CHAPTER 1

Climate, People, and Vegetation of the West Indies

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The definition of the West Indies varies depending on the group of organisms that one considers, and in this book, the region is delineated in the south by "Koopman's Line," which passes between Saint Vincent and Bequia, the northernmost of the Grenadine Islands (Genoways et al. 2010). Islands north of this boundary support at least some species of bats that are endemic to the region, whereas islands to the south are primarily inhabited by species that also live on mainland South America. Hence, the West Indies includes three island chains: the Lesser Antilles from Saint Vincent to the Virgin Islands, the Greater Antilles, and the Bahamas and Turks and Caicos Islands. The total number of islands probably exceeds 7000, because many smaller islets are associated with each major land mass. For example, the governmental entity known as Puerto Rico is really an archipelago of 660 individual islands, including cays as small as 0.001 ha (Lugo et al. 2016). The region spans a latitudinal range of 14°, from Saint Vincent (13° N) to Little Abaco in the Bahamas (27° N). Geographers consider all these islands "tropical," except the northern half of the Bahamas, which lie above the Tropic of Cancer (23.4° N).

The diversity of animals in any part of the West Indies is strongly dependent on the type of plant community that is present. The goal of this chapter is to present a realistic overview of contemporary vegetation in these diverse archipelagos and describe how it is shaped by abiotic factors and human activity. The interrelationships among plants, climate, and anthropic change are central to understanding the following introductory chapters that concern the historical biogeography of bats, their modern ecology, and current conservation needs, as well as the details of the species accounts that follow.

The Importance of Elevation on Temperature and Rainfall

Elevation plays an important role in the climate of these islands, which consist of two types of landmasses—high and low. High islands have elevations from near sea level up to 3.1 km at Pico Duarte on Hispaniola, the highest point in the West Indies. Different sites on high islands typically experience several distinct climatic regimes, ranging from dry woodlands (500–1000 mm of annual rainfall) to rain forests (>4000 mm). Low islands, in contrast, such as Anguilla, Antigua, and Barbuda, are usually small in area and are typically dry.

Prevailing winds that bring moisture to each island also influence climate. In the Northern Hemisphere, the trade winds blow across the Atlantic Ocean from the northeast and strike the Lesser Antilles from Dominica southward. Those southern islands are described as windward, whereas islands to the north and not in the direct flow are leeward. Thus, islands can be low or high, based on topography, and windward or leeward, depending on their position relative to the trade winds. For example, Barbados is a low windward island, whereas Dominica, a high island, is leeward.

The classification of entire islands as leeward or windward is applied mostly to the Lesser Antilles, but the Greater Antilles and other high islands have windward and leeward aspects. Elevation, combined with a persistent direction of moisture-laden winds, greatly affects the amount and distribution of rain on these landmasses. Moist air blowing over the ocean strikes the uplands of any high island and rises upward, cooling the air, condensing the water vapor, and resulting in rain. Thus, the windward side of high islands receives more rainfall and supports wet forests, while a rain shadow occurs on the leeward side, which sustains only dry to moist forests. Overall, annual rainfall is greater on high windward islands and lower on low leeward islands. Most islands experience a wet and a dry season, with annual rainfall typically ranging from 800 to 2000 mm but reaching more than 5000 mm on the highest peaks.

Hurricanes, with strong winds and intense rainfall, occur anytime between May and December, although the "official" Atlantic hurricane season is between 1 June and 30 November (Neumann et al. 1978). Hurricanes have passed over the West Indies for millions of years and have affected the vegetation by limiting tree height and resulting in high species dominance in plant communities (Lugo 1991). On average, daily maximum air temperature on the islands ranges from the upper 20s °C in winter to the lower 30s °C in spring and summer; nighttime temperatures are about 6 °C cooler. Frost, which determines the types of plants that can grow, does not occur in the lowlands of the West Indies, and the resulting life zones range from tropical to subtropical (Holdridge 1967). Nevertheless, frost is a regular occurrence above 2200 m in elevation in the pine forests of Hispaniola and is a factor in the reduced diversity of plants, as well as bats, high in the mountains of that island (Martin et al. 2011; Núñez-Novas et al. 2021).

The Effect of Humans, History, and Economics on the Landscape

> Three sea-crossing technologies—canoe, caravel, and container ships—serve as symbols of the main periods of Caribbean history. . . . Each of these vessels carried with them whole cultures, representing an increasingly global cargo.
>
> —Higman (2011, 327)

Human activity in the West Indies dates to about seven millennia before present and involves periods of distinct activities, such as hunting and gathering, subsistence agriculture, plantations, industry, and political dominance, including colonialism, rebellions, democracies, and dictatorships (Higman 2011). The canoe of indigenous peoples represents 5000 years of history, whereas the European caravel spanned 500 years; the modern container ship, in contrast, involves only a short period of 50 years. Each technology had consequences to the people, the economy, and the ecosystems of the region. From its beginning, the progression of human history in the West Indies is characterized by the changing diversity of peoples and cultures inhabiting the various isles, with each island evolving along different trajectories than the others, even if distances among them were short (Horowitz 1971), resulting in contrasting levels of economic development and environmental effects.

The population of the region, as of 2010, is forty-one million people, with 90% living in the Greater Antilles. Of this population, 66% live in urban environments, with the greatest densities occurring in Anguilla, the Cayman Islands, and Puerto Rico (Fig. 1.1). On most inhabited islands more than half the population is classified as urban, and such populations increased by 81% between 1980 and 2010. Overall, average population density is about 180 people/km^2, ranging from 664 in Barbados and 449 in Puerto Rico to 31, 46, and 50 people/km^2 for the Bahamas, Turks and Caicos, and Montserrat, respectively. The human population is not continuing to grow on all islands, as Puerto Rico and many of the Lesser Antilles lost population between 1980 and 2010, and this decline accelerated in multiple locations after Hurricane Maria in 2017 (Lugo 2019).

The landscapes of the Caribbean islands reflect the development of their local economies (Lugo 1996). Human economic activity influences the kinds of ecosystems that prevail on each island, as well as their species composition. Indeed, all components of the social-ecological-technological systems of the West Indies function in synchrony, responding and adapting to extreme events originating either in the anthropogenic realm, such as wars, political actions, and economic turmoil, or the nonanthropogenic realm, such as hurricanes and volcanoes.

The effects of severe events on landscapes are epitomized by Puerto Rico over the last 125 years, as changes in political regimes, economic upheavals, and differing agricultural practices combined with periodic high-intensity hurricanes to alter the landscape of

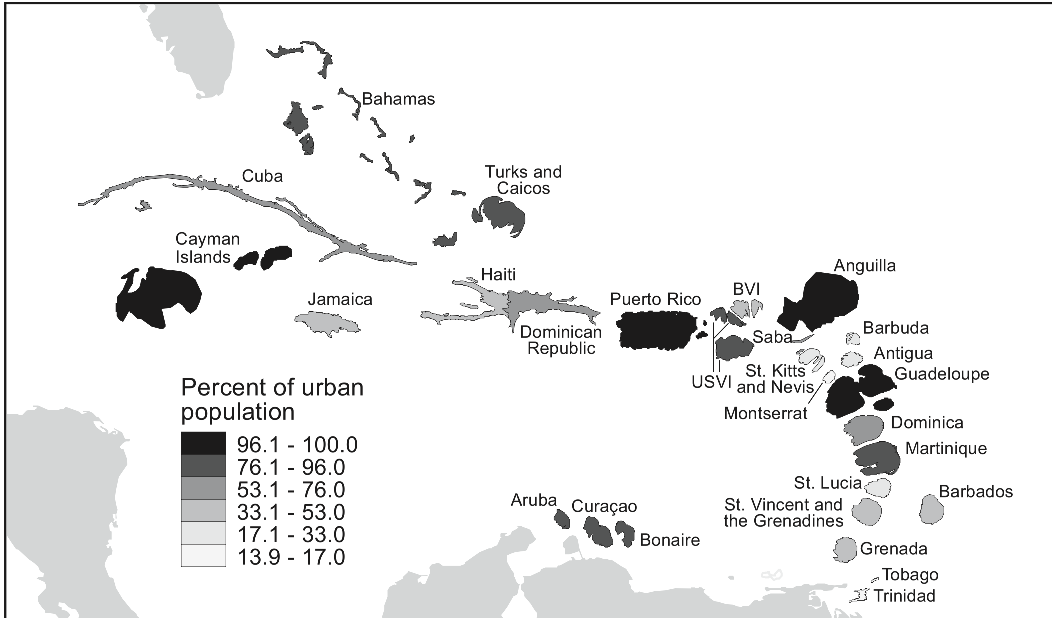

Figure 1.1. Cartogram of the West Indies based on the density of urban populations in 2010 (from López Marrero et al. 2012). Courtesy of Tania López Marrero.

the island and the composition of the bat community. Native plant species once maintained high concentrations of soil organic matter in historic forests, but by the early 1900s, deforestation and widespread agriculture had degraded soils and greatly reduced soil organic matter. After the collapse of agriculture following Hurricane San Ciprián in 1932, the reforestation that followed involved introduced species that are now contributing to increased forest cover and soil organic matter. Both the agricultural activity and the prevailing condition of the landscape, including forests, changed after the passage of each intense storm. By 2020, the local vegetation had shifted from the pre-twentieth-century indigenous combinations of species to maturing, novel plant communities dominated by introduced species (Lugo 2019, 2020); consequently the plant communities that feed and shelter bats today are not the same as those 200 years ago. All West Indian islands share the key events in the Puerto Rican story, but they occurred at different times, with varying intensity, and with different long-term effects, because each island has its own unique culture, level of economic activity, governance, historical context, and ecosystems. Regardless of inter-island differences, human activity is linked with the state of the landscape and its ecological systems, and it is impossible to study one without considering the other.

The Vegetation of the West Indies

> This climax [plant community] is that which develops not only in the entire absence of anthropic influences, but in the absence of all natural accidents, catastrophes and "abnormal" disturbances.
>
> —Egler (1952, 74)

When thinking about the vegetation of the West Indies, one usually imagines the green fringe of mangroves lining low-energy coastal and estuarine waters, beautiful dry forest shrublands, magnificent lower montane forests, impressive windward mountain slopes dominated by palm forests with even-height canopies, or cloud-shrouded montane forests and woodlands. These are all iconic examples of Caribbean flora. However, modern tourists flock to the West Indies to spend time on beaches lined with coconut palms (*Cocos nucifera*) that originated somewhere in Indomalaya. As visitors travel along island roads, people marvel at the beautiful flowers of flamboyan (*Delonix regia*) from Madagascar and those of the African tulip tree (*Spathodea campanulata*) from Ghana and Kenya, or observe the large fruits of the breadfruit tree (*Artocarpus altilis*) from New Guinea via Tahiti. In fact, tourists typically encounter vegetation quite different from the climax communities described in the classic botanical literature of the West Indies (Stehlé 1945; Beard 1949).

Egler (1952) observed that the writings and classification systems of Beard (1949) and Stehlé (1945) reflected the different experiences and worldviews of those authors, resulting in an incomplete picture of reality, because of what they did not consider when developing their respective frameworks. Egler (1952) believed that the frequent description of plant associations by Beard (1949) and Stehlé (1945) as ruinate, reduced, defective, or degraded suggested a bias that supported their idealistic model of a vegetation adapted to climatic conditions. Moreover, he noted that most plant studies focused on the mountains, where human effects were less apparent, and less so in the lowlands, where humans were more prevalent. In the spirit of Egler (1952), the following discussion concerning the modern flora of the West Indies takes a broad view and examines the importance of non-native species of plants; explores the interactions among climate, topography, soil, and extreme events; and concludes with a description of the role that animals play in structuring plant communities in the islands.

The Present-Day Flora Consists of Native and Novel Species Assemblages

Technically, botanists classify the flora of the West Indies as part of the Antillean subregion of the Caribbean province of the Neotropical kingdom (Good 1953; Borhidi 1991). Within the subregion, there are six distinct floras associated with different islands or groups of islands. These six include the Lesser Antilles, Cuba, Jamaica, Hispaniola, Puerto Rico plus the Virgin Islands, and the combination of south Florida, the Bahamas, and Bermuda.

The West Indies is a global hot spot of endemism, with at least 2% of the world's endemic plant and vertebrate species on only 0.4% of the earth's land surface (Myers et al. 2000). The number of native plant species, which reflects development over millennia, is 10,948 (Acevedo Rodríguez and Strong 2008). Furthermore, there are 1899 introduced species that have become naturalized over the last 500 years, for a total of 12,847 species, with introduced plants representing 14.8% of this total. The number of introduced forms on an island is positively related to the amount of urban cover, which is an index of the level of human activity; such activity, in turn, creates opportunities for the importation and ultimate naturalization of more species (Lugo et al. 2012b). Because naturalized species are recent additions to the flora, their presence has created novel assemblages of species that, unlike native plants, can colonize deforested and degraded lands and rehabilitate their productivity and biodiversity.

Effects of Topography, Climate, Soils, and Extreme Events on the Flora

Depicting a realistic scenario for the development of vegetation in the West Indies requires an examination of four principal conditions—topography, climate, soils, and extreme events—that, together, determine the ecological space available for the growth and dispersal of plants and their assembly into interacting communities. This space is characterized in Figure 1.2 by four quadrants, one for each condition. The totality of the flora is represented by a central circle at the intercept of the four quadrants, and components of the vegetation (species) spread outward along environmental gradients, according to their life-history traits and physiological tolerances. The diagram illustrates eighteen such continuums, because empiric data support the distribution of species along those gradients within the West Indies. Although the diagram depicts the gradients and quadrants as discrete entities, they interact with each other in determining which plants occupy an area.

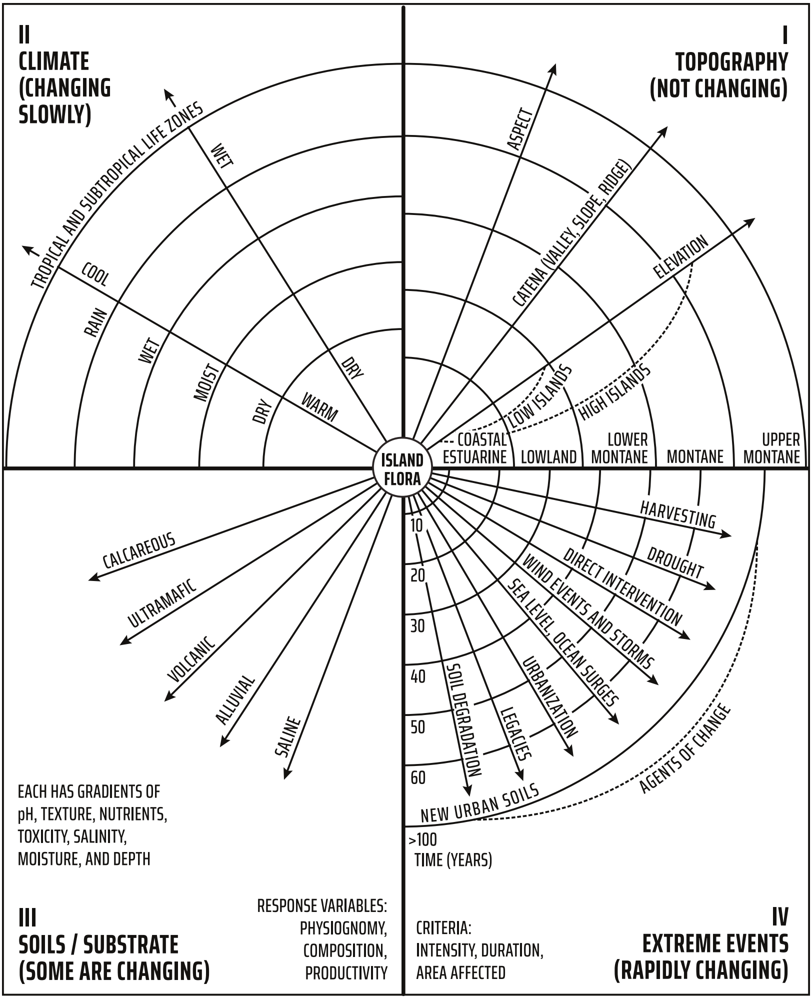

Figure 1.2. Four-quadrant diagram depicting the environmental conditions or ecological space within which the vegetation of the West Indies grows and functions. Each quadrant represents a major group of environmental conditions to which vegetation responds. The eighteen radiating lines represent environmental gradients along which the insular flora (including naturalized species) is distributed. Prepared by Ariel E. Lugo.

Quadrant I represents topography. At the scale of the West Indies, the topography of the islands is the most stable of the four quadrants and provides the basal conditions for classifying vegetation according to elevation (Beard 1949). However, at smaller scales, forces of change from within this quadrant and from other quadrants can significantly affect the vegetation of a particular area. For example, tectonic forces slowly move the geologic plates of the Caribbean, inducing earthquakes and volcanic activity that can alter surface features in either the short or the long term. Landslides, because of the interaction of climate and topography (quadrants I and II), also change surface conditions, and some geologic substrates in quadrant III are significantly more susceptible to sliding than others. In addition, use of heavy machinery and explosives (quadrant IV) modifies significant portions of the topography of the West Indies, thus affecting the cover of vegetation on montane (quarries), coastal (construction over sand dunes), wetland (drainage and filling), and lowland (urbanization) locations.

Within quadrant I, there are three principal gradients—elevation, catena, and aspect. The high islands of the West Indies contain the range of vegetation types described by Beard (1949), including coastal, lowland, lower montane, montane, and cloud forests. Each elevational belt is associated with a particular group of species distributed along the catena and aspect. The catena (a gradient of location—from a valley, along a slope, to the top of a ridge) represents contrasting conditions for the establishment of vegetation, as well as community organization and functioning (Scatena and Lugo 1995). Aspect (direction that a site faces), especially in relation to rainfall (quadrant II) and wind exposure (quadrant IV), is another critical component regulating community composition and its physical appearance.

Quadrant II represents the climate of the islands, which both Beard (1949) and Stehlé (1945) used to classify climax plant communities. However, the tropical climate of the West Indies is slowly but measurably changing (Jennings et al. 2014) because of human activity at the global scale (quadrant IV). For instance, climate change in the Luquillo Mountains of Puerto Rico is affecting some avian species, such as the endemic lizard cuckoo (*Coccyzus vieilloti*), which has shifted its range upslope because of environmental warming (Campos-Cerqueira et al. 2017). Although global climate models also predict future reductions in rainfall (Henareh Khalyani et al. 2016), so far there is no evidence that such a decrease is happening (but see Hernández Ayala and Heslar 2019), perhaps because the climate of islands is too complicated and difficult to predict with global-scale models.

There are two major climatic gradients affecting vegetation in the West Indies. One is the moisture gradient caused by differences in rainfall. This gradient is closely linked to the topographic conditions in quadrant I, with more precipitation at higher elevations (García Martinó et al. 1996). The other gradient, temperature, defines the West Indies as tropical and subtropical because of the absence of frost in the lowlands, as indicated earlier. Furthermore, air temperature differs with elevation, time of day, and season of the year, with more variation at higher latitudes. Plant and ecosystem processes respond to all of these variations.

Quadrant III represents the rocky substrates and soils that are ultimately derived from the bedrock. These gradients represent the simplest aggregation of substrates possible, as geologists recognize many others. This quadrant is complicated because of the diversity of soils and complexity of the substrates that occur in the West Indies. Even in the absence of human activity, the conditions in this quadrant result from forces associated with time, topography, and elevation. For example, karst substrates occur in areas submerged by the ocean earlier in geologic time, but the soils that are present may originate on volcanic mountain slopes; in addition, the climate in karst areas may be dry, moist, or wet, depending on elevation and aspect. Although the geology of the islands is well known, as are the locations and identities of the soils, ecologists understand less about how these substrates and soils affect vegetation than they do about the effects of climate.

Nevertheless, vegetation does change dramatically along the five gradients of quadrant III. Changes in vegetative structure and functioning along gradients of soil moisture and salt concentration were detected long ago (Gleason and Cook 1926). Mangroves, as an illustration, become smaller and less productive as salinity increases (Cintrón et al. 1978; Lugo and Medina 2014), and tree height decreases with elevation on high islands, culminating in elfin woodlands on mountaintops (Odum 1970).

Quadrant IV comprises the forces of anthropogenic change acting on the West Indies. There are eight gradients depicted, each associated with events that have a measurable intensity and duration (Lugo 2020). In contrast to older historic vegetation in quadrants I and II, the vegetation that predominates in quadrant IV is novel and generally less than 100 years old. When historic vegetation is subjected to extreme events, it recovers through pathways of succession that evolved over thousands of years, but historic vegetation yields to novel vegetation when site conditions change so that the older species assemblages cannot compete with novel assemblages (Álvarez Ruiz and Lugo 2012). For example, the native tree that normally grows at the beginning of succession, the trumpet tree (*Cecropia schreberiana*), cannot successfully colonize lowland pastures, because soil moisture is too low, and its seeds are consumed by predators (Silander 1979). Instead, non-native trees such as guava (*Psidium guajava*) and African tulip now fulfill the role as colonizers (Aide et al. 1995, 1996).

In the upper montane forests of Hispaniola, the complexity of plant distribution makes it difficult to anticipate changes in response to global warming and increased frequency of hurricanes (Martin et al. 2004). However, anthropogenic effects on vegetation are measurable and already reflect that introduced species account for 29% of the "importance value" (an index derived from the frequency, density, and basal area) of all tree species. Despite the prevalence of introduced species on Hispaniola, the structure (e.g., height and canopy closure) of woody vegetation in secondary riparian forests approaches the structure of mature forests within a 40-year span, which is similar to results from the mountains of Puerto Rico (Aide et al. 1995, 1996).

The Role That Animals Play in Structuring Plant Communities

The list of plants used as food by bats (Gannon et al. 2005) contains numerous introduced species, indicating that these mammals are providing pollination and seed dispersal for the non-native as well as the native flora. This dietary behavior of bats is consistent with their frequent reliance on remnant blocks of forest, which are mostly dominated by naturalized species of plants (Rodríguez-Durán and Feliciano Robles 2016). In fact, there are many examples of symbiotic relationships between native and non-native plants and animals other than bats. These include the role of Africanized honey bees in pollinating the endangered endemic beautiful goetza (*Goetzea elegans*) (Caraballo Ortiz 2007) and synchrony between the swarming behavior of European honey bees (*Apis mellifera*) and the massive flowering of Sierra palms (*Prestoea montana*) (Snyder et al. 1987).

Naturalized animal species are ubiquitous in the West Indies and include representatives of most animal groups (Kairo et al. 2003). The number of introduced species varies with the size and location of each land mass, with the larger islands of the Greater Antilles having more than the smaller isles of the Bahamas or Lesser Antilles. Like introduced plants, non-native animals assemble into novel combinations of indigenous and introduced species that function within historic and novel environmental conditions on each island (Lugo et al. 2012a).

In so doing, animals become part of the functioning of these new ecological systems. One of the key ecological roles of birds, for example, is bringing tree seeds into pastures, whereby the animals contribute to the establishment of novel plant communities that include both native and non-native species (Carlo and Morales 2016). Bats play an analogous role by accelerating the transition of tree plantations to secondary forests, and these flying mammals also influence the dispersal of both native and introduced plants in novel forests, such as those dominated by the African tulip tree (Abelleira Martínez 2008; Abelleira Martínez et al. 2015).

Species diversity of bats changes with alterations in land use (Mendes and Srbek Araujo 2020) and also with floral succession (Martínez-Ferreira et al. 2020). Populations of bats respond to the overall physical structure of plant communities, such as the height of the canopy and the density of the understory, as well as the ability of plants to produce food suitable for the animals.

In general, the vegetation of the West Indies consists of a diverse matrix of communities within a small geographic space; this distribution likely helps maintain a diverse bat community more effectively than in continental regions, where individual vegetation types span a much larger area, necessitating a greater flying distance to access a similar variety of plants. Moreover, the development of novel communities may not be as detrimental to bats as expected by preservationists, who deny a positive role to introduced species, because the structure of these novel forests resembles that of mature historical woodlands (Aide et al. 1995, 1996), thus not affecting connectivity among communities in the West Indies. Habitat heterogeneity is one of the most important predictors of bat species richness in the Caribbean (Hoffman et al. 2019; see Chapter 2), and the current trend toward novel communities contributes to this heterogeneity, as evidenced by the use of remnant habitats by many species of bats in an urban matrix on Puerto Rico (Rodríguez-Durán and Feliciano Robles 2016).

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