Luquillo Experimental Forest: Research History and Opportunities

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Editors

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1. Introduction

N.L. Harris

Tropical forests cover an area of approximately 1.8 billion hectares (ha), or nearly 50 percent of the world's total forest area (Food and Agriculture Organization 2003). Tropical forest ecosystems are often introduced to students of ecology by dividing them into two types, based solely on rainfall patterns—rain forests and dry or seasonal forests. Although this representation may provide a simple, approachable view, it fails to illustrate the true diversity of all tropical forest types and promotes the extrapolation of limited data sets over large and heterogeneous regions to produce broad, sweeping generalizations about all tropical forests worldwide.

The Holdridge Life Zone System (Holdridge 1967), which is based on empirical data and ecophysiological principles, provides a more comprehensive picture of tropical forest types: of the world's 112 life zones, more than one-half (66) are tropical and 33 include forests (out of 52 forested life zones in the world; Lugo and Brown 1991) (fig. 1). Thus, from a climatic perspective, tropical forests are more diverse than all other forest types combined. Understanding this diversity has posed a challenge even to seasoned ecologists, because describing the diversity of forest types becomes even more complicated when considering local factors, such as geologic formation, soils, topography, and aspect, as well as forest function and responses to natural and anthropogenic disturbances.

When using the life zone approach, the guiding principle that underlies the diversity of tropical forests is that multiple environmental conditions—not just precipitation regime—dictate the organization, composition, and functioning of ecosystems from local to global scales. Therefore, ecological comparisons among ecosystems require a clear understanding of factors relevant at the various spatial, temporal, and biological scales.

The Luquillo Mountains in Puerto Rico provide an excellent natural research laboratory in which to study the diversity of tropical forest types, because five subtropical life zones are represented within an area of just over 11,000 ha: wet forest, rain forest, lower montane wet forest, lower montane rain forest, and a small tract of land in the southwest portion that falls within the moist forest life zone. Puerto Rico falls within the subtropical belt of the Holdridge Life Zone System because of the temperature regime; frost is absent from all tropical and subtropical life zones. The region is also steeped in a rich tradition of forestry research that is unique among tropical forests; scientists have been active there since the end of the 19th century.

In 1983, Brown et al. summarized major findings of past research that once had been scattered among obscure papers and

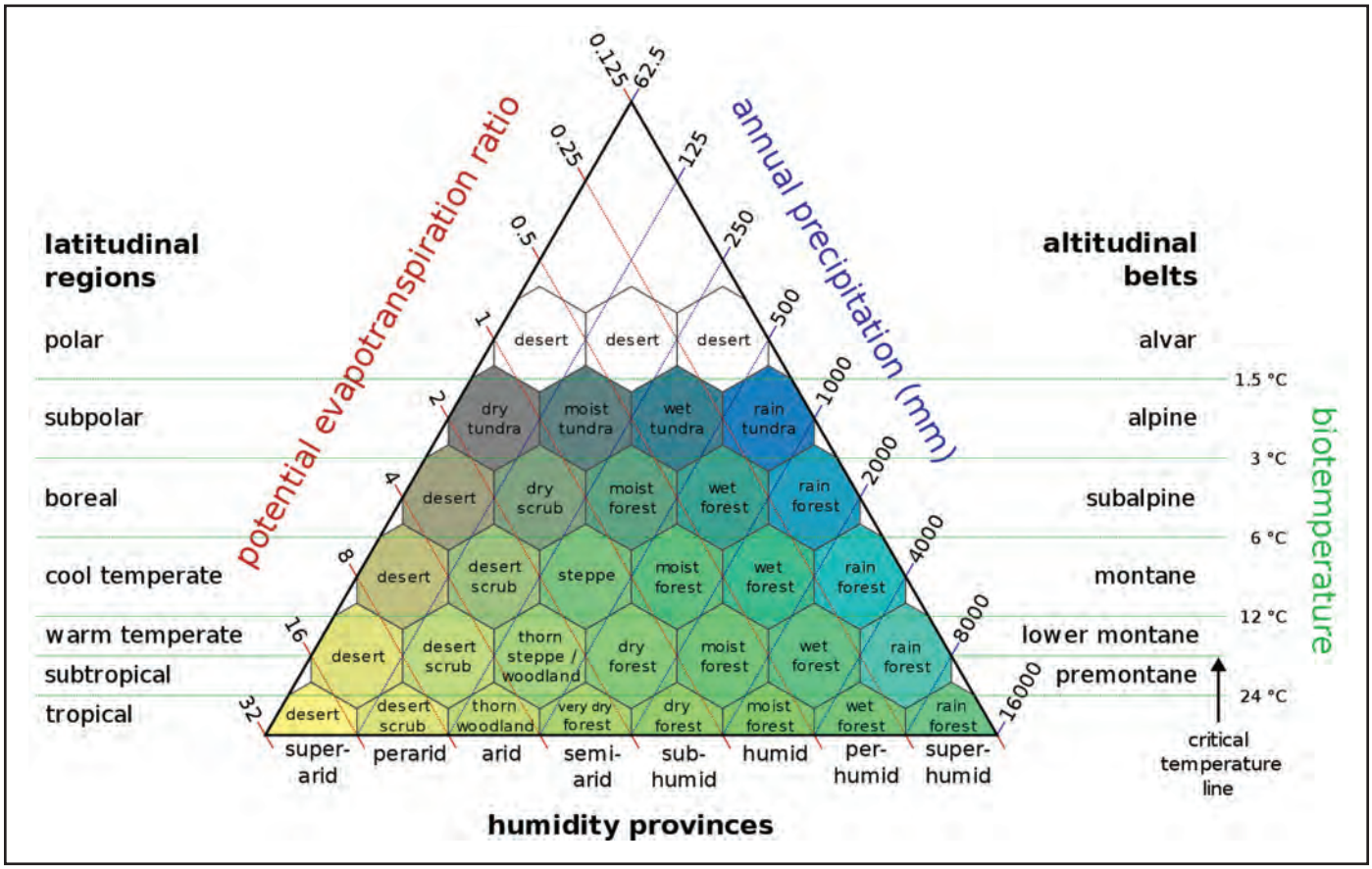

Figure 1.—Holdridge Life Zone System. From http://en.wikipedia.org/wiki/Holdridge_life_zones.

large and inaccessible volumes to produce a succinct yet data-rich summary that is still widely cited more than 25 years later. Since the publication of Brown et al. (1983), significant new research has led to new hypotheses and new conclusions about how tropical forests function. Improvements in technology and data storage over the past 25 years have resulted in vast new data sets, syntheses, and models for the Luquillo Experimental Forest (LEF) that were once unimaginable due to data storage and processing limitations (e.g., Harris et al. 2008; Harris et al. in press; Heartsill Scalley et al. 2007; Wang et al. 2002; Wu et al. 2006a, 2006b).

The goals of this *Luquillo Experimental Forest: Research History and Opportunities* are to synthesize the new research that has emerged from the LEF since the publication of Brown et al. (1983) into a concise summary of key research findings and to highlight opportunities for future research that will contribute to a greater understanding of the structure and function of tropical forested ecosystems in a changing world. The basic structure of this publication remains similar to the Brown et al. version, but the data presented in each chapter reflect new knowledge and new ideas that have arisen through the extensive work of modern-day researchers. Although some basic information from the Brown et al. (1983) version remains included in this version, it is assumed that the interested reader will consult the original version for detailed information on data published before 1983.

2. General Description of the Research Area

N.L. Harris

Located at 18º N latitude and 66º W longitude in the northeastern Caribbean Sea, Puerto Rico is an archipelago, encompassing Vieques, Culebra, Mona, Desecheo, Caja de Muertos, and numerous cays. The main island is the smallest (8,895 square kilometers (km^2)) in the Greater Antilles island chain. The island boasts a population of nearly 4 million people, however, making Puerto Rico one of the most densely populated places on Earth (429 inhabitants km^{-2}; U.S. Census Bureau 2000). The Luquillo Experimental Forest (LEF) is located in the Luquillo Mountains in the northeast corner of the island, approximately 30 miles (48.3 km) east of the capital of San Juan and southwest of the municipality of Luquillo (fig. 2). Ocean and trade winds moderate the island's climate. Another large mountain chain in the middle of the island (the Cordillera Central, or Central Mountain Range) creates a rain shadow, such that annual precipitation across the island spans a gradient of almost 5,000 millimeters (mm) from the Luquillo Mountains on the windward northeast coast to the Guánica dry forest (800 mm of annual rainfall) on the leeward southwest coast. One of the deepest points of the Atlantic Ocean lies several kilometers northwest of the Luquillo Mountains, a factor that, coupled with the long wind fetch of the Atlantic, contributes to high-energy conditions and thus frequent hurricanes on the north coast of the island (Lugo 2008). Of the land surface of Puerto Rico, 85 percent falls within the subtropical moist and subtropical wet life zones (Thomlinson et al. 1996).

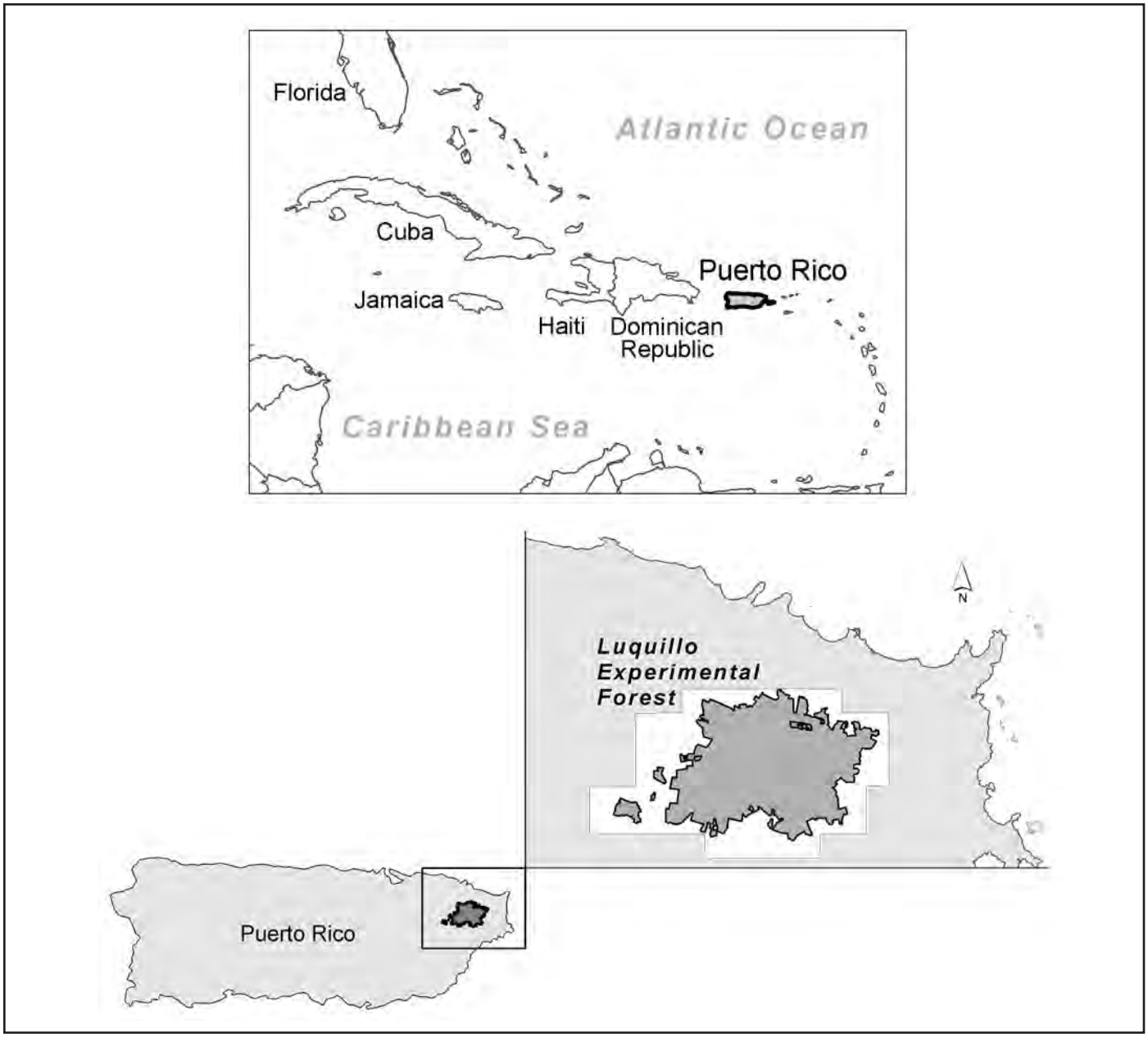

Figure 2.—The Luquillo Experimental Forest in Puerto Rico. From Lugo and Heartsill Scalley (in press).

The Luquillo Mountains rise from the coast to over 1,000 meters (m) above sea level, with El Yunque Peak (1,065 m in elevation) located 8 km (straight line distance) from the nearest beach (fig. 3). Other mountain peaks include El Toro (1,075 m), Pico del Este (1,050 m), Pico del Oeste (1,020 m), El Cacique (1,020 m), Los Picachos (968 m), Mount Britton (937 m), and La Mina (925 m). Moist air from the trade winds coming off the Atlantic Ocean cools and condenses as it rises up the steep, dissected mountain slopes, resulting in mountain peaks shrouded in cloud cover most of the time. Heavy rainfall at the peaks serves as the headwaters for six major rivers: Río Espíritu Santo, Río Grande de Loíza, Río Blanco, Río Mameyes, Río Fajardo, and Río Sabana (fig. 3). These rivers provide the main water supply to approximately 20 percent of the island's population. Air temperature decreases up the mountain, with average monthly temperature ranging between 23.5 and 27 ºC (74 to 81 ºF) at the base of the mountain to between 17 and 20 ºC (63 to 68 ºF) on the mountain peaks (García Martinó et al. 1996).

Variation in climatic conditions in the Luquillo Mountains results in a shift in vegetation and community structure over a relatively small area. Tabonuco trees (*Dacryodes excelsa*) dominate forests at low elevations in the LEF (fig. 4a), while palo colorado (*Cyrilla racemiflora*) with reddish leaves and bark dominates at mid-elevations (fig. 4b). Palm forests, dominated by the sierra palm (*Prestoea montana*), occur at all elevations wherever very steep slopes and saturated soils prevail (fig. 4c). Forests at the mountain peaks are known as elfin forests (fig. 4d) because trees are short in stature in response to chronically saturated soils that limit transpiration rates and low solar radiation that limits photosynthesis (Wang et al. 2003; Harris 2006; Wu et al. 2006b; Harris et al. in press). Although these broad forest types characterize the vegetation of the LEF, clear boundaries between where one forest type stops and another starts are nonexistent. Rather, the distribution of vegetation corresponds to multiple environmental gradients such as solar radiation, temperature, rainfall, soil type, and topographic position that

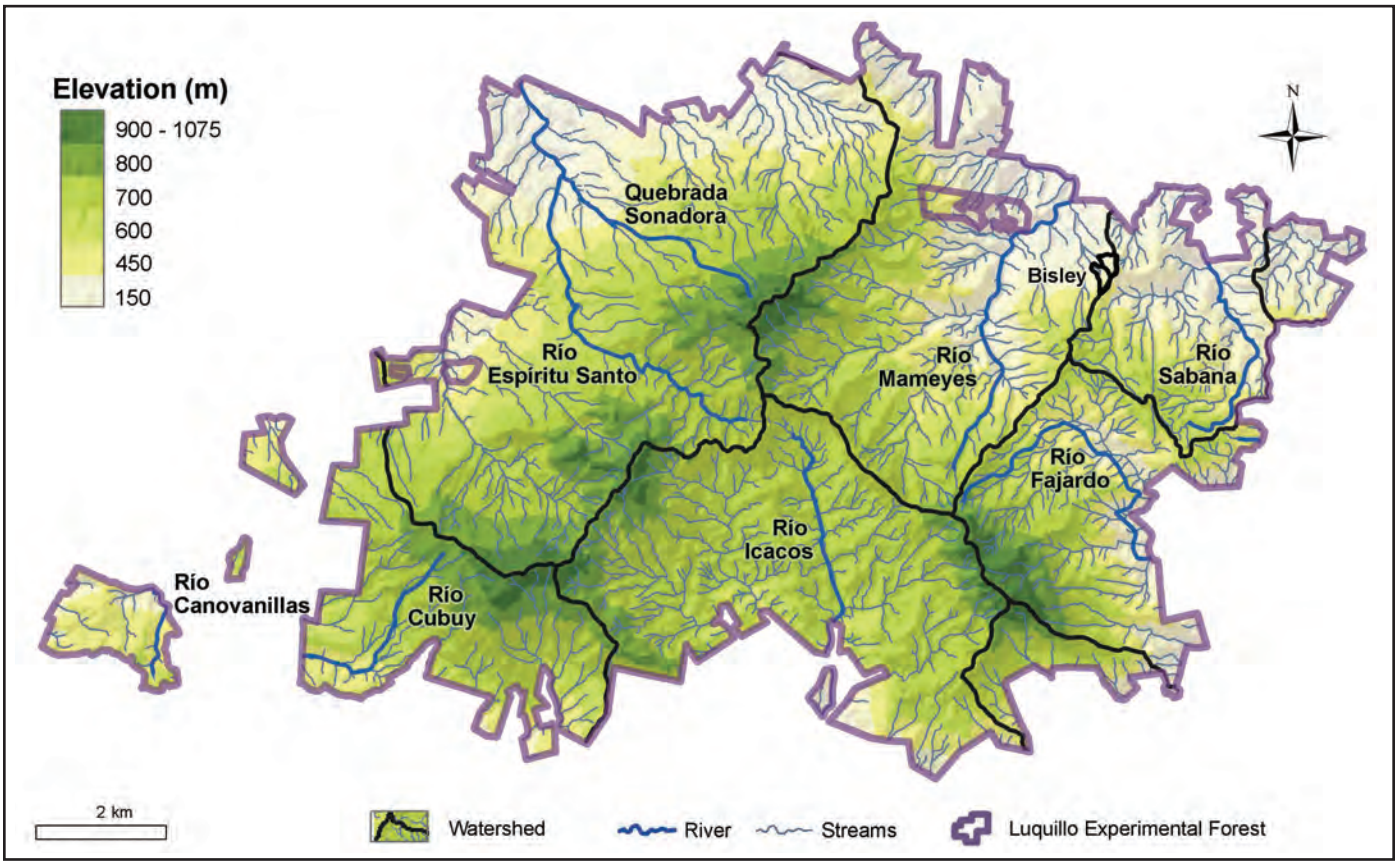

Figure 3.—Elevation and rivers of the Luquillo Experimental Forest.

Figure 4.—Representative forest types within the Luquillo Experimental Forest. (a) Tabonuco forest in the lowlands, dominated by *Dacryodes excelsa*; (b) palo colorado forest at mid-elevations, dominated by *Cyrilla racemiflora*; (c) palm brake forest in areas with steep slopes and saturated soils, dominated by the sierra palm (*Prestoea montana*); and (d) elfin forest at mountain peaks, with *Micropholis garciniifolia* as a representative tree species. Photos by G. Bauer.

vary continuously over the landscape rather than as discrete categories. Also, many specialized communities occur across the landscape, such as floodplain forests, riparian vegetation, herbaceous bogs, plantations, and roadside vegetation.

Hurricanes and severe tropical storms are common in the LEF and occur mainly during the late summer months. More than 70 severe storms have occurred in Puerto Rico since the early 1700s, and the most recent storms to pass over Puerto Rico (since 1989) are shown in figure 5. The last two hurricanes to hit the LEF were Hurricane Georges in 1998 and Hurricane Hugo 9 years earlier in 1989. Hurricanes can be expected to pass directly over the forest once every 62 years and pass within 60 km once every 22 years (Scatena 1989).

In comparison with tropical forests in the Atlantic lowlands of Costa Rica and the lowlands of central Panama—other well-known sites of long-term research activity (Gentry 1990)—the Luquillo Mountains are cooler, wetter, and less seasonal (Scatena 1998a). Unlike areas with monsoonal tropical climates that receive most of their annual rainfall during a well-defined rainy season, rainfall in the Luquillo Mountains is relatively evenly distributed throughout the year. Dry periods in these mountains last days and weeks rather than months and are only moderately seasonal in occurrence. Rainfall in the Luquillo Mountains has a nutrient-rich oceanic chemical signature, and the precipitation regime is a high frequency of low-intensity showers punctuated by periodic high-intensity storms (Heartsill Scalley et al. 2007).

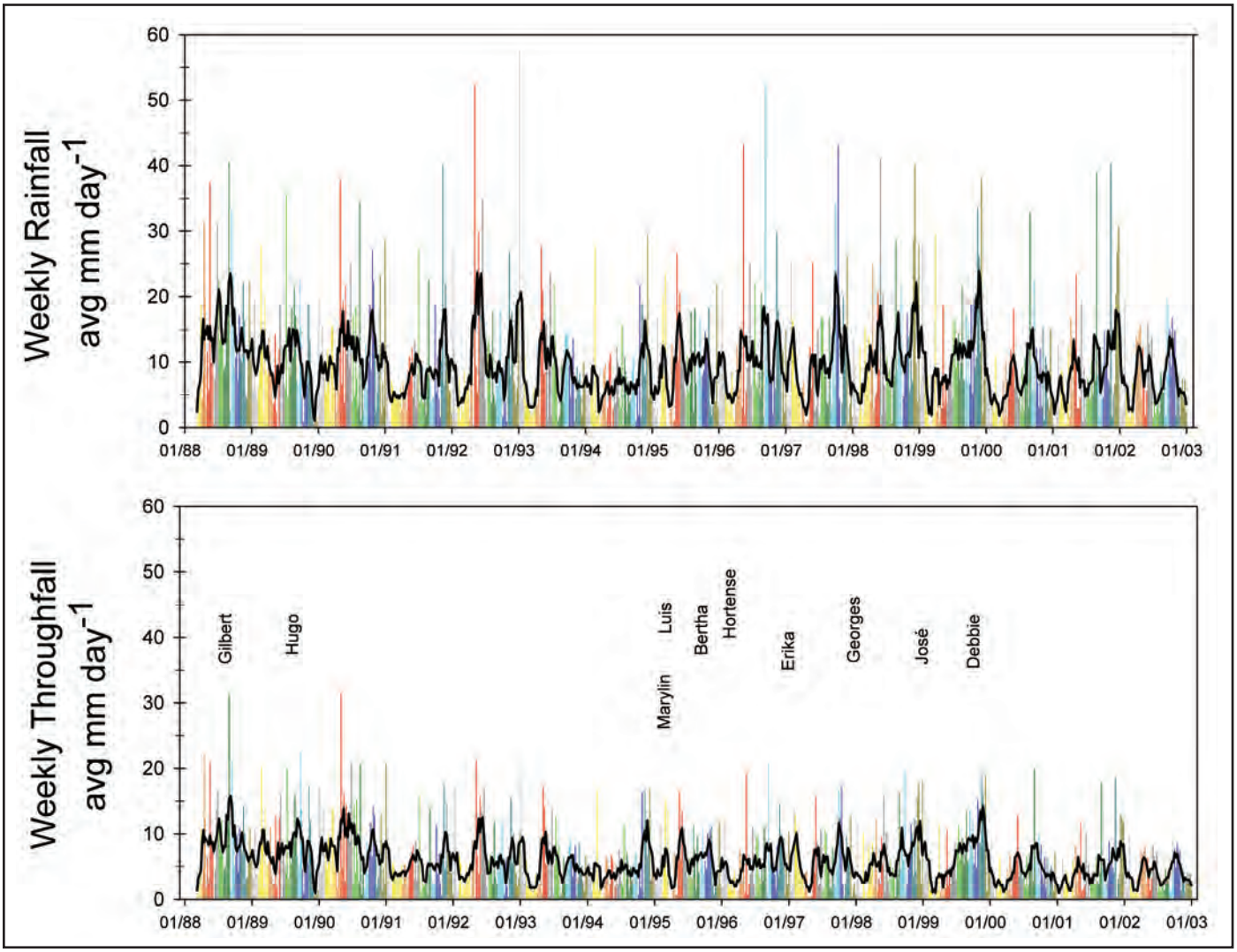

Figure 5.—Weekly rainfall and throughfall at the Bisley Watersheds in the Luquillo Experimental Forest and the names of storms and hurricanes passing over Puerto Rico from 1988 to 2003. Weekly means are expressed in mm day^{-1}. The black color line is a running average. Bar colors represent January in gray, February in yellow, March in dark yellow, April in orange, May in red, June in dark gray, July in light green, August in dark green, September in light blue, October in dark blue, November in cyan, and December in olive. From Heartsill Scalley et al. (2007).

3. Historical Perspective

N.L. Harris

The Origins of Forestry in the Luquillo Experimental Forest: 1903 to 1956

When Puerto Rico became part of the United States territory in 1898, 5,018 hectares (ha) of forest land in the Luquillo Mountains were under the protection of the Spanish Crown. The Luquillo Forest Reserve was established by the United States in 1903 and renamed the Luquillo National Forest in 1907. The Division of Forestry managed the area between 1898 and 1905. The Forest Service has managed the area continuously since 1905, and the first supervisor of the national forest was appointed in 1917. The forest was renamed the Caribbean National Forest in 1935. In 2007, the name was changed again to the El Yunque National Forest to better reflect the cultural and historical attitudes of the Puerto Rican people. During the past century, the size of the forest under Forest Service ownership increased from the original 5,018 ha to 11,300 ha. In 1956, this forest area–with the same boundaries as today's El Yunque National Forest–was also designated as the Luquillo Experimental Forest (LEF).

Initial Forest Service programs began about 1920 and included large-scale trial plantings with both introduced and native tree species. With the onset of the Great Depression in the early 1930s, the Civilian Conservation Corps program did extensive work in reforestation, forest road construction, and recreational and administrative improvements to the forest. The Forest Service started the first timber management plan for the Luquillo Mountains in 1934 (Muñoz 1965). Before this plan, management of public lands was minimal, and most privately owned areas were either cleared for agriculture or selectively cut for desirable species. Sugarcane production was at its peak in the Luquillo municipality in the late 1940s (Thomlinson et al. 1996). The 1956 forest management plan suggested that about 6,700 ha of the Caribbean National Forest, now El Yunque National Forest, could support timber production and were thus designated as commercial lands. Close to one-half of these lands came under active management, including both the management of natural stands and the development of plantations.

The Odum Years: 1963 to 1968

In the 1960s, the Atomic Energy Commission (now the U.S. Department of Energy) and the University of Puerto Rico provided funding for Howard T. Odum and dozens of other scientists and technicians to conduct the first large-scale ecosystem study on the effects of disturbance caused by radiation in the tabonuco forest. Odum's experiments established the foundation for long-term ecological research in Puerto Rico and the tropics in general (Odum and Pigeon 1970). Through his radiation experiment, Odum found that the structure and function of the tabonuco forest ecosystem were highly resistant to the effects of radiation (Odum 1970a). Odum's research legacy in the Luquillo Mountains transcends the radiation experiment, however. Odum also described in detail the climate of the Luquillo Mountains (Odum et al. 1970) and demonstrated how to measure forest metabolism on a large scale by isolating a section of forest within a giant plastic cylinder (Odum and Jordan 1970). Scientists involved in the Rain Forest Project also made comparisons with other tropical forests, both insular and continental (Odum 1970a, 1970b), and raised countless questions for future studies. Many of Odum's questions concerned key methodological and monitoring approaches of the time, while others emphasized fundamental issues for research in tropical forests (see Lugo 2004a).

For Howard Odum, the Luquillo Mountains functioned as an integrated ecosystem connected to the rest of the globe by regional flows of energy and cycling of materials. He recognized the connection between the tabonuco forest and latitudinal wind patterns through inputs of water and nutrients. Odum also recognized the role of wind and hurricanes in shaping the canopy of the forest (Odum 1970b), demonstrated the hierarchical nature of forest function, and integrated the functions of organisms from microbes to humans (Odum 1970c). Through research on fundamental ecosystem structure and function, Odum developed models of sustainable land use for the tropics, including the design of ecosystems for human uses, such as waste recycling and wood production (Odum 1995).

The LTER Network: 1988 to Today

Most research conducted in the Luquillo Mountains until 1988 was of relatively short duration, from less than a year to a decade. Even H.T. Odum's Rain Forest Project, which in its time was the most comprehensive study of a tropical forest ever conducted, lasted only 5 years (1963 to 1968). Notable longer term studies include (from 1942) monitoring of tree growth and survival under natural and managed conditions (Drew et al. 2009; Brown et al. 1983), the recovery of vegetation after ionizing radiation (Taylor et al. 1995), and the recovery project for the endangered Puerto Rican Parrot (Snyder et al. 1987).

The National Science Foundation's Long Term Ecological Research (LTER) Network began with 6 sites in 1980 and has grown to 26 sites today, including 2 sites in Antarctica and 1 coral reef site off the coast of Tahiti (fig. 6). The LEF (known as LUQ in the LTER Network) was added to the LTER Network in 1988 and remains the only terrestrial tropical site in the network. At the time that the LUQ site was established, data on tropical forests were limited and basic information on topics such as carbon and nutrient dynamics, disturbance effects, and trophic interactions was largely lacking; the LUQ site already had a strong research basis on which the LTER could build. Establishing an LTER program at the LEF initiated a new research focus on ecosystem forcing functions of long duration, infrequent occurrence, or incremental effect. Now, some 20 years later, more than 1,000 publications addressing all these topics and more have come out of the LUQ LTER.

Figure 6.—The National Science Foundation's Long Term Ecological Research Network consists of 26 sites. The Luquillo Experimental Forest is the only terrestrial tropical site in the LTER.
From http://www.lternet.edu/sites/.

4. Land Use and Land Cover

N.L. Harris

Most of Puerto Rico was forested at the time of European arrival. Although pre-Columbian Arawak and Taíno agriculturalists cleared small tracts of land in the mid-elevation forests of Puerto Rico, their activities probably had little effect on the vegetation of the Luquillo Experimental Forest (LEF) because the coastal plains and the drier intermountain valleys were better suited to their needs than the Luquillo range (Wadsworth 1949; Walker in press).

Land-clearing activities and the extent of human-induced disturbances increased rapidly at the onset of European colonization, but then slowed with the development of the continental New World. The first two major settlements of Puerto Rico, Caparra and San Germán, were established by 1510, but a third town was not established for another 136 years (Scatena 1989). During the first three centuries of colonization, the relatively inaccessible nature of the Luquillo Mountains limited their use.

Extensive agricultural activity did not begin in the LEF until the onset of government land distribution programs in the early 1800s. By 1831, coffee was grown in the region, but most of Fajardo and Luquillo were forested and sparsely populated (Wadsworth 1949). Between 1830 and 1890, as a result of the government land distribution programs, the flanks of the mountain became cultivated with coffee, bananas,

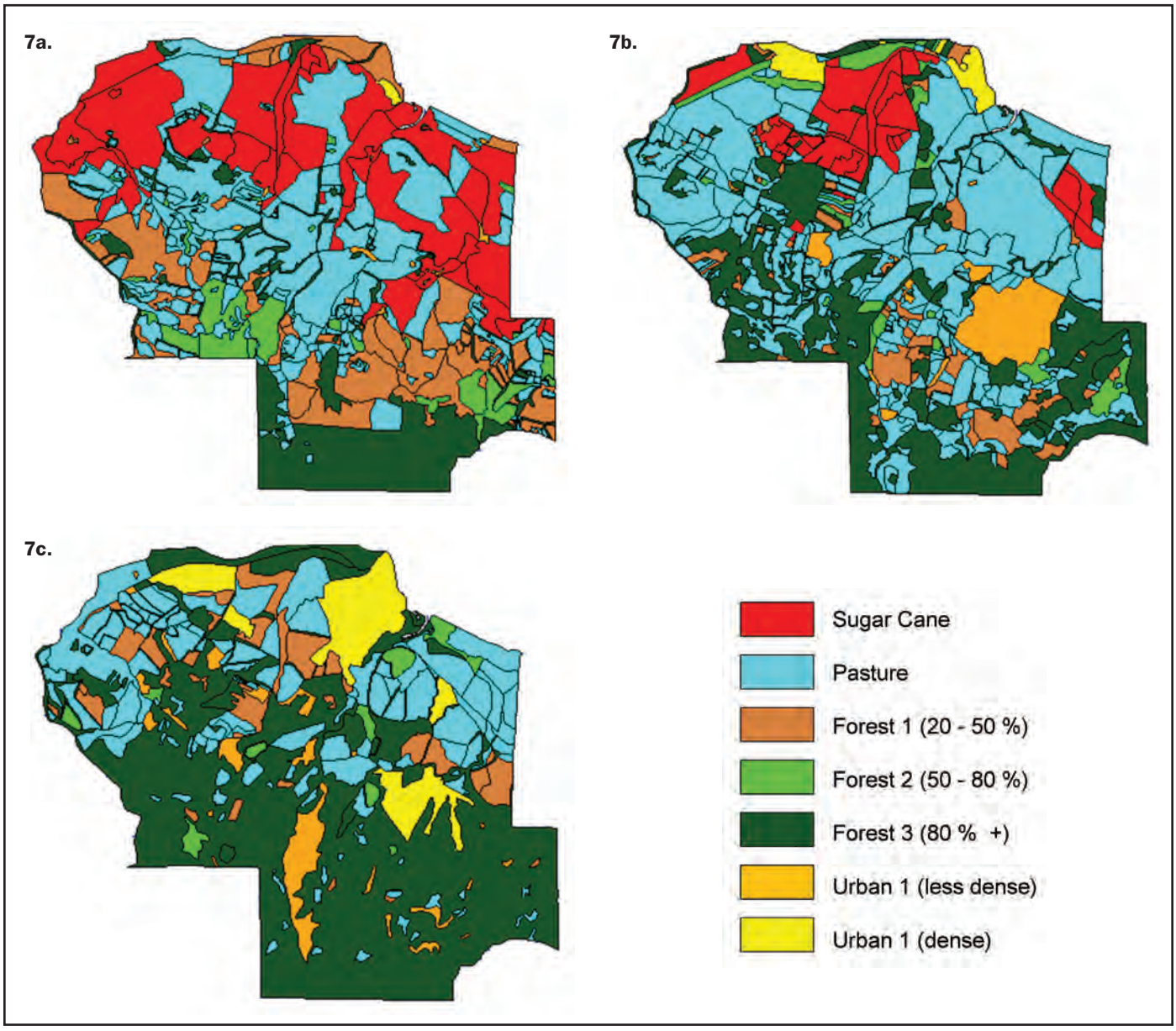

Figure 7.—Land use classes in the municipality of Luquillo, Puerto Rico in (a) 1936, showing the dominance of sugar cane and pasture; (b) 1964, showing the increasing area of pasture, largely due to abandonment of sugar cane crops; and (c) 1988, showing the dominance of dense forest. Values in parentheses in the legend show the percent canopy closure for each of the three forest classes. From Thomlinson et al. (1996).

and subsistence crops including upland rice. The forest also supplied wood products and water resources to the surrounding communities, and local residents made charcoal for personal use. The extent of cultivated land in the Luquillo Mountains increased steadily from 1800 until a hurricane passed in 1899 (Wadsworth 1949). After the hurricane hit, many affected farms and coffee plantations were abandoned and allowed to reforest naturally. By 1934, all original coffee plantations had been destroyed, but many original shade trees (*Inga fagifolia* and *Inga vera*) remained. This decline in agricultural activity and the subsequent reforestation predates the general trend of natural reforestation in Puerto Rico that began about 1950 (Birdsey and Weaver 1982).

Helmer (2004)—who summarized islandwide land cover change over the time period between 1977 to 1978 and 1991 to 1992—found that the largest land cover change on the island was a 64-percent (~119,000 ha) decrease in agricultural lands, with about one-third of this decrease corresponding to an increase in coffee cultivation and secondary forest. In an earlier study, Thomlinson et al. (1996) analyzed aerial photographs of the municipality of Luquillo, within which part of the LEF is located, and found that the pattern of land use between 1936 and 1988 followed the islandwide trend of a transition from high-intensity agriculture to dense forest (fig. 7). Sugar cane cropland and pasture were the dominant land uses in Luquillo in 1936, occupying about one-third of the study area each, while dense forest was rare. By 1988, pasture still occupied about one-fourth of the area, mainly because most of the area under sugar cane production was transformed to pasture after abandonment. Urban areas also increased by more than 2,000 percent between 1936 and 1988 and continue to encroach on forested areas today. Between 1988 and 1993, urbanization around the LEF in the municipality of Luquillo increased by 31 percent and represented a 5-percent loss in vegetative cover, more than 80 percent of which was dense forest (Thomlinson and Rivera 2000).

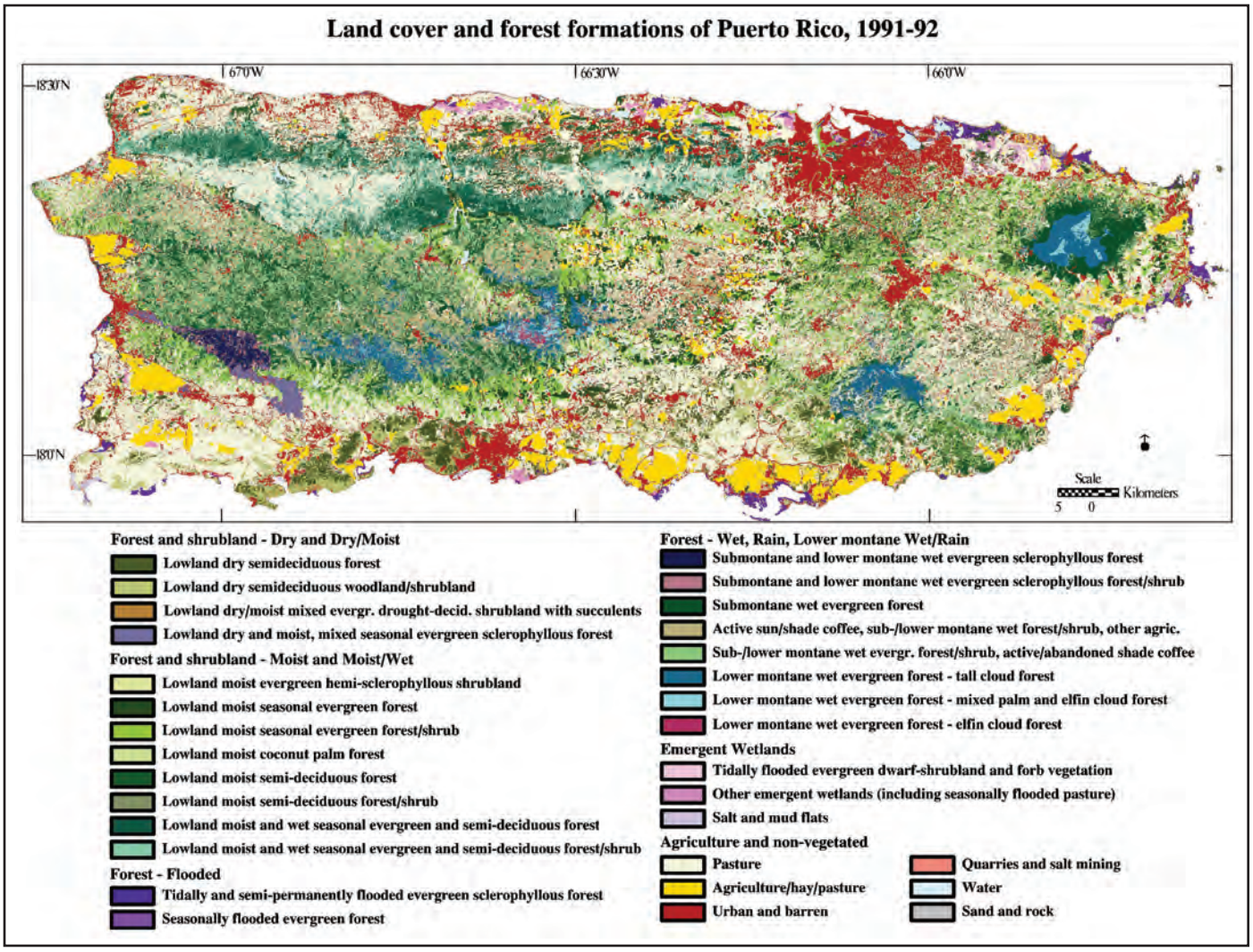

Figure 8.—Land cover map of Puerto Rico in 1991-1992. The Luquillo Experimental Forest is located in the northeastern corner. From Helmer et al. (2002).

Suburbanization, or the transition of other land cover types to low-density urban areas, continues to encroach on the lowlands of the Luquillo Mountains. Thus, the LEF can be viewed as an "island within an island" because the forest is embedded within a broader mosaic of forested and nonforested land (fig. 8). What was once actively managed for timber production, charcoal, coffee, and sugar cane is now managed primarily for research and recreation. Hundreds of visitors from Puerto Rico and mainland United States visit the El Yunque National Forest each day, with July and August as peak months for tourism (fig. 9).

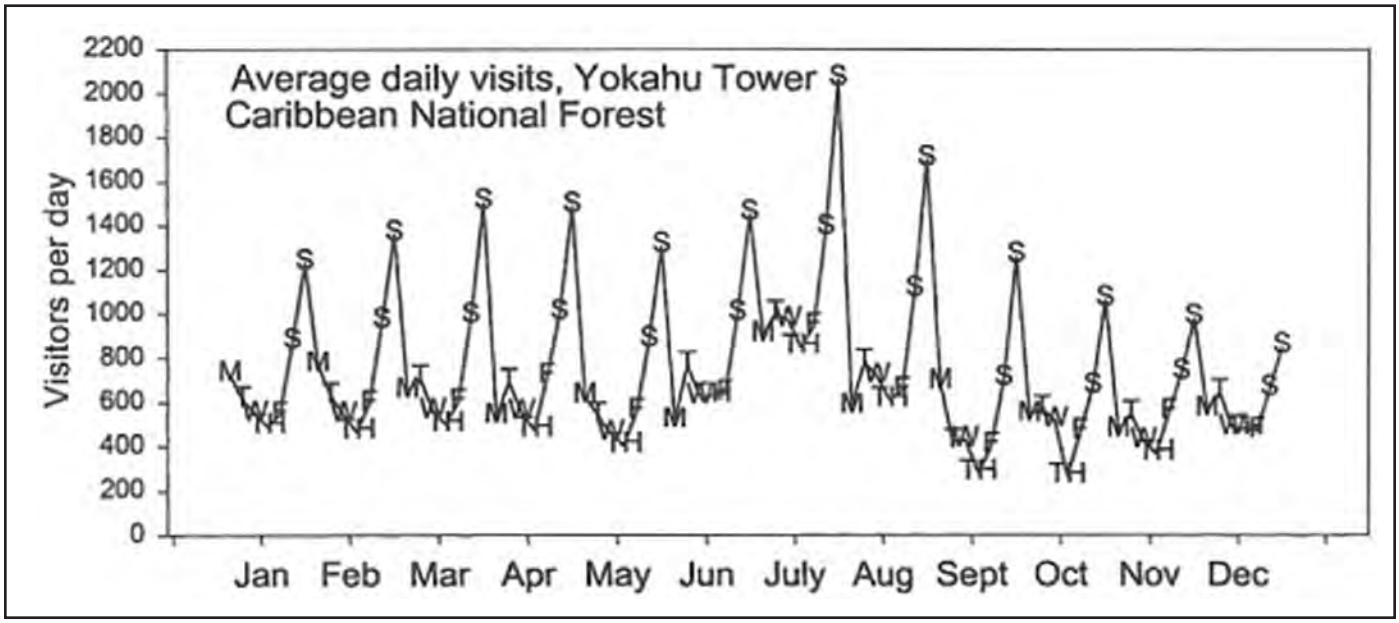

Figure 9.—Average daily visits to Yokahu Tower, a major visitor center in El Yunque National Forest. Letters represent the day of the week, with Sunday being the most popular day. From Scatena (2001).