete dam built for agricultural irrigation against the advice of geologists. Because it is a dry valley, the dam has never retained any water, not even during heavy rains.

People build homes in doline landscapes, only to see them fall into collapsed depressions. These depressions are also used to deposit garbage. Vertical caves are also used for garbage disposal. Wegrzyn et al. (1984) document examples. For example, a drainage pit was located at the entrance of H.R. Robins Pharmaceutical at km 63 of Highway PR 2. During December 13 to 15, 1981, a 740 mm storm filled the pit to capacity. In 45 seconds, 5,500 m³ (1.2 million gallons) of water drained into the ground with a roaring sound as four large sinkhole openings (one with a diameter of 12 m) developed at the bottom of the pit (Wegrzyn et al. 1984).

tourism, as well as vast reaches of surface and underground rivers with high water quality.

Human habitation entails problems in this region (box 16). The topography is extremely rugged; soils are unsuitable for cultivation on the karst belt; and construction through or over the karst is particularly hazardous, very costly, and requires constant high levels of maintenance. Traditional urban settlements have been located outside the karst belt, usually on flatlands with alluvial or blanket sands and soil. The karst belt is an area of Puerto Rico where people can find space and natural resources

to sustain and enhance their quality of life. It is an area whose best use is the conservation of its natural resources so that the dense populations outside the karst belt can benefit from the use and services of its natural resources.

The view of the karst belt as a source of products and services for the rest of Puerto Rico is already tested in the construction of the super aqueduct, which transfers water from the northern karst region to the San Juan metropolitan area. Another example would be the use of the region for recreation and tourism, using public lands as the destination for recreationists and tourists. Other

examples of locations within the karst that attract users from throughout the island and the world are the following: Las Cavernas Río Camuy National Park (photo 66), Río Abajo



Photo 66. Las Cavernas de Camuy National Park. Photo by A.E. Lugo.

Commonwealth Forest, Guajataca Commonwealth Forest, the estuaries of Río Grande de Manatí and Río Grande de Arecibo, Laguna Tortugero, Caño Tiburones, and the Encantado, Camuy, and Tanamá rivers.

Conservation of the Karst Belt

The karst belt needs to be conserved for a variety of reasons:

- its biodiversity (photo 67),



Photo 67. Santa Lucia (*Sphaerodactylus* sp.). Photo by J. Colón.



Photo 68. Steep-walled mogote in Ciales, Puerto Rico. Photo by L. Miranda Castro.



Photo 69. Participants of an educational activity in a Laguna Tortugero, Vega Baja, Puerto Rico. Photo by L. Miranda Castro.

- for recovery of endangered species,
- its wilderness nature and spectacular scenery (photo 68),
- the scientific and educational opportunities in the region (photo 69),
- its open space and recreation potential, and
- its many environmental functions, such as providing vast amounts of freshwater for natural and human dominated systems, absorbing reasonable amounts of waste, and buffering humans from disturbances (photo 70).

There are also some powerful self-survival reasons for conserving all karst, and indeed, all natural resources (box 17). Yet, three reasons tower above the rest: uniqueness, value, and its vulnerable condition.

Nowhere in the United States is there tropical karst comparable to that found in Puerto Rico. Nowhere in the world would one find landscapes of zanjones



Photo 70. A young consumer of pure water from the karst belt. Photo L. Miranda Castro.

Box 17. Why conserve?

The environmental assets of the karst belt are the result of a web of biotic and abiotic factors that are interconnected and interrelated in complex ways and are the result of eons of geologic and biologic evolution.

The way human activity has been obliterating Puerto Rican karst makes it almost impossible to restore what took nature millions of years to develop. We are unknowingly destroying our life support system. Destruction of sand dunes, wetlands, caves, unique landforms, and riverine estuaries—done for the sake of human development for the short-term—ends up threatening ourselves in the long-term because we are creating environmental problems with known consequences.

In this human voyage into the future, we have decided which species survive, sentencing to extinction many species without noticing that their extinctions are an early and urgent warning to humans of what will happen to us unless we conserve the karst as well as the rest of the island.

- In summary, conservation is essential; it is our best approach to resource use that will:
- sustain advances that have been achieved,
- allow us to keep a natural and public patrimony,
- protect us from nature's catastrophic events,
- guarantee sufficient supplies of quality air and water,
- reduce development costs, and
- improve the quality of life.

within a short distance of other landscapes of tower karst, cone karst, doline karst, zanjones karst, and world class underground cave river systems, such as the Río Encantado and Río Camuy. The karst belt of Puerto Rico is simply a unique place in the world and should be conserved.

The value of the northern karst is beyond measurement. Its water yield alone makes it one of the richest in the Caribbean. The sustainability of economic development in Puerto Rico and the quality of life for future generations of Puerto Ricans will be assured if the water resources of the karst

belt are protected. Maintaining the natural forest and underground wilderness that now cover and underly the karst belt is a sure way of achieving this goal.

Conserving the karst belt of Puerto Rico requires action. We have shown that current trends of land use in this region are making the karst vulnerable to irreversible damage. Conservation does not mean preserving the region and disallowing human activity. Many of the desired activities of people can continue, but they must be directed and organized in such a way as to minimize irreversible

Box 18. Alternative development for Puerto Rico and the karst belt

Human activity should be organized to recognize the ecological footprint of humans. For future generations to have the ability to meet their needs, changes are required today. People's quality of life can only be maintained if the biosphere, of which Puerto Rico is part, can meet their needs without being eroded. We have to recognize that today we live on an island with more consumption, more waste, more people, but with less available fresh water, less soil, and less agricultural land than anytime in its history. Today's island biodiversity is different from yesterdays. The internationally accepted system of national economic accounting calculates the gross domestic product (GDP) but neglects the depreciation of natural capital, such as the loss of topsoil, destruction of forests, and loss of many other services provided by the biosphere. Therefore, the use of GDP greatly overstates progress and in failing to reflect reality, generates destructive economic policies. An expanding economy based on an incomplete accounting system slowly undermines itself until it collapses through the destruction of its support systems.

Human activity in the karst belt has to be carefully planned because of the particular geologic makeup and because its northern sector contains the largest freshwater aquifer of the island, which already is partially contaminated.

Freshwater is vital for the survival of life, including human life. Therefore, it is imperative to curtail any activity that can further threaten the quality and quantity of water in the aquifer. Aquifer contamination, as already explained elsewhere, is very difficult or impossible to clean and, where feasible, can take decades.

The development scenarios for the karst belt require that urban sprawl be contained and that existing urban centers grow vertically to reduce demand for land. In cities like Curitiba in Brazil and Portland, Oregon, services are provided more efficiently and at a lower cost; and collective transportation is a necessary alternative. Quality of life has improved, and both cities have dynamic economies based on a smaller use per capita of natural resources and reduced waste. Puerto Rico deserves no less.

harm to the karst landscape (box 18). Some activities, such as the wholesale removal of mogotes from the landscape, might be unacceptable. Conservation is the only approach available to balance economic development with the wilderness experience.

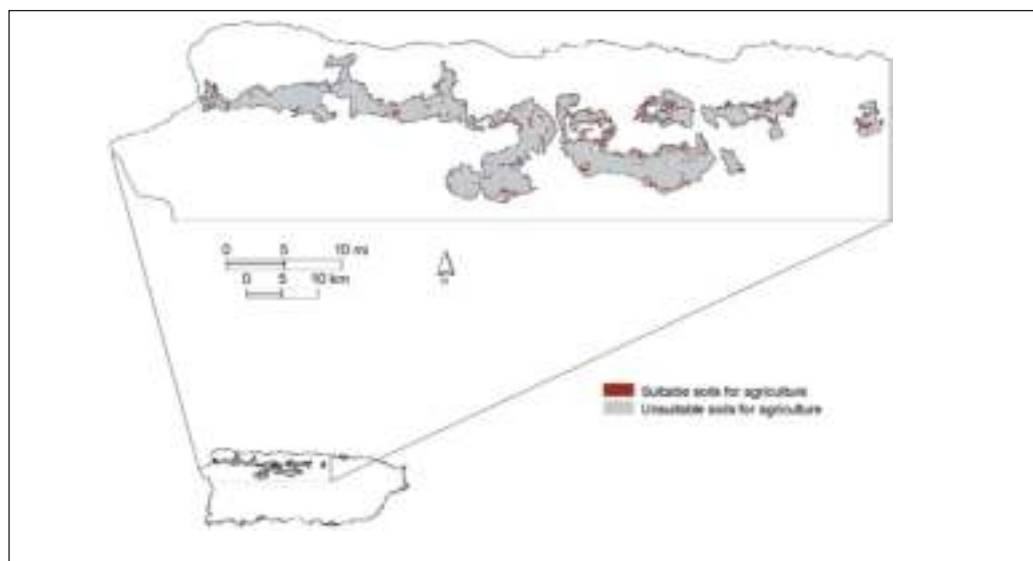


Figure 32. Map of soil types in the karst belt proposed to be transferred to the public domain.

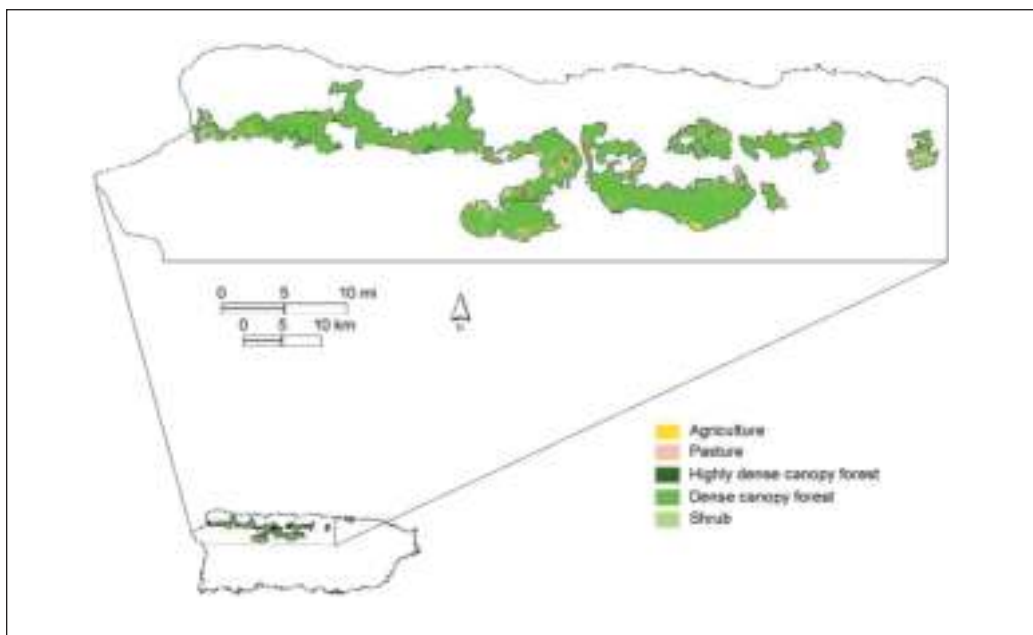


Figure 33. Map of land cover types in the area of the karst belt proposed to be transferred to the public domain.

Proposal for Transferring a Portion of the Karst Belt to the Public Domain

We advocate a conservation ethic to all land uses in Puerto Rico, including the limestone region. We also advocate that a greater fraction of the island’s land base be set aside for

preservation. The advantage of preserved natural areas is that they provide a buffer around, and ecological services to, lands under heavier intensity of use. The presence of bats in the caves of the karst belt, for example, contributed to the rapid reforestation of abandoned agricultural lands in Puerto Rico.

Preserved karst areas can contribute significantly to the sustainability of developed lands in Puerto Rico.

We propose that the forest cover of the karst belt be protected under the public domain. Such action would assure the protection of significant recharge areas of the north coast aquifer and thus the water supply

of this aquifer. The water from the aquifer will in turn maintain coastal wetlands, river and stream flows, and water supplies to sustain human activity. As an additional benefit, this action will conserve biodiversity, protect endemic and endangered species, and provide open natural space for the ever-increasing human population on the island.

This proposal does not detract from any significant present use of these lands. The rugged portions of the karst belt do not contain soils that are useful for commercial agriculture (figure 32) nor space suitable for construction of houses or road infrastructure. In fact, such uses are very sparse in the region. In spite of all the growth of urban and built up land in Puerto Rico, this part of the island has remained forested and demonstrates that natural forest cover is the most sensible use of the region. Uses of the region would include freshwater production and protection, wilderness, restoration of wildlife populations, conservation of biodiversity, passive recreation, ecological tourism, forest products and services, education, and research.

Research in the karst region has relevance to its own conservation and also to the karst problems in the United States (Peck et al. 1988) and the rest of the world (White 1988).

We propose that a portion of the karst belt (figure 33) be acquired and transferred to the public domain. This proposal

focuses on a band of karst covering 39,064 ha—mainly on Aguada and Lares limestones. At this time, this region has essentially no human habitation (only 1.5 percent of the land was developed in 1994, table 2) but has continuous forest cover (86 percent) on soils that are unsuitable for agricultural or other economic uses (figure 32). Soil maps (Gierbolini 1975, Acevedo 1982) show that 92 percent of these lands are classified as capability VII. These are soils and miscellaneous areas that have very severe limitations—due to erosion potential, poor soil condition, or too much moisture—that make them unsuitable for cultivation (tables 2 and 16).

Referring to soils in the San Sebastián association, which covers over 24,282 ha in the northern karst region, Gierbolini (1975) wrote (p. 7):

“Most of the soils have little or no farming value because they are steep and shallow to bedrock. Most areas are inaccessible, and those that do have foot trails also have large amounts of rocks that make walking difficult. The soils on the footslopes and in the narrow valleys

between the steep hills are more useful than those in other areas. Rainfall is generally high throughout the area and is well distributed throughout the year. Few highways and few farm roads cross this association. Laying out and constructing highways and roads are costly.”

The proposed designation of public lands focuses on 27 percent of the karst belt or 16 percent of the limestone region (table 2), as well as a small fraction of lands unsuitable for cultivation. Protection of these lands will contribute to aquifer recharge for the region and assure the availability of the largest wilderness on the island to sustain all the compatible human uses necessary for high-quality life styles. The landscapes to be protected are not found anywhere else in the United States, and the services that it will provide Puerto Ricans cannot be duplicated elsewhere in the highly urbanized island. Protection of the karst belt assures high-quality ground water supplies; conservation of biodiversity; open space for recreation and ecotourism; and mature ecosystems for education, research activities, and forest products and services.

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Literature Cited

- Abruña, F., M.A. Lugo López, and R. Pérez Escobar. 1977. Los suelos de Puerto Rico. In *Geovisión de Puerto Rico*. M.T.B. de Galiñanes, ed. Río Piedras, PR: Editorial Universitaria. 120-157 p.
- Acevedo Rodríguez, P. and F.S. Axelrod. 1999. Annotated checklist for the tracheophytes of Río Abajo forest reserve, Puerto Rico. *Caribbean Journal of Science*. 35:265-285.
- Acevedo, G. 1982. *Soil survey of Arecibo area of northern Puerto Rico*. Washington, DC: USDA Soil Conservation Service. 169 p. + maps.
- Aguayo, C.G. 1966. Una lista de los moluscos terrestres y fluviales de Puerto Rico. *Stablia*. 5:1-17.
- Allen, J.A. 1916. An extinct Octodont from the island of Porto Rico, West Indies. *Annals of the New York Academy of Sciences* 27:17-22.
- Alvarez, M., P. Acevedo Rodríguez, and M. Vázquez Otero. 1983. Quantitative description of the structure and diversity of the vegetation in the limestone forest of Río Abajo Forest. Progress Report, Project W-10. San Juan, PR: Puerto Rico Department of Natural Resources.
- Alvarez Ruiz, M., P. Acevedo Rodríguez, and M. Vázquez. 1997. Quantitative description of the structure and diversity of the vegetation in the limestone forest of Río Abajo, Arecibo-Utuado, Puerto Rico. *Acta Científica*. 11:21-66.
- American Ornithologist's Union. 1976. Report of the committee on conservation. *Auk*. 93(4, supplement): 1DD-19DD.
- Anthony, H.E. 1916a. Preliminary diagnosis of an apparently new family of insectivores. *Bulletin American Museum Natural History*. 35:725-728.

- Anthony, H.E. 1916b. Preliminary report of fossil mammals from Porto Rico, with descriptions of a new genus of Hystricomorph rodents. *Annals New York Academy of Sciences*. 27:193-203.
- Anthony, H.E. 1917. New fossil rodents from Porto Rico, with additional notes on *Elasmodontomys obliquus* Anthony and *Heteropsomys insulans* Anthony. *Bulletin American Museum of Natural History*. 37:183-189.
- Arana Soto, S. 1969. Nuestra Isla Mona. Barcelona, Spain: Minguza. 82 p.
- Aron, J.M. 1973. Geology and mineral resources of Isla de Mona. In Mona and Monito Islands: an assessment of their natural and historical resources. Puerto Rico San Juan, PR: Environmental Quality Board. 2: B1-B7.
- Atkins, J.B., F. Pérez Blair, and J.L. Parman. 1999. Analysis of flow durations for selected streams in Puerto Rico through 1994. Water Resources Investigations Report 98-4189. San Juan, PR: U.S. Geological Survey. 32 p.
- Beard, J.S. 1949. Natural vegetation of the windward and leeward islands. *Oxford Forestry Memoirs*. 21:1-192.
- Beard, J.S. 1955. The classification of tropical American vegetation types. *Ecology*. 36:89-100.
- Behrensmeyer, A.K., J.D. Damuth, W.A. DiMichele, R. Potts, H.D. Sues, and S.L. Wing, editors. 1992. *Terrestrial ecosystems through time*. Chicago, IL: The University of Chicago Press. 568 p.
- Biaggi, V. 1997. *Las aves de Puerto Rico*. Río Piedras, PR: Editorial Universitaria, University of Puerto Rico. 5th edition.
- Birdsey, R.A. and P.L. Weaver. 1982. *The forest resources of Puerto Rico*. Resource Bulletin SO-85. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station.
- Birdsey, R.A. and P.L. Weaver. 1987. *Forest area trends in Puerto Rico*. Research Note SO-331. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station.
- Borges, S. and A.G. Moreno. 1990. Contribución al conocimiento de los oligoquetos terrestres de Puerto Rico: Las "pheretimas." *Caribbean Journal of Science*. 26(3-4): 141-151.
- Borges, S. and A.G. Moreno. 1992. Redescipción de *Trigaster rufa* (Gates 1962) (Oligochaeta: Octochaetidae). *Caribbean Journal of Science*. 28(1-2): 47-50.
- Bowdish, B.S. 1902. Birds of Porto Rico. *Auk*. 19: 357-366.
- Bowdish, B.S. 1903. Birds of Porto Rico. *Auk*. 20: 10-23.
- Briggs, R.P. 1966. The blanket sands of northern Puerto Rico. Transactions of the third Caribbean geological conference. Robinson, E. ed. Kingston, Jamaica: Geological Survey Department of Jamaica. pp. 60-69.
- Bunkley Williams, L. and E.H. Williams Jr. 1994. Parasites of Puerto Rican freshwater sport fishes. Sportfish disease project. Lajas, PR: Department of Marine Sciences, University of Puerto Rico. 164 p.
- Carlo Joglar, T.A. 1999. Diet, Fruit Preference and Seed Dispersal Capabilities of Fruit-eating Birds in North-central Puerto Rico. Raleigh, NC: Department of Zoology, North Carolina State University. 109 p. Thesis.
- Calvesbert, R.J. 1973. The climate of Mona Island. In Mona and Monito Islands: an assessment of their natural and historical resources. San Juan, PR: Puerto Rico Environmental Quality Board. 2: A1-A11.
- China, J.D. 1980. *The Forest Vegetation of the Limestone Hills of Northern Puerto Rico*. Ithaca, NY: Cornell University. 70 p. Thesis.
- Chubb, L.J. 1963. Bauxite genesis of Jamaica. *Economic Geology*. 58: 286-289.
- Cintrón, B.B. 1979. Effects on introduced animals on the vegetation of Mona Island. In Memorias del tercer simposio de los recursos naturales. San Juan, PR: Departamento de Recursos Naturales. pp. 88-99.
- Cintrón, B. and L. Rogers. 1991. Plant communities of Mona Island. *Acta Científica*. 5(1-3): 10-64.
- Cintrón, G., A.E. Lugo, D.J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica*. 10(2): 110-121.
- Comer, J.B. 1974. Genesis of Jamaican Bauxite. *Economic Geology*. 69(8): 1251-1264.
- COE. 1973. Flood plain information Río Cibuco, and Río Indio, Vega Baja and Vega Alta, Puerto Rico. Jacksonville, FL: U.S. Army Corps of Engineers. 37 p. + 14 plates.
- Conde Costas, C. and F. Gómez Gómez. 1999. Assessment of nitrate contamination of the upper aquifer in the Manatí -Vega Baja area, Puerto Rico. Water Resources Investigations Report 99-4040. San Juan, PR: U.S. Geological Survey. 43 p.
- Cortés Burgos, S. 1990. Estudio de la transferencia de agua del acuífero artesiano al acuífero llano en la costa norte. In Memorias del decimosexto simposio de los recursos naturales. San Juan, PR: Departamento de Recursos Naturales. pp. 93-96.

- Courbon, P., C. Chabert, P. Bosted, and K. Lindsley. 1989. Puerto Rico. Atlas of the great caves of the world. In *Cave Book*. St. Louis, MO. pp. 84-86.
- Covich, A.P. and W.H. McDowell. 1996. The stream community. In *The food web of a tropical rain forest*. D.P. Reagan and R.B. Waide, editors. Chicago, IL: University of Chicago Press. pp. 433-459.
- Cruzado Torres, D.G. 1996. Preliminary investigation of bauxite deposits in the Florida area, Puerto Rico. Mayagüez, PR: Department of Geology, University of Puerto Rico. 37 p. Undergraduate Research Report.
- Culver, D.C., L.L. Master, M.C. Christman, and H.H. Hobbs. 1999. Obligate cave fauna of the 48 contiguous United States. *Conservation Biology*. 14: 386-401.
- Danforth, S.T. 1931. Puerto Rican ornithological records. *Journal of Agriculture University of Puerto Rico*. 15: 33-106.
- Danford, S.T. and J.A. Smyth. 1935. The Puerto Rican form of the broad-winged hawk. *Journal of Agriculture University of Puerto Rico*. 19: 485-486.
- Delannoy, C.A. 1992. Status surveys of the Puerto Rican broad-winged hawk (*Buteo platypterus brunnescens*). Final status report submitted to the U.S. Fish and Wildlife Service, contract no. 14-16-0004-82-047. 66 p.
- Delannoy, C.A. 1997. Status of the Broad-winged Hawk and Sharp-shinned Hawk in Puerto Rico. *Caribbean Journal of Science*. 33: 21-33.
- del Llano, M. 1988. Map of the wetlands of Puerto Rico. *Acta Científica*. 2: cover.
- Domínguez Cristóbal, C.M. 1989a. La situación forestal pre- hispánica de Puerto Rico. *Acta Científica*. 3: 63-66.
- Domínguez Cristóbal, C.M. 1989b. La situación forestal de Puerto Rico durante el siglo XVI. *Acta Científica*. 3: 67-70.
- Dopazo, T. and W.L. Molina Rivera. 1995. Estimated water use in Puerto Rico, 1988-89. Open File Report 95-380. San Juan, PR: U.S. Geological Survey. 31 p.
- Dugger, K.R., J.E. Cardona, J. González Liboy, and D.J. Pool. 1979. *Habitat evaluation in the wet limestone forest of Río Abajo*. Final Report, Project W-8. San Juan, PR: U.S. Fish and Wildlife Service and Puerto Rico Department of Natural Resources. 186 p.
- Erdman, D.S. 1961. Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. *Bulletin of Marine Science of the Gulf and Caribbean*. 3: 448-456.
- Erdman, D.S. 1967. *Inland game fishes of Puerto Rico*. Department of Agriculture, Federal Aid Project F-1-R. San Juan, PR: Commonwealth of Puerto Rico.
- Erdman, D.S. 1972. *Inland game fishes of Puerto Rico*. 2nd edition. San Juan, PR: Department of Agriculture, Commonwealth of Puerto Rico. 96 p.
- Erdman, D.S. 1984. Exotic fishes in Puerto Rico. In *Distribution, Biology and Management of Exotic Fishes*. W.R. Courtenay Jr. and J.R. Stauffer, Jr., eds. Baltimore, MD: John Hopkins University Press, 430 p.
- Field, M.S. 1999. *A lexicon of cave and karst terminology with special reference to environmental karst hydrology*. Washington, DC: U.S. Environmental Protection Agency, Office of Research and Development. EPA/600/R-99/006. 195 p.
- Figueroa Colón, J. 1995. Phytogeographical trends, centers of high species richness and endemism, and the question of species extinctions in the native flora of Puerto Rico. In *The scientific survey of Puerto Rico and the Virgin Islands: an eighty year reassessment of the islands' natural history*. J. Figueroa Colón, ed. *Annals of the New York Academy of Sciences*. New York.
- Figueroa, J.C., L. Totti, A.E. Lugo, and R. Woodbury. 1984. *Structure and composition of moist coastal forests in Dorado, Puerto Rico*. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station. Research Paper SO-202. 11 p.
- Francis, J.K. 1995. Forest plantations in Puerto Rico. In *Tropical forests: management and ecology*. A.E. Lugo and C. Lowe, eds. New York, NY: Springer Verlag. 210-223 p.
- Franco, P.A., P.L. Weaver, and S. Eggen-McIntosh. 1997. *Forest resources of Puerto Rico, 1990*. USDA Forest Service Southern Research Station. Resource Bulletin SRS-22. 45 p.
- Frank, E.F. 1998a. A radiocarbon date of 380 + 60 BP for a Taino site, Cueva Negra, Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 101-102.
- Frank, E.F. 1998b. History of the guano mining industry, Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 121-125.
- Frank, E.F., C. Wicks, J. Mylroie, J. Troester, E.C. Alexander Jr., and J. Carew. (1998a). Geology of Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 69-72.

- Frank, E.F., J. Mylroie, J. Troester, E.C. Alexander Jr., and J. Carew. 1998b. Karst development and speleogenesis, Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 69-72.
- García Díaz, J. 1967. Rediscovery of *Bufo lemur* (Cope) and additional records of reptiles from Puerto Rico. *Stablia*. 10: 1-6.
- García Ríos, C.I. 1998. *Listado de los peces que viven en aguas territoriales de Puerto Rico*. Humacao, PR: Departamento de Biología, Colegio Universitario de Humacao, Mimeo. 38 p.
- Gierbolini, R.E. 1975. *Soil survey of Mayagüez area of western Puerto Rico*. Washington, DC: USDA Soil Conservation Service. 296 p. + maps.
- Giusti, E.V. 1978. *Hydrogeology of the karst of Puerto Rico*. Geological Survey Professional Paper 1012. Washington, DC: U.S. Government Printing Office. 68 p. + map.
- Giusti, E.V. and G.D. Bennett. 1976. *Water resources of the north coast limestone area, Puerto Rico*. Water-Resources Investigations 42-75. San Juan, PR: U.S. Geological Survey Water Resources Division. 42 p.
- Gleason, H.A. and M.T. Cook. 1926. Plant ecology of Porto Rico. *Scientific Survey of Porto Rico and the Virgin Islands 7*: 1-173. New York, NY: New York Academy of Sciences.
- Goebel, A.M. 1996. *Systematics and conservation of Bufonids in North America and in the Bufo boreas species group*. Boulder, CO: University of Colorado. Dissertation
- Gómez Gómez, F. 1984. *Water resources of the lower Río Grande de Manatí valley, Puerto Rico*. Water Resources Investigations Report 83-4199. San Juan, PR: U.S. Geological Survey. 42 p.
- Gómez Gómez, F. 1991. Ground water development in the artesian aquifer in north-central Puerto Rico and possible effects of future withdrawals. In 23rd International Congress of the International Association of Hydrogeologists. Tenerife, Canary Islands. 221-225 p.
- Gómez Gómez, F. and H. Torres Sierra 1988. *Hydrology and effects of development on the water-table aquifer in the Vega Alta quadrangle, Puerto Rico*. San Juan, PR: U.S. Geological Survey. Water Resources Investigations Report 87-4105. 54 p.
- Gómez Gómez, F., F. Quiñones, and M. López. 1984. *Public water supplies in Puerto Rico, 1983*. Open File Report 84-126. San Juan, PR: U.S. Geological Survey. 102 p.
- González Azar, J. 1992. *Guía para la pesca recreativa en los embalses de Puerto Rico*. Programa de educación de recursos acuáticos. San Juan, PR: Departamento de Recursos Naturales y Ambientales, Estado Libre Asociado de PR. 201 p.
- Graham, A. 1996. Paleobotany of Puerto Rico—from Arthur Hollick's (1928) scientific survey paper to the present. In The scientific survey of Puerto Rico and the Virgin Islands: an eighty year reassessment of the Islands' natural history. J.C. Figueroa Colón, ed. *Annals of the New York Academy of Sciences* 776. New York, NY. 103-114 p.
- Grana Raffucci, F.A. 1993. *Catálogo de nomenclatura de los peces de Puerto Rico y las Islas Vírgenes*. 2nd edition. San Juan, PR: Department of Natural and Environmental Resources, Commonwealth of Puerto Rico. 201 p.
- Grant, C. 1933. Notes on *Epicratres inornatus*. *Copeia*. 1933: 224-225.
- Guzmán Ríos, S. 1983. *Reconnaissance of the principal springs of Puerto Rico, 1982-83*. Open File Data Report 83-683. San Juan, PR: U.S. Geological Survey.
- Guzmán Ríos, S. and Quiñones Márquez, F. 1985. *Reconnaissance of trace-organic compounds in ground water throughout Puerto Rico, October 1983*. Open-File Data Report 84-810. San Juan, PR: U.S. Geological Survey.
- Halton, P. 1996. Cave photo course and the Río Encantado expedition. *National Speleological Survey News*. September: 233-243.
- Hernández, B. 1978. Geología de los yacimientos de bauxita de Pedranales. In Memoria primer seminario sobre el sector minero. R.A. Llinás and A.V. Malagón, eds. Santo Domingo, República Dominicana. pp. 133-138.
- Hernández Prieto, E. 1980. Estudio de aves, reptiles y anfibios en la reserva forestal de Carite. Río Piedras, PR: Programa de Mantenimiento Ambiental, Facultad de Ciencias Naturales, Universidad de Puerto Rico.
- Hernández Prieto, E.N. 1993. *Ecological comparison of the land bird fauna of two subtropical dry forests in the West Indies*. Boulder, CO: Department of Environmental, Population and Organismic Biology, University of Colorado-Boulder. Dissertation.
- Hernández Prieto, E. 2001. *Status review of the Puerto Rican Crested Toad (Peltophryne lemur) on the northwestern coast Puerto Rico*. Final Report to the U.S. Fish and Wildlife Service. Humacao, PR: University of Puerto Rico. 25 p.
- Hertz, P.E. 1992. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *Anolis cristatellus*: A field test using null hypotheses. *Oecologia*. 90(1): 127-136.
- Hickenlooper, I.J. 1967. *Floods at Barceloneta and Manatí, Puerto Rico*. Hydrologic Investigations Atlas HA-262. Washington, DC: U.S. Geological Survey.

- Hildebrand, F.A. 1960. *Occurrences of bauxitic clay in the karst area of north central Puerto Rico*. In Short papers in the geological sciences. Geological Survey Research 1960. U.S. Geological Survey Professional Paper 400B. pp. B360 - B371.
- Hill, R.T. 1899. Porto Rico. *National Geographic*. 10: 93-112.
- Hill, V.G. and S. Ostojic. 1982. The bauxite deposits of Jamaica. A.A. Lyew, ed. A distinctive karstic type. In Proceedings of the bauxite symposium no. 5. *Journal of the Geological Society of Jamaica*. Kingston, Jamaica. pp. 9-18.
- Holdridge, L.R. 1967. *Life zone ecology*. San José, Costa Rica: Tropical Science Center. 206 p.
- Hollick, A. 1924. A review of the fossil flora of the West Indies, with descriptions of new species. *Bulletin New York Botanical Gardens*. 27: 2 23-227.
- Hollick, A. 1926. Fossil walnuts and lignite from Porto Rico. *Journal of the New York Botanical Gardens*. 27: 97-102.
- Hollick, A. 1928. *Paleobotany of Puerto Rico*. Scientific Survey of Puerto Rico and the Virgin Islands 7(3). New York, NY: New York Academy of Sciences.
- Hubbard, B. 1923. *The geology of the Lares district, Puerto Rico*. New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands 2(1): 1-115.
- Jennings, J.N. 1971. *Karst*. Cambridge, MA: MIT Press. 241 p.
- Joglar, R.L. 1998. *Los Coquíes de Puerto Rico: su historia natural y conservación*. Río Piedras, PR: Editorial Universitaria, University of Puerto Rico. 232 p.
- Joglar, R.L. and P.A. Burrowes. 1996. Declining amphibian populations in Puerto Rico. In *Contributions to West Indian Herpetology: A tribute to Albert Schwartz*. R. Powell, and R. W. Henderson, eds. Ithaca, New York: Society for the Study of Amphibians and Reptiles. pp. 371-380.
- Lafalaise, B. 1980. La bauxite de la République d'Haiti. In Presentations et transactions du 1er colloque sur la geologies d'Haiti. F.J.M.R., ed. Port au Prince. pp. 112-115.
- Little, E.L. and F.H. Wadsworth. 1964. *Common trees of Puerto Rico and the Virgin Islands*. Agriculture Handbook No. 249. Washington, DC: USDA Forest Service. 548 p.
- Little, E.L., R.O. Woodbury, and F.H. Wadsworth. 1974. *Trees of Puerto Rico and the Virgin Islands*. Washington, DC: USDA Forest Service Agriculture Handbook 449. 1024 p.
- López, T. del Mar, T.M. Aide, and J.R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio*. 30: 49-54
- Lugo, A.E. 1991. Dominancia y diversidad de plantas en isla de Mona. *Acta Científica*. 5: 65-71.
- Lugo, A.E. In press. Bosques húmedos y muy húmedos sobre lomas de roca caliza. In A.E. Lugo, Los bosques de Puerto Rico. Río Piedras, PR: Editorial Universidad.
- Lugo, A.E. and A.R. García Martínó. 1996. Cartilla del agua para Puerto Rico. *Acta Científica*. 10(1-3): 1-89 .
- Lugo, A.E. and G. Cintrón. 1975. The mangrove forests of Puerto Rico and their management. In Proceedings of international symposium on biology and management of mangroves. G. Walsh, S. Snedaker, and H. Teas, eds. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida. pp. 825-846.
- McDowell, B. 1962. Puerto Rico's seven-league bootstraps. *National Geographic*. 122: 755-793.
- McFarlane, D.A. 1999a. Late Quaternary fossil mammals and last occurrence dates from caves at Barahona, Puerto Rico. *Caribbean Journal of Science*. 35: 238-248.
- McFarlane, D.A. 1999b. *A note on dimorphism in Nesophontes edithae* (Mammalia: Insectivora), an extinct island-shrew from Puerto Rico. *Caribbean Journal of Science*. 35: 142-143.
- McGuinness, C.L. 1963. *The role of ground water in the national water situation*. U.S. Geological Survey Water Supply Paper 1800. Washington, DC: U.S. Government Printing Office.
- Martin, F.D. and J.W. Patus. 1988. Clave para los peces teleósteos de Puerto Rico. In Compendio enciclopédico de los recursos naturales de Puerto Rico. J.L. Vivaldi and C. Paniagua, eds. San Juan, PR: Department of Natural Resources. 3: 1-191.
- Martorell, L.F. 1945. A survey of the forest insects of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*. 29(1-2).
- Miller, T.E. 1987. Fluvial and collapse influences on cockpit karst of Belize and eastern Guatemala. In B. Beck and W. Wilson, editors. *Karst hydrogeology: engineering and environmental applications*. Orlando, FL: Florida Sinkhole Research Institute, University of Central Florida. pp. 53-57.
- Miller, T.E. 2000. Karst processes in Puerto Rico. Nineteenth annual symposium of Caribbean Geology. February 23-26, Mayagüez, PR: University of Puerto Rico.

- Miller, T.J. 1985. Husbandry and breeding of the Puerto Rican Toad (*Peltophryne lemur*) with comments on its natural history. *Zoo Biology*. 4: 281-286.
- Molina Rivera, W.L. 1997. *Ground water use from the principal aquifers in Puerto Rico during calendar year 1990*. Fact Sheet FS-188-96. San Juan, PR: U.S. Geological Survey, Caribbean District. 3 p.
- Molina Rivera, W.L. 1998. *Estimated water use in Puerto Rico, 1995*. Open File Report 98-276. San Juan, PR: U.S. Geological Survey. 28 p.
- Molina Rivera, W.L. and T. Dopazo. 1995. *Estimated water use in Puerto Rico, 1986-87*. Open File Report 95-358. San Juan, PR: U.S. Geological Survey. 31 p.
- Monroe, W.H. 1966. Formation of tropical karst topography by limestone solution and reprecipitation. *Caribbean Journal of Science*. 6: 1-7.
- Monroe, W.H. 1967. *Geologic map of the Quebradillas quadrangle, Puerto Rico*. Miscellaneous Geologic Investigations (Map I-498). Washington, DC: Department of the Interior, U.S. Geological Survey.
- Monroe, W.H. 1971. *Geologic map of the Manatí quadrangle, Puerto Rico*. Miscellaneous Geologic Investigations Map I-671. Washington, DC: Department of the Interior, U.S. Geological Survey.
- Monroe, W.H. 1976. *The karst landforms of Puerto Rico*. U.S. Geological Survey Professional Paper 899. Washington, DC: U. S. Government Printing Office. 69 p. + map.
- Monroe, W.M. 1980. *Geology of the middle Tertiary Formations of Puerto Rico*. U.S. Geological Survey Professional Paper 953. Washington, DC: : Department of the Interior, U.S. Geological Survey. 93 p. + map.
- Morales Cardona, T., B. Ruiz, A.E. Lugo, and G. Morris. 1994. Un llamado a la acción para salvaguardar el patrimonio natural y la calidad de vida en Puerto Rico. *Acta Científica*. 8: 67-70.
- Moreno, J.A. 1991. Accounts of those species considered to be concern. In Status y distribución de los reptiles y anfibios de la región de Puerto Rico. J.A. Moreno, editor. San Juan, PR: Publicación Miscelánea del Departamento de Recursos Naturales de Puerto Rico. pp. 9-10.
- Morris, G.L. and J. Fan. 1997. *Reservoir sedimentation handbook: design and management of dams, reservoirs, and watersheds for sustainable use*. New York, NY: McGraw Hill.
- Negrón González, L. 1986. Las lagunas de Puerto Rico. Compendio enciclopédico de los recursos naturales de Puerto Rico 9: 1-248. San Juan, PR: Area de Investigaciones Científicas, Departamento de Recursos Naturales.
- Nelson, A.E. and W.H. Monroe. 1966. *Geology of the Florida quadrangle Puerto Rico*. Bulletin 1221-C. Reston, VA: U.S. Geological Survey. 22 p.
- Neváres, R. and J. Villamil. 1980. Laguna de Tortuguero: recopilación comprensiva de datos sobre la estructura, funcionamiento y utilización de este recurso natural. CEER T-068. Río Piedras, PR: Center for Energy and Environmental Research, University of Puerto Rico. 116 p.
- Nieves Rivera, A.M. 1999. El mar prehistórico de Puerto Rico. Ancestro del tiburón blanco. *Boletín Marino Sea Grant*. 20(1-3): 1-6.
- Office of Economic Research. 1999. Puerto Rico directory of manufacturers. San Juan, PR: Economic Development Administration Commonwealth of Puerto Rico. 300 p.
- Olson, S.L. 1976. Fossil woodcocks: an extinct species from Puerto Rico and an invalid species from Malta (Aves: Scolopacidae: Scolopax). Proceedings of Biological Society. Washington, DC. 89: 265-274.
- Olson, S.L. 1982. A new species of palm swift (Tachornis: Apodidae) from the Pleistocene of Puerto Rico. *Auk*. 99: 230-235.
- Olson, S.L. and M.C. McKittrick. 1981. A new genus and species of Emberizine finch from Pleistocene cave deposits in Puerto Rico (Aves: Passeriformes). *Journal of Vertebrate Paleontology* 1: 279-283.
- Ortiz, P.R. 1979. *Behavioral comparison of anoline competitors: Anolis cooki and Anolis cristatellus (Reptilia: Iguanidae)*. Blacksburg, VA: Virginia Polytechnic Institute and State University. Thesis.
- Ortiz, P.R. 1985. Distribution of the lizard *Anolis cooki*, with comments on its possible future extinction. *Herpetological Review*. 16(4): 99-102.
- Ortiz, P.R. and T.A. Jensen. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Zeitschrift für Tierpsychologie*. 60: 227-238.
- Peck, S.B. 1974. The invertebrate fauna of tropical American caves, Part II: Puerto Rico, an ecological and zoogeographic analysis. *Biotropica*. 6: 14-31.
- Peck, S.B. 1981. Zoogeography of invertebrate cave faunas in southwestern Puerto Rico. *National Speleological Society Bulletin*. 43: 70-79.
- Peck, S.B. and J. Kukalova Peck. 1981. The subterranean fauna and conservation of Mona Island (Puerto Rico): a Caribbean karst environment. *National Speleological Society Bulletin*. 43: 59-68.

- Peck, D.L., J.W. Troester, and J.E. Moore. 1988. *Karst hydrogeology in the United States of America*. Open File Report 88-476. San Juan, PR: U.S. Geological Survey. 19 p.
- Pérez Rivera, R.A. and R. Cotté Santana. 1977. Algunas notas sobre los falconiformes residentes en Puerto Rico. *Science-Ciencia*. 4: 89-95.
- Petrunkevitch, A. 1929. The spiders of Puerto Rico, Part I. Transactions of the Connecticut Academy of Arts and Sciences. 30: 1-158.
- Petrunkevitch, A. 1930a. The spiders of Puerto Rico, Part II. Transactions of the Connecticut Academy of Arts and Sciences. 30: 159-355.
- Petrunkevitch, A. 1930b. The spiders of Puerto Rico, Part III. Transactions of the Connecticut Academy of Arts and Sciences. 31: 1-191.
- Picó, R. 1950. *The Geographic Regions of Puerto Rico*. Río Piedras, PR: University of Puerto Rico Press. 256 p.
- Picó, R., Z. Buitrago de Santiago, and H.H. Berrios. 1975. Nueva geografía de Puerto Rico. Río Piedras, PR: Editorial Universidad, University of Puerto Rico. 460 p.
- Pool, D.J. and G. Morris. 1979. Land use in the mogotes. In Memorias del tercer simposio de los recursos naturales. San Juan, PR: Departamento de Recursos Naturales. 124-132 p.
- Post, W. and J.M. Wiley. 1976. The Yellow-Shouldered Blackbird: present and future. *American Birds*. 30: 13-20.
- Pregill, G.K. 1981. Late Pleistocene herpetofaunas from Puerto Rico. Miscellaneous Publications, University of Kansas Museum of Natural History. 71: 1-72.
- Pregill, G.K. and S.L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics*. 12: 75-98.
- Quiñones Aponte V. 1986. *Water resources of the lower Río Grande de Arecibo alluvial valley, Puerto Rico*. Water Resources Investigations Report 85-4160. San Juan, PR: U.S. Geological Survey. 38 p.
- Quiñones Márquez, F. and L.A. Fusté. 1978. *Limnology of Laguna Tortuguero*. Water Resources Investigations 77-122. San Juan, PR: U.S. Geological Survey. 86 p.
- Raffaele, H. 1973. Assessment of Mona Island avifauna. In Mona and Monito Islands: an assessment of their natural and historical resources. San Juan, PR: Puerto Rico Environmental Quality Board. 2: K1-K32.
- Raffaele, H. 1992. *A Guide to the Birds of Puerto Rico and the Virgin Islands*. Princeton, NJ: Princeton University Press. 254 p.
- Ramos, O.M. and A.E. Lugo. 1994. Mapa de la vegetación de Puerto Rico. *Acta Científica*. 8(1-2): 63-66.
- Raúl Díaz, J. 1973. *Chemical quality of water in Caño Tiburones, Puerto Rico*. U.S. Geological Survey Open File Report Map Series No. 2. San Juan, PR. 2 Plates.
- Reagan, D.P. and C.P. Zucca. 1982. Inventory of the Puerto Rican Boa (*Epicrates inornatus*) in the Caribbean National Forest. CEER T-136. San Juan, PR: Center for Energy and Environment Research, University of Puerto Rico. 42 p.
- Ricart Morales, C.M. 1999. *Frugivory by birds in two subtropical dry forest tree species (almácigo, Bursera simaruba and guayacán, Guaiacum officinale) in Guánica, Puerto Rico*. Boulder, CO: Department of Environmental, Population and Organismic Biology, University of Colorado. Dissertation.
- Richard, R.T., J.W. Troester, and M.I. Martínez. 1998. An electromagnetic geophysical survey of the freshwater lens of Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 115-120.
- Ríos Lavienna, G. 1933. *Guía del agricultor isla de Puerto Rico*. Arecibo, PR: Editorial Pozo. 372 p.
- Rivera, L.W. 1998. *Secondary succession in Caribbean karst forests*. Río Piedras, PR: University of Puerto Rico. 153 p. Dissertation.
- Rivera, L.W. and T.M. Aide. 1998. Forest recovery in the karst region of Puerto Rico. *Forest Ecology and Management*. 108: 63-75.
- Rivera, M. 1994. Aspectos sobre la biología del cangrejo de agua dulce *Epilobocera sinuatifrons* (BURUQUENA) en Puerto Rico. In Memorias del Decimotercer simposio de la flora y fauna del Caribe. Humacao, PR: Universidad de Puerto Rico, Recinto Universitario de Humacao. 7-10 p.
- Rivera Milán, F.F. 1993. Standardization of roadside counts of columbids in Puerto Rico and Vieques Island. *USDI National Biological Survey Resource Publication*. 197: 1-26.
- Rivero, J.A. 1998. Los anfibios y reptiles de Puerto Rico. San Juan, PR: Universidad de Puerto Rico. Editorial Universitaria. 510 p.
- Rivero, J.A., H. Mayorga, E. Estremera, and I. Izquierdo. 1980. Sobre el Bufo lemur (Cope) (Amphibia, Bufonidae). *Caribbean Journal of Sciences*. 15(3-4): 33-40.
- Rivero, J.A. and D. Seguí Crespo. 1992. Anfibios y reptiles en nuestro folklore. Imprenta San Rafael, Quebradillas.
- Roberts, R.C. 1942. *Soil survey of Puerto Rico*. USDA Soil Survey Report No. 8, Series 1936. Washington, DC. 503 p.

- Rodríguez Durán, A. 1996. Foraging ecology of the Puerto Rican Boa (*Epicrates inornatus*): bat predation, carrion feeding, and piracy. *Journal of Herpetology*. 30: 533-536.
- Rodríguez Durán, A. 1998. Distribution and non-random aggregations of the cave bats of Puerto Rico. *Journal of Mammalogy*. 79: 141-146.
- Rodríguez Durán, A. and A.R. Lewis. 1985. Seasonal predation by merlins on sooty mustached bats in western Puerto Rico. *Biotropica*. 17: 71-74.
- Rodríguez Durán, A. and A.R. Lewis. 1987. Patterns of population size, diet, and activity for a multispecies assemblage of bats. *Caribbean Journal of Science*. 23: 352-360.
- Rodríguez Martínez, J. 1995. *Hydrogeology of the north coast limestone aquifer system of Puerto Rico*. Water Resources Investigations Report 94-4249. San Juan, PR: U.S. Geological Survey. 22 p.
- Rodríguez Martínez, J. 1997. *Characterization of springflow in the north coast limestone of Puerto Rico using physical, chemical, and stable isotopic methods*. Water Resources Investigations Report 97-4122. San Juan, PR: U.S. Geological Survey. 53 p.
- Rodríguez Ramírez, J.G. 1991. Reproducción en los teidos de Puerto Rico *Ameiva exsul* y *Ameiva wetmorei*. *Herpetologica*. 47(4): 395-403.
- Rodríguez Ramírez, J.G. 1994. *Status survey of Ameiva wetmorei*. Report to the U.S. Fish and Wildlife Service. Ponce, PR: University of Puerto Rico.
- Rogers, L. 1974. The vegetation of Mona island. In *Memorias del primer simposio de los recursos naturales*. San Juan, PR: Departamento de Recursos Naturales. 41-46 p.
- Román Más A. and R.W. Lee. 1987. Geochemical evolution of waters within the north coast limestone aquifers of Puerto Rico: a conceptualization based on a flow path in the Barceloneta area. Water Resources Investigations Report 86-4080. San Juan, PR: U.S. Geological Survey. 28 p.
- Ruiz, C. and J.L. Chabert. 1989. Notas sobre el comportamiento y ecología de los cabros en Isla de Mona. In *Memorias del decimoquinto simposio de los recursos naturales*. San Juan, PR: Departamento de Recursos Naturales. 1-46 p.
- Santiago de Rohena, E. 1974. *Taxonomy and geographic distribution of the Chilopoda of Puerto Rico*. Río Piedras, PR: Department of Biology, University of Puerto Rico. Thesis.
- Santiago Blay, J. 1984. *The scorpions of Puerto Rico*. Río Piedras, PR: Department of Biology, University of Puerto Rico. Thesis.
- Seiglie, G.A. and M.T. Moussa. 1984. Late Oligocene-Pliocene transgressive-regressive cycles of sedimentation in northwestern Puerto Rico. In *Interregional unconformities and hydrocarbon accumulation*. J.S. Schlee, editor. American Association of Petroleum Geologists Memoir 36. pp. 89-98.
- Sepúlveda, N. 1999. *Ground-water flow, solute transport, and simulation of remedial alternatives for the water-table aquifer in Vega Alta, Puerto Rico*. Water Resources Investigations Report 97-4170. San Juan, PR: U.S. Geological Survey. 96 p.
- Snyder, N.F.R., J.W. Wiley, and C.B. Kepler. 1987. *The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot*. Los Angeles, CA: Western Foundation of Vertebrate Zoology. 384 p.
- Solley, W.B., R.R. Pierce, and H.A. Perlman. 1998. *Estimated use of water in the United States in 1995*. Circular 1200. Denver, CO: U.S. Geological Survey. 71 p.
- Soto, A.E. and W. Morales. 1984. Collapse sinkholes in the blanket sands of the Puerto Rico karst belt. Proceedings of the first multidisciplinary conference on sinkholes. Orlando, FL. 143-146 p.
- Struthers, P.H. 1923. Observations on the bird life of Puerto Rico. *Auk*. 40: 469-478.
- Tarhule-Lipps, R.F.A. and J. Carew. 1998. Condensation corrosion in caves on Cayman Brac and Isla de Mona. *Journal of Cave and Karst Studies*. 60(2): 84-95.
- Taylor, E.C. 1864. Five months in the West Indies. II. Martinique, Dominica, and Puerto Rico. *Ibis*. 3: 157-173.
- Torres González, A. 1985. *Simulation of ground-water flow in the water-table aquifer near Barceloneta, Puerto Rico*. Water Resources Investigations Report 84-4113. San Juan, PR: U.S. Geological Survey. 39 p.
- Torres González, A. and J.R. Díaz. 1984. *Water resources of Sabana Seca to Vega Baja Area, Puerto Rico*. Water Resources Investigations Report 82-4115. San Juan, PR: U.S. Geological Survey. 53 p.
- Torres González, A. and R.M. Wolansky. 1984. *Planning report for the comprehensive appraisal of the ground-water resources of the north coast limestone area of Puerto Rico*. Open-File Data Report 84-427. San Juan, PR: U.S. Geological Survey. 32 p.
- Torres Sierra, H. and A. Avilés. 1986. *Estimated water use in Puerto Rico, 1980-82*. Open File Data Report 85-557. San Juan, PR: U.S. Geological Survey. 77 p.

- Tossas, A.G. 1995. *Nesting site habitat description and space requirements of the Puerto Rican broad-winged hawk*. Mayagüez, PR: University of Puerto Rico. 59 p. Thesis.
- Troester, J.W. 1999. *Geochemistry and hydrogeologic framework of the saline-freshwater interface and the calculation of net recharge in the Dorado Area, North-Central Puerto Rico*. Water Resources Investigations Report 98-4030. San Juan, PR: U.S. Geological Survey. 36 p.
- Troester, J.W., E.L. White, and W.B. White. 1984. A comparison of sinkhole depth frequency distributions in temperate and tropical karst regions. In *Sinkholes: their geology, engineering, and environmental impact*. B.F. Beck, editor. A.A. Balkema, Rotterdam, The Netherlands. 65-73 p.
- Troester, J.W. and J. Rodríguez Martínez. 1990. *Field trip guide. International Symposium on Tropical Hydrology and Fourth Caribbean Island Water Resources Congress*. San Juan, PR: American Water Resources Association. 40 p.
- Tucci, P. and M.I. Martínez. 1995. *Hydrology and simulation of ground-water flow in the Aguadilla to Río Camuy Area, Puerto Rico*. Water Resources Investigations Report 95-4028. San Juan, PR: U.S. Geological Survey. 39 p.
- U.S. Fish and Wildlife Service. 1984. *Puerto Rican Whip-poor-will Recovery Plan*. Atlanta, GA. 16 p.
- U.S. Fish and Wildlife Service. 1986. *Puerto Rican Boa Recovery Plan*. Atlanta, GA. 21 p.
- U.S. Fish and Wildlife Service. 1987a. *Beautiful Goetzea Recovery Plan*. Atlanta, GA. 35 p.
- U.S. Fish and Wildlife Service. 1987b. *Vahl's Boxwood Recovery Plan*. U.S. Atlanta, GA. 34 p.
- U.S. Fish and Wildlife Service. 1991a. *Banara Vanderbiltii Recovery Plan*. Atlanta, GA. 22 p.
- U.S. Fish and Wildlife Service. 1991b. *Bariaco (Trichilia triacantha) Recovery Plan*. Atlanta, GA. 21 p.
- U.S. Fish and Wildlife Service. 1992a. *Calyptronoma rivalis (palma de manaca) Recovery Plan*. Atlanta, GA. 18 p.
- U.S. Fish and Wildlife Service. 1992b. *Recovery Plan for the Puerto Rican Crested Toad (Peltophryne lemur)*. Atlanta, GA. 19 p.
- U.S. Fish and Wildlife Service. 1994a. *Chamaecrista glandulosa var. mirabilis Recovery Plan*. Atlanta, GA. 18 p.
- U.S. Fish and Wildlife Service. 1994b. *Ottoschulzia rhodoxylon (palo de rosa) Recovery Plan*. Atlanta, GA. 27 p.
- U.S. Fish and Wildlife Service. 1996a. *Myrcia paganii and Auerodendron pauciflorum Recovery Plan*. Atlanta, GA. 17 p.
- U.S. Fish and Wildlife Service. 1996b. *Puerto Rican Endangered Ferns Recovery Plan*. Atlanta, GA. 23 p.
- U.S. Fish and Wildlife Service. 1996c. *Yellow-Shouldered blackbird (Agelaius xanthomus) Revised Recovery Plan*. Atlanta, GA. 77 p.
- U.S. Fish and Wildlife Service. 1997a. *Puerto Rican Broad-winged Hawk and Puerto Rican Sharp-shinned Hawk Recovery Plan*. Atlanta, GA. 30 p.
- U.S. Fish and Wildlife Service. 1997b. *Technical/Agency Draft Recovery Plan for Pleodendron macranthum and Eugenia haematocarpa*. Atlanta, GA. 36 p.
- U.S. Fish and Wildlife Service. 1999. *Technical/Agency Draft Revised Recovery Plan for the Puerto Rican Parrot (Amazona vittata)*. Atlanta, GA. 77 p.
- Van der Schalie, H. 1948. *The Land and Freshwater Mollusks of Puerto Rico*. Ann Arbor, MI: University of Michigan Press.
- Vélez, M.J. 1967a. Checklist of the terrestrial and freshwater decapoda of Puerto Rico. *Caribbean Journal of Science*. 7: 41-44.
- Vélez, M.J. 1967b. New records of Puerto Rican Diplopoda with notes on their geographic distribution. *Stablia*. 8: 1-11.
- Vélez, M.J. 1979a. Bibliografía selecta de la fauna y de las comunidades naturales de Puerto Rico. *Science-Ciencia*. 6(3): 106-126.
- Vélez, M.J. 1979b. Bibliografía selecta de la fauna y de las comunidades naturales de Puerto Rico, segunda parte. *Science-Ciencia*. 6(4): 145-166.
- Vélez, M.J. 1979c. Bibliografía selecta de la fauna y de las comunidades naturales de Puerto Rico, tercera parte. *Science-Ciencia*. 6(5): 189-218.
- Wadsworth, F.H. 1973. The historical resources of Mona Island. In *Mona and Monito Islands: an assessment of their natural and historical resources*. San Juan, PR: Puerto Rico Environmental Quality Board. 2: N1-N37.
- Wadsworth, F.H. and G.H. Englerth. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. *Caribbean Forester*. 20: 38-51.
- Wege, D.C. and A.J. Long. 1995. *Key areas for threatened birds in the Neotropics*. Birdlife Conservation Series, No. 5. Washington, DC: Birdlife International, Smithsonian Institution Press. 311 p.

- Wegrzyn, M.J., A.E. Soto, and J.A. Perez. 1984. Sinkhole development in north-central Puerto Rico. Pages 137-142 in Proceedings of the first multidisciplinary conference on sinkholes. Orlando, FL.
- Wetmore, A. 1916. *Birds of Puerto Rico*. Washington, DC: U.S. Department of Agriculture. Bulletin. 326. 59 p.
- Wetmore, A. 1920. *Five New Species of Bird from Cave Deposits in Porto Rico*. Proceedings Biological Society of Washington. 33: 77-78.
- Wetmore, A. 1922. Bird remains from the caves of Porto Rico. *Bulletin American Museum of Natural History*. 46: 297-333.
- Wetmore, A. 1927. The birds of Puerto Rico and the Virgin Islands. Scientific Survey of Puerto Rico and the Virgin Islands. New York, NY: New York Academy of Sciences. Vol. IX: 322-323.
- White, W.W. 1988. *Geomorphology and Hydrology of Karst Terrains*. New York, NY: Oxford University Press. 464 p.
- Wicks, C.M. and J.W. Troester. 1998. Ground water geochemistry of Isla de Mona, Puerto Rico. *Journal of Cave and Karst Studies*. 60(2): 107-114.
- Wiewand, T.A. 1973. Mona amphibians, reptiles, and mammals. In Mona and Monito Islands: an assessment of their natural and historical resources. San Juan, PR: Puerto Rico Environmental Quality Board. 2: L1-L13.
- Williams, E.E. and K.F. Koopman. 1951. A new fossil rodent from Puerto Rico. *American Museum of Natural History Novitates*. 1515: 1-9.
- Wolcott, G.N. 1948. The insects of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*. 32(1-4).
- Woodbury, R.O. 1973. The vegetation of Mona Island. In Mona and Monito Islands: an assessment of their natural and historical resources. San Juan, PR: Puerto Rico Environmental Quality Board. 2: G1-G2.
- Zack, A.L. and A. Class Cacho. 1984. *Restoration of Freshwater in the Caño Tiburones area, Puerto Rico*. U.S. Geological Survey Water Resources Investigations Report 83-4071. San Juan, PR. 33 p + map.
- Zack, A., T. Rodríguez Alonzo, and A. Roman Más. 1986. Puerto Rico. Ground-water quality. In National water summary 1986. U.S. Geological Survey Water-Supply Paper 2325. Washington, DC. 437-442 p.
- Zans, V.A. 1959. Review, bauxites, their mineralogy and genesis. *Economic Geology* 54: 957-965.

Terminology

The geologic definitions have been taken mainly from Monroe (1976). Consult Field (1999) for a comprehensive lexicon of cave, karst, and karst hydrology terminology.

allochthonous: Said of material originating from a different locality than the one in which it has been deposited.

aggressive water: Water having the ability to dissolve rocks. In the context of limestone and dolomite, this term refers especially to water containing dissolved carbon dioxide.

anadromous: Aquatic organisms that migrate up a river or stream from an ocean or lake to spawn.

beachrock: A friable to indurated rock consisting of sand grains of various minerals cemented by calcium carbonate; naturally cemented beach sand.

bicarbonate: A salt containing the radical HCO_3^- , such as $\text{Ca}(\text{HCO}_3)_2$.

blind valley: A valley that ends suddenly downstream at an upward slope or rock face; any stream in the valley that disappears underground in swallow holes or in a cave.

bogaz: A solution-enlarged joint 2 to 4 m wide and extending linearly for some tens of meters.

caliche: Mantle of chalk and chalky limestone of secondary origin.

casehardening: In the context of karst terminology, the induration of the surface of limestone by solution and reprecipitation of calcium carbonate.

cathadromous: Aquatic organisms that migrate down a river or stream to spawn in a lake or ocean.

cave breakdown: (a) Enlargement of parts of cave system by falling rock masses from walls and ceiling. (b) Rock that has collapsed from the walls and ceiling of a cave.

cave system: An underground network of connected cavities.

clastic: Pertaining to a rock or sediment composed principally of broken fragments that are derived from pre-existing rocks or minerals and that have been transported some distance from their place or origin.

cliffed cone karst: Cone karst in which a vertically walled tower surmounts each cone.

cliff-foot cave: A cave formed at the foot of a cliff by solution by standing water in a lake or a swamp; cliff-foot caves are common at sea level or former stillstands of sea level. Commonly called *Fussöhhl*.

closed depression: A general term for any enclosed topographic basin having no external drainage, regardless of origin or size.

cockpit: (a) Any closed depression having steep sides. (b) More exactly, the irregularly shaped depressions surrounding conical hills in cone karst.

collapsed doline, collapsed sink: A closed depression formed by the collapse of the roof of a cave.

condensation corrosion: Where water condensing onto cave walls in soluble rock is undersaturated with respect to the mineral—calcite, dolomite, gypsum, etc.—the potential exists for dissolution to occur.

cone karst: A type of karst topography, common in the tropics, characterized by many steep-sided cone-shaped hills surrounded by more or less star-shaped depressions; equivalent to **Kegelkarst** or **lapiés**.

congeners: Of the same genus.

corridor: Open or closed valley, commonly straight, cut in soluble rock, having steep or overhanging sidewalls. Mostly located on joints or zones of weakness.

cuesta: A hill or ridge with a gentle slope on one side and a steep slope on the other; the gentle slope generally conforms with the dip of resistant beds that form it, and the steep slope or scarp is formed by the outcrop of the resistant strata.

cuesta karst: A type of karst formed on a *cuesta*, characterized by a steep slope or scarp at one side of an area and sinks and towers on the gentle slope.

detritivores: Organisms that feed on waste, such as guano, or dead organic matter, such as wood and leaves.

diagenesis:

Postdepositional physical and chemical changes in sediments.

doline: A simple closed karst depression with subterranean drainage, having a shape like a dish, a funnel, or a cauldron. Its diameter normally exceeds its depth. Dolines may have asymmetric longitudinal or cross sections. They are subdivided according to their shapes or supposed origin.

doline karst: A type of karst topography characterized mainly by dolines.

dome pit: A vertical overhead cavity in a cave, generally with an arched ceiling and underlain by a vertical shaft.

drip line: A line at the entrance to a cave that is directly below the top of the entrance.

dripstone: Hanging or standing concretion of calcium carbonate formed by dripping water; collective term for such features as stalactites, stalagmites, columns, drapery, and so forth.

dry valley: A valley that at present lacks a surface stream or river because of underground drainage.

eccentric: European term for a speleothem having an abnormal shape; in the United States eccentrics are generally called **helictites**.

emergence: Karst springs generally flowing with a large quantity of water. These springs are classified, where possible, into exurgences and **resurgences**.

estuary: A place in the coastal zone where seawater and freshwater mix.

exceedence probability: A higher stream flow or discharge than measured at a percent of the time at a particular location. For example, if a river or stream reach experiences a flow or discharge of 1 m³/s 99 percent of the time, the 1 percent exceed probability of flow would have to be > than 1 m³/s.

exurgence: An emergence with no known surface headwaters.

guano: A phosphorus-rich fertilizer product of bat and/or bird dung.

haystack hill: Mogote.

helictite: A curved or angular twig-like projection from the side or bottom of a stalactite.

herbivores: An organism that obtains energy by feeding on primary producers, usually green plants.

herpetofauna: Amphibian and reptile species within a given area.

hydraulic conductivity: The response of the aquifer to hydraulic gradients. It is the rate of water flow through a 1-m² section of aquifer measured in m³/day under a gradient of 1 m per m—units are canceled and results are reported in m/d.

hydraulic gradient: A measure of the slope of a water surface between two points along a stream channel or aquifer flow.

hydrograph: A plot of the stage—water level—of a river or stream over time.

hydroperiod: Describes the depth, length, and frequency of inundation in a wetland or water body.

impermeable confining bed: A nearly impervious stratum above or below an aquifer; formerly called aquaclude.

impounded karst: A karstified body of limestone of limited area completely surrounded by rocks of low permeability. A term proposed by Jennings (1971) for the French karst barré.

importance value: An index of a species importance in a plant community. It includes the relative density, relative frequency and relative basal area of the species. Values range from 0 to 300 or can be expressed in percent.

karren: The surface and subterranean minor solution features of the karst landscape, consisting of channels, furrows, or basins dissolved on surfaces of limestone.

karst, karst landscape: A terrain in which subterranean drainage follows cavities in readily soluble rocks (karstifiable rocks) and in which characteristic surface and underground features appear (karst phenomena). Readily soluble rocks are chiefly limestone, but include dolomite, other carbonate rocks, gypsum, salt, and so forth.

karst denudation: The removal of carbonate rocks by solution. The term is generally used in determining the rate of lowering of the surface by solution.

karstifiable rocks: Collective term for all those rocks in which, owing to their solubility in water, karst phenomena can develop.

karstification: The process of forming a type of terrain in soluble rocks with surface and subterranean phenomena that are the result of solution.

karstify: To form karst phenomena by solution. karst spring: Any overflow or point of escape of karst water to the surface or into a cave.

karst type: A karst landscape whose surface is characterized by the occurrence of a single dominant karst feature or a group of features. The names of the types of karst depend on dominant geographical, geological, hydrological, climatic, and genetic aspects. Examples are tropical karst, and tower karst.

kegelkarst: German term for cone karst. lapiés: French term for karren; commonly also used in English-speaking areas.

life form: The characteristic form or appearance of a species at maturity, e.g., tree, herb, worm, fish, etc.

macrophyll: Leaves with surface area >164,025 mm².

mesic: Of intermediate moisture content. Moist habitat.

mesophyll: Leaves with surface area between 18,225 mm² and 164,025 mm².

microphyll: Leaves with surface area from 2,025 mm² to 18,225 mm².

mogote: A steep-sided hill of limestone generally surrounded by nearly flat alluviated plains; karst inselberg. See **tower karst**.

nanophyll: Leaves with surface area from 225 mm² to 2,025 mm².

natural arch: A rock arch or very short **natural tunnel**.

natural bridge: A rock bridge spanning a ravine and not yet eroded away.

natural tunnel: A nearly horizontal cave open at both ends, generally fairly straight in direction and fairly uniform in cross section.

pepino: Name used by Hill (1899) and Hubbard (1923) for mogote.

phanerozoic: Designating or of a geologic eon that includes the Paleozoic, Mesozoic, and Cenozoic eras.

physiognomy: The appearance of vegetation as determined by **life forms** and the plant species dominance.

piper diagrams: Multiple tri-lineal diagrams containing a plot of the concentration of chemicals in waters sampled along their flow pathway. The diagram shows trends in the data.

polje: Extensive depression in karst terrain closed on all sides, having a flat bottom and steep walls. In many places the walls form a sharp angle with the floor. There is no outflowing surface stream. A polje may be completely dry, have a surface stream originating and ending within it, or be inundated all the year round or temporarily.

potentiometric surface:

Water level of aquifers.

resurgence: Reemergence of a stream that has earlier sunk underground; the term is also commonly but incorrectly used for any emergence.

rillenkarren: Shallow channels eroded by solution in limestone, separated by sharp ridges 2-3 cm apart.

rinnenkarren: Flat-bottomed grooves several centimeters apart separated by sharp ridges.

river cave: A cave in which a stream flows. The stream may be perennial or intermittent.

rock shelter: A natural shallow cave, generally under an overhanging ledge and having a more or less flat bottom.

salinization: The intrusion of seawater into the aquifer.

sclerophyll: A tough or leathery, usually evergreen, leaf adapted to resist water loss.

sclerophyllous: Vegetation with leaves possessing sclerophylls.

shaft: A vertical cave on the surface or a vertical passage in a cave.

shelter cave: A small cave in which the maximum horizontal extension seldom exceeds the width of its mouth.

sink, sinkhole: Term used generally for closed depressions, especially referring to dolines, vertical caves, and swallow holes.

sinter: Calcareous concretionary material, generally crystalline, deposited from flowing water both on the surface and in caves.

siphon: Place where the ceiling of a cave dips beneath either quiet or running water; this immersion separates parts of the cave which otherwise belong together.

solution: The change from a solid or gaseous state to a liquid state by combination with a liquid. In the scientific study of karst phenomena, the erosion of **karstifiable** rocks by chemical means with the aid of acids, especially carbon dioxide in water.

solution pan: Shallow solution basin formed on bare limestone, generally characterized by flat bottom and overhanging sides. Synonyms: Kamenitza, Opferkessel, panhole, and tinajita.

species dominance: Refers to the percentage of a stand's basal area accounted by a tree species. Species with high dominance have the largest fraction of the basal area.

speleologist: A scientist engaged in the study and exploration of caves, their environment, and their biota.

speleothem: A secondary mineral deposit formed in caves, such as stalactite or stalagmite.

spitzkarren: Vertical spear-like or steeple-like spikes of limestone left by solution; from a few centimeters to more than 1 m long.

stalactite: A cylindrical or conical deposit of minerals, generally calcite, formed by dripping water, and hanging from the roof of a cave or at the bottom of a cliff. Most stalactites have a hollow tube at the center.

stalagmite: A deposit of mineral matter, commonly calcite, rising from the floor of a cave, formed by precipitation of minerals from solutions dropping from above.

stream sink: Point at which a surface stream sinks into the ground; swallow hole.

struga: A corridor or trench formed by solution along a bedding plane in steeply inclined strata of limestone.

subsidence: Gradual sinking or settling to a lower level, as the slow descent of the roof of a cave or of the surface of the ground above a cavity.

swallow hole: The place where a surface stream disappears underground; a stream sink.

sympatric: Refers to the origin or area of occupation of two or more closely related species in the same geographic area.

thalweg: A line of maximum depth of stream cross-section.

tower: A steep-sided hill in a karst terrain.

tower karst: General term for a karst terrain dominated by steep-sided hills, such as cone karst and mogote karst.

transmissivity of water by an aquifer: The volume of water that flows per day through a section of the aquifer (the hydraulic conductivity) multiplied by its thickness— $[(m^3/d)/m^2]m$; units are canceled and the results reported in m^2/d .

travertine: Limestone precipitated from a flowing stream, generally more tightly cemented and stronger than calcareous tufa.

troglobitic: or troglobite. An animal living permanently underground in the dark zone of caves and only accidentally leaving it. A creature that is fully adapted to life in total darkness and can only complete its life cycle underground.

troglophilic: or troglophile. An animal that enters beyond the daylight zone of a cave intentionally and habitually spends part of its life in underground environments, for example, bats.

uvala: A large, dish-shaped or elongate karst depression having an uneven bottom, commonly containing scattered dolines.

vertical cave: A natural cavity that is vertical, or nearly so, on the surface or in a cave; in which the depth exceeds the width. Also known as a shaft, natural well, a pit, or pothole.

wilderness: Uncultivated, uninhabited area where natural conditions predominate over anthropogenic ones.

xeric. Dry habitat.

zanjón: A solutional trench in limestone, generally ranging from a few centimeters to several meters in width, from about 1 to 4 m deep, and from a few tens to more than a thousand meters long. Puerto Rican term for corridor.

zanjón karst: A karst terrain dominated by zanjones.

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