Caribbean Islands

The thousands of islands and cays composing the Greater and Lesser Antilles are among the most biologically interesting areas of the world. Centrally located in the West Indies, Puerto Rico and the Virgin Islands are in the eastern extreme of the Greater Antilles at 18° north latitude, about halfway between the southern tip of Florida to the north and the Caribbean coast of Venezuela to the south (Fig. 1). Although Puerto Rico and the Virgin Islands are in the tropics (south of the Tropic of Cancer), the seas around the islands keep them cooler than tropical mainland Central America. Because the mean annual temperature of the region at sea level is lower than 24°C, the lower limit of the tropical region, these islands are actually classed as subtropical (Ewel and Whitmore 1973).

Columbus visited Puerto Rico on his second voyage in 1493; the island remained a Spanish colony until it passed to the United States after the Spanish–American War of 1898. The island has been in a commonwealth relationship with the United States since 1952. The Virgin Islands have been governed by several countries, including France and Denmark. After the United States purchased the islands of St. John, St. Thomas, and St. Croix from Denmark in 1917, they became an unincorporated territory of the United States. The remainder of the Virgin Islands are possessions of Great Britain.

The many islands that make up the Virgin Islands and Puerto Rico are separated by water today, although at the time of maximum lowering of the seas during the ice ages, Puerto Rico and most of the Virgin Islands, including St. John, St. Thomas, and the British Virgin Islands, were one piece of land called the Puerto Rican Bank (Pregill 1981). The islands of Mona (Puerto Rico) and St. Croix (U.S. Virgin Islands), though, were never connected to the Puerto Rican Bank because they were separated by channels of deep water. At the end of the last Ice Age (about 8,000 years ago) and after sea levels rose, the Puerto Rican Bank fragmented and separated into Puerto Rico and the Virgin Islands. Because the small islands were connected with most other land masses in the Puerto Rican Bank until fairly recently in evolutionary terms (Pregill 1981), none of them have more than a few unique species. In contrast, Mona Island and St. Croix have higher numbers of endemic animals and plants because these islands have been isolated from Puerto Rico for a longer time and may never have been connected to other islands of the Puerto Rican Bank.

General Description of Puerto Rico

The main island of Puerto Rico is roughly rectangular in shape, 178 kilometers long by 58 kilometers wide, with an area of 8,802 square kilometers. The three principal geographic regions of Puerto Rico are the mountains and foothills of the Cordillera Range (highest elevation 1,353 meters), which transects the island from east to west; a discontinuous fringe of mostly flat Coastal Plain; and rugged limestone or karst regions occurring in the north-central and northwestern part of the island.

The Commonwealth of Puerto Rico consists of the main island and several satellite islands, including Mona Island (5,517 hectares) and its satellite, Monito (15 hectares); Desecheo Island (122 hectares); Caja de Muerto (202 hectares); Vieques Island (13,606 hectares); and the Culebra archipelago (Culebra Island, the main island, is 2,696 hectares; Fig. 1). The Cordillera de Fajardo stretches from eastern Puerto Rico toward

Courtesy V. Vincente, National Oceanic and Atmospheric Administration

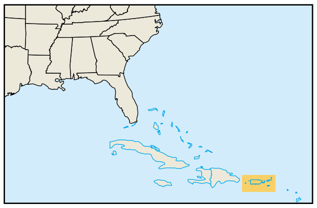

Fig. 1. Puerto Rico and the U.S. Virgin Islands.

Culebra and Vieques islands and consists of many small cays (islets). Numerous other small cays lie offshore of Puerto Rico.

Average annual rainfall varies widely in the different areas and indicates the range of local climates and associated plant communities. Southwestern Puerto Rico is the driest region and receives about 75 centimeters of rain each year, whereas more than 700 centimeters fall annually in the eastern Sierra de Luquillo.

General Description of the U.S. Virgin Islands

Although the U.S. Virgin Islands are on the same submarine bank as Puerto Rico, they are relatively low and have little rainfall compared with Puerto Rico. The fewer numbers of life forms in the Virgin Islands are the result of the smaller size, the lower relief, and the restricted variety of habitats of these islands. Annual rainfall averages about 140 centimeters, with wetlands expanding and contracting considerably depending on the amount and frequency of rain. Animals and plants that live in these wetlands experience population changes related to the amount of rainfall.

St. Croix is physically similar to the other Virgin Islands but is separated from them by a sea passage more than 3,600 meters deep, whereas the other islands are separated from each other by relatively narrow passages only a few meters deep. Aside from the main U.S. Virgin Islands, 54 small islands flank St. Thomas, St. Croix, and St. John. These cays are particularly important for native reptile species and nesting seabird colonies (Tolson 1988; Dammann and Nellis 1992).

St. Croix is the largest (34 kilometers long by 9.6 kilometers wide; 219 square kilometers) and most southern of the U.S. Virgin Islands; it is about 64 kilometers south of St. Thomas and St. John. The highest point on the island is Mount Eagle, with an elevation of 355 meters. As a consequence of this relatively low elevation and the forest clearing that has occurred on St. Croix, the area is much drier than most of the Greater Antilles, averaging only 102 centimeters of rain in the west and about 76 centimeters in the east. The average mid-island temperature is 26°C, with a variation of only 3°C to 5°C between the warmest and coolest months.

St. Thomas is about 19 kilometers by 5 kilometers (90.3 square kilometers), with a maximum elevation of 477 meters. Although little agricultural activity has occurred on St. Thomas in the recent past, it does suffer from high urban and tourist developmental pressure.

St. John is about 13 kilometers long, with an area of 53 square kilometers, and a maximum elevation of 392 meters. This island has a relatively small human population compared with St. Thomas and St. Croix.

Status of Ecosystems

Terrestrial Ecosystems

Virgin Forests

Recent environmental change in the West Indies has been dramatic. In contrast to the warm and moist climate of the region today, dry, cool climates prevailed 15,000–20,000 years ago, and savannas and other ecosystems adapted to this climate were probably widespread (Pregill 1981; Olson and Hilgartner 1982). Plants and animals of the islands' lowlands and lower montane areas were typical of a dry, savannalike habitat until about 13,000 years ago, when a shift to the current moister conditions occurred. As a result, the animal and plant communities gradually evolved toward their present composition (Pregill 1981).

The environmental shifts resulting from human activities have been just as dramatic as these earlier climatic changes (Garcia-Montiel and Scatena 1994). A human population that is too large for its supporting resources and a broad array of associated environmental problems have greatly changed the ecosystems and native plants and animals of Puerto Rico and the Virgin Islands.

Several kinds of natural processes are important in shaping the environments of islands, including earthquakes, landslides, fires, and hurricanes (Guariguata 1990; Larsen and Torres-Sanchez 1990; Reilly et al. 1990; Scatena and Larsen 1991). Puerto Rico and the Virgin Islands were covered with luxuriant forests that consisted of more than 500 tree species when Columbus arrived (Little and Wadsworth 1964). Extensive cutting and modification of natural forests, widespread agriculture, and introduction of many nonindigenous plants from other parts of the tropics have fragmented the original plant associations into remnants of the once-extensive tracts of forest.

Typical mountain forests are confined to Puerto Rico. The most magnificent of these forests probably occurred from 150 meters to

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650 meters in elevation in the eastern mountains, known as the Sierra de Luquillo, and up to 920 meters in the central mountains, the Cordillera Central. At this forest's maximum development, its trees reached 33 meters in height, with some trees 2.5 meters in diameter. Three forests of distinctive size and composition grew together, each forming a separate plant layer. Probably about 170 tree species grew throughout this forest.

Life Zones

Biologists divide Puerto Rico and the Virgin Islands into six regions, each characterized by an association of certain animals and plants. These life zones range from dry forest to rain forest in the Coastal Plain, and wet forest and rain forest in the mountain areas (Ewel and Whitmore 1973; Fig. 2). Subtropical lower montane rain forest occupies the smallest area, accounting for only 0.1% of the islands, whereas subtropical moist forest is the most extensive life zone, covering about 60% of the area.

Subtropical Dry Forest

The subtropical dry forest is the driest life zone of the six (mean annual rainfall, 60–110 centimeters), and it covers substantial areas in the Virgin Islands, Vieques Island and southwestern Puerto Rico, and all of Mona, Culebra, and Desecheo islands. The vegetation of the subtropical dry forest zone tends to form a complete ground cover, and on most soils the trees are almost entirely leafless during the dry season, even though vegetation in the Virgin Islands is mostly evergreen. Many of the tree species common on the north side of Puerto Rico were excluded by the harsher climate on the island's dry, southern side. Instead of the more common trees found on the island's north side, this life zone supports a few other species adapted to such arid conditions. Palms are usually absent. Plants often have small, succulent or leathery leaves, and plants with thorns and spines are common. Trees are usually less than 15 meters tall and their crowns are broad, spreading, and flattened, with sparse foliage. Fire is common on the better soils where the successional vegetation includes many grasses, and large amounts of organic debris accumulate on the soil surface during the dry season (generally December–April). Agriculture is marginal at best and is only possible with irrigation. Pasturing of livestock (mainly cattle and goats) has been extensive. In the past, charcoal manufacturing and nonindigenous livestock took their toll on the native dry forests. Growth of cities has proceeded rapidly but is limited primarily by water supplies.

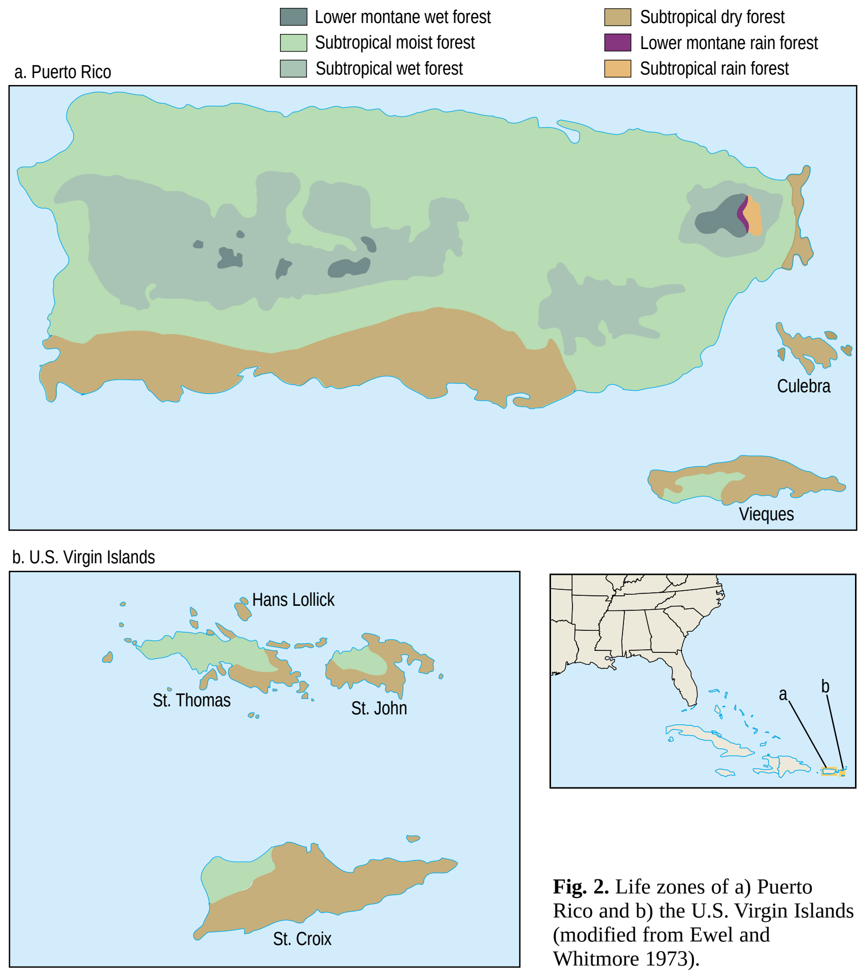

Fig. 2. Life zones of a) Puerto Rico and b) the U.S. Virgin Islands (modified from Ewel and Whitmore 1973).

The dry coastal forests of Puerto Rico support many species of animals and plants. Of 700 plant species (including 246 tree species) in the Guánica Forest, informal evaluations suggest that 45 (6.4%) are considered rare and endangered (Hill 1975; Woodbury et al. 1975; Lugo 1983; Fig. 3). The trees of the dry coastal forest include gumbo limbo, mesquite, oxhorn bucida, common lignumvitae, red manjack, and indio (see Table 1 for a more complete list). Mangroves line the coasts of this zone, but the trees do not attain the height of mangrove species in the subtropical moist forest zone. Forests of this life zone have more bird species than the wetter life zones (Kepler and Kepler 1970), although lizard and frog populations are comparatively larger in wetter zones (Rivero 1978).

Excessive soil drainage accentuates the dryness in the inland limestone region of the southern coast of Puerto Rico, as it does on the northern coast. These extreme conditions exclude some kinds of vegetation, and hardier species take their places. The trees of the dry limestone forest include corcho bobo, guayacán blanco, willow bustic, and alelí (see Table 1 for a more complete list).

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Courtesy F. J. Vilella, USGS

Fig. 3. *Epidendrum krugii*, an endemic orchid of dry limestone forests of Puerto Rico at Guánica Biosphere Reserve. Although limestone forests are not as well known by the general public as rain forests, tropical dry forests are characterized by high species richness and are hot spots of biodiversity.

Subtropical Moist Forest

The subtropical moist forest zone is characterized by a mean annual rainfall of 100–220 centimeters and a mean temperature of 18°C–24°C. Most of the subtropical moist forest zone has been cleared of forest because the region's climatic conditions and soils are generally favorable for agriculture. Only small, scattered pieces of the original forest remain. Historically, the species composition of vegetation varied with locality but included a mixture of many species, with at least 200 kinds of trees. On the northern Coastal Plain of Puerto Rico, trees grew to 35 meters or more in height. In contrast, on the southern Coastal Plain and in the moist limestone region of Puerto Rico and the Virgin Islands the forest trees grew only 13 to 20 meters tall. Characteristic trees in the moist forest of the coasts include the endemic Puerto Rican royal palm (found only in Puerto Rico), ausubo, false mastic, roble blanco, box-briar, and white prickle (Table 1). Many of the characteristic trees, shrubs, and lianas are leafless during the dry season. Epiphytes are common. Grasses, in both natural and improved pastures, dominate the landscape today in this Puerto Rican zone. Mangroves, which line the coasts in the subtropical moist forest zone, are under heavy developmental pressure (Lugo 1988; U.S. Department of the Interior 1994). In addition, human activities have extensively altered this zone's coastal freshwater swamps, which may be Puerto Rico's most endangered ecosystem (Cintrón 1983; U.S. Department of the Interior 1994).

Inland from the coastal forest is the moist forest of the limestone hills. This forest is similar to the subtropical moist forest along the Coastal Plain and includes many of the same species. Drier soils on the well-drained limestone hills and the greater humidity in protected areas among the hills caused most of the chief differences between the inland moist forests and the Coastal Plain forests, especially in the southern part of Puerto Rico close to the central mountains. Common trees in this forest include palma de lluvia, uvilla, cupey, and white prickle (see Table 1 for a more complete list).

Table 1. Characteristic plants of life zones in Puerto Rico and the U.S. Virgin Islands (from Ewel and Whitmore 1973).

Life zone	Characteristic plants
Subtropical dry forest	Alelí, bitter-ash, calambreña, common lignumvitae, corcho bobo, Royen's tree cactus, Florida fiddlewood, guayacán blanco, gumbo limbo, indio, leadtree, mesquite, oxhorn bucida, pricklypear, red manjack, sarrasuela, silk cotton tree, Spanish lime, sweet acacia, tachuelo, tamarind, willow bustic
Subtropical moist forest	Ausubo, box-briar, common guava, cupey, false mastic, guaba, guama, gumbo limbo, matchwood, mountain immortelle, palma de lluvia, palo de pollo, Puerto Rico acrocomia, Puerto Rican royal palm, roble blanco, shortleaf fig, Spanish cedar, trumpet tree, tulipán africano, uvilla, West Indian locust, white prickle
Subtropical wet forest	Ausubo, balsa, giant tree-fern, higuillo, Honduras mahogany, matchwood, motillo, sierra palm, tabonuco, teak, trumpet tree
Subtropical rain forest	Ausubo, giant tree-fern, motillo, sierra palm, spiny tree-fern, tabonuco
Subtropical lower montane wet forest	Caimitillo, caimitillo verde, guayabota de sierra, jusillo, nemocá, oreganillo, palo colorado, roble de sierra
Subtropical lower montane rain forest	Similar to lower montane wet forest, but with greater abundance of epiphytes

Subtropical Wet Forest

The subtropical wet forest zone occupies most of the higher mountains of Puerto Rico but is not found in the Virgin Islands or Puerto Rico's outlying islands. Rainfall is high, averaging 200–400 centimeters each year, and accounts for a rich flora with more than 150 species of trees. Forests are diverse, and the second-growth trees grow rapidly. Epiphytic ferns, bromeliads (air plants), and orchids are common. Remnants of mature forest remain in three protected areas. The plant community of this zone is sometimes called the *tabonuco* type after the dominant tree, which is also known as candlewood. Other prominent trees include the common tree-fern, motillo, and ausubo (Table 1). The natural forest forms a closed canopy at about 20 meters. Mahogany and teak have been successfully established in plantations; the International Institute of Tropical Forestry has carried out extensive research on the tabonuco forest type and on the plantations (Mosquera and Feheley 1984).

Much of this life zone in Puerto Rico is covered by second-growth vegetation as a result of farm failures and abandonment. Formerly, much of this zone in western Puerto Rico was converted to shade coffee plantations, but the coffee crop, as is typical of most agriculture in Puerto Rico, has greatly declined since about 1950 (Birdsey and Weaver 1987). As in all other zones, land use has shifted toward grazing livestock. On abandoned lands, higuillo, yagrumo macho, yagrumo hembra, and balsa are early successional species. Sierra palm is common in the wetter parts of the zone.

Courtesy J. Wiley, USGS

Fig. 4. Upper Luquillo Forest, Puerto Rico.

Subtropical Rain Forest

The subtropical rain forest zone occupies only 13.2 square kilometers and is restricted to the windward faces of the Sierra de Luquillo in Puerto Rico (Fig. 4). It is the wettest of the sea-level belt of subtropical life zones, with an annual rainfall of about 380 centimeters. Plant species are essentially the same as those found in the surrounding subtropical wet forest, with the main features the high frequency of sierra palms and a superabundance of epiphytes. The spiny tree-fern is more abundant here than in the subtropical wet forest. Much of this zone has remained intact, originally under the protection of the Spanish Crown lands, then within the federally protected Caribbean National Forest.

Subtropical Lower Montane Wet Forest

Of the two lower montane life zones in Puerto Rico, the subtropical one is by far the most extensive, occurring in both the eastern and central parts of the island from about 700 meters to the summits of most mountains above 1,000 meters. Annual rainfall ranges from about 170 to 340 centimeters. The palo colorado, the dominant tree in the colorado forest zone, is the species that endangered Puerto Rican parrots use most often for nest sites (Fig. 5). This forest has fewer species of animals and plants than the adjacent subtropical wet forest; only about 53 tree species have been recorded (Wadsworth 1950). Other characteristic plant species include nemocá, caimitillo, and caimitillo verde (Table 1). This zone includes the elfin (dwarf) forest association and the palm brake, consisting of pure stands of sierra palm. The vegetation of this zone has been extensively altered from cutting and agriculture; the best-preserved tract occurs within the Caribbean National Forest.

Subtropical Lower Montane Rain Forest

This zone occurs only on the windward slopes of the Sierra de Luquillo, just above the subtropical rain forest, and has the smallest area of any Puerto Rican life zone. Average annual rainfall is 450 centimeters, and the mean annual temperature is 18.6°C. The plants of this zone are similar to those of the lower montane wet forest but with a greater abundance of epiphytes, palms, and tree-ferns (Little and Woodbury 1976). The steep slopes and poor timber quality of the tree species in the subtropical lower montane rain forest zone have not attracted agriculture or timber interests. Because this zone is within the Caribbean National Forest, it has been protected from most human-caused disturbances.

Reforestation and the Natural Habitat of Today

Although Puerto Rico was covered with various kinds of forests when Europeans arrived in 1493, by 1912 nearly all of the island had been clear-cut for agriculture (Murphy 1916). Although considerable secondary forest cover exists today, only about 0.2% of the original forest remains. With these sweeping changes in the environment, many plants and animals declined or disappeared. Despite the near-complete ruin of natural habitat, only a few species are known to have been completely lost from the island's ecosystems. Other species, though, may have been eliminated before they were recorded by naturalists.

Nevertheless, this extreme habitat fragmentation has placed many species at great risk. Several species survive only as tiny clusters of a few individuals separated from other small groups by inhospitable expanses of unsuitable habitats. Not only are such populations at risk of extinction because of their small sizes and

Courtesy J. Colón, U.S. Fish and Wildlife Service

Fig. 5. Puerto Rican parrot perched on the entrance vine of its nesting cavity in a tabonuco tree. This is the first record of parrots nesting in this tree species since the Puerto Rican parrot project began in 1968 (see Vilella and García 1995). These trees dominate the overstory of lower elevation forests in the Sierra de Luquillo (in the subtropical lower montane rain forest zone).

their lack of genetic interchange, but they are also more susceptible to any chance natural or unnatural events such as fires, diseases, or hurricanes. Extinction could be caused by random events that often have little effect on larger, more continuous populations.

The severe tropical storms that strike these islands at fairly frequent intervals are the most powerful forces shaping the ecology of the West Indies. In the past, such fierce storms had only moderate, and usually short-lived, effects on most island ecosystems. Some of the islands' ecosystems are largely determined by these storms. For example, such storms flush the debris from mangroves, making way for aquatic communities, particularly fish nurseries. In addition, these storms open mature forest canopies, which allow succession of plants and animals (Fig. 6). However, as human activities have substantially fragmented habitats of the West Indies and reduced their size, hurricanes have posed more serious threats to the survival of organisms and communities (reviewed in Askins and Ewert 1991; Walker et al. 1991; Wiley and Wunderle 1993). For example, the Puerto Rican parrot was historically widespread and abundant throughout the main island, Culebra Island, and probably other Puerto Rican satellite islands. Even the strongest of hurricanes would have cut a damaging swath through only a relatively small part of these islands, allowing the parrot to survive. Now that the parrot is limited to the Sierra de Luquillo, though, a direct hit by a hurricane poses much more serious consequences: when such a hurricane did strike the Luquillo Forest in 1989, about half the wild parrot population was destroyed (Vilella and García 1995; Fig. 7).

Effects of Human Activities

Humans probably had little real effect on the region's forests until the colonial period. The cutting of the islands' forests, partly to harvest

Courtesy F. J. Vilella, USGS

Fig. 7. Damage by Hurricane Hugo to sierra palm forest in the Sierra de Luquillo. Puerto Rican parrots synchronize their breeding activities to coincide with the fruiting peaks of this forest palm. Sierra palm fruit was scarce during 1990, the year after the hurricane, and only one pair of wild parrots successfully fledged two young that year.

timber but more generally to clear land for farming, took place primarily in the nineteenth century. That cutting eliminated tree growth from the more fertile and accessible lands, but left small forest remnants on steep slopes, rocky mountain summits, or poor soils. Thus, the best-developed forests are gone, and the remaining forests are quite different from those seen by the early explorers. The most valuable trees, both in terms of species and size, have been removed. Few trees exceed 30 centimeters in diameter, and those that do generally have little timber value. Even within the best-preserved examples of original forest, selective harvesting of some species has altered forest structure and species composition.

In the second half of the twentieth century, Puerto Rico shifted away from an agrarian-based economy to a modern industrial and tourism-based economy (Fig. 8). Considerable areas of agricultural land, particularly the least

Courtesy F. J. Vilella, USGS

Fig. 6. View of Hurricane Hugo's damage to the Caribbean National Forest. Hurricane damage was not evenly distributed—notice the ridge on the right side of the photograph. The right side of the ridge (facing northwest) suffered severe damage, whereas the left side of the ridge (facing northeast) suffered little damage.

productive, were abandoned as people migrated away from rural areas to cities. Those abandoned croplands have subsequently reforested, either through management programs to improve watersheds or through natural succession. Today, about 38% (284,000 hectares) of Puerto Rico's surface area (9,000 square kilometers) is forested, with secondary forest and abandoned coffee plantation shade accounting for 76% of all forestland (Birdsey and Weaver 1987; Ortiz 1989; Fig. 9). Along with second-growth reforestation of abandoned agricultural lands, many nonindigenous species became established in the island. Some of these, such as teak and mahogany, were established in timber plantations, whereas others were imported as ornamentals for gardening and landscaping.

The natural plant cover in the Virgin Islands suffered the same fate as did the forests in Puerto Rico. Uplands that were originally covered with seasonal deciduous or evergreen forests were clear-cut to cultivate the land. Distribution and composition of vegetation were completely controlled by large-scale cultivation, heavy grazing by goats and sheep, and the periodic burning of "brush." St. Thomas and St. Croix still have large human populations and considerable agriculture and grazing; consequently, these islands remain extensively deforested. In contrast, St. John was gradually abandoned by people after 1848, and vegetation has again covered more than 75% of the island (Robertson 1962).

Aquatic Ecosystems

Marine Environments

Like most of the Caribbean, the islands in the Puerto Rican Bank often share the following confining physical and biological coastal scenario: a limited coastline extension, a restricted shelf dimension, a permanent temperature gradient, oligotrophic waters, and a sparsity of upwelling zones. Nonetheless, the littoral systems surrounding the islands of the Puerto Rican Bank are nuclei of biodiversity and are responsible for coastal organic production. St. Croix and Mona islands are surrounded by deep water on all sides and have comparatively narrow shelves. The shelf and its adjacent coastal fringe support several important ecosystems.

Coral Reefs

Coral reefs support small island fisheries, protect the shoreline from erosion, create or nourish sandy beaches, and represent perhaps the most valuable coastal resource of the islands in the Caribbean. Although coral reefs generally have low biomass (280 grams of organic carbon per square meter per year), they are highly productive (2,900–4,200 grams of organic carbon per square meter per year) and support a wide diversity of taxa, many of commercial or recreational importance (Goenaga and Boulon 1991; Bohnsack 1992; Fig. 10).

These reefs provide homes for most of the islands' fishes and marine invertebrates. Patch reefs are scattered all around the islands but are most abundant behind major reef formations. The best-formed reefs are in the shallow waters surrounding the drier islands or adjacent to those parts of Puerto Rico where few rivers deposit sediments on coral formations.

Coral reefs are subjected to many natural disturbances. Hurricanes frequently and intensely weaken coral reefs in the Caribbean through the physical destruction caused by storm wave activity and through sediment runoff from the surrounding coastal areas. However, random events such as storms may

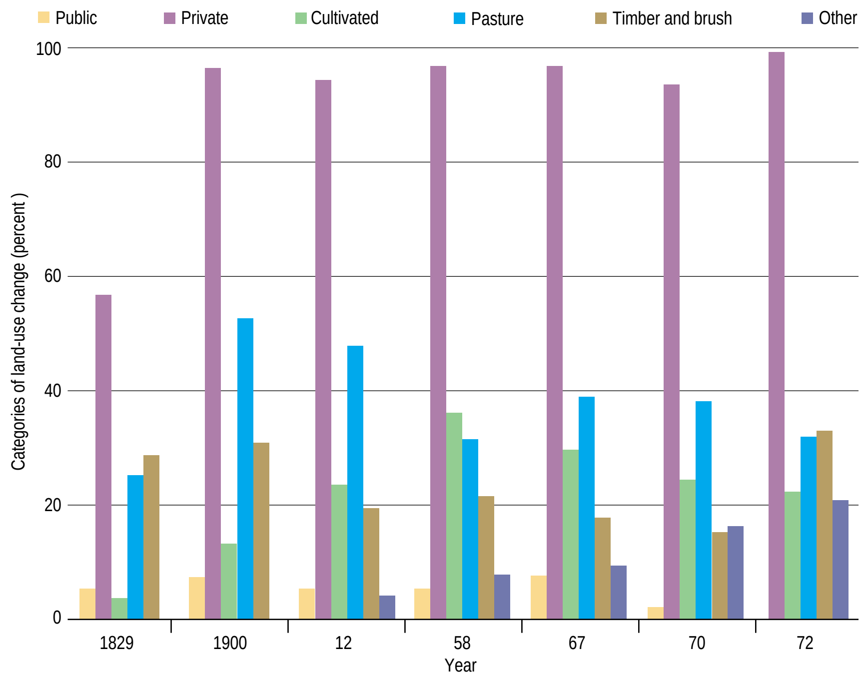


Fig. 8. Historical land-use changes (in percentage of area) in Puerto Rico, 1829–1972 (modified from Lugo 1983).

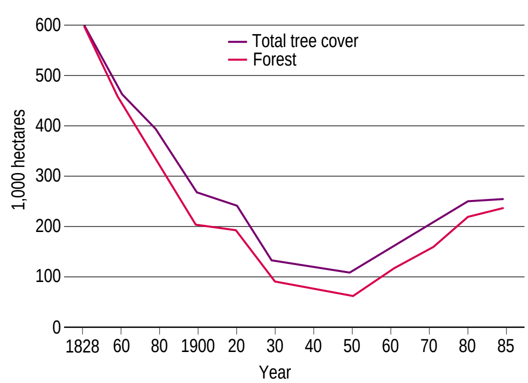
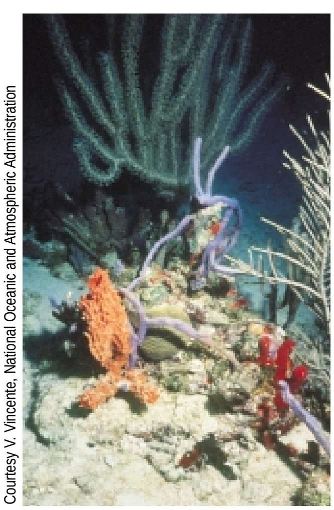


Fig. 9. Area with tree cover in Puerto Rico, 1828–1985. Forest does not include nonstocked forestland (modified from Birdsey and Weaver 1987).



Courtesy V. Vincente, National Oceanic and Atmospheric Administration

Fig. 10. Coral reef community featuring gorgonian corals and calcareous and tubular sponges.

Coral Reefs of the U.S. Virgin Islands

Most of the coral reefs around St. Thomas, St. John, and St. Croix are shallow fringing reefs that parallel the islands' coastlines. Many of them are true coral reefs, established on a framework of coral skeletons deposited over thousands of years. Elsewhere, coral reef organisms grow on submerged boulders and rock ridges near shore. Submerged bank reefs are also found in deeper water, some with spur and groove formations. Reef-building organisms grow on the walls of Salt River Canyon, a drowned river valley on the north shore of St. Croix. Extensive barrier reefs with well-defined lagoons do not occur around St. John or St. Thomas, but such reefs are found around Buck Island Reef National Monument north of St. Croix and along the island's southeastern shore. In some locations, fringing reefs extend out from rocky headlands at bay entrances, cutting off back-reef areas and eventually leading to the formation of salt ponds. More than 40 species of scleractinian corals have been found on U.S. Virgin Islands reefs (Beets and Lewand 1986; C. Rogers, U.S. Geological Survey, Virgin Islands National Park, St. John, personal observation). The total coverage of living coral on U.S. Virgin Islands reefs is typically less than 40%, although some reef zones have higher coverage (Beets et al. 1986).

Coral reefs in the U.S. Virgin Islands face the same pressures as reefs elsewhere in the Caribbean (Rogers 1985; Beets et al. 1986). Hurricanes and other major storms, higher than normal water temperatures, and coral diseases, together with destruction caused by boat anchors and boat groundings, careless land use, dredging, pollution, and overfishing, cause reef deterioration. Within the last 15 to 20 years, the amount of live coral cover has declined, while the abundance of algae has increased (Fig. 1). The increase in algae probably reflects both the increase in substrate available after the death of coral and the inability of the herbivorous fish and sea urchins to keep the algal growth in check.

Long-term monitoring of reefs around St. John began in 1989 with the establishment of five permanent transects at depths of 12 to 14 meters in Lameshur Bay off the island's southern coast (Fig. 2). Similar transects were established off Buck Island at the same time. In 1991 other long-term sites were established around St. John in Newfound and Francis bays. These sites have provided detailed information about the effects of storms and the recovery of reefs from storms and anchor damage (Rogers et al. 1991; Rogers 1992). Maps of the major benthic habitats around St. John and early studies at Buck Island provide valuable baseline information about U.S. Virgin Islands reefs (Gladfelter et al. 1977, 1979; Beets et al. 1986).

Perhaps the most conspicuous change on U.S. Virgin Islands coral reefs over the last few decades is the decline in elkhorn coral, one of the primary reef-building corals in the Caribbean (Fig. 3). Elkhorn corals often form shallow crests near the water's surface, creating physical barriers to ocean waves, thereby reducing coastal erosion. In the late 1970's, the elkhorn zone on the east end of Buck Island's barrier reef was described as perhaps the best in the Virgin Islands (Gladfelter et al. 1979). Fifteen to twenty years ago it was possible to find entire stands and impressive, isolated colonies of this species around Buck Island and St. John, but few large, live colonies can be found now. The primary culprit appears to have been white band disease, first observed in the U.S. Virgin Islands in the early 1970's

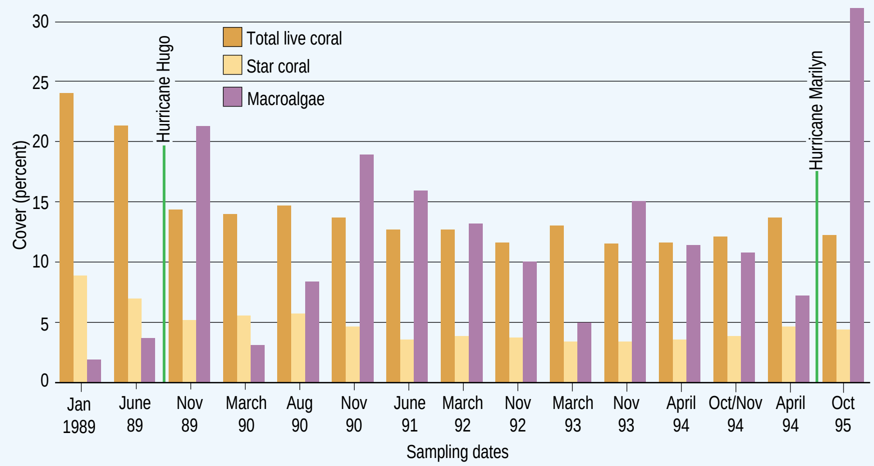


Fig. 1. Percent of cover of total live coral, star coral, and macroalgae at Yawzi Point, St. John, from January 1989 to October 1995.

Courtesy Virgin Islands National Park

Fig. 2. Coral reef in Lameshur Bay, U.S. Virgin Islands.

Fig. 3. Elkhorn coral at Virgin Islands National Park.

(Robinson 1973; Gladfelter 1982). This disease, which has yet to be correlated with pollution or any other human activity, generally kills the colonies it infects, although occasionally patches of live tissue survive.

At Buck Island, white band disease and physical destruction from Hurricane David and Tropical Storm Frederic (1979) reduced the live coverage of elkhorn coral from 85% to 5% (Rogers et al. 1982; Gladfelter 1991); in 1989 Hurricane Hugo led to even further declines (Gladfelter 1991). Numerous new colonies of elkhorn coral, which had developed from sexually produced larvae and from branch fragments, were seen at Buck Island in the summer of 1995. A few months later, Hurricanes Marilyn and Luis destroyed several of these (Z. Hillis-Starr, National Park Service, Buck Island Reef National Monument, Christiansted, U.S. Virgin Islands, personal observation).

In 1987 a study of 50 individual elkhorn coral colonies in Hawksnest Bay off the north shore of St. John indicated that only 10 remained undamaged 7 months after initial observation (Rogers et al. 1988). Heavy ground seas and damage from snorkelers and boats were probably responsible for the observed decline. The elkhorn coral population in Hawksnest Bay appeared to be recovering when it suffered damage from Hurricanes Luis and Marilyn in September 1995. Though little quantitative information exists, staghorn coral and finger coral also appear to have declined substantially around the U.S. Virgin Islands.

The U.S. Virgin Islands have been hit by 4 hurricanes and numerous tropical storms in the last 15 years. Some of the most severe damage was associated with Hurricane Hugo in 1989 (Edmunds 1991a; Hubbard et al. 1991; Rogers et al. 1991; Bythell et al. 1992). This category 4 storm flattened reefs off the south side of Buck Island, creating widespread areas of rubble. Transport of rubble and coral resulted in movement of the southern reef crest 30 meters toward the island (Hubbard et al. 1991). In contrast, little damage from Hurricane Hugo was noted off the north shore of the island.

At long-term monitoring sites around St. John and Buck Island, coral cover, initially less than 30%, dropped to 8%–18% following Hugo (Edmunds 1991a; Rogers et al. 1991; Bythell and Bythell 1992; Rogers 1992). The dominant coral species, star coral, declined about 35% in Lameshur Bay. Studies have shown that no substantial recovery in total coral cover has occurred, although coral recruitment is occurring. Decreases in the amount of living star coral are of particular concern because it is one of the major reef-building species in the Caribbean.

During Hurricane Hugo, gorgonian corals and sponges were torn apart and ripped off their bases. Many collected in sand channels and other depressions on the reefs, and piles of them washed up on the beaches. Along long-term transects in Lameshur Bay, the number of species and the size of colonies of gorgonians and sponges increased between 1991 and 1992 (Gladfelter 1993). Although there was a slight decrease in the number of sponge colonies during this time, the number of gorgonian colonies increased. These results may indicate ongoing recovery of the sponge and gorgonian communities from Hurricane Hugo.

In September 1995 two hurricanes (Luis and Marilyn) hit the U.S. Virgin Islands within a 10-day period. Reefs off the north side of Buck Island and the south side of St. John suffered severe damage. Although damage was conspicuous at Lameshur Bay, the percentage of live coral cover along the permanent study transects did not decrease, perhaps because of the uneven nature of hurricane damage or because so little coral remained to be damaged (Rogers, unpublished data). In some bays on the north shore of St. John, more physical destruction was caused by boats that had broken loose and dragged across coral colonies than by the storm itself. Large coral colonies, some perhaps more than 100 years old, were split into pieces by boat keels. At the long-term study site in Newfound Bay, little damage from Marilyn was observed; total live coral cover there has remained at about 23% for the last 6 years (Rogers, unpublished data).

Although the physical destruction from hurricanes and white band disease has produced the most drastic changes in U.S. Virgin Islands reefs, other stresses are also taking their toll. Probably the greatest potential threat to the reefs around the U.S. Virgin Islands is sedimentation associated with runoff from coastal development sites. The steepness of the islands exacerbates this problem. A theoretical study of sediment runoff indicated that reef distribution around St. John is a function of watershed size, bay exposure and bathymetry, distance from sources of land-derived sediments, and storms (Hubbard 1987). Cores taken from large coral colonies off St. John give some clues as to the sedimentation regime before, during, and after extensive clearing of vegetation for sugarcane plantations in the eighteenth and nineteenth centuries. Growth data from these cores suggest gradual declines over the last 200 years (Hubbard 1987). Limited data from cores in Hawksnest Bay indicate that upland construction in the early 1980's led to significant decreases in annual growth rates (Hubbard et al. 1987), presumably a response to increased sedimentation. Current developments of private land inside and adjacent to park boundaries, as well as construction of new roads, have increased the sediment flow into nearshore waters (Anderson 1994). U.S. Geological Survey scientists are conducting research on this issue.

Black band disease has also been reported for several species of hard corals, including star corals and brain corals, around St. John (Edmunds 1991b) and at Buck Island Reef National Monument (Bythell et al. 1992). This disease has not been conclusively linked to human activities. Edmunds (1991b) found that less than 1% of the corals in Lameshur Bay were infected. Even though the effects of black band disease are small compared with other stresses, the disease should not be ignored because it infects primary reef-building species. Like coral bleaching, which was observed in the U.S. Virgin Islands in 1987 and 1990, this disease appears to be correlated with higher seawater temperatures. If algae grow on the bare substrate that becomes available after the infected coral tissue dies, recolonization by hard corals and other reef organisms will be inhibited.

The abundance of algae on the long-term transects in Lameshur Bay has fluctuated between 2% and 32% cover, with the highest amounts occurring in the fall of each year (Rogers, unpublished data). Increases in algal biomass result from nutrient input and reductions in herbivory, but no direct correlations have been documented. In spite of some excellent early studies on herbivorous fishes in Lameshur Bay (Earle 1972), further research is needed to unravel the complex relationship among herbivorous fishes, invertebrates, and the species of algae (primarily *Dictyota*) that predominate on the reefs around St. John. Some fishes and sea urchins graze on algae and open up new space on the reef for colonization by nonalgal reef organisms. It is not clear how the decline in predatory fishes has affected these herbivores (see box on Reef Fishes).

With respect to natural resource protection, national parks are a mixed blessing. Virgin Islands National Park attracts nearly one million visitors a year, most of them arriving on cruise ships or smaller boats. A single anchor drop from a cruise ship in 1988 led to the destruction of almost 300 square meters of reef. Monitoring at this site reveals no significant recovery of hard coral 8 years later (Rogers 1993; Rogers, unpublished data). A survey of 186 boats in 1987 revealed that 32% were anchored in seagrasses and 14% in coral communities. About 40% of the anchors in coral and 58% in seagrass beds caused damage (Rogers et al. 1988). Small boats continue to run aground on reefs within Buck Island Reef National Monument and Virgin Islands National Park. The installation of mooring buoys and limits on the size of vessels allowed in park waters have resulted in less pressure on these reefs, but in some areas there is little coral left to protect.

Coral reefs are highly diverse and complex ecosystems. We have only limited understanding of the ecological processes that occur within and among reefs and associated mangrove and seagrass bed systems. Interactions among these systems include transfer of nutrients and the movements of organisms (primarily fishes). Seagrass beds and prop roots of red mangroves provide critical feeding and nursery areas for reef fishes. The degradation of reefs in the U.S. Virgin Islands is a result of a combination of stresses that sometimes act synergistically. There is no doubt that the reefs have suffered serious declines from hurricanes and white band disease. The hurricanes have scoured out large portions of the seagrass beds around St. John and, in combination with a severe drought in 1994–1995, have killed extensive mangrove areas. The full effects of the changes that have occurred on the associated reefs are impossible to quantify.

Sedimentation, overfishing, and damage from boats continue to degrade U.S. Virgin Islands reefs (see box on Reef Fishes, this chapter). On reefs off the north coast of Jamaica, similar stresses have resulted in a drastic, probably irreversible, decline in the amount of live coral cover to less than 5%, as well as increases in algal biomass of up to 90% (Hughes 1994). Only time will determine if the amount of living coral on the reefs in the U.S. Virgin Islands will drop to these levels, leading to further increases in algae. Future hurricanes, combined with human-related stresses, may tip the balance so that recovery becomes impossible.

See end of chapter for references

Author

Caroline S. Rogers
U.S. Geological Survey
Biological Resources Division
Virgin Islands National Park
P.O. Box 710
St. John, U.S. Virgin Islands 00831

also enhance local reef diversity, provided they disturb the system at an intermediate level (Connell 1978).

Humans also disturb coral reefs. Collection of corals by people and breakage of corals by boat anchoring have considerably damaged these reefs. Anchoring buoys have been installed in some of the best-preserved reef sanctuaries of Puerto Rico, including Caja de Muerto Island. Coral reefs have also been negatively affected by sedimentation caused by poor land-use practices (Loya 1976; Rogers 1977). Of even greater concern are the extensive losses of coral reefs and their dependent species worldwide, including those in Puerto Rico and Mona Island (Williams and Bunkley-Williams 1990). Marine ecologists are concerned that many reefs may not be able to survive as functional ecosystems if bioerosion rates exceed reef accretion rates (± 10 millimeters per year) for extended periods (Smith and Buddenmeier 1992). This poses particular problems for Caribbean reefs, which are more prone to bioerosion than reefs elsewhere (Highsmith 1980).

Seagrass Beds

The tropical Atlantic seagrass beds (that is, beds of species such as turtle grass and manatee grass) may have the highest primary productivity rates of all natural systems in the world. In Puerto Rico, primary production and biomass are extremely high, even under nonoptimal conditions. Under pristine conditions, seagrass primary production may exceed 10,000 grams of organic carbon per square meter per year. Any of the six Caribbean seagrass species may form isolated patches or vast meadows, depending on water quality, nature of the substrate, and geomorphology of the coast (Vicente 1992).

Seagrasses greatly modify the physical, chemical, and geological properties of coastal areas. They provide nutrients, primary energy, and habitats to sustain coastal fishery resources; create foraging grounds for endangered species; and enhance biological diversity and productivity. Seagrass beds have characteristic fish populations and sometimes serve as nurseries for young reef fishes. These meadows are also

Reef Fishes of St. John, U.S. Virgin Islands

Of the 24,618 known fish species in the world (Nelson 1994), more than 400 reef-associated or inshore-ranging pelagic species (that is, living in open seas) are found in the nearshore waters surrounding St. John, U.S. Virgin Islands (Virgin Islands National Park, unpublished data). Many species, such as the foureye-butterflyfish and the butter hamlet, depend on coral reefs for shelter from predation, as a source of food, or as a place to spawn; juvenile fishes of many species (such as great barracuda and gray snappers) also find shelter amidst red mangrove prop roots. Some species, such as the bucktooth parrotfish and fringed filefish, live their entire lives in seagrass beds, whereas other species use the seagrass beds as nursery areas (such as French grunts; Fig. 1) or for nocturnal feeding (many snappers and grunts). Even habitats dominated by gorgonians (soft corals), sand, or algae and sponges are essential for some fishes, including the scrawled filefish, which feeds on gorgonians; the spotted snake eel, which lives in sand; and the chalk bass, which lives on the algal plain.

Both natural events and human activities can directly kill fish and degrade habitats, adversely affecting the habitat-dependent species. When Hurricane Hugo swept through the Virgin Islands in September 1989, the total abundance of fishes and number of species on two St. John reefs decreased significantly for 2 to 3 months after the storm (Beets and Friedlander 1990). Blue chromis declined sharply in number; surgeonfishes were observed in significantly greater abundance, feeding on the increased amount of algae, and normally secretive squirrelfishes appeared in the open, probably because of extensive reef damage (Beets and Friedlander 1990). It is interesting to note that when Hurricanes Luis (6 September 1995) and Marilyn (15 September 1995) struck St. John, no changes in either the number of fish species or the abundance of fishes were detected (V. H. Garrison, U.S. Geological Survey, Virgin Islands National Park, St. John, unpublished data and personal observation).

In the Virgin Islands today, many human activities are damaging coral reefs (see box on Coral Reefs), seagrass beds, and mangroves. Long-term effects of these activities on the reef fish assemblages are not yet fully understood. Fishing damages habitats when anchors and traps are set on the reef and lines become entangled on the bottom, but, more importantly, fishing can directly affect the abundance, average size, and assemblage of fish species.

Since about 800 B.P., human inhabitants of the Virgin Islands have harvested a variety of reef fishes for food (Wild 1989). Fishing initially involved gleaning fish by hand in the shallows, then advanced with the development of tools and technology. Today, most fishing in the Virgin Islands is conducted by using traps (or *pots*) made of 3- to 5-centimeter wire mesh reinforced with a wooden or steel frame (Fig. 2). Traps are not selective; they harvest most reef fish species that are too large to escape through the mesh. Some species are trapped frequently whereas others are seldom caught, despite their absolute abundance. Groupers, in particular, tend to be attracted to traps, perhaps by the lure of a meal from the concentration of prey inside. Most types of fishes trapped in the Virgin Islands are eaten (Swingle et al. 1970; Olsen and McCrain 1980), putting pressure on a large number of species. Unfortunately, even the unpalatable species that escape the dinner plate and are discarded (bycatch) do not usually survive (Harper et al. 1994; Garrison, personal observation). Once the larger fish have been removed from an intensely fished area, immature fish make up a greater proportion of subsequent catches. *Recruitment overfishing* can result, which could seriously compromise the future abundance of reef species.

The rapid growth of coastal human populations has fueled the increased demand for marine resources worldwide (Wilkinson and Buddemeier 1994); St. John is no exception. The 1929–1930 Virgin Islands census counted 765 people living on the 52-square kilometer island of St. John, out of a total of 22,012 people living in the U.S. Virgin Islands (Fiedler and Jarvis 1932). As of 1990 the island had 3,500 permanent

Courtesy D. Burks, Virgin Islands National Park

Fig. 1. French grunts off St. John, U.S. Virgin Islands.

Courtesy J. Sneddon, Virgin Islands National Park

Fig. 2. Commercial fisherman using wire traps in the U.S. Virgin Islands.

residents (out of 100,000 total in the U.S. Virgin Islands; U.S. Bureau of the Census 1994) and more than one million visitors per year (Virgin Islands National Park statistics). This 55-fold increase in the number of people has greatly increased the demand for local fish. Consequently, the economic incentive to catch more fish has become so compelling that the local Nassau grouper spawning aggregation has been fished out of existence (Olsen and LaPlace 1979; Beets and Friedlander 1992). Yet fishing pressure continues to increase (Virgin Islands Division of Fish and Wildlife, unpublished statistics). In 1987 the Virgin Islands Division of Fish and Wildlife reported the following trends in the fishery: a continuing decline in the average size of trapped fish; an increase in fishing effort with no significant increase in landings; and prespawning juveniles making up most of the catch (deGraf and Moore 1987). Whereas groupers and snappers made up 33% of the catch in 1967–1968 (Dammann 1969), parrotfishes dominated the fishery in 1987 (deGraf and Moore 1987). Parrotfish populations are now beginning to exhibit signs of overfishing; specifically, the average size of trapped parrotfishes has decreased (Appeldoorn et al. 1992).

In 1992 the Research Division (now part of the U.S. Geological Survey's Biological Resources Division) of Virgin Islands National Park commenced a 3-year study designed to assess the effects of fishing (primarily by trap) on the reef fishes in the waters of St. John and to elucidate trends in species composition, abundance, and sizes of fishes. Park regulations allow fishing in park waters by trap, hook and line, and cast net only; no other fishing methods or types of gear are permitted (Fig. 3). Thus, another objective of the study was to evaluate the effectiveness of park fishing regulations in preserving and protecting the reef fish resource. The research involved several interrelated studies that were carried out and completed through the cooperative efforts of a number of agencies and universities (National Biological Service [now part of the U.S. Geological Survey], National Park Service, the Virgin Islands Department of Planning and Natural Resources Division of Fish and Wildlife, the Florida Marine Research Institute, and the universities of Rhode Island, Richmond, and Hawaii). A comprehensive view of the state of the reef fish and fishery resource of St. John is emerging from analyses of historical data and the results of these projects. The following information summarized from these projects to date is both exciting and disturbing.

- Fish traps have decreased the number of fishes and changed the relative abundance of species on St. John's reefs. Throughout 6 months of experimental trapping on a single reef in the park, the number of groupers, snappers, squirrelfishes, surgeonfishes, and total number of fishes caught in 8 traps declined significantly (Beets 1996). During the same period, visual census data also showed a decrease in the numbers of piscivorous (fish-eating) fishes, squirrelfishes, snappers, grunts, parrotfishes, and surgeonfishes, and in the total number of fishes (Beets 1996).

The results of a study that compared the fishes trapped on a reef in 1982–1983 with those caught on the same reef in 1993–1994 clearly document the decline in numbers and percentage of grunts, porgies, groupers, snappers, goatfishes, and boxfishes (Beets 1996; Table 1). Also, the mean length of most species decreased. Eleven of the species present in 1982–1983 were not observed or trapped during the 1993–1994 study; 4 of the 11 were groupers (rock hind, mutton hamlet, red grouper, and black grouper; Beets 1996).

- There was a decline in the average number of fishes caught per trap and a decrease in the average length of fishes in visually censused fish traps. Over the study period, the average catch was 4.7 fish per trap and the mean length of each fish was 25.0 centimeters.

Table 1. The ten most numerically abundant fish families in one fisherman's trap catches in 1982–1983 and in experimental trap sampling in 1993–1994 at Yawzi Point reef, St. John Island, U.S. Virgin Islands (Beets 1996).

Family common name	Percent	
	1982–1983	1993–1994
Surgeonfishes	25.7	45.2
Grunts	23.1	11.3
Porgies	10.0	3.5
Sea basses (groupers only)	8.8	4.7
Snappers	8.1	5.5
Goatfishes	5.6	3.7
Parrotfishes	5.4	15.4
Boxfishes	2.5	0.6
Squirrelfishes	2.0	5.4
Angelfishes	1.1	2.2

Blue tangs (surgeonfish family) were trapped in greater numbers than any other species; they averaged 15.4% of the catch. Porgies were the second most abundant (11.7%), and gray angelfish the third (9.4%). The highly prized food fish, the Nassau grouper, made up only 0.4% of the catch. The surgeonfishes accounted for 19.5% of the fishes trapped, increasing from 8.6% in 1992 to 34.6% in 1994; the surgeonfishes, butterflyfishes, angelfishes, and boxfishes made up over 50% of the catch. Table 2 summarizes the relative abundance in catches by trophic level. Note the increase in the percentage of herbivorous fishes and the decrease in fish-eating fishes.

- Catch rates (number of fish per trap), species composition, and sizes were similar on reefs inside and outside park waters in the experimental and general trapping studies (Beets 1996) and visual censusing. The results seem to indicate that park regulations and enforcement are not protecting a natural resource the park is mandated to protect.

Courtesy V. Garrison, Virgin Islands National Park

Fig. 3. A fish trap on Yawzi Reef, Virgin Islands National Park.

Table 2. Percentage of number of fish by trophic level in visually censused traps in St. John, U.S. Virgin Islands.

	Percent			
	All years	1992	1993	1994
Herbivores	28.1	23.5	22.8	41.8
Omnivores	16.4	18.7	19.1	9.5
Invertivores (invertebrate-eating)	41.2	41.0	44.1	36.2
Piscivores (fish-eating)	14.3	16.8	14.0	12.5

- Within park waters, 86% of the traps were set on organisms (live corals, soft corals, seagrasses) living on the sea floor. Damage to the live substrate has far-reaching negative effects on the marine ecosystem because the available amount of shelter and food often decreases as damage increases.
- Forty-nine percent of the traps in the park (35% of all traps) did not have a functioning biodegradable panel. Without the required panel, lost traps continue to kill fish for years.

In sum, our analyses have shown that the direct effects thus far from the trap fishing of reef fishes in the waters surrounding St. John include a change in the relative abundance of reef fish species, a change in the species composition, a decrease in the numbers of many species of fishes, and a decrease in the size of fishes.

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Author

Virginia Haney Garrison
U.S. Geological Survey
Biological Resources Division
Virgin Islands National Park
P.O. Box 710
St. John, U.S. Virgin Islands 00831

important grazing areas for the green sea turtle and the West Indian manatee. In some areas, intensive recreational use has extensively disturbed the shallow seagrass meadows. Other beds have suffered from siltation caused by changing land-use practices or from dredge and fill operations during creation of shipping channels and docking accommodations. High turbidity levels generated by such activities can decrease the depth limit of seagrass beds (Vicente and Rivera 1982) and reduce the depth limit of corals, thereby diminishing the amount of deeper seagrass beds and coral reef habitats.

Mangroves

Only 4 of the 80 mangrove species found worldwide occur in the Caribbean Islands. Like coral reefs and seagrass beds, the functional values of mangrove forests are often critical to fisheries, wildlife resources, and biodiversity. Furthermore, these systems are also highly productive. Mangroves at Joyuda Lagoon, on the southwestern coast of Puerto Rico, produce more than 20 metric tons of organic matter per hectare per year (Levine 1981).

Mangrove forests consist of several salt-tolerant tree species, including black-mangrove, white-mangrove, and red mangrove, and the buttonwood-mangrove. Small islands (*manglares*) formed by clumps of red mangrove trees are important in extending land masses seaward because the trees capture sediments and debris (Fig. 11). The network of manglares, cays, and channels provides inland areas with a buffer from the action of stormy seas.

The extensive prop root systems of fringing mangroves have been reported to contribute to coastal accretion by as much as 25–200 meters per year (Maul 1993). This accretion may play a pivotal role in mitigating the present

Courtesy J. Colón, U.S. Fish and Wildlife Service

Fig. 11. Mangrove forest at Humacao Wildlife Refuge, Puerto Rico.

and projected sea-level rises and coastal erosion problems. Mangroves also play an important role in protecting uplands from storm winds and surge (Dammann and Nellis 1992).

Mangrove forests also serve as nurseries for many reef and marine fishes, including commercially important species (Austin 1971). Mangrove ecosystems are also important to birds and other animals that depend on the fishes and invertebrates concentrated there. Manglares serve as relatively safe nesting habitat for some birds, including the white-crowned pigeon (Dammann and Nellis 1992). Two bird species listed as endangered, the brown pelican and the yellow-shouldered blackbird, as well as many species of herons and egrets, roost and nest on the mangrove canopy.

Development by humans has greatly reduced the amount of mangrove forests throughout the islands, although these forests have been protected in both Puerto Rico and the Virgin Islands during the last 20 years. In some cases, such protection has resulted in natural restoration of mangrove forest; for example, in Puerto Rico, 6,426 hectares of mangrove forest remained in 1974, following a period of destruction from 1950 to 1970. At present, there are 8,959 hectares of mangrove forests, an increase of 39.5% (Torres-Rodriguez 1993).

Rocky Coast, Beachrock, and Offshore Rocks

Rocky coast, beachrock, and offshore rock habitats receive heavy wave action and often have algal ridge reefs associated with them. Because of the wave action and salt spray, these areas are typically without vegetation. Only a few species of plants are able to survive in these areas, and the survival of the hardiest of plants is influenced by seasonal and storm-induced wave action. Aside from the importance of coastal rock formations for a wide array of invertebrates, these formations are also routinely used as roosts by shorebirds, gulls, and wading birds (Dammann and Nellis 1992).

Saltwater Ponds

Saltwater ponds are formed as a result of the growth of corals across the mouth of an indented shoreline (Dammann and Nellis 1992). Storm-deposited materials eventually form a berm separating the pond from the sea, and thereafter the pond gradually fills with trapped debris, forming a land mass. These inshore ponds may exchange water and organisms during unusually high tides or through remnant channels. Ponds that are not connected to the sea do not support fish. Water salinity, oxygen content, and temperature are highly variable and influence the fauna of these ponds (Dammann and Nellis 1992). During periods when conditions are favorable, insects and small invertebrates are common and form an important prey base for shorebirds such as plovers and sandpipers. Saline ponds and lagoons are particularly important to migratory waterfowl such as blue-winged teal, as well as the resident white-cheeked pintail and several waders. The usual fringe of mangroves surrounding these saltwater ponds provides habitat for nesting populations of herons, pigeons, and many songbirds.

Spoil Islands

Spoil from dredging a shipping channel in St. Croix was stockpiled offshore, forming spoil islands. Some of these islands have been colonized by terrestrial vegetation and are used by several species of birds (Dammann and Nellis 1992). A major hurricane did not destroy the largest of these islands, and some have been recognized as potential habitat for naturalized plants and animals (Dammann and Nellis 1992).

Freshwater Environments

Problems with freshwater ecosystems are a major environmental issue in Puerto Rico and the Virgin Islands. Water pollution, siltation of reservoirs, and excessive withdrawals of fresh water from rivers are problems associated with the growing human populations of the islands. Also, unauthorized filling of wetlands is a substantial and continuing problem (U.S. Department of the Interior 1994). Detailed descriptions of the freshwater communities in Puerto Rico are available (U.S. Army Corps of Engineers 1978).

Reservoirs

Puerto Rico and the Virgin Islands have no natural inland bodies of fresh water (lakes). In Puerto Rico, 20 reservoirs, varying from 6 to 390 surface hectares, were constructed for the purposes of potable water, irrigation, water power, and flood control. The large native shrimp, gobies, and mountain mullet may come into some of the reservoirs from the rivers, but there are no native fauna adapted to such water bodies. Several game fish, including peacock bass, largemouth bass, and channel catfish, have been introduced into Puerto Rican reservoirs.

Artificial Freshwater Bodies

Ponds are important habitats in Puerto Rico and the Virgin Islands; almost all are artificial and mostly intended for irrigation, livestock, or aesthetic reasons. Most go dry during the year. Fish are stocked in some of the ponds for sport fishing and for mosquito and weed control.

Canals irrigating the sugarcane fields are also important habitats for fishes and aquatic invertebrates. Introduced fishes such as guppies and mosquitofish are often kept in cisterns and water troughs to control mosquitos.

Rivers and Streams

Puerto Rico has about 1,200 rivers, streams, and creeks. Twenty of these rivers have a permanent minimum water flow of at least 0.28 cubic meters per second and are important to the island's fishery. Major river systems are the Rixo Grande de Loíza (64 kilometers), Bayamón (41 kilometers), La Plata (73 kilometers), Arecibo (64 kilometers), Culebrinas (40 kilometers), and Añasco (65 kilometers). The character of the streams changes radically from rapidly flowing in the steep mountains to slower and more winding courses across the narrow Coastal Plain, creating habitats for fishes and other aquatic animals. Many fishes migrate up- or downstream to or from saltwater habitats.

Following heavy rains, many active freshwater streams can be found in St. Croix and the other Virgin Islands. These streams are short-lived now, although previously some did flow permanently. Even the pools left behind dry up during the annual cycle. Near the shoreline, some depressions and beaches retain brackish pools throughout the year. Despite the ephemeral nature of these streams, fish can usually be found in them during the rainy season (Ogden et al. 1975).

Lagoons

All of the lagoons have shallow water, usually with mud bottoms, are weedy over large stretches, and, if brackish or salty, are surrounded by mangrove forests. Cartagena Lagoon, formerly perhaps the most important wetland in Puerto Rico (Danforth 1926), has been greatly degraded by nearby agricultural practices. The lagoon has recently been acquired as a national wildlife refuge, and restoration is proposed. Other important lagoons include Joyuda, San José, Torrecillas, Tortuguero, and Piñones.

Status and Trends of Animals and Plants

The Fossil Record, Extinctions, and Extirpations

Island ecosystems are, in general, more susceptible to change than are those on continents, and the West Indies are no exception. Deforestation and fire, introduction of grazing animals, cultivation, and the introduction of weedy plants are all important causes of island extinctions (Heywood 1979), but deliberate or accidental species introductions have been singled out as disproportionately critical (Elton 1958). Extinction rates are generally higher on islands because island species typically have small populations, restricted genetic diversity, and narrow geographic ranges (MacArthur and Wilson 1967; Vitousek 1988). In addition, human-caused extinction rates are much higher on islands than on continents (Vitousek 1988).

Large-scale extinctions in the late Ice Age and during more recent prehistory drastically altered the West Indian vertebrate fauna, especially the nonflying terrestrial mammals. Many of these species disappeared from the West Indies about 10,000 years ago as a result of climatic change and the post-Ice Age rise in sea level (Pregill 1981). The species composition of the fossil faunas indicates that the environment of parts of Puerto Rico was a dry, savannalike habitat, quite in contrast to the moist conditions there now. Undoubtedly, the plant community changed with this climatic shift, and probably many rare plants disappeared from the islands or were confined to postglacial ecological refugia (Little and Woodbury 1980). No endemic tree species in Puerto Rico and the Virgin Islands are known to have become extinct, although the fossil flora of Puerto Rico is poorly known. Small, mountainous islands usually lack favorable sites (that is, freshwater lakes) for fossil pollen deposition and preservation.

A second and probably more extensive wave of extinctions took place from about 4,500 years ago to the present, after the arrival of humans on the islands (Morgan and Woods 1986). Many extinctions in the Antilles during the post-Ice Age prehistoric period were probably human-caused, resulting from direct exploitation, habitat destruction, or introduction of nonindigenous species (Olson 1982; Steadman et al. 1984b).

Reptiles and Amphibians

In a review of the world's amphibians and reptiles that are presumed to have become extinct since 1600, Honegger (1981) found that most were island taxa. All of the extinct lizards and snakes had island distributions, and West Indian species made up half of the world's extinctions (Henderson 1992). Pregill (1981) reported 21 fossil reptiles and amphibians from Puerto Rico; these species consisted of 16 genera and 12 families. One of these, *Cyclura portoricensis*, is an extinct form closely allied to the endangered Mona Island ground iguana.

Several reptiles have recently disappeared. In the Virgin Islands, the St. Croix tree snake, once common on St. Croix Island, became extinct about 1950. Similarly, the Puerto Rican racer snake is now extinct on St. Thomas. In Puerto Rico, the Culebra Island giant anole lizard, known only from Culebra Island, seems to have become extinct and thus represents the first of Puerto Rico's reptiles known to have become extinct since Columbus's arrival.

Birds

Although fewer than one-fifth of the world's bird species are restricted to islands, more than 90% of all historical bird extinctions have occurred on islands. The effects of nonindigenous animals introduced on islands by humans are the major cause of such losses. Human activities have precipitated a long history of decline for the approximately 250 native bird species known from Puerto Rico and the Virgin Islands (Raffaele 1989). This number includes ten extinct and two extirpated species. The crested caracara (Olson 1976a), Puerto Rican quail-dove, and Puerto Rican woodcock (Olson 1976b) almost certainly disappeared before Columbus's arrival, although the Puerto Rican barn-owl may have survived into the colonial period (Wetmore 1927). DeBooy's rail, known from Native American middens, probably did not survive long after Columbus's arrival.

Four (1.6%) of Puerto Rico's native birds are known to have become extinct or extirpated since about 1850: Hispaniolan parakeet, white-necked crow, Cuban (lesser Puerto Rican) crow, and limpkin. Another three species no longer breed on the island but are still occasional visitors: black-bellied whistling-duck, black rail, and greater flamingo. The now-extinct Culebra Island race of the Puerto Rican parrot survived until at least 1899.

In the U.S. Virgin Islands, Raffaele (1989) lists 199 native bird species; 70 breed there. Several species have disappeared since the arrival of the Spanish colonists. Some species now absent from certain islands still survive on others. For example, St. Croix has lost the masked booby, red-footed booby, and the least bittern, and St. Thomas and St. John no longer have populations of the Antillean mango and Antillean nighthawk.

Several species are known from the U.S. Virgin Islands only from bone remains, including a petrel and snow goose from St. Croix; DeBooy's rail from St. Thomas, St. Croix, and St. John; and the purple gallinule, St. Croix macaw, white-necked crow, and Cuban (lesser Puerto Rican) crow from St. Croix (Wetmore 1918, 1937; Olson and Hilgartner 1982). Because the DeBooy's rail is well represented in St. Croix's pre-Columbian refuse heaps, it was probably an important part of the aboriginal diet (Wetmore 1925, 1938). The rail possibly survived up to the twentieth century in the Virgin Islands (Nichols 1943; Ripley 1977).

Mammals

Twenty-two mammal species are known historically from Puerto Rico and neighboring islands; this group includes 1 insectivore, 1 sloth, 4 rodents, and 16 bats (Woods 1990). The number of mammal species in the original mammal fauna was high among the West Indies and was exceeded only by the number of mammal species in the much larger islands of Cuba and Hispaniola in the Greater Antilles. Despite the original high diversity of mammals, all Puerto Rican mammals except bats have been extirpated. Bats have fared much better—only 14% of known West Indian bat species went extinct during the period when terrestrial mammal species dramatically declined.

Likewise, many terrestrial mammal species of the Antilles are also extinct; these losses have a common basis. Taxa evolving in isolation on oceanic islands without competition or predators may not be able to adapt to rapidly changing conditions, such as the extensive climatic fluctuations of the Ice Ages or sudden competition or predation from introduced animals (Woods 1990). The combination of island invasions by aboriginal humans and competition and predation by introduced animals is the most probable reasons for the extinction of several West Indian mammal species (Woods 1989a).

Biodiversity, Endemism, and Endangered Species

Plants

Puerto Rico and the Virgin Islands are rich in plants not found elsewhere. Fortunately, most native trees are protected in natural or near-natural forests on public forestlands and parks. Puerto Rico and the Virgin Islands combined have about 551 species of native trees, of which 539 are found in Puerto Rico. More than one-fourth (142) of these species are known only from these islands. Forty-six plant species are listed as endangered or threatened, including 30 tree or shrub species, 8 fern species, 2 cacti species, 2 orchid species, and 4 herbaceous plant species (Silander 1992; S. Silander, U.S. Fish and Wildlife Service, Caribbean Field Office, personal communication). About 100 other tree species listed as rare are native but are found elsewhere in the West Indies (Little and Woodbury 1980). More than 70 Puerto Rican and Virgin Islands' plant species are candidates for listing or are species of concern (U.S. Fish and Wildlife Service 1993, 1994a; Table 2).

Only 26 (18%) of the region's native endemic trees still grow wild on one or more of the Virgin Islands (Little et al. 1974); this small number of local species is related to lack of isolation. Only five tree species are endemic to the Virgin Islands.

Invertebrates

Invertebrates are important components of the islands' ecosystems, but knowledge of the status of invertebrate wildlife is not nearly as complete as that for the region's vertebrates. Even the functional roles of such fundamental elements as soil microfauna are poorly known in the region (Madge 1965; Coleman 1970). Although the total number of invertebrate species is low in the tropical forests of Puerto Rico and the Virgin Islands—no greater than that of temperate forests—species richness is much higher than in temperate forests (Odum et al. 1970). The richness of insect species has been demonstrated by Drewry (1970a), who reported 1,200 species from the Sierra de Luquillo in Puerto Rico. In the Sierra de Luquillo, the most common herbivores are invertebrates, primarily snails and plant-eating insects, which have a major influence on forest foliage (Martorell 1945; Van der Schalie 1948; Willig and Camilo 1991; Torres 1994). Vélez (1967) listed 36 species of terrestrial and freshwater crustaceans for Puerto Rico.

Researchers have noted invertebrate species in need of special attention. For example, because of the threats to cave ecosystems in

Table 2. Endangered and threatened wildlife and plants in Puerto Rico and the U.S. Virgin Islands. E = Endangered, T = Threatened, and * = extirpated.

Species	Range in region	Federal status
Birds		
Brown pelican	Puerto Rico	E
Puerto Rican sharp-shinned hawk	Puerto Rico	E
Puerto Rican broad-winged hawk	Puerto Rico	E
American peregrine falcon	Puerto Rico, Virgin Islands	E
Arctic peregrine falcon	Puerto Rico, Virgin Islands	T
Roseate tern	Puerto Rico, Virgin Island	T
Piping plover	Puerto Rico, Virgin Islands	T
Puerto Rican plain pigeon	Puerto Rico	E
Puerto Rican parrot	Puerto Rico	E
Puerto Rican nightjar	Puerto Rico	E
White-necked crow	Puerto Rico	E*
Yellow-shouldered blackbird	Puerto Rico	E
Red siskin (introduced)	Puerto Rico	E
Reptiles		
Culebra Island giant anole	Puerto Rico (Culebra Island)	E
Mona boa	Puerto Rico (Mona)	T
Puerto Rican boa	Puerto Rico	E
Virgin Islands tree boa	Virgin Islands	E
Monito dwarf gecko	Puerto Rico (Monito)	E
Mona ground iguana	Puerto Rico (Mona)	T
St. Croix ground lizard	Virgin Islands	E
Green turtle	Puerto Rico, Virgin Islands	T
Hawksbill	Puerto Rico, Virgin Islands	E
Kemp's ridley	Puerto Rico, Virgin Islands	E
Leatherback	Puerto Rico, Virgin Islands	E
Loggerhead	Puerto Rico, Virgin Islands	T
Amphibians		
Golden coqui	Puerto Rico	T
Puerto Rican ridge-headed toad	Puerto Rico	T
Plants		
Ferns and allies		
Brake family		
Adiantum vivesii	Puerto Rico	E
Shield fern family		
Elaphoglossum serpens	Puerto Rico	E
Polystichum calderonense	Puerto Rico	E
Tectaria estremerana	Puerto Rico	E
Thelypteris family		
Thelypteris inaborensis	Puerto Rico	E
T. verecunda	Puerto Rico	E
T. yaucoensis	Puerto Rico	E
Tree-fern family		
Elfin tree-fern	Puerto Rico	E
Monocot plants		
Grass family		
Aristida chaseae	Puerto Rico	E
Pelos del diablo	Puerto Rico	E
Orchid family		
Cranichis ricartii	Puerto Rico	E
Lepanthes eltoroensis	Puerto Rico	E
Palm family		
Palma de manaca	Puerto Rico	T
Dicot plants		
Bignonia family		
Higuero de sierra	Puerto Rico	E
Boxwood family		
Vahl's boxwood	Puerto Rico, Virgin Islands	E
Buckthorn family		
Auerodendron pauciflorum	Puerto Rico	E
Cacti		
Higo chumbo	Puerto Rico	T
Leptocereus grantianus	Puerto Rico	E
Canella family		
Chupacallos	Puerto Rico	E
Citrus family		
St. Thomas prickly-ash	Virgin Islands	E
Flacourt family		
Palo de Ramón	Puerto Rico	E
Heath family		
Lyonia truncata var. *proctorii*	Puerto Rico	E
Holly family		
Cook's holly	Puerto Rico	E
Ilex sintenisii	Puerto Rico	E
Icacine family		
Palo de rosa	Puerto Rico	E
Madder family		
Mitracarpus maxwelliae	Puerto Rico	E
M. polycladus	Puerto Rico	E
Mahogany family		
Bariaco	Puerto Rico	E
Mezereum family		
Daphnopsis hellerana	Puerto Rico	E
Myrtle family		
Calyptranthes thomasiana	Puerto Rico, Virgin Islands	E
Eugenia woodburyana	Puerto Rico	E
Uvillo	Puerto Rico	E
Myrcia paganii	Puerto Rico	E
Nightshade family		
Erubia	Puerto Rico	E
Matabuey	Puerto Rico	E
Olax family		
Schoepfia arenaria	Puerto Rico	T
Pea family		
Chamaecrista glandulosa var. *mirabilis*	Puerto Rico	E
Cóbana negra	Puerto Rico	T
Pepper family		
Wheeler's peperomia	Puerto Rico	E
Snowbell family		
Palo de jazmín	Puerto Rico	E
Sunflower family		
Vernonia proctorii	Puerto Rico	E
Tea family		
Palo colorado	Puerto Rico	E
Ternstroemia subsessilis	Puerto Rico	E
Verbena family		
Capá rosa	Puerto Rico	E
Palo de nigua	Puerto Rico	E

Puerto Rico, the Mona Cave shrimp has been designated as a species of concern (Groombridge 1993), and the Tuna Cave roach has been listed as a candidate for federal listing as endangered or threatened (U.S. Fish and Wildlife Service 1994b).

The Queen conch and the Caribbean spiny lobster, two commercially important invertebrates, are at risk throughout the Caribbean because of heavy commercial demand for their use as human food (Groombridge 1993). Both species have been federally listed, along with the common land crab, as deserving special attention in Puerto Rico (Raffaele et al. 1973).

In Puerto Rico, freshwater shrimp are not only important in the food chains of freshwater streams (Covich et al. 1991); they are also a much sought-after recreational resource in the island and are heavily harvested from some rivers. In Puerto Rico, competition of native snail species with introduced snail species has probably caused the decline of several populations of native snails, including *Physa cubensis* (Erdman 1972). V. Mestey-Villamil (Colegio Universitario de Cayey, Cayey, Puerto Rico, unpublished report) evaluated the status of marine mollusks in Puerto Rico, suggesting that

16 species and one subspecies were of special concern because of possible declining populations (Table 3).

Housing development and pollution in neighboring areas seriously threaten several of Puerto Rico's most spectacular natural areas, including Phosphorescent Bay at La Parguera and Mosquito Bay in Vieques. On dark, moonless nights, tiny marine dinoflagellates (*Gonyaulax* spp.) emit a phosphorescent glow, creating a spectacular light display. At La Parguera, past pollution problems (that is, oil spills) and recent increases in housing and tourism development may jeopardize the future of these phosphorescent dinoflagellates. The lagoons and surrounding mangroves at Mosquito Bay on Vieques Island, managed by the Vieques Conservation Trust, are currently protected, however. The topography of the area around Mosquito Bay and the absence of intense development on Vieques Island help maintain this system as the most pristine and spectacular luminescent lagoon in the region.

Table 3. Status of marine mollusks of concern in Puerto Rico (after V. Mestey-Villamil, Colegio Universitario de Cayey, Cayey, Puerto Rico, unpublished data).[a]

Name	Suggested status
Flame helmet	Undetermined
Cameo helmet	Undetermined
Cameo helmet subspecies	Undetermined
Caribbean helmet	Undetermined
West Indian topsnail	Undetermined
Atlantic trumpet triton	Undetermined
Mangrove oyster	Vulnerable
Angular triton	Undetermined
Angelwing	Undetermined
Clench's nerite	Endangered
Zebra nerite	Vulnerable
Sad nerite	Endangered
Milk conch	Undetermined
Roostertail conch	Undetermined
Queen conch	Undetermined
West Indian fighting conch	Undetermined
Hawkwing conch	Undetermined

[a] Populations of these species have substantially declined and those declines are of concern, but no good quantitative data have been collected.

Fishes

Although Puerto Rico has the fourth-largest insular land mass in the region, it has no native freshwater fishes; it does, however, support 24 established nonindigenous introductions as well as 60 peripheral marine invaders (Erdman 1972, 1974; Burgess and Franz 1989). Similarly, the Virgin Islands have no native freshwater fishes (Ogden et al. 1975), although numerous species have been intentionally or accidentally introduced, and peripheral marine species use freshwater streams during wet seasons.

The Commonwealth of Puerto Rico's Department of Agriculture established a fishery division in 1934 to support the growing interest in sport fishing and to supply a protein source for local residents. Several species were subsequently introduced into Puerto Rico's waters. Rainbow trout eggs were imported and hatched in the Caribbean National Forest in 1934; these trout introductions were unsuccessful because Puerto Rican waters were too warm for trout to breed. A hatchery at Maricao, once managed by the Puerto Rican Department of Agriculture, is now operated by the Fisheries Division of the Puerto Rico Department of Natural and Environmental Resources. In the last 3 to 4 years, the hatchery has been expanded and improved in order to produce various species of game fish, including peacock bass, which are stocked in the island's system of reservoirs.

Considerable habitat loss for freshwater fishes and invertebrates has resulted from water withdrawal from streams for domestic and industrial purposes. This problem will worsen as human populations grow and demands for water resources increase; recent periods of severe water shortage already highlight this problem (Lugo 1994). Inshore marine fisheries have declined as growing human populations have increased pollution levels and the amount of fish harvests. The fisheries have also been harmed because of habitat destruction, especially in the critical mangrove estuaries that serve as nurseries for fishes and their food.

Reptiles and Amphibians

Fifty reptiles and twenty-three amphibians are known from Puerto Rico and adjacent waters. Among the amphibians, 15 species are endemic, and 4 have been introduced. There are 29 endemic reptiles, and 2 introduced species may now be established.

Puerto Rico's 18 indigenous amphibians include the ridge-headed toad, the common mud frog, and 16 species of tiny frogs commonly called coquis. The amphibian fauna of the U.S. Virgin Islands is composed of 4 coquis, the Caribbean white-lipped frog, and 2 introduced species, the marine toad and the Cuban treefrog. All 20 species found in Puerto Rico and the Virgin Islands are unique to the region.

In the Caribbean National Forest of Puerto Rico, leptodactylid frogs (primarily coquis) are the most numerous vertebrates (Drewry 1970b; Rivero 1978). The most common species, the common coqui, existed at high densities (estimated at 20,570 animals per hectare) in the early 1980's (Stewart and Woolbright 1996). Abundant amphibians play important roles as predators on and prey of other species in the island ecosystems. Researchers estimate that in each hectare of forest, common coquis eat 114,000 prey items each night (Stewart and Woolbright 1996). Frogs are also important prey for numerous predators, including birds, snakes, and spiders and their relatives.

Habitat destruction is generally considered the most critical threat to the amphibians and reptiles of Puerto Rico and the Virgin Islands, although the introduction of nonindigenous mammals, such as black rats, has also had a substantial negative effect (Henderson 1992). Puerto Rico's native frogs are experiencing dramatic population declines, even though Puerto Rico's forest cover has recently increased. Many species were still common in their preferred habitats as late as the mid-1970's, but several species and formerly common populations are severely declining.

Several species of Puerto Rican amphibians have experienced drastic population declines in the last 20 years; in fact, almost two-thirds of Puerto Rico's endemic amphibians are declining (R. L. Joglar, University of Puerto Rico, San Juan, personal communication; Table 4). Some species have not been found for several years, including the web-footed coqui (not seen since 1974), the golden coqui (not seen since 1981), and the mottled coqui (not seen since 1990). Furthermore, 3 of 7 populations of amphibians studied in Puerto Rico on a long-term basis were declining (Joglar, personal communication). In the last 8 years, 5 other amphibian populations went extinct in 2 study sites; no recolonization has occurred. At least one Virgin Islands species is also in decline. All declining and disappearing species are highly specialized (morphologically or ecologically) and occur at high elevations. Paradoxically, amphibians in the Caribbean National Forest, the best-conserved forest in Puerto Rico and formerly home to the greatest variety of frog species, seem more negatively affected than amphibians in other localities. The reasons for this decline are unclear but may be related to declines in amphibian populations in many other parts of the world (for example, Barinaga 1990; Wyman 1990; Burrowes and Joglar 1991; Joglar 1992; Carey 1993; Vial and Saylor 1993; Blaustein et al. 1994; Pounds and Crump 1994).

Among the region's amphibians, only the Puerto Rican ridge-headed toad (Fig. 12) and the golden coqui have been listed under provisions of the U.S. Endangered Species Act of 1973 (Table 2). Three species of coquis are also candidates for listing under the Endangered Species Act: the rock coqui, the mottled coqui, and the web-footed coqui (Silander, personal communication). Local and international committees, though, recognize that several other amphibian species need special attention (Moreno 1991; Groombridge 1993; Table 4).

Puerto Rico's 50 reptilian species include 48 indigenous forms: 33 lizards (2 extinct), 8 snakes, 1 freshwater turtle, 1 land tortoise (extinct), and 5 sea turtles. In the Virgin Islands, 26 reptile species are known, including 15 lizards, 5 snakes (1 extinct), 1 tortoise (introduced), and 5 sea turtles. The 60 reptile species that occur in Puerto Rico and the Virgin Islands show a high rate of endemism, with 42 species (70%) found only in these islands. Twelve of the region's species, including all sea turtles, are listed under the U.S. Endangered Species Act of 1973 (Fig. 13; Table 2).

As in other parts of the world, sea turtle populations have greatly declined in the waters surrounding Puerto Rico and the Virgin Islands (see box on Sea Turtles). Once an important resource in regional waters, the green turtle fishery is nearly gone. Coral reefs and turtle grass meadows in the Virgin Islands and the Culebra archipelago are prime habitat for immature green turtles (Carr 1977; Tucker 1988; Collazo et al. 1992). Construction, sediment runoff, pollution, and increased boating and fishing activities in Culebra's coastal zone are threats to the islands' surrounding coral reefs and seagrass beds (Loya 1976; Rogers 1977; Lugo 1978; Goenaga and Canals 1980). The hawksbill, leatherback, and loggerhead sea turtles have also declined, in large part because of killing for food and loss of their habitat. Sea turtles are the subject of intensive research in the Virgin Islands (Eckert et al. 1986; Basford 1988; Groshens 1993; Starbird 1993).

Table 4. Status, including International Union for the Conservation of Nature (IUCN) categories, for 12 species of Puerto Rican and Virgin Island amphibians (as recommended by R. L. Joglar and P. A. Burrowes, University of Puerto Rico, San Juan, personal communication).

Species	Status
Rock coqui	Vulnerable
Mottled coqui	Extinct in the wild
Cricket coqui	Declining
Tree-hole coqui	Declining
Golden coqui	Extinct in the wild
Web-footed coqui	Extinct in the wild
Warty coqui	Vulnerable
Puerto Rican coqui	Declining
Ground coqui	Endangered
Virgin Islands coqui	Declining
Wrinkled coqui	Declining
Ridge-headed toad	Endangered


Courtesy F. J. Vilella, USGS

Fig. 12. A Puerto Rican ridge-headed toad, Guánica Biosphere Reserve.


Courtesy J. Wiley, USGS

Fig. 13. Endangered St. Croix ground lizard, Green Cay National Wildlife Refuge, St. Croix, U.S. Virgin Islands.

Sea Turtles of the Virgin Islands and Puerto Rico

The Virgin Islands and Puerto Rico include a complex of islands and small cays surrounded by coral reefs and seagrass beds adjacent to deep water. These islands provide critical nesting, foraging, and developmental habitat for three species of sea turtles: the leatherback and the hawksbill, both endangered species, and the green turtle, a threatened species. In addition, rare olive ridleys have only been reported in Puerto Rico once (Caldwell 1969); loggerhead turtles are transitory and are only occasionally seen in the area.

Sea turtles have been nesting on these islands since well before recorded history. Leatherback turtles, found in the Virgin Islands only during their nesting season, require for nesting open sand beaches with no nearshore reef; such beaches are found on Culebra Island and the north shore of Puerto Rico; Trunk Bay, St. John; and Sandy Point, St. Croix. Green turtles and hawksbill turtles nest in vegetated dunes, low scrub, and beach forested areas, which are often fringed by shoreline reefs (Hillis and Mackey 1989).

Green turtles and hawksbill turtles forage throughout the coastal areas surrounding the Virgin Islands and Puerto Rico. Juvenile sea turtles live in coral reef and seagrass habitats and remain there until they reach sexual maturity (Limpus 1990; Frazer et al. 1994). Adult female leatherback turtles, which are primarily pelagic (that is, living in open seas), migrate to the tropics every 2 to 3 years to nest (Boulon et al. 1996).

During the nineteenth century, the sea turtle fishery in the Virgin Islands and Puerto Rico was for subsistence only. Leatherback turtles were slaughtered on the nesting beaches for their oil, and their eggs were harvested for food. A substantial green turtle fishery for food and export to Europe existed historically, though the Virgin Islands were not a significant green turtle nesting area but instead were a juvenile foraging ground. Hawksbill turtles are solitary nesters throughout their range. In the Virgin Islands, hawksbills supplied the tortoiseshell industry beginning in the 1920's; the harvest was so great that turtle carcasses were common on the beaches, and hawksbill populations declined dramatically. These animals were killed for their shells only, the keratinized plates of which were exported to be made into curios and jewelry.

In the 1930's, Joe LaPlace, a former Department of Planning and Natural Resources/Division of Fish and Wildlife officer, noted heavy sea turtle nesting in three bays (Wilks, Hard, and Sandy) in St. Thomas, but coastal development boomed in the late 1950's, eliminating many of these sea turtle nesting areas around St. Thomas (Eckert 1992). By the 1950's the sea turtle populations were severely depleted, especially the formerly abundant juvenile populations of green and hawksbill turtles. Subsistence hunting continued, and to meet the demands of a growing human population, sea turtles were imported from other islands. By 1992 only 5 to 10 turtles nested in these bays each year; in some areas where all three species once nested, only an occasional hawksbill turtle now nests (Eckert 1992). In the 1960's, 40 to 50 green turtles were seen nesting on St. Croix's 3-kilometer-long Sandy Point beach during the nesting season (Eckert 1992). Today fewer than 10 females nest there each year, and fewer than 20 females nest on the entire island of St. Croix (Mackay 1994; Mackay and Rebholz 1995; R. Boulon, Jr., Virgin Islands Department of Planning and Natural Resources, St. Thomas, Virgin Islands, personal observation).

In 1972 Virgin Islands' law finally made it illegal to harvest sea turtles on their nesting beaches and allowed harvest in the water only between October and April. In 1973 leatherback and hawksbill turtles were protected under the U.S. Endangered Species Act; in 1978 the green turtle was listed as a threatened species. At present, populations seem stable, and juvenile green turtle populations seem to be increasing in the seagrass beds around the Virgin Islands (Boulon 1989; Boulon, personal observation), but there are no significant signs of recovery despite more than a decade of protection (Eckert 1991).

The greatest threats to sea turtles in the Virgin Islands and Puerto Rico today are coastal and upland development, introduction of domestic and nonindigenous animals, boating (both commercial and recreational), incidental take in fisheries, illegal harvest of adults and eggs, ingestion of and entanglement in marine debris, inadequate local protection and enforcement of laws, and insufficient regional cooperation for turtle protection. Coastal and upland developments that are constructed without concern for their downstream effects cause degradation of nesting beaches, seagrasses, coral reefs, and mangrove areas, which are all critical components of sea turtle habitat. Upland developments also result in increased lighting of nesting beaches, which disorients both hatchlings and adults (Philibosian 1975; Witherington and Bjorndal 1991; Witherington 1992). Such light forces nesting turtles to move away from protected public beaches into adjacent areas, where they are more vulnerable to poaching. Beach landscaping for recreational use causes loss of sand and native vegetation, thereby changing the temperature regime of the nesting beach. Recreational activities also affect nesting beaches. Off-road vehicles (illegal on Virgin Islands beaches) can crush nests and leave deep tire tracks that trap hatchlings on their way to the sea. Introduced domestic and nonindigenous animals (dogs, pigs, goats, horses, and mongooses) harass nesting females and destroy nests and hatchlings. Mongooses destroyed 24% of the nests recorded on St. John in 1980–1981 (Small 1982), and feral hogs destroyed between 44% and 100% of hawksbill nests outside of fenced beaches on Mona Island, Puerto Rico, from 1985 to 1987 (Kontos 1985, 1987, 1988). Before 1981, when mongooses were removed from Buck Island Reef National Monument, St. Croix, they destroyed more than 50% of all hawksbill nests annually (Small 1982).

Local fishing practices, such as trap fishing and gill netting, are hazardous to sea turtles in nearshore waters throughout the Virgin Islands. Offshore, long-line fishermen targeting 1,000 fathoms set trap lines, which are 30 to 65 kilometers in length and which hold more than 400 hooks on each line. Long lines are set to catch swordfish and tuna but have accidentally snagged, or *foul hooked,* leatherback sea turtles. Once snagged by a hook, a turtle becomes entangled and either drowns or is attacked by sharks (W. Tobias, Department of Planning and Natural Resources, St. Croix, Virgin Islands, personal communication). Abandoned fishing gear is especially deadly, entangling and drowning turtles, especially nesting females, which remain near shore between nestings. Young sea turtles also may become entangled in or ingest marine debris. In recent years the number of sea turtles killed by boat collisions has increased, especially along ferry routes where turtles forage (Boulon, personal observation).

The illegal take of sea turtles (eggs, juveniles, and adults) is still a significant threat in the Virgin Islands and in Puerto Rico. Twelve persons were arrested in Puerto Rico in 1994 for selling sea turtle meat in several local restaurants (M. Evans, U.S. Fish and Wildlife Service, St. Croix, Virgin Islands, personal observation). Insufficient enforcement of protective laws greatly limits the effectiveness of legal protection for nesting sea turtles.

Public education programs have become the most effective weapon against the continued killing of sea turtles. Still, inconsistent regional protection of sea turtles, which use a variety of habitats in different areas during the various phases of their life cycle, offers them little overall protection in their foraging grounds or on their nesting beaches. Despite protective legislation in the U.S. Virgin Islands and Puerto Rico, the subsistence use of sea turtle meat and eggs and the harvest of hawksbills for their shells continue in adjacent island nations, posing a significant threat to the survival of sea turtles in this region.

The period for which data have been collected on sea turtles is extremely short compared with the long life of an individual sea turtle, which may require 20 to 30 years to reach sexual maturity and may be reproductive for 30 or more years (Frazer et al. 1994). Sea turtles are highly mobile and tend to return to particular nesting beaches (Hillis 1992; Melucci et al. 1992); in fact, genetic studies of female nesting populations indicate that female sea turtles may return to their natal beaches to nest (Bass et al. 1996). Once a nesting population is extirpated (removal of all eggs and adults) from a particular beach, it is unlikely that the nesting population will recover in the near future.

Sandy Point National Wildlife Refuge, St. Croix, is the principal nesting beach for leatherbacks in the northern Caribbean (Fig. 1). Tagging studies have shown movement by females among regional nesting beaches in Puerto Rico, Anguilla, and St. Croix (Eckert et al. 1989; Boulon et al. 1994; McDonald et al. 1995). A long-term saturation tagging program now provides essential information on leatherback turtle population trends in U.S. properties. Since 1981, of the 342 leatherback turtles tagged, 18–55 females have nested each year, laying between 82 and 700 nests (McDonald et al. 1995; Boulon et al. 1996). Researchers believe that before protection of leatherbacks, possibly 100% of the nests laid at Sandy Point were either destroyed by poaching or lost to beach erosion (seasonally a 50% to 60% loss). Since 1981 the beach at Sandy Point has been protected, and nests threatened by erosion have been relocated; nest loss is now less than 5% annually. Biologists speculate that the increase in the numbers of females nesting per season (given an average age to maturity for leatherbacks of 10 to 15 years) is a direct result of beach protection and nest relocation (Boulon et al. 1996; Fig. 2).

Observations of green turtle nesting populations have been collected incidentally by both leatherback and hawksbill turtle research programs in the Virgin Islands and Puerto Rico since the 1980's. In 1993 and 1994 daytime beach surveys were conducted for green and hawksbill turtles on St. Croix (Mackay 1994; Mackay and Rebholz 1995). The number of green turtle nests remains low for all the islands, but there appears to have been a gradual increase in the numbers of juveniles observed in the foraging grounds since the mid-1970's (Boulon, personal observation). The only island that still supports any green turtle nesting is St. Croix, which had an average of 100 nests per year between 1980 and 1990 (Eckert 1992). The largest concentration of green turtle nesting occurs on St. Croix's east-end beaches, which average 15 nests per year (Mackay and Rebholz 1995). This pristine area is now threatened by private development plans. In 1992 several green turtle nests were recorded on Isla Caja de Muertos, Puerto Rico, where illegal take of eggs and adults is still a risk (Diaz 1994).

There are very few places in the Caribbean where any large numbers of hawksbill turtles remain today (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993). In the Virgin Islands and Puerto Rico, hawksbill turtles nest on St. Croix (Buck Island Reef National Monument and east-end beaches), a few isolated beaches on St. John, St. Thomas (primarily on the offshore cays), and on Mona Island, Puerto Rico, as well as some scattered locations on mainland Puerto Rico, Culebra, and Vieques (Fig. 3). In 1993 only 32 hawksbill nesting activities were observed on all of St. John's beaches, even though more than 50% of the island remains an undeveloped national park (Mendelson 1993). In 1994, 100 hawksbill nesting activities were recorded on St. Thomas's offshore cays, 61% of which were on

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Fig. 1. A leatherback turtle nesting on the beach at the Sandy Point National Wildlife Refuge, St. Croix.

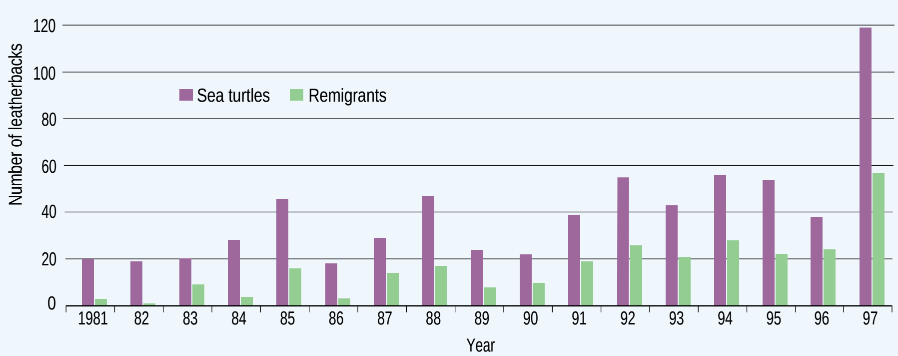

Fig. 2. The number of leatherback turtles and leatherback remigrants (that is, a nesting female who returns to nest at a particular site in subsequent nesting seasons) returning to nesting grounds at Sandy Point, St. Croix, U.S. Virgin Islands, 1981 to 1997 (modified from Boulon et al. 1994).

Courtesy Z. M. Hillis-Starr, National Park Service

Fig. 3. A hawksbill nesting.

Greater Hans Lollick, which is threatened by a proposed major hotel development (Boulon 1994).

The most important concentrations of hawksbill turtles are on Mona Island, Puerto Rico, St. Croix, and on Buck Island Reef National Monument, St. Croix's east-end beaches (Jack's Bay, Isaac's Bay, east-end bays). Mona Island supports more than 160 hawksbill nests annually, laid by about 30 to 40 adults (Kontos 1985, 1987, 1988; van Dam and Sarti 1989; Richardson 1990; van Dam 1990; van Dam and Pares 1991). Hawksbill nesting on Mona Island is still subject to illegal take and feral pig predation, but the Puerto Rico Department of Natural Resources continues conservation and enforcement efforts (Pares-Jordan et al. 1994).

Buck Island and St. Croix's east-end beaches support two remnant populations of between 20 and 30 nesting hawksbill turtles per season (Hillis 1994a; Mackay 1994). Since 1988, 84 individual hawksbill turtles have been tagged while nesting on Buck Island Reef National Monument. Hawksbill turtles return to nest every 2 to 4 years, indicating a high degree of nesting beach fidelity (Hillis 1992). Of these remigrants, between 50% and 80% have returned to nest in subsequent years, which demonstrates the high survivorship of adult sea turtles (Hillis 1994b; Frazer et al. 1996). Although annual survival of adult hawksbill turtles is high (Frazer et al. 1996), unfortunately, annual recruitment to the Buck Island population remains low (10%–15%; Hillis 1994b; Fig. 4). In 1994 a saturation tagging program began on St. Croix's east-end beaches; 14 hawksbill turtles were tagged that season (Mackay 1994), but to date, no Buck Island hawksbill turtles have been observed nesting there. These two populations are possibly distinct from each other (Mackay and Rebholz 1995; Bass et al. 1996). To successfully manage the highly migratory hawksbills, it is essential to resolve the identities of their reproductive populations in the Caribbean (Bass 1994; Bass et al. 1996).

Recent studies of juvenile foraging populations of hawksbill turtles at Mona Island and Buck Island Reef show juvenile hawksbill turtles residing in particular sections of reef over time (van Dam and Diez 1995; Hillis and Phillips 1996). Because juveniles stay in nearshore habitats, coral reefs, and seagrass beds, and because of their slow growth to maturity (15–30 years), their chances increase of being harmed through interactions with humans before they reach sexual maturity. Human actions that harm juvenile sea turtles living in nearshore habitats include boat–turtle collisions, turtle entanglement in abandoned fishing gear, ingestion of marine debris, degradation of habitat and food sources, and illegal capture. If a sea turtle reaches reproductive age, it faces a potential absence of mates and lack of suitable nesting habitat.

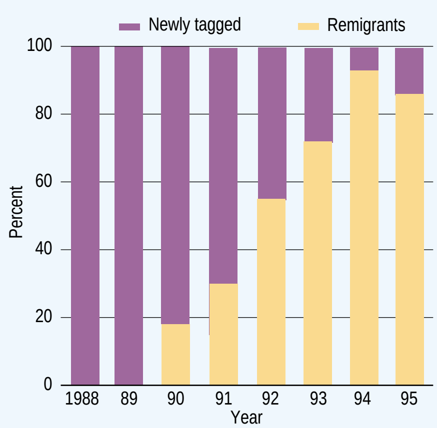

Fig. 4. Results of saturation tagging efforts of remigrant versus newly tagged hawksbills at Buck Island (Z. M. Hillis-Starr, National Park Service, Buck Island Reef National Monument, St. Croix, Virgin Islands, unpublished report).

Any discussion of status and trends of sea turtle populations in the U.S. Virgin Islands and Puerto Rico is incomplete without mention of conflicting regulations in the adjacent British Virgin Islands. About a kilometer east of St. Thomas and St. John, the British Virgin Islands have a 4-month open season (December to March), allowing legal take of sea turtles. In addition, the sale of tortoiseshell items is legal year-round there. This unresolved conflict between two neighboring jurisdictions is the single greatest threat to sea turtle protection in the U.S. Virgin Islands and Puerto Rico.

The British Virgin Islands have historically supported a large turtle fishery. Leatherback turtles were harvested for oil, and all sea turtle eggs were collected for consumption. In the 1920's, during one nesting season, six leatherback females came ashore to nest each night on two beaches in Tortola (Eckert et al. 1992). By 1990 only ten leatherback females came ashore to nest in all of Tortola. By 1991 only four females were observed nesting, and two of those were slaughtered (Eckert et al. 1992). On many beaches, leatherbacks have been completely extirpated. Records of harvest during open season show a similar decline for green turtle and hawksbill populations. In 1981, 700 green turtles were taken, compared with 71 in 1990–1991. In 1981, 400 hawksbill turtles were captured, compared with 32 in 1990–1991 (Eckert 1992). The dramatic decline of sea turtle populations in the British Virgin Islands has prompted the recommendation of stricter regulations to the British Virgin Islands Ministry of Natural Resources, for adoption by the UNEP/Widecast Sea Turtle Recovery Action Plan of 1992. Until such regulations are adopted and enforcement is improved, there is still no protection for sea turtle eggs and no size restriction on turtles harvested during open season in the British Virgin Islands.

Today, illegal trade in tortoiseshell persists and illegal take of turtles for meat continues. Confusion exists among U.S. and British Virgin Island residents about sea turtle products purchased outside the jurisdiction of the United States. Turtle products legally purchased in the British Virgin Islands are frequently brought to the U.S. Virgin Islands with the owner having no knowledge of the prohibitions on importation of sea turtle products. The items are seized and fines are possibly levied (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993).

See end of chapter for references

Authors

Zandy-Marie Hillis-Starr
National Park Service
Buck Island Reef National Monument
Danish Customs House
Kings Wharf
Christiansted, U.S. Virgin Islands 00820-4611

Ralf Boulon
Government of the Virgin Islands
of the United States
Department of Planning and Natural Resources
Division of Fish and Wildlife
101 Estate Nazareth
St. Thomas, Virgin Islands 00820

Michael Evans
U.S. Fish and Wildlife Service
Sandy Point National Wildlife Refuge
Federal Building
3013 Golden Rock
Christiansted, Virgin Islands 00820-4355

Birds

A combined total of 247 native bird species live in Puerto Rico (239 species) and the U.S. Virgin Islands (199 species; Raffaele 1989). In addition, many nonindigenous bird species from other areas of the world were introduced to the islands over the last 200 years. The rate of introduction of nonindigenous birds has greatly increased in recent decades; these additions have increased the region's total number of species by 37, with most (36) of these nonindigenous releases known for Puerto Rico. Far fewer species (11) have been introduced to the Virgin Islands (Raffaele 1989). Of Puerto Rico's 239 native bird species, 12 (5%) are endemic to the island. The Virgin Islands have no endemic species, although they share two species that occur only in common with Puerto Rico.

Twelve resident or migrant bird species or populations have been listed under the U.S. Endangered Species Act because of declining populations; the red siskin, an introduced species, is also listed (see Wiley 1985; Table 2). An additional eight species of Puerto Rican and Virgin Islands birds have been proposed as species of concern (S. Silander, personal communication). These include four native waterbird species (the white-cheeked pintail, the West Indian whistling-duck, the West Indian ruddy duck, and the Caribbean coot), as well as two species of forest birds (the elfin woods warbler and the Virgin Islands screech-owl).

Recovery efforts have been made for some of the federally listed species, including the Puerto Rican parrot (Fig. 14), Puerto Rican nightjar (Fig. 15), Puerto Rican plain pigeon, and the yellow-shouldered blackbird (Fig. 16). These efforts have been particularly intense for the pigeon, parrot, and blackbird (Fig. 17) and include population monitoring; nest monitoring; habitat management; predator, competitor, and parasite control; and management of captive populations (parrot and plain pigeon). Recovery efforts for the nightjar have been


Courtesy J. Wiley, USGS

Fig. 14. Endangered Puerto Rican parrot.

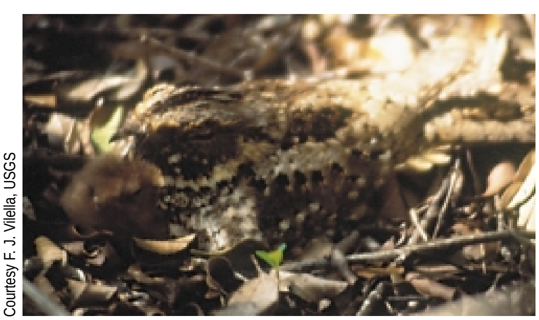
Courtesy F. J. Vilella, USGS

Fig. 15. Adult male Puerto Rican nightjar brooding a 3-day-old chick at Guánica Forest, Puerto Rico.


Courtesy J. Wiley, USGS

Fig. 16. Endangered yellow-shouldered blackbird, endemic to Puerto Rico.

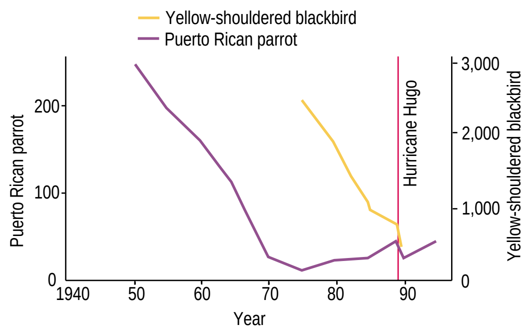

Fig. 17. Population trends of two critically endangered bird species, the Puerto Rican parrot and the yellow-shouldered blackbird.

primarily limited to field research for mapping geographic distribution and abundance and for identifying ecologically limiting factors.

Mammals

Bats are the only native terrestrial mammals left on Puerto Rico and the Virgin Islands. Presumably, bats had adaptations that helped them elude the invading nonindigenous predatory and competitive species. Nevertheless, several of the native bats are threatened by human-caused disturbances and habitat change. Puerto Rico has 13 species of bats, including 7 that are endemic to the Antilles, but none are exclusive to Puerto Rico. The Virgin Islands have 4 bat species, one of which is an endemic of the Greater and Lesser Antilles, but none are endemic to the Virgin Islands (Griffiths and Klingener 1988).

Ten of the thirteen extant bat species in Puerto Rico are cave dwellers. Cave-dwelling bats in Puerto Rico have low reproductive rates and are especially vulnerable to environmental disturbances (A. Rodríguez-Durán, Interamerican University of Puerto Rico, San Juan, personal communication). Bats that inhabit caves are particularly sensitive to direct disturbances, such as the entrance of people into the caves, as well as to indirect disturbances, including the spraying of pesticides or microclimatic changes in caves due to alterations to the cave opening. About 31% of Puerto Rico's caves host bat colonies varying in size from a few to hundreds of thousands of individuals (Rodríguez-Durán 1993). Increasing interest in caves for tourism and the use of chemical agents in insect control pose serious threats to the island's cave bat populations. The red fig-eating bat is a species of concern (U.S. Fish and Wildlife Service 1994b).

Nonindigenous Species

The native ecosystems of Puerto Rico and the Virgin Islands have been seriously disrupted by the introduction of many nonindigenous plant and animal species. At least 118 nonindigenous plant species are reproducing in Puerto Rico (Francis and Liogier 1991). In addition, an undetermined (but likely large) number of invertebrates have become established in Puerto Rico and the Virgin Islands. The nonindigenous vertebrate faunas are better known for the islands, with 24 fishes, 2 reptiles, 4 amphibians, more than 37 birds, and 13 mammals established in breeding populations. Although these introductions may be viewed by some as offsetting the losses of species through extinctions and extirpations, nonindigenous species do not usually fit smoothly into the new ecosystems but instead become aggressive predators on or competitors with native species. Species that have developed on remote oceanic islands in the absence of such predators or competitors are usually at a great disadvantage and may easily fall victim to such invaders.

The history of introductions to Puerto Rico and the Virgin Islands is a long one, perhaps pre-dating the arrival of Europeans in the region. Even so, the rate of introductions, as in other parts of the world, has greatly accelerated as human travel became faster and easier. Rapid and frequent transportation among the islands and mainlands has provided easy access to what were formerly remote regions. Furthermore, our society's increasing interest in stocking gardens with nonindigenous plants and in keeping exotic pets has also aided in the higher rate of nonindigenous species becoming established in the region. These introduced organisms pose a critical problem in the islands, not only because they sometimes threaten food crops but also because they challenge the existence of native species.

Ironically, Puerto Rico may be viewed as an important sanctuary for several nonindigenous species that are experiencing severe population declines or are facing extinction in their native ranges elsewhere in the world. For example, numerous parrot species, including some of those resident in Puerto Rico, are being excessively harvested for the pet trade industry, and continued removal of these birds from their home countries will likely result in more species listed as endangered. The endangered red siskin was probably introduced to Puerto Rico in the nineteenth century and may now occur there in greater numbers than in its native Venezuela and Colombia (Raffaele 1983). In recent years, the Department of Natural and Environmental Resources in Puerto Rico has considered extending protected status to the red siskin, despite its status as an introduced species (J. L. Chabert, Puerto Rico Department of Natural and Environmental Resources, San Juan, personal communication). Such concern stems from the fact that in Puerto Rico, red siskins are being captured by bird collectors

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who can legally trap nonindigenous species for export. At present, red siskins are extremely rare in Puerto Rico (F. F. Rivera-Milan, U.S. Fish and Wildlife Service, Washington, D.C., personal communication). Similarly, the Cuban ground iguana is classified as vulnerable in its native range of Grand Cayman and Cuba, but introduced populations in Puerto Rico are thriving. It is conceivable that Puerto Rican populations of such species may someday be valuable as reservoirs for reintroducing species into reserves in their native lands.

Plants

Because of the extensive cutting and modification of natural forests, widespread agriculture, and introduction of many nonindigenous species, little remains of the original vegetation found in Puerto Rico and the U.S. Virgin Islands. Many introduced nonindigenous tree species have become naturalized in the forests of the islands. Common naturalized trees in the humid forests of Puerto Rico include pomarrosa, emajagua, almendra, mountain immortelle, and tulipán Africano. On the dry southwestern coast of Puerto Rico, bayahonda has become naturalized in pastures. In the U.S. Virgin Islands, an outstanding naturalized tree in the forest (particularly in St. Croix) is Dominican mahogany and, in pastures, tibet.

The native vegetation of these islands developed in the absence of large herbivorous mammals and, consequently, may have been quite susceptible to introduced goats and cattle (Fig. 18). Dry forests, which are restricted in Puerto Rico but widespread in Mona, Desecheo, Vieques, and Culebra islands, and also in the Virgin Islands, have been damaged by grazing animals. Nonetheless, Desecheo and Mona islands have been free of permanent human occupation for many years because of the absence of abundant sources of fresh water, the islands' small sizes, and their rough topography. Thus, these islands include some of the best examples of dry forest left in the region. The naturalization of introduced grasses usually occurs as dry forest areas are subjected to selective cutting and high grazing pressures. Periodic fires during the height of the dry season can become a recurring problem at disturbed sites and prevent native trees from becoming established.

Animals

The introduction of animals has had enormous effects on island ecosystems throughout the world (Vitousek 1988). The most disruptive species include vertebrate and invertebrate predators and herbivorous mammals. Most

Courtesy J. Wiley, USGS

Fig. 18. Seabird nesting habitat damaged by feral livestock, Culebra National Wildlife Refuge.

extinctions of birds (King 1985) and mammals (Morgan and Woods 1986) in the West Indies have been attributed to habitat loss and the introduction of rats, cats, dogs, and mongooses. Puerto Rico and the Virgin Islands are now home to all of these nonindigenous species.

Invertebrates

Native populations of freshwater snails, including *Physa cubensis*, have been affected by several introduced snails (Erdman 1972). An African species, the quilted melania, is now the most abundant snail in Puerto Rico. At least one introduced snail species has had a more direct effect on humans; for example, the snail *Australorbis glabratus*, a possible introduction from South America, is an intermediate host for the debilitating human parasite *Schistosoma mansoni* (Erdman 1972).

European honey bees, now established throughout the islands, were introduced by the earliest colonists. Honey bees have proven to be fierce competitors for natural cavities used as nests and roost sites for several native species, including the endangered Puerto Rican parrot. Africanized honey bees recently became established in Puerto Rico (Vilella 1995). These aggressive bees pose an even more serious threat to native cavity nesters and to wildlife managers maintaining nesting sites for some species.

Freshwater Fishes

Numerous established nonindigenous species have been intentionally or accidentally released into native waters from aquarium stocks. Several other species have been established as game species. About 24 species are

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established in Puerto Rico and 9 in the Virgin Islands (Erdman 1972; Ogden et al. 1975; Burgess and Franz 1989).

Reptiles and Amphibians

Three nonindigenous reptile species and four nonindigenous amphibian species have become established in Puerto Rico and the Virgin Islands. Common caimans, probably escaped or released pets, have become established in some swamps on Puerto Rico. The green iguana was apparently introduced on the island of Icacos in the Cordillera de Fajardo around 1970; others have been sighted on Culebra Island. Breeding populations of the common iguana are found in eastern Puerto Rico. In Fajardo, groups of nesting iguanas are commonly seen near the beach in the coastal forest reserve of Las Cabezas de San Juan, which is owned and managed by the Puerto Rico Conservation Trust. The red-footed tortoise has also been introduced to the Virgin Islands.

The marine toad, which is native to tropical America, was introduced to Puerto Rico around 1919 to control insect pests of sugarcane. The species proliferated and helped reduce cane pests, but it also competes with the endangered ridge-headed toad for food, habitat, and spawning sites. The bullfrog was introduced from North America in 1935–1936 with the intent of supplying an additional source of nutrition for poor people who lived directly off the land (Erdman 1972). Although the bullfrog became established in moderate numbers in many of the swamps and ponds of the Coastal Plain, it has never been accepted as a potential human food source.

Birds

At least 32 species of nonindigenous birds have become established in breeding populations in Puerto Rico and the Virgin Islands (Raffaele 1989); an additional 5 species are suspected of breeding in the region. Most nonindigenous bird introductions are probably the result of accidental releases, but some species were purposely released. Populations of northern bobwhite, introduced as game to Puerto Rico and the Virgin Islands, may survive in small populations, probably because of a lack of suitable habitat and because of predation by introduced mammals. The well-established troupial and turkey vulture were also intentionally introduced to Puerto Rico (V. Barnés [deceased], Puerto Rico Division of Fisheries and Wildlife, personal communication). Many species of cage birds have become established in Puerto Rico. Whereas certain nonindigenous species (for example, some estrildid finches inhabiting grasslands) have had no apparent effect on native wildlife or plants, others are a current or potential threat to native wildlife or crops. House sparrows and European starlings have become entrenched in metropolitan areas within the last 20 years, although the European starling remains uncommon, if not rare (Rivera-Milan, personal communication). Nonindigenous hill mynas and white-vented mynas compete with native cavity-nesting species, such as the Puerto Rico screech-owl, and with introduced psittacines (J. Wiley, U.S. Geological Survey, Grambling, Louisiana, personal observation) for the limited nest sites available. More than 14 species of nonindigenous parrots breed in Puerto Rico (Raffaele 1989) and may pose a threat to the endangered Puerto Rican parrot as competitors for nest sites and food resources, and perhaps through interbreeding and diseases they may carry. Fortunately, none of the nonindigenous parrots have yet entered the virgin forest of Luquillo. However, several nonindigenous species of parakeets, such as the monk parakeet and the orange-fronted parakeet, have become locally abundant and nest in areas of secondary forest surrounding the Luquillo Forest Reserve.

Another nonindigenous species, the shiny cowbird, was indirectly aided by human land-use changes in its invasion of the Virgin Islands and Puerto Rico. The cowbird "island hopped" north from its native South America through the West Indies as original forests were cut to make way for agriculture and pasturelands (Post and Wiley 1977). It arrived in Puerto Rico sometime in the 1940's or early 1950's. The cowbird is a brood parasite (that is, it lays its eggs in other birds' nests), and its parasitic habits have caused some populations of native species to decline (Cruz et al. 1989). Of particular concern is the dramatic decline of Puerto Rico's endemic yellow-shouldered blackbird.

Introduced Mammals

Possibly the earliest human-aided introduction of mammals to the Puerto Rican Bank was the Puerto Rico hutia, a large edible rodent (Steadman et al. 1984a,b), which was brought to Puerto Rico from Hispaniola by native people. The arrival of European colonists accelerated the decline of hutias through increased demand for meat, clearing of forests, and introduction of predators (Allen 1942).

Perhaps the hutia had little effect on native faunas and floras of Puerto Rico and the Virgin Islands, but many subsequent introductions made in colonial times and more recently have had devastating effects on native ecosystems. The combination of competition and predation by introduced forms is the most likely reason for the extinction of several West Indian mammals (Woods 1989b).

Introduced Rodents

The house mouse and black and Norway rats probably arrived when Columbus landed on the western Puerto Rican beaches. Rats are now distributed throughout all natural habitats in the West Indies and occur in large numbers (Woods et al. 1985). Rodents have been implicated in the declines of several native mammal, bird, and reptile populations.

Mongoose

The small Indian mongoose was introduced in various islands of the West Indies from 1872 to 1925 to help control rats and snakes (Wadsworth 1949; Wolcott 1953; Nellis and Everard 1983; Hoagland et al. 1989). Today, mongooses occur in a wide variety of habitats in the West Indies, from sea level to more than 2,000 meters, and have been accused of considerable damage to the natural faunas in those regions (Allen 1911; Seaman 1952; Seaman and Randall 1962; Raffaele 1989). Mongoose populations established on small cays and islands can be highly destructive to native fauna, particularly to reptiles and colonial seabirds (Philibosian and Ruibal 1971). On larger islands like Puerto Rico, though, the effect of mongooses as a primary limiting factor for terrestrial vertebrates is harder to elucidate (Vilella and Zwank 1993).

Cats and Dogs

Cats and dogs are particularly destructive to native wildlife on small islands. Although cats and dogs were introduced into the West Indies hundreds of years before the mongoose (Crosby 1991), it is only relatively recently that they have been implicated for any damage inflicted on native animal populations (for example, Mittermeier 1972; Wiewandt 1977; Iverson 1979; Tolson 1988; Woods 1989a).

Monkeys

A group of 57 rhesus macaques was released on Desecheo Island in 1966 so that researchers could study the process of adaptation in free-ranging monkeys (Morrison and Menzel 1972). The project was subsequently abandoned, and Desecheo was designated a national wildlife refuge in 1976. Meanwhile, the once-important brown booby and red-footed booby colonies there underwent dramatic declines, which some biologists have attributed to the predation of booby eggs by these nonindigenous monkeys (Evans 1989; Meier and Crider *in* Evans 1989). Efforts to trap the monkeys began in 1977 and continued through 1987 (summarized in Evans 1989). Some monkeys, however, remain on the island, and seabird colonies have not begun to recover (Evans 1989; J. González-Martínez, Caribbean Primate Research Center—University of Puerto Rico, Sabana Seca, personal communication).

Macaques were also established on islands off the coast of Puerto Rico, but escapees from those colonies have reached Puerto Rico, where they range widely through the southwest (J. González-Martínez, personal communication). The degree of threat posed by these nonindigenous animals is unknown. Aside from the inappropriateness of the species in the ecosystem, there is a threat to native animals such as the endangered Puerto Rican nightjar (a ground-nesting species) and the yellow-shouldered blackbird.

Several acts of vandalism from 1976 to 1978 resulted in the escape of 107 common squirrel monkeys at Sabana Seca, Puerto Rico (González-Martínez, personal communication). That population is now free-ranging and in 1984 consisted of about 155 individuals. By 1994 the population consisted of about 35 individuals; the decline is possibly related to damage by Hurricane Hugo in 1989. Escaped squirrel monkeys have also been found in the Luquillo Forest and at Lago de Cidra—both areas harbor endangered native species.

Game Mammals

Several attempts have been made to establish various game species in Puerto Rico and the Virgin Islands. White-tailed deer were released on Culebra Island in 1966 and have become established in small numbers. White-tailed deer were introduced to the Virgin Islands before 1800. The deer survive on St. Thomas and St. Croix islands (Seaman 1966).

Feral Livestock

Habitat stripping by grazing livestock (domestic and feral) is commonplace in the West Indies, where stock was introduced by the early colonists (Rudman 1990). As previously discussed, competition among feral and native animals does occur, as does predation of birds and lizards by feral pigs. Feral animals have also been implicated in the decline of certain endangered plants; including Wheeler's peperomia and higo chumbo (Lowe et al. 1990). Hunting of feral pigs and goats is allowed on Mona Island.

Knowledge Gaps and Ecological Outlook

The islands in the Puerto Rican Bank have been practically denuded of native vegetation, have extremely dense human populations, and face an associated array of environmental problems. Not surprisingly, the number of species heading toward extinction, or recently extinct, is rapidly increasing. Still, with continued aggressive conservation efforts, Puerto Rico and the U.S. Virgin Islands may retain the best-preserved examples of certain natural ecosystems in the West Indies. Unfortunately, most other islands of the West Indies are undergoing accelerating habitat destruction for agriculture, leaving little reason for optimism regarding the future of their natural resources. Changing trends in the economics of Puerto Rico and the Virgin Islands have created an environment favorable for conservation of natural resources. Showcases of natural ecosystems as part of the image of these tropical islands are vital to the tourist industries, which are important to the economies of Puerto Rico and the Virgin Islands. Moreover, there is an increased awareness and concern about environmental and conservation issues among local residents, especially young people.

Most forested lands of the islands are second-growth. The role of plantations and second-growth forests in the rehabilitation of degraded ecosystems should be a priority for research investigations (Parrotta 1992) because a clear understanding of the ecology of plantations and recovering habitats is essential for managing the flora and fauna (Cruz 1988).

Human population growth in Puerto Rico and the Virgin Islands is of concern because human populations will continue to increase in the islands. Although human populations are concentrated in cities, there is a trend toward dispersion of tourist facilities and residential country homes. Many examples of relict ecosystems have been set aside in various state and federal reserves, although lack of money and other resources hampers the management of these areas. Because of the extensive fragmentation of habitats, many populations of plants and animals remain at extremely low levels, which puts them at great risk of local or rangewide extinctions. Forest cover is increasing with the shift away from an agricultural economy, but the resulting second-growth forests are often a mixture of native and nonindigenous species, or are replaced with monocultures of timber-producing trees. Such environments may not provide native species with appropriate habitats. In addition, saline flats, freshwater marshes, and freshwater swamp forests all face developmental pressures in Puerto Rico and the Virgin Islands. Mangrove forests and freshwater wetlands face the greatest risks; these highly productive ecosystems need greater protection. Also, if predictions for global warming prove correct, the frequency of hurricanes in the Caribbean is expected to increase (O'Brien et al. 1992). Consequently, ecosystems can be expected to change in response to the warming trend and to the increase in the frequency of tropical storms.

Scientific knowledge about several groups of organisms is lacking; the frog species undergoing precipitous population declines in the last two decades are cases in point. Likewise, little is known about the status of many invertebrate groups.

The West Indies are critical wintering habitat for certain migratory animals, especially birds. We need to determine the ecology of resident and migrant populations, particularly as related to remnant tracts of natural habitat and areas of recovering vegetation.

With proper maintenance of these reserves, most species of plants and animals will survive as remnant populations. Still, it is vital to ensure that populations are distributed among several parts of the islands as insurance against such natural disasters as hurricanes or the possibility of exotic diseases.

It is likely that Puerto Rico and the Virgin Islands will be able to maintain showcase ecosystems into the future. Because their economies are largely based on tourism, the establishment and maintenance of such examples of original ecosystems are beneficial to these countries. Beyond maintaining the biotic remnants of what now survives in the islands, an exciting opportunity is available to islanders: restoration of some original ecosystems (Wiley 1985). Even though extinctions have caused the disappearance of certain components of recently pristine ecosystems, other species, although extirpated from Puerto Rico or the Virgin Islands, still survive in other islands. Some of those surviving populations are rapidly declining, however, and may become extinct within decades.

Citizens of Puerto Rico have developed a strong conservation ethic. Such an ethic, along with well-enforced regulations to safeguard plants and animals, provides an excellent environment for restructuring some of the original ecosystems. Examples of the wet limestone forest of northwestern Puerto Rico, in large part within the state forest system, could be rehabilitated and, through introductions of native species, critical elements of the original ecosystem could be restored to the area. To do this, the current network of state limestone forest reserves must be expanded and, whenever possible, connected by conservation corridors. At present the area encompassed by limestone forest reserves totals approximately 4,586 hectares, with two of these, the Cambalache and the Vega, existing as small sets of forest fragments isolated from each other. Together, all these forest reserves are less than half the area of the Luquillo Forest Reserve (10,920 hectares; Fig. 19). Additionally, all but one of these limestone forest reserves (Guajataca) are being further degraded and fragmented by a major highway project.

Puerto Rican parrots and plain pigeons, now surviving as small populations in other parts of the island, are scheduled for release in the limestone forest. White-necked crows, limpkins, and rock iguanas, all surviving on other islands, could be reintroduced to these forests. Such restoration attempts should not be delayed too long, though, because the numbers of some surviving species from the original ecosystems are severely declining.

Ironically, Puerto Rico may become a sanctuary for several species facing extinction in their natural ranges. Through innovative reintroductions, entire ecosystems may be reestablished in these islands.

Fig. 19. Public forestlands of Puerto Rico. Green areas represent the Commonwealth Forests (Bosques Estatales) and the Caribbean National Forest, including the Luquillo Experimental Forest. Forestlands are represented by yellow areas (after Little et al. 1974).

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Authors

James W. Wiley
U.S. Geological Survey
Biological Resources Division
Division of Cooperative Research
Grambling Cooperative Wildlife Project
P.O. Box 4290
Grambling State University
Grambling, Louisiana 71245

Francisco J. Vilella
U.S. Geological Survey
Biological Resources Division
Division of Cooperative Research
Mississippi Cooperative Fish and Wildlife Research Unit
Mail Stop 9691
Mississippi State University
Mississippi State, Mississippi 39762

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