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Ecological Paradigms for the Tropics
Old Questions and Continuing Challenges

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Abstract and Keywords

This chapter focuses on the ecological response mechanisms of the Luquillo Mountains to natural and human-induced disturbances, such as hurricanes and land cover change. It identifies the ecosystems of the Luquillo Mountains as a perfect representation of large masses of a non-frost tropical land because of its naturally occurring features: high rainfall, hurricane disturbances, maritime climate, and insularity. It then sets out the Luquillo Long-Term Ecological Research (LTER) program as a by-product of the 20th and 21st century experimentations, and discusses its contributions to the basic understanding of the ecological make-up and biogeochemistry of the Luquillo Mountains.

Keywords: Luquillo Mountains, anthropogenic disturbances, maritime climate, insularity, non-frost tropical land, Luquillo Long-Term Ecological Research program, biogeochemistry

Key Points

- • The ecosystems of the Luquillo Mountains are representative of large areas of the frost-free tropical world, particularly those with high rainfall, periodic hurricane disturbances, a maritime climate, and insularity.
- • The natural history of the Luquillo Mountains spans over 30 million years, whereas human presence has been an influence over the past 2,200 years.
- • Indigenous peoples, Spanish conquistadors, and a steady stream of 20th and 21st century scientists have observed, studied, and experimented with the ecosystems of the Luquillo Mountains, and in the process they have left a legacy of ideas and heuristic models concerning ecosystem organization and function. The Luquillo Long-Term Ecological Research (LTER) program is rooted in this legacy.
- • Important contributions to tropical science made by the Luquillo LTER program are a systematic investigation of disturbance and the identification of a number of mechanisms that contribute to the resistance and resilience of forested ecosystems.
- • The LTER program has also contributed to a basic understanding of the ecology and biogeochemistry of the Luquillo Mountains and to an understanding of the long-term consequences of human activity on populations, communities, and ecosystem function.
- • This book focuses on the response of the ecosystems of the Luquillo Mountains to natural and anthropogenic disturbances, with a particular focus on hurricanes and land cover change.

(p.4) Introduction

The Tropics and Tropical Forests

Tropical forests cover an area of approximately 1.8 billion hectares, and they account for about 45 percent of the world's forests (Food and Agriculture Organization [FAO] 2003). Based on rainfall, ecology textbooks (e.g., Ricklefs 1997) usually represent tropical forests as belonging to one of two biomes: rain forests and dry or seasonal forests. This representation fails to appreciate the diversity of tropical forest types and perpetuates the myth that tropical forests are dichotomous in nature. The Holdridge Life Zone System (Holdridge 1967), which is based on empirical data and ecophysiological principles, provided a different picture of tropical forest types. Of the world's 112 life zones, over half (66) are tropical, and 33 include forests (out of 52 forested life zones in the world [Lugo and Brown 1991]). Thus, in climatic terms alone, tropical forests are more diverse than all other world forests combined. The diversity of tropical forest types increases even more when local factors such as geologic formation, soils, topography, and aspect are considered.

The Tropics of Cancer and Capricorn, at 23.5 degrees north and south of the equator, are usually used to define the geographical limits of the tropics. However, the distribution of the conditions amenable to the development of tropical forests does not always conform to these latitudinal criteria (figure 1-1). Tropical forest species respond to environmental factors, of which freezing temperatures is one of the most critical. Species richness decreases sharply in the presence of freezing temperatures, even within tropical latitudes, as evidenced by elevational patterns. Holdridge (1967) defined the tropics and subtropics by the absence of frost in the lowlands (figure 1-2).

Most lowland tropical species cannot tolerate frost, and this explains why tropical forests occur in frost-free areas beyond the Tropics of Cancer (India) and Capricorn (Madagascar) or contract within these geographic limits in areas such as Mexico or Australia, where frost occurs in the lowlands. Frost also occurs on tropical mountains, such as Mount Kilimanjaro, which experiences "summer every day and winter every night" (Hedberg 1997:185). In response to the dramatic diurnal temperature variation in these tropical mountain systems, plants and animals exhibit unusual adaptations such as the diurnal movement of leaves, the production of antifreeze substances, and day/night changes in behavior (Hedberg 1964). The distribution of tropical forests in relation to frost-free conditions is an example of how ecological space, defined by the distribution of environmental factors, differs from a distribution based on geographic space (i.e., the Tropics of Cancer and Capricorn) (see chapter 2).

The diversity of tropical forests is a challenge to ecologists. The task of describing the diversity of forest types is daunting, and it becomes even more complicated when considering forest function and responses to natural and anthropogenic disturbances. The tradition in tropical ecology was to compare forests with little consideration of differences in their climate or disturbance regimes (e.g., Gentry 1990). However, our research in Puerto Rico, and that of colleagues in other parts **(p.5)**

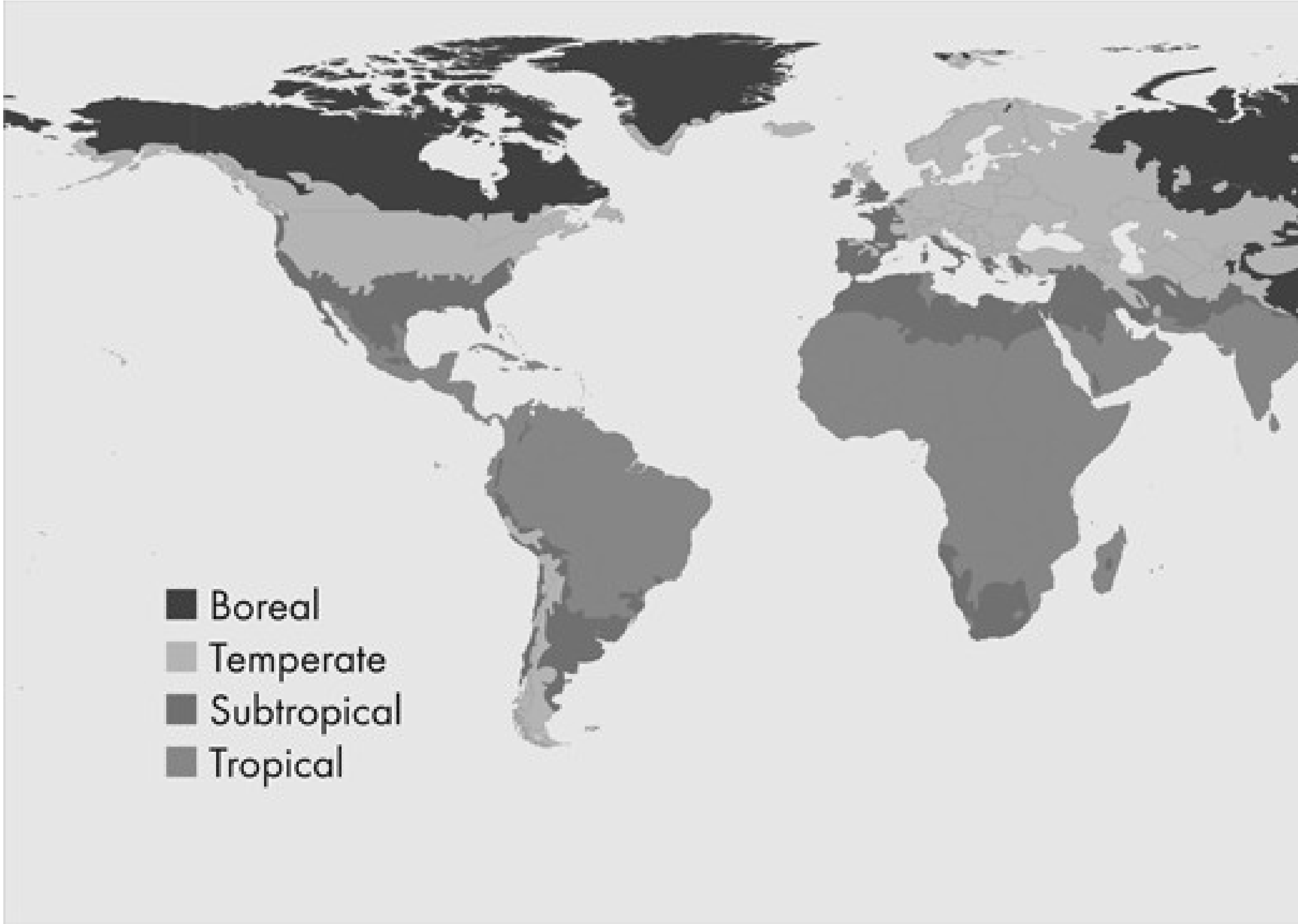
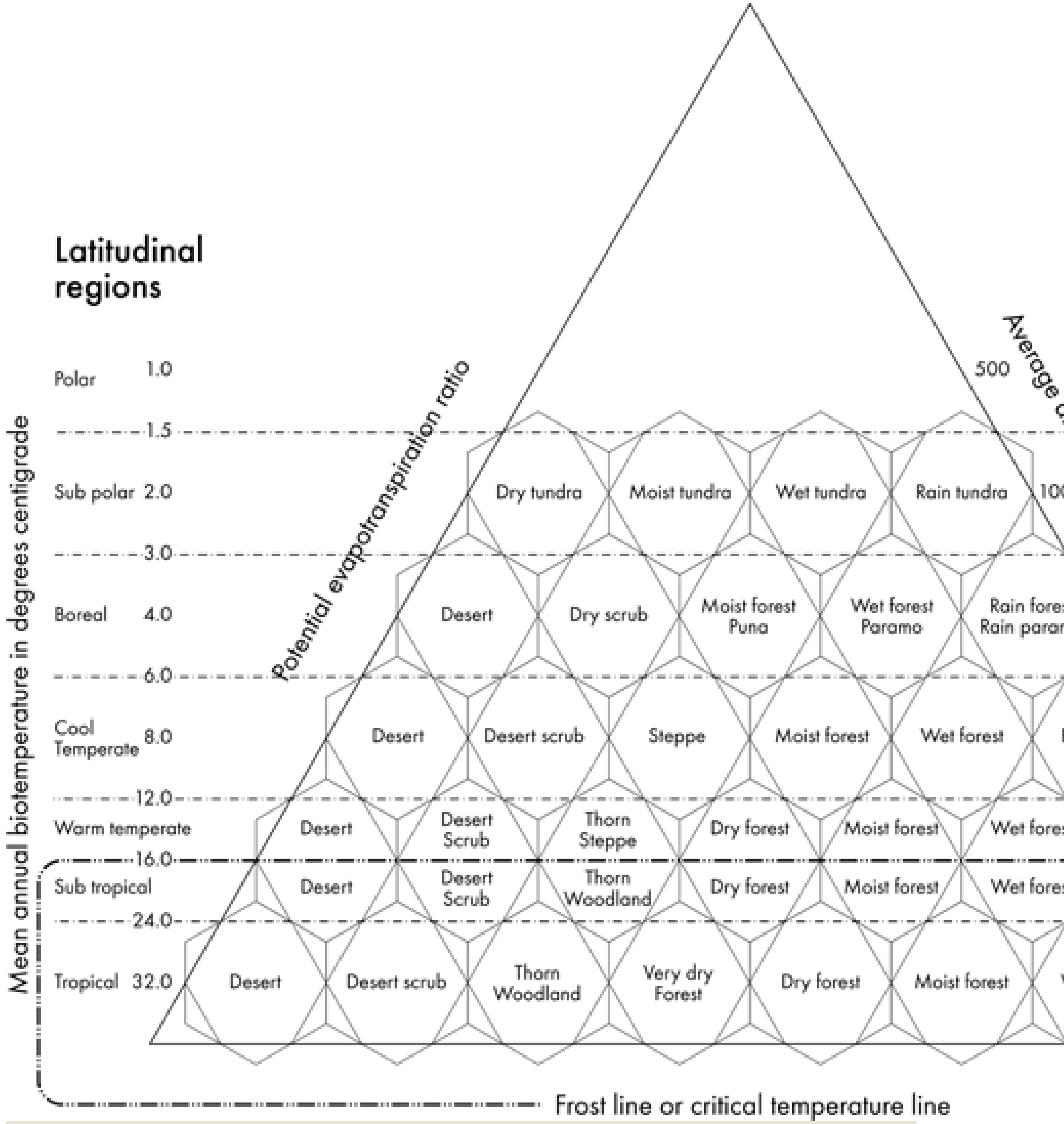


Figure 1.1 The global frost line defines the ecological space in which tropical forests occur. This map, prepared by R. P. Neilson, illustrates four levels of frost throughout the world. The tropics correspond to the area with a 12-month growing season and no frost. The long-term average monthly temperatures for all 12 months exceed the average monthly temperature associated with spring green-up (Neilson 1995). The other thermal zones are as follows: Boreal = supercooled freezing point (−40°C) reached annually; long-term minimum average monthly temperature < −16°C. Temperate = hard frosts annually (24 h < 0°C); long-term minimum average monthly temperature < −1.25°C. Subtropical = frequency of hard frosts ranging from less than annual to relatively rare; nearly zero days annually when the maximum temperature is < 0°C; long-term minimum average monthly temperature < 13°C. The definitions of “tropical” and “subtropical” in this system are different from the designations used by Holdridge (1967), who considers subtropical zones as also frost-free. Thus, “tropical” in this map coincides with “tropical” and “subtropical” in the Holdridge Life Zone System (figure 1-2).


Latitudinal regions
Polar 1.0
1.5
Sub polar 2.0
3.0
Boreal 4.0
6.0
Cool Temperate 8.0
12.0
Warm temperate
16.0
Sub tropical
24.0
Tropical 32.0
Mean annual biotemperature in degrees centigrade
Potential evapotranspiration ratio
500
Average
100
Dry tundra
Moist tundra
Wet tundra
Rain tundra
Desert
Dry scrub
Moist forest Puna
Wet forest Paramo
Rain fores
Rain paran
Desert
Desert scrub
Steppe
Moist forest
Wet forest
Desert
Desert Scrub
Thorn Steppe
Dry forest
Moist forest
Wet fores
Desert
Desert Scrub
Thorn Woodland
Dry forest
Moist forest
Wet fores
Desert
Desert scrub
Thorn Woodland
Very dry Forest
Dry forest
Moist forest
Frost line or critical temperature line

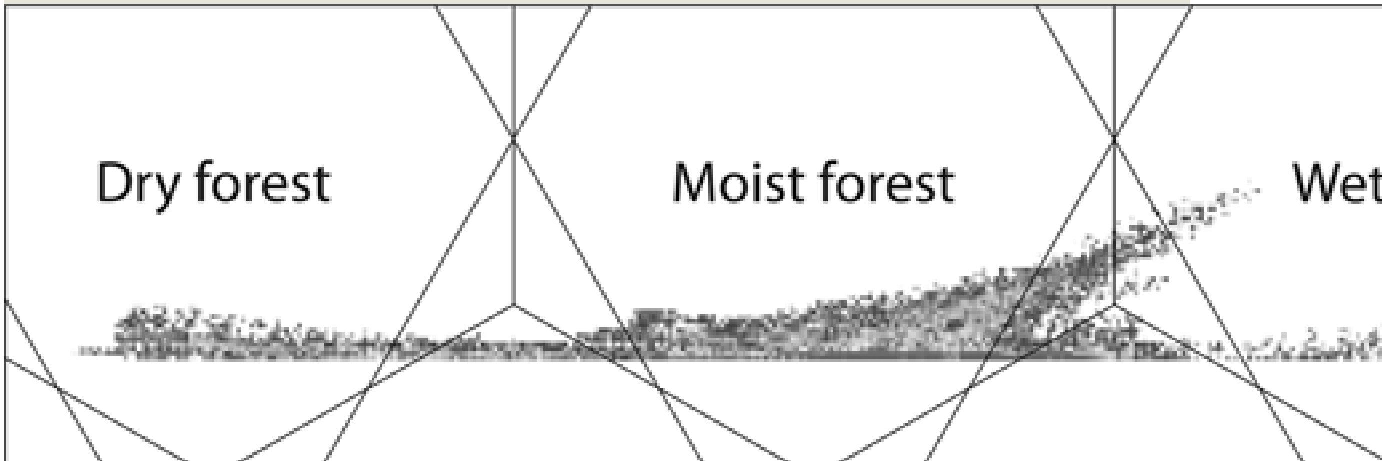

Dry forest
Moist forest
Wet

Figure 1.2 The Holdridge ternary classification system (opposite page; Holdridge 1967) defining life zones with latitudinal regions, altitudinal belts, and potential eva potranspiration ratios based on biotemperature and precipitation. A Holdridge Life Zone map program generated the scatter plot above indicating the continuous distributions of classifications in Holdridge ternary space. This scatter plot represents the biotemperature x precipitation setting in Puerto Rico, that is, the climatic ecological space of the island. Both panels, the program that generates life zones for particular locations, and the scatter plot are from Helmer and Plume (personal communication, 2005) and Plume and Helmer (2005).

(p.7) (p.8) of the world, shows that comparisons among tropical forests require knowledge and a consideration of environmental conditions, the age of forest stands, and the disturbance regime under which forests function (Lugo et al. 2002). Different features of the forest ecosystem, such as species composition, canopy structure, and rates of primary productivity, respond differently to various driving forces. These features affect comparisons among forests and generalizations about their processes. Dry and wet forests, for example, might respond similarly to wind in terms of their canopy structure but differently in terms of their phenology, as a result of water availability and species composition (Lugo et al. 2002). Using the life zone approach, the guiding principle underlying the definition of “tropics” and the diversity of tropical forests is that environmental conditions—or ecological space, as discussed in chapter 2—dictate the organization, composition, and functioning of ecosystems from local to global scales. Therefore, ecological comparisons among ecosystems require a clear understanding of the environmental conditions that are relevant at the various spatial, temporal, and biological scales.

Puerto Rico and the Luquillo Mountains

Puerto Rico is within the geographic tropics and the global frost-free zone (figure 1-1), but it falls within the subtropical belt of the Holdridge Life Zone System because of its temperature regime (figure 1-2). The location of Puerto Rico within the Caribbean basin results in the island’s being subjected to frequent hurricanes (chapter 4). Ocean and trade winds moderate the island’s climate. One of the deepest spots in the Atlantic Ocean is several kilometers northwest of the Luquillo Mountains, a factor that, coupled with the long wind fetch of the Atlantic, contributes to high-energy conditions on the north coast of the island. A mountain chain in the middle of the island creates a rain shadow so that the annual precipitation in Puerto Rico spans a gradient of almost 5,000 mm from the Luquillo Mountains on the windward north coast to the Guánica dry forest (800 mm) on the leeward south coast.

The Luquillo Mountains loom large to observers from any vantage in the northeastern corner of Puerto Rico (figure 1-3). They rise to over 1,000 m above sea level, and the El Yunque peak is only 8 km in a straight line from the nearest beach. Because of their height, the Luquillo Mountains intercept moist air blown from the Atlantic Ocean by the steady trade winds; the peaks are under cloud cover most of the time. 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 1998). 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 (figure 1-4) with a high frequency of low-intensity showers punctuated by periodic high-intensity storms.

Discussions about the ecology of Puerto Rico raise the issue of insularity. Insularity has well-documented effects on the rate of species migrations and turnover (MacArthur and Wilson 1967), but the implications of insularity for the functional aspects of forests or the density of species remain poorly understood (Whittaker 1998). The effects of hurricanes and human disturbance on **(p.9)** ecosystems in the Luquillo Mountains are difficult to disentangle from the effects of insularity.

Figure 1.3 The Luquillo Mountains.

(Photo by A. E. Lugo.)

This Book

This book is a synthesis of ecological knowledge about the Luquillo Mountains and its application to the conservation of biodiversity and the improvement of paradigms in the biological, ecological, and earth sciences. In this first chapter we review and synthesize ecological studies from eight decades of research, beginning with Gleason and Cook’s (1926)vegetation survey and Wadsworth’s (1947) examination of long-term forest growth 15 to 20 years after Hurricanes San Felipe (1928) and San Ciriaco (1932) struck the forest. An examination of the history of ecological research in the Luquillo Mountains reveals the gradual development of more refined and complex conceptual models, as well as the punctuated development of ideas across decades of research by different groups of scientists. All of these investigations have their conceptual roots in long-term assessments of the biotic and abiotic characteristics of the Luquillo Mountains. As part of our synthesis, we demonstrate in this chapter how our conceptualization of the ecosystems of the Luquillo Mountains contributes to a general understanding of the dynamics of forested ecosystems. In other chapters, the focus is principally on research conducted by the Luquillo Long-Term Ecological Research (LTER) program in response to Hurricane Hugo, after which we launched a series of studies in order to understand the effects of disturbances on forest dynamics, structure, and composition. **(p.10)**

Figure 1.4 Box plots of standardized values of the bulk precipitation and soil pool size for various humid tropical forests (Scatena 1998). Values for Bisley (B), Luquillo Experimental Forest, are highlighted for comparison with other sites. Each box encompasses the 25th through 75th percentiles and has horizontal lines at the 10th and 90th percentiles. Circles represent data outside the range of the 10th and 90th percentiles. Dividing the value from a particular site by the meridian value of all the sites and then multiplying by 100 gives standardized values. The abbreviations IN-NA, IN-CA, IN-MG, IN-CL, IN-K, IN-NH$_4$, and IN-NO$_3$ denote the annual average inputs by bulk precipitation for sodium, Ca, Mg, Cl, K, NH$_4$-N, and NO$_3$, respectively. The abbreviations S-CA, S-MG, S-K, S-P, S-N, and pH denote the concentrations of extractable soil nutrients in surface soils. The coefficients of variation and sample size are as follows: IN-NA = 0.96, 11; IN-CA = 0.77, 14; IN-MG = 1.04, 14; IN-CL = 0.90, 9; IN-K = 0.65, 14; IN-NH$_4$ = 0.82, 7; IN-NO$_3$ = 0.73, 8; S-CA = 1.42, 23; S-MG = 1.18, 23; S-K = 1.36, 23; S-P = 0.88, 17; S-N = 0.76, 17; pH = 0.20, 23.

Models of Forest Structure and Functioning

Humans have visited and modified the Luquillo Mountains since prehistoric time. Each wave of visitors, including modern scientists, has no doubt marveled at the beauty and contemplated the mysteries of these mountains. Each group has also formulated questions and sought answers in an effort to understand the sights and sounds and to derive benefits from the ecosystems of these mountains.

A number of conceptual models of the ecosystems of the Luquillo Mountains have emerged. The Taíno Indians were among the first inhabitants of Puerto Rico and most likely generated the first conceptual models of the Luquillo Mountains (Domínguez Cristóbal 1989, 2000). Several scientists have summarized the scientific understanding of the Luquillo Mountains during the 20th century (Gleason and Cook 1926; **(p.11)** Holdridge 1947; Beard 1949; Wadsworth 1949, 1950; Odum 1970a; Lugo and Scatena 1995; Reagan and Waide 1996). Robinson (1997) recently published a popular version of the natural history and historic events of the Luquillo Mountains. Each of the works mentioned above represents a particular concept of the world that was descriptive of the state of knowledge at the time of its formulation. These works mentioned the role of large and infrequent disturbances but gave little attention to them. In this book, we offer a new synthesis of information that will certainly be modified in the future as our understanding of ecological phenomena increases through additional research.

Indigenous Peoples—The Forest as a Sacred Place

Humans arrived in Puerto Rico some 2,200 years ago by island hopping from South America (Domínguez Cristóbal 2000). These indigenous peoples included three successive groups or cultures: the Saladoides, the Taínos, and the Caribs. The Saladoides were the first to arrive via the Orinoco River and from Saladero, across the sea in Venezuela. They were hunters and gatherers who were replaced in Puerto Rico by the Taínos, who had mastered agriculture. By 1490, indigenous peoples had spread throughout the island. Their activities modified the flora and fauna by introducing new species to Puerto Rico (Francis and Liogier 1991) and caused the extinction of numerous native animal species (Brash 1987). The Carib Indians, known for their superior navigational skills, were becoming prominent in the Caribbean region when the Europeans interrupted their expansion after 1493.

The Taíno Indians are the best known among the three indigenous groups. They left rock carvings within the Luquillo Mountains that depict creatures, both alive and dead (dead people were represented with the soul leaving the body above the deceased’s head). The writings of early European observers and subsequent inquiries suggested that the Taíno’s view of the Luquillo Mountains was both religious and pragmatic (Domínguez Cristóbal 2000). To the Taíno people, the Luquillo Mountains were a sacred place where the good god *yucahu* or *yucayú* resided; this god protected them from the bad god *mabuya* or *juracán*. The modern term *hurricane* originates from the Taíno word *juracán*. The existence of this term and its connection to the Taíno religion suggests some knowledge of the most severe natural disturbance of the Luquillo Mountains. Clearly, questions about the nature and origin of hurricane disturbances and forest recovery from them had to be of concern to these early inhabitants of the Luquillo Mountains. Long-term records of hurricane tracks show two lanes to the north and south of Puerto Rico with a high number of tracks, and a lower number of hurricane tracks over the island (Neuman et al. 1978). This pattern, locally known as the “Puerto Rico split,” correlates with the Taíno belief that the Luquillo Mountains somehow influenced the passage of hurricanes and protected their island.

Taínos also believed in totems and, possibly inspired by the Luquillo Mountains and the Central Cordillera, visualized the whole island as being carried by a large animal, which evolved into a figure with a human face and feet (Domínguez Cristóbal 2000). This animal figure is a *cemí* (figure 1-5), representations of which are sold today as decorations and as a tourist curiosity. The movement of the cemí was thought to contribute to the periodic earthquakes that affected the island.

(p.12)

Figure 1.5 A Taíno cemí illustrates the idea that the island of Puerto Rico is steadied by an anthropogenic being.

(Photo by Jerry Bauer.)

The sacred nature of the Luquillo Mountains, however, did not stop the Taínos from using natural products from its forests. They used the resin of the tabonuco tree (*Dacryodes excelsa*) to caulk their canoes, a custom that the Spaniards adopted after arriving on the island. Although the Taínos used tabonuco and other plants and animals for food, construction materials, and medicinal purposes, there is no evidence that suggests a sophisticated understanding of the relationship between ecosystem disturbance and response. Taínos also used the Luquillo Mountains as a haven during their conflict with the Spanish conquistadors (Scatena 1989).

Spanish Conquistadors—The Forest as a Resource

Europeans first saw Puerto Rico during the second voyage of Columbus in 1493 (Morison 1974). As Columbus’s ships approached from the east, it is likely that the Luquillo Mountains were the first part of Puerto Rico that the sailors saw, which made them believe they were the tallest mountains on the island. The conquistadors subsequently used the Luquillo Mountains as a beacon to guide their ships as they sailed between the Atlantic and the Caribbean. The predominant paradigm of Spanish colonization involved economics, focusing on the exploitation of people and resources. The Taínos disappeared as a people under the 400 years of Puerto Rico’s Spanish rule. The main focus of the Spaniards in Puerto Rico was on products, and what was available on the island for export to Spain or to support local Spanish activities. The conquistadors began an inventory of the island’s wood and minerals in order to exploit them. These inventories represent the first description of the **(p.13)** biodiversity and ecosystem services provided by the Luquillo Mountains and Puerto Rico (Domínguez Cristóbal 1992).

The Spanish government established a forest service in Puerto Rico (*Inspección de Montes*) between 1876 and 1889 (Domínguez Cristóbal 1992). This agency focused on timber production and land management. Land management and harvesting plans were developed, and timber harvesting had begun in the Luquillo Mountains by 1880. Tabonuco and ausubo (*Manilkara bidentata*) were species targeted for extraction. A tabonuco tree was valued at

1.50 pesos, whereas an ausubo tree was worth 2.25 pesos, assuming a minimum height and circumference for extraction of 8.5 and 1.58 m (0.5 m in diameter at breast height), respectively (a Spanish peso in the 19th century was equivalent to 60 U.S. cents in modern currency). Trees were harvested by the end of January and extracted during the somewhat drier months of January to March. A 9,000 ha area in the Luquillo Mountains yielded 19,630 m^3 of wood, or 15,857 pesos y^{-1}. Enforcement activities involved arrests, as was reported in 1889 when two people were arrested for cutting dozens of laurel sabino (*Magnolia splendens*), an endemic timber tree species.

The Spanish government's approach to forestry included the planned use of the forests and the protection of their watershed value. The government passed laws and proclamations to protect the forest timber for the crown, and they also designated buffer areas along rivers and streams in order to protect the water quality (Wadsworth 1949). A large area of the Luquillo Mountains and other forest locations in Puerto Rico were designated as public forests in 1876, making it one of the earliest such designations in the Western hemisphere. These actions anticipated the modern understanding of sustainable management practices and the effects of anthropogenic disturbance. However, no evidence suggests that the Spanish government actually estimated the watershed values of the Luquillo Mountains. This would not occur until the 1990s, when scientists in the LTER program developed a technical justification for the protection of these resources.

Early Foresters—Focus on Forest Management

North American foresters started writing about the Luquillo Mountains immediately after the Spanish–American War of 1898 (Hill 1899; Gifford 1905). The foresters surveyed the forest resources of the Luquillo Mountains from a utilitarian viewpoint. However, their approach touched on modern issues of functional diversity, ecosystem resilience, and species introductions. For example, they noted the abundance of "useless palms" (*Prestoea montana*) and asked how to control them (Gifford 1905). One suggestion was to import pigs to eat the palm fruit and thereby control the palm populations. Murphy (1916) published a comprehensive analysis of forestry in Puerto Rico and predicted that if timber exploitation continued at the rate observed, all forest cover would be lost from the island in the next 11 years. Murphy also considered the best approaches for the reforestation of slopes degraded by subsistence agriculture, but the early foresters did not know which species to use on particular sites or how to plant them. Early foresters spent a short time in Puerto Rico, and their contribution was observational rather than experimental.

(p.14) In 1903, 2 years before the establishment of the U.S. Forest Service and the National Forest System, the U.S. government created the Luquillo Forest Reserve. In 1907, the Luquillo Forest Reserve was proclaimed the Luquillo National Forest, and in 1935 it was named the Caribbean National Forest. The use of the forest for research purposes was recognized in 1956, when the Caribbean National Forest was also designated as the Luquillo Experimental Forest; this is the only example in the National Forest System of a National Forest that also is designated as an Experimental Forest. In 1976, the Luquillo Experimental Forest was designated as a United Nations Educational, Scientific, and Cultural Organization

(UNESCO) Biosphere Reserve, and in 2007 the Caribbean National Forest was renamed the El Yunque National Forest.

Natural Historians—Focus on Biodiversity

In the beginning of the 20th century, over a period of some 30 years, Nathaniel Lord Britton led an impressive number of scientists from the New York Academy of Sciences and the University of Puerto Rico on a scientific survey to describe the natural history of Puerto Rico and the Virgin Islands (Britton 1919). Figueroa Colón (1996) updated many aspects of this survey. The natural historians answered many taxonomic and botanical questions and created the taxonomic foundation for most of the research that would follow on the Luquillo Mountains. Expeditions from the New York Academy of Sciences made fundamental contributions to many subjects, including geology (Meyerhoff 1933), botany (Britton and Wilson [1923, 1924, 1925, 1926] 1930), ecology (Gleason and Cook 1926), paleobotany (Hollick 1928), Pteridophyta (Maxon 1926), bryophytes (Britton 1924; Crum and Steere 1957), fungi (Seaver and Chardón 1926; Seaver et al. 1932; Hagelstein 1932), and mammals (Anthony 1925). On the 80th anniversary of the beginning of the scientific survey, the state of knowledge on birds (Wiley 1996) and insects (Maldonado Capriles 1996) was updated, as were other topics (Figueroa Colón 1996).

Gleason and Cook (1926) were the first to propose models on the successional relations of vegetation in Puerto Rico. Their studies initiated investigations into the community ecology on the island and specifically addressed the relationship between community composition and disturbance. They were interested in the effects of agricultural activities on the species composition of plant associations. The work of Gleason and Cook (1926) provided the basis for subsequent long-term studies and experiments.

Modern Foresters—Focus on Control of Production

A series of hurricanes struck Puerto Rico between 1928 and 1932 and had severe effects that changed the land uses and economy of the island. In the 1940s, research turned once again toward methods to stimulate tree growth and the harvesting of forest timber. The first mechanistic studies and long-term experiments began during this period. J. S. Beard (1942, 1945) and Frank Wadsworth (1949), for example, both addressed questions about the “useless palms” that grew on steep slopes with saturated soils and on the sites of large landslides (Lugo et al. 1995). Studies of the **(p.15)** tree growth of both palms and dicotyledonous trees led to the conclusion that although palm brakes had no potential for wood production, they were of significant watershed value because they grew on the wettest slopes of the Luquillo Mountains and protected significant catchment areas for lowland water supplies.

The failure of reforestation efforts within and outside of the Luquillo Mountains led to the establishment in 1939 of the Tropical Forest Experiment Station, later to become the International Institute of Tropical Forestry. The mission of this institution was to develop a scientific basis for effective reforestation and ecosystem restoration (Wadsworth 1995).

Leslie Holdridge, the first scientist of the Tropical Forest Experiment Station, addressed the relationship between vegetation and climate and developed the concept of the life zone based on observations about the Luquillo Mountains and the mountains of Haiti (Holdridge 1947, 1967). Ewel and Whitmore (1973)published a map of the life zones of Puerto Rico; however, they performed no validation of the correspondence of life zones with vegetation parameters such as species composition or the physiological limits of plant growth. Nevertheless, life zone studies highlighted the importance of environmental gradients in the distribution of communities and ecological processes. They provided the groundwork for later studies on the interrelationships among disturbance, vegetation, and climate, and they established the baseline information for the depiction of ecological space in Puerto Rico (see chapter 2).

Frank Wadsworth, a U.S. Department of Agriculture (USDA) Forest Service scientist, asked whether tree growth could be accelerated to make all trees in a stand grow as fast as the fastest-growing ones. He addressed the relationship between disturbance and productivity by establishing forest inventory plots under a variety of conditions in which he cut down trees in order to manipulate the basal area and measured the growth of the remaining trees. Wadsworth also measured the natural rates of tree growth and their variation over time (Wadsworth 1947). Wadsworth and other USDA Forest Service scientists continued these long-term studies (Crow and Weaver 1977; Weaver 1979, 1983; Wadsworth et al. 1989). However, with one exception (Crow 1980), the temporal changes in the structural and functional characteristics of forest stands received little attention until the 1980s.

José Marrero (1947, 1950) conducted tree-planting experiments in collaboration with Charles Briscoe and Frank Wadsworth, who worked in the tree plantation program of the USDA Forest Service. These foresters provided information on the correspondence between tree species and site conditions. Additional autecological research resulted in detailed life history observations for a number of tree species (McCormick 1995) and a summary of the silviculture of tropical tree species in Puerto Rico and the Caribbean (Francis and Lowe 2000). Plantation experiments led to greater success in reforestation efforts (Francis 1995; Wadsworth 1995), but no consideration was given to the effects of the planted species on the soils, site productivity, and successional outcome of planted sites. More recently, research on nutrient cycling, carbon dynamics, plant succession, and the relationship between diversity and function in plantations (Lugo et al. 1990b; Cuevas et al. 1991; Lugo 1992; Cuevas and Lugo 1998; Silver et al. 2000, 2004) has been carried out and continues today in plantations that now exceed 70 years of age (figure 1-6). Two **(p.16)** syntheses of forestry research and experience in Puerto Rico and their applications in tropical forest production were recently published (Wadsworth 1997; Francis and Lowe 2000). Lugo et al. (2003)summarized the experience with mahogany plantations.

Monitoring Soils, Climate, and Hydrology

Scientists in the Agriculture Experiment Station of the University of Puerto Rico studied the soils of Puerto Rico and developed a detailed map of the island’s 165 soil series (Roberts 1942) that is still in use today. According to Beinroth et al. (1996), the state of soil characterization in Puerto Rico is unmatched anywhere else in the tropics. In one data set, they report an analysis of a soil pedon per approximately 4,500 ha, or one data point for every plot in a grid of 6.5 by 6.5 km. Soils in Puerto Rico are extremely diverse and include

10 of the 12 soil orders of the USDA Soil Classification System. The monitoring of climate in Puerto Rico is also comprehensive. The National Weather Service operates over 90 weather stations, of which 12 have been keeping continuous records for over 100 years (Larsen 2000). Some stations contain records from the time of the Spanish government. These weather stations are complemented with an island-wide U.S. Geological Survey network of stream-gauging and well-monitoring stations.

Figure 1.6 A mature artificial forest in the *Dacryodes excelsa* zone of the Luquillo Mountains. Dr. F. H. Wadsworth (right) was responsible for the management of this site.

(Photo by A. E. Lugo.)

(p.17) Modern Ecologists

H. T. Odum’s Rain Forest Project

Howard T. Odum and dozens of scientists and technicians, supported by the Atomic Energy Commission and the University of Puerto Rico, conducted the first large-scale ecosystem study on the effects of disturbance on the tabonuco forest. Their experiments using radiation and tree harvesting established the foundation for long-term ecological research in Puerto Rico and the tropics in general (Odum and Pigeon 1970). The Odum research legacy in the Luquillo Mountains transcends the radiation experiment in which he found that the tabonuco ecosystem’s structure and function had a high resistance to radiation (Odum 1970a). Odum also described in detail the climate of the Luquillo Mountains (Odum et al. 1970b) and demonstrated how to measure forest metabolism on a grand 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, 1970c), and raised many questions for future studies. Many of Odum’s questions concerned key methodological and monitoring approaches of the time, and others emphasized fundamental issues for research in tropical forests (table 1-1).

Studies of nutrient cycling in the tabonuco forest addressed plant biomass and nutrient content (Ovington and Olson 1970), soil nutrients (Edmisten 1970b), nitrogen (N) (Edmisten 1970a) and phosphorus (P) (Luse 1970) cycles, nutrient input in litterfall (Wiegert 1970a), litter decomposition (Wiegert and Murphy 1970), and nutrient losses in leachate (Sollins and Drewry 1970; Tukey 1970). These and other subsequent studies identified key aspects of biogeochemical cycling in tropical forests that have been applied to other tropical forest environments. These include the following:

- • Tukey (1970) measured phosphorus leaching and foliar phosphorus absorption in bromeliads, thus demonstrating a mechanism by which these epiphytes receive nutrients from the atmosphere.
- • Odum et al. (1970a), Witkamp (1970), Kline (1970), and others measured the radioactive fallout retention of epiphytes, epiphylls, and other forest surfaces,

Table 1.1 Ecosystem functioning questions raised by Odum (1970a: I-273–I-274) with annotations regarding any progress made

• What controls forest functioning? This continues to be a research priority.
• How much diversity is needed for stability and control? This hotly debated question

remains unanswered.

- What is the weight of nervous tissue in the forest? Nervous tissue per unit area was proposed as an index of the animal contribution to the control system of the forest, but its value has not been determined beyond the early estimates of Canoy (1970).
- What is the significance of regenerative specialists for the planning of systems of man and nature where complex chemicals are used? There is considerable interest in designing new ecosystems (Lugo 1997), but we have very little knowledge of the functions of individual species that would compose these ecosystems.

(p.18) thus showing the global connection of tropical forests to atmospheric systems originating in temperate latitudes.

- The global role of tropical forests in accumulating carbon in biomass and soils was a subject of study and synthesis in the Luquillo Mountains, beginning with a study by Odum and Pigeon (1970), which was followed by the work of Brown and Lugo (1982), Lugo and Brown (1982), Brown et al. (1984), Aide et al. (1995), and Silver et al. (2000). These studies have documented that tropical forests in Puerto Rico are carbon sinks under both natural and human-altered conditions.

Jordan et al. (1972) summarized the results of mineral cycling research in the Luquillo Mountains and proposed several hypotheses regarding the ways in which elements cycle in temperate ecosystems compared to cycling in tropical ecosystems. They also hypothesized that the size of a given ecosystem compartment would have a proportional effect on variations in the mineral cycling. For example, in the tabonuco forest of the Luquillo Mountains the relatively small litter pool would be more sensitive to disturbances than would the stemwood or root biomass pools, owing to their larger size and greater potential buffering capacity.

Before the LTER program, the animal species that received the greatest research attention included termites (McMahan 1970; Wiegert 1970b), earthworms (Lyford 1969), birds (Kepler and Kepler 1970; Recher 1970; Snyder et al. 1987), lizards, frogs (Turner and Gist 1970, Pough et al. 1983; Stewart and Pough 1983; Stewart 1985; Narins and Smith 1986), and snails (Heatwole et al. 1970; Stiven 1970). Collectively, these studies represent an effort to understand the population and community dynamics of animals in the forest, explore the relationship between their activity and vegetation dynamics, and hypothesize their importance to the overall functioning of the forest.

For Odum, the Luquillo Mountains functioned as an integrated ecosystem connected to the rest of the globe via 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 1970b). Through research on the 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 or wood production (Odum 1995).

Government and Academic Scientists

Even today, we lack answers for many of the questions posed by Odum and other scientists. Many institutions are currently working together to answer these questions, including government (U.S. Department of the Interior [USDI] Geological Survey, USDA Forest Service, U.S. Department of Energy, USDI Fish and Wildlife Service, U.S. National Aeronautic and Space Administration) and academic (University of Puerto Rico and other universities in Puerto Rico and mainland United **(p.19)** States) institutions. Together we are addressing many lines of research in order to advance our knowledge of the Luquillo Mountains from the 1960s to the present. The overarching contribution of these efforts is to diversify the scope of science in the Luquillo Mountains, introduce the latest research technologies, and consolidate the reputation of the Luquillo Mountains as a tropical site with intense monitoring and experimental investigations of ecological phenomena. In the following sections we present summaries of the major conclusions of these studies, so as to lay the foundation for new material presented later in this book.

Managed Systems in Relation to Soils and Succession

Research regarding tree plantations has received considerable attention in the Luquillo Mountains. These studies have attempted to increase site productivity by matching selected tree species to particular site conditions and have thus addressed issues relevant to our present ideas about ecological space. Some of the oldest tree plantations in the tropics (approximately 70 years old) grow in the Luquillo Mountains. These plantation ecosystems were established by the USDA Forest Service in the 1930s, and the subsequent monitoring of these ecosystems has provided an unprecedented opportunity to conduct comparative research in managed and unmanaged forests. Research on tree plantations has focused on key ecosystem storages and fluxes, including the following:

- • the determination of standing stocks, flow rates, and nutrient-use efficiencies in pine (*Pinus caribaea*) and mahogany (*Swietenia macrophylla*) plantations in comparison with those in nearby secondary forests of similar age (Cuevas et al. 1991; Lugo 1992);
- • the documentation of species differences in rates of nutrient retranslocation and nutrient use efficiency (Cuevas and Lugo 1998);
- • the quantification of the effects of tree plantations on soil carbon and nutrient dynamics (Lugo et al. 1990b; Silver et al. 2004) and on organismal diversity (Cruz 1987, 1988; González et al. 1996); and
- • the assessment of the responses of tree plantations to hurricanes (Fu et al. 1996; Wang and Scatena 2003; Ostertag et al. 2005).

Trees in plantations grow faster at low elevations (<500 m), where soils are better aerated and the rainfall is lower than at high elevations. Plantations attempted at higher elevations and rainfall levels have generally failed. On degraded sites, plantations contributed to the recovery of nutrient and organic matter pools in the soil (Lugo et al. 1990b; Cuevas et al. 1991; Cuevas and Lugo 1998). This recovery took decades (Silver et al. 2004). In addition, the plantation understories were invaded by a number of native tree species, although their richness was not as high as that of natural forest stands (Lugo 1992). Native species reinvade plantations, eventually contributing to the tempo and direction of succession. The long-term consequences of this reinvasion are still under investigation (Parrotta and Turnbull 1997).

Topographic Control of Vegetation and Soils

Tree species are not evenly distributed across ridges, slopes, and valleys (Wadsworth 1949; Weaver 1987). Some species, such as the tabonuco, prefer ridge habitats with well-aerated soils, **(p.20)** whereas others—for example, *Pterocarpus officinalis*—grow in valleys where the soils are saturated. Still other species, such as *Sloanea berteriana*, occur on slopes. The pattern of species distributions on these catenas occurs throughout the Luquillo Mountains, but the relationships among the topography, disturbance regimes, and vegetation dynamics were not understood in a comprehensive fashion until the LTER program explored them (Silver et al. 1994; Scatena and Lugo 1995; see also chapter 3).

Nutrient Cycles and Soil Organic Matter

In addition to the studies in the tabonuco forest discussed above, nutrient cycles have been studied in the Luquillo Mountains in mature (Lugo 1992; Silver 1992, 1994; Silver and Vogt 1993; Silver et al. 1994; McDowell 1998), successional (Lugo 1992; Silver 1992; Scatena et al. 1996; Silver et al. 1996), and plantation forests (Lugo et al. 1990b; Cuevas et al. 1991; Lugo 1992; Fu et al. 1996; Cuevas and Lugo 1998; Silver et al. 2004). These studies provided estimates of the storages and the main fluxes of nutrients and organic matter, the relative distribution of organic matter and nutrients between above- and belowground compartments, and the efficiency of nutrient cycling. The results indicate the following:

- • Nitrogen and calcium (Ca) do not limit the productivity of tabonuco forest, but phosphorus (P) and potassium (K) might be limiting.
- • The distribution of nutrients and biomass in a forest is a function of the forest’s age, topographic position, and climate.
- • The efficiencies of cycling differ among nutrients (for example, high for P and low for N).
- • The large quantity of belowground nutrients and organic matter contributes to the resilience of the forest.
- • Nutrients in natural forest stands cycle at faster rates with relatively less storage in biomass as compared to that in plantations.

In the late 1960s, the Arnold Arboretum of Harvard University conducted a set of integrated studies of the biology, ecology, and ecophysiology of elfin forests in the Luquillo Mountains. These studies contributed basic information about, and some of the first observations of, the biogeochemistry in upper montane elfin forest plants and soils (Howard 1968, 1969, 1970; Lyford 1969; Wagner et al. 1969). Studies included the description of the canopy soil (complete with earthworms), the saturated surface soils, and the foliar chemistry of upper montane forest species. This interdisciplinary study gave us the first comprehensive overview of the short stature elfin forest as a saturated wetland on a mountaintop, and it described the many biotic adaptations of the flora and fauna to the extreme conditions of wind and wetness of this forest.

Soil Oxygen and Greenhouse Gases

Wet tropical forests, such as those in the Luquillo Mountains, are commonly characterized by low or fluctuating soil oxygen availability, a factor that has a significant effect on the structure and functioning of the ecosystem. High-clay soils, warm temperatures, and abundant water lead to conditions in which the oxygen consumption by roots and soil organisms **(p.21)** exceeds the rate of replacement from the atmosphere. These conditions, together with pockets of saturated and waterlogged soils (Wadsworth and Bonnet 1951), led to the description of the forests of the Luquillo Mountains as “slope wetlands” (Frangi 1983; Lugo et al. 1990a). The most extreme case of poorly oxygenated upland soils occurs on the peaks and ridges of the upper elevation elfin forests, where Lyford (1969) found organic soils at all levels of the forest from the ground to the canopy. He suggested that the canopy roots and arboreal earthworms were escaping the strongly reducing conditions of the terrestrial soil environment. Odum (1970c) noted mottling and gleying in the soil profile, a tendency for roots to concentrate near the surface, and the low redox potential of these soils. Silver et al. (1999) quantified the soil oxygen concentrations in soils along elevation and topographic gradients (figure 1-7). They found that the soil oxygen decreased with increasing annual rainfall, as well as from ridgetops to valley bottoms, and they interpreted the importance of these observations for patterns in tree species richness, nutrient cycling, primary productivity, and greenhouse gas emissions.

Tropical forests are involved in the circulation of greenhouse gases, and the dynamic redox of the Luquillo soils contributes to strong patterns in the production and emissions of carbon dioxide, nitrous oxide, and methane (Keller et al. 1986; Steudler et al. 1991; Silver et al. 1999; McGroddy and Silver 2000; Silver et al. 2001; Teh et al. 2005). Patterns in carbon dioxide emissions are complex and are affected by a combination of the rates of net primary production, the soil redox status, and past disturbance (Keller et al. 1986; McGroddy and Silver 2000).Tropical forests are the largest natural source of nitrous oxide, a potent greenhouse gas. Flood plains and upper elevation soils are large natural sources of this gas in the Luquillo Mountains (Keller et al. 1986; Erickson et al. 2001; McSwiney et al. 2001; **(p.22)** Silver et al. 2001). Tropical wetlands are a natural source of methane, which is also a potent greenhouse gas, but upland tropical forests were thought to be a net sink. Research in the Luquillo Mountains suggests that slope wetlands and valley bottoms are actually a net source, owing to the abundance of anaerobic soil microsites, even in well-drained soils (Keller et al. 1986; Silver et al. 1999; Teh et al. 2005).

Figure 1.7 The soil oxygen gradient in the Luquillo Mountains (Silver et al. 1999).

Nutrient cycles are fundamentally affected by soil oxygen as redox states change with the onset of anaerobic conditions. This is particularly true for phosphorus, an element generally thought to limit the net primary production on highly weathered tropical soils. Phosphorus cycling is tightly coupled with the redox state of iron, and it can be released through the reduction of abundant iron oxides (Silver et al. 1999). Soil redox dynamics, both spatial and temporal, create sharp interfaces in the soil (aerobic versus anaerobic microbial physiologies) and between plants and soil (anoxia tolerant versus intolerant species) that help shape the structure and function of the forest.

Root Grafting and Tree Unions

Wadsworth and Englerth (1959) observed the resistance of trees on ridges to high winds, and later Odum (1970a, 1970c) reported the presence of root grafting in the tabonuco forest. These two independent observations have profound importance for the understanding of several phenomena in the tabonuco forest. They might help explain the success of monospecific stands of tabonuco on ridges, which are the most oxygen-rich sites in the forest (Silver et al. 1999). They might also help explain the high respiration rates of tabonuco shade leaves (Odum et al. 1970c), which could benefit from the translocation of sugars among tabonuco trees connected through root grafts. Chapter 3 reviews the long-term ecological research that placed these early observations in context with regard to the dominance and functioning of tabonuco forests on ridges.

Food Webs and Functional Diversity

The animal species richness of the Luquillo Mountains is less than that found in similar-sized mainland tropical forests (Waide 1987), in part because of biogeographical and historical conditions. Communities comprise a small number of abundant or functionally important animal species, and this provides an excellent opportunity to examine the influence that animals have on ecosystem structures and processes.

Vertebrates are abundant in the Luquillo Mountains. Frogs and lizards each average more than two individuals per square meter; this density is among the highest recorded for these types of animals (Reagan 1996; Stewart and Woolbright 1996). On average, the body size of vertebrates is smaller in the Luquillo Mountains than in mainland tropical forests. However, because of their high density in Puerto Rico, vertebrates have a significant effect on the movement of mass, nutrients, and materials in forest stands. For example, lizard and frog populations consume about a million insects per hectare per day (Reagan 1996; Stewart and Woolbright 1996). Birds, bats, and insects pollinate and disperse seed for most tree species (Garrison and Willig 1996; Waide 1996; Willig and Gannon 1996). Among invertebrates, termites accelerate the decomposition of woody materials (Wiegert 1970b; Wiegert and Murphy 1970), and earthworms aerate low-oxygen-saturated soils (Lyford **(p.23)** 1969) and accelerate litter decay (González and Seastedt 2001). These studies have been expanded greatly in the LTER program (see chapter 3).

The functional relationships among taxa emerged only as a result of a research program at the El Verde Field Station in the 1980s. Reagan and Waide (1996) synthesized over 30 years' worth of research to develop a comprehensive picture of the food web structure in the tabonuco forest (see chapter 3). Several important observations about food webs in the tabonuco forest have influenced contemporary theory about the trophic organization of ecosystems. The following five examples from Reagan et al. (1996)illustrate the insights gained from this long-term and intensive study of the biota in the tabonuco forest at El Verde (see also chapter 3).

- • Although feeding loops or cycles (e.g., species A consumes species B, which in turn consumes species A) within a community should be rare for theoretical reasons associated with the destabilization of population dynamics, they are quite common in the tabonuco forest. Approximately one-third of all (ca. 20,000) food chains in the forest involve at least one species that is part of a food loop. The more dominant vertebrate taxa, such as frogs and lizards, participate in food loops through ontogenic dietary shifts (e.g., adult vertebrates consume some invertebrates that in turn consume immature vertebrates).

- • Connectance in a food web, or the proportion of possible feeding relations realized in a community, is hypothesized to be an invariant characteristic of communities such that, on average, each species should interact trophically with approximately 14 percent of the other species. This pattern is present in the tabonuco forest at the lowest level of trophic species resolution (100 to 300 species). However, as the trophic species resolution increases (>1500 species), the connectance decays to a value of approximately 2 percent.
- • Although trophic ratios are hypothesized to be scale-invariant, the ratios of basal to intermediate to top species and links among top to intermediate to basal species in the tabonuco forest vary significantly with the number of trophic species. In particular, top predators, even at the lowest level of taxonomic resolution, were significantly less common (by an order of magnitude) than theoretically predicted.
- • Food web theory and thermodynamic constraints indicate that omnivory (species feeding on multiple trophic levels) should be rare and that food chains should be short (three to five links). Nonetheless, in the tabonuco forest, omnivores are pervasive and include about one-quarter of the bird species (Waide 1996), many of the bat species (Willig and Gannon 1996), and keystone species of frogs (Stewart and Woolbright 1996) and anoline lizards (Reagan 1996). Similarly, the range of food chain lengths in tabonuco forest is from 2 to 19 links, with a mean of 8.6 and a mode of 8.
- • The reticulate hypothesis of food web organization suggests that the compartmentalization of trophic interactions should not occur within well-defined habitats. In contrast, in the tabonuco forest, a strong dichotomy in the food web organization exists, with nocturnal and diurnal compartments dominated by frogs and lizards, respectively.

(p.24) The structure and dynamics of foods webs in the Luquillo Mountains are closely related to the biogeography, habitat heterogeneity, and disturbance, as discussed in chapters 2 through 5.

Land–Water Interactions

A review of the available literature on land–water interactions in the Luquillo Mountains prior to the LTER program suggested that the connectivity within and among the ecosystems of the Luquillo Mountains is enhanced by interfaces involving water (Lugo 1986). During heavy rains, a continuous film of water covers the land from all surfaces of high-elevation forests (palm, colorado, and elfin forests) to streams and via the two-way movement of biota between the tops of the mountains and the ocean. The ecological importance of this connectivity rests in the coupling of the ecosystems of the Luquillo Mountains through a variety of alternative avenues for the exchange of materials and organisms. The support for this proposal includes the following:

- • The cloud condensation level is around 600 m, which means that the whole aboveground structure of the forests above this elevation is immersed frequently within clouds. This increases humidity, decreases radiation input, saturates all plant and soil surfaces, and supports epiphytic growth and aquatic systems in tank bromeliads and other crevices.
- • High rainfall coupled with clay-rich soils results in low redox soils and saturated decaying logs. The high clay content also limits the infiltration of rain, and this contributes

to overland runoff. This also results in a high proportion of fine roots located near or on the soil surface and in the canopy of plants, instead of deep in the soil. Therefore, the typical role of roots in water uptake from deep in the soil is reduced compared to that in lowland ecosystems. Waterlogged decaying logs on the forest floor also become sites of water storage, with reduced rates of wood decay by aerobic organisms. The waterlogged soils and logs form a continuous film of water that aquatic organisms can use for mobility or the transport of larvae and, in the case of algae, spores.

- • The forest canopy and tank bromeliads harbor 126 species of aquatic algae (Foerster 1971). These tank bromeliads are aquatic microcosms within the terrestrial community that support aquatic food chains connected to terrestrial food webs. Maguire (1970) found that these communities had as many as 76 kinds of aquatic organisms. He described a minimum of eight stable associations of fauna with two consistent community characteristics: they were highly resistant to ionizing radiation, and they showed rapid and effective dispersal mechanisms. In 12 days, 40 experimental microcosms with distilled water accumulated 180 different types of organisms.
- • Sedges and aquatic plants with abundant aerenchyma and specialized gas exchange structures occur in bogs at high elevations. The presence of lowland wetland species (e.g., the sawgrass *Cladium jamaicensis*) in bogs within elfin forests is associated with long hydroperiods, saturated soils, and the possibility of groundwater movement along catenas.
- **(p.25)** • Shrimp, fish, mollusks, and crustaceans in the streams of the Luquillo Mountains migrate to the ocean to reproduce. These migrations establish another form of contact among montane forests, estuaries, and coastal systems. The food webs of streams and rivers are also connected to terrestrial food webs in the Luquillo Mountains (Covich and McDowell 1996).

Long-Term Ecological Research Program: An Integration of Approaches

Most of the research conducted in the Luquillo Mountains until 1988 was of relatively short duration (from less than a year to a decade). Even Odum’s Rain Forest Project, which in its time was the most comprehensive study ever conducted of a tropical forest, lasted only 5 years (from 1963 to 1968). Notable longer and ongoing studies include (from 1942) the monitoring of tree growth and survival under natural and managed conditions (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 establishment of an LTER site in the Luquillo Mountains in 1988 initiated a new research focus on ecosystem-forcing functions of long duration, infrequent occurrence, or incremental effect. The passage of Hurricane Hugo in 1989 and Hurricane Georges 9 years later directed attention to the key role that repeated disturbances play in tabonuco forests. These hurricanes also brought into focus the qualitative and quantitative differences in the types of disturbances common in tabonuco forests, such as hurricanes, floods, droughts, landslides, treefalls, and a wide range of human activities. Finally, LTER studies have identified the interactions among different kinds of disturbances as an important factor when interpreting the existing distributions of organisms, biomass, and nutrients. Each of these conceptual advances has contributed to the understanding of the Luquillo Mountains that we put forward in this book.

The LTER program has encouraged coordination among a variety of scientific disciplines, as well as broadened our understanding and stimulated comparisons of the fundamental characteristics of the different ecosystems of the Luquillo Mountains. Pre-LTER observations of forests become increasingly relevant and important for current research, as they provide a context for the long-term study of natural phenomena. Since 1988, we have studied the Luquillo Mountains using a coordinated research program involving the population, the community, and the ecosystem, as well as landscape ecologists, hydrologists, soil scientists, geologists, foresters, climatologists, atmospheric scientists, and modelers. Results from the LTER program have been compared to those from other sites in the LTER Network (e.g., decomposition, N cycling, productivity, landscape diversity, watershed hydrology, and disturbance effects) and from other national (Land Margin Ecosystem Research, Long-Term Intersite Decomposition Team Project) and international (Flow Regimes from International Experimental and Network Data, Soil Biology and Fertility Program of UNESCO—Man and the Biosphere Program, Taiwan Ecological Research Network, Chinese Ecological Research Network, Center for Tropical Forest Science) programs studying soil organisms, landslide revegetation, hydrological characteristics, hurricane/typhoon effects, **(p.26)** and tree communities, as well as to data from the Smithsonian's Center for Tropical Forest Science forest dynamics plot network. The breadth of the current research program is proving to be an asset in support of comparative ecological studies and synthesis across scales that transcend the Luquillo Experimental Forest.

Paradigm Shifts and the Improvement of Understanding

The analysis of the ecological effects of the passage of Hurricane Hugo over the Luquillo Mountains provided first-hand evidence in support of a paradigm shift that had started decades earlier concerning forest ecosystems. Until 1989, the focus of ecological research in the Luquillo Mountains had been the functioning of forest stands from the perspective of microbes, plants, and animals, and the priority for ecologists was an understanding of the structure and function of complex tropical forests, without an emphasis on natural disturbances as an integrating force (Odum and Pigeon 1970). In part, this priority arose because Puerto Rico had not been impacted by a major hurricane since 1932 or a tropical storm since 1956. Therefore, scientists had not had the opportunity to study windstorm events and their effect on forests. Research in Luquillo, as in temperate and other tropical forests, had mainly explored the long-term effects of small, discrete disturbances such as branch falls, treefalls, and clearing (Whitmore 1978, 1984, 1989; Denslow 1980, 1984; Frangi and Lugo 1985; Pickett and White 1985). Notable exceptions are the studies of Whitmore (1974), Garwood et al. (1979), and Foster (1980). At the same time as when these short-term studies were being published, evidence of the crucial effects of hurricanes in the Caribbean was slowly building. For example, Odum (1970a, 1970c) explained the canopy structure of Caribbean forests as being the result of trade winds and hurricanes. Doyle (1981) created a model that suggested that hurricanes maintained the species richness of the tabonuco forest. Crow (1980) interpreted structural changes in tabonuco forests as being caused by the 1932 hurricane. Willig et al. (1986) suggested that key consumer species might play a critical role in nutrient dynamics and succession after disturbance. Lugo et al. (1983) documented the effects of Hurricane

David on the tabonuco forests of Dominica. Together, these observations formed the core basis for the first proposal for an LTER site in the Luquillo Mountains.

The recognition of the importance of disturbances to the species composition, structure, and functioning of ecosystems has its roots in early 20th century science, and the development of this disturbance paradigm has been the subject of several literature reviews (Walker 1999; White and Jentsch 2001). In fact, the rain forest experiment carried out by Odum and many colleagues (Odum and Pigeon 1970) was an experiment in human-produced disturbance. Nevertheless, the passage of Hurricane Hugo over our research sites was a significant turning point in our LTER research, as it unequivocally demonstrated the critical nature of such events with regard to forests (Walker et al. 1991, 1996). Our research benefited from the presence of a research infrastructure that allowed scientists to take full advantage of the event and from a strong partnership between the University of Puerto Rico, the U.S. Forest Service, and the National Science Foundation LTER program.

(p.27) After Hurricane Hugo, we were surprised by the rapid rate of forest recovery in the Luquillo Mountains. It became evident that hurricanes and other disturbances had continually disrupted the forest and that this state of constant change had led to the development of adaptations to disturbance by forest organisms. In particular, the large-scale effects of hurricanes meant that most areas in the Luquillo Mountains were always responding to previous disturbances. Large and infrequent disturbances introduce pulses of high primary productivity with lagging respiration, followed by long periods of gradual forest changes and readjustment toward maturity (figure 1-8). The LTER program that we review and synthesize in this book signaled the completion of a shift toward an integrated disturbance paradigm and an effort to quantify the processes associated with the dynamic responses to disturbances in the Luquillo Mountains.

The disturbance paradigm has had fundamental effects on many other ecological ideas used to guide research and conservation in the Luquillo Mountains. For example, under a steady-state paradigm, forests were believed to be fragile, as any disturbance would shift them away from maturity and balance into states that were deemed incompatible with long-term stability. However, as hurricanes are recurrent, it was immediately obvious that the species in the forests of the Luquillo Mountains possessed adaptations that allowed them to resist or recover when confronted with these disturbance events. This insight led to a search for mechanisms that provided resilience in these forests (Lugo et al. 2002). Similarly, the changes in plant and animal population distributions and abundance observed after the passage of Hurricanes Hugo and Georges (Walker et al. 1991, 1996; Gannon and Willig 1994; Secrest et al. 1996) contributed to the recognition of environmental gradients (Hall et al. 1992) that shift in time and space. We recognized that geographic space couldn’t always be equated to ecological space. The shift of environmental gradients results in the dynamic redistribution of the biota (plant and animal) and in the demonstration by individual species of characteristic types and rates of response to changing environmental conditions. The discovery of the importance of these dynamic responses provided an impetus for the integration of ideas about environmental gradients, disturbance, and response into a conceptual model relating geographic and ecological space (see chapter 2).

Our improved understanding of how species and ecosystems respond to environmental change provides a means with which to approach the restoration of degraded tropical forests. An example is the experience with plantations on degraded sites and the rapid establishment of species-rich understories within these plantations in the Luquillo Mountains (Lugo 1992, 1997). The rapid recovery of species richness and biomass in abandoned pastures further illustrated the possibilities for the restoration of tropical forests (Aide et al. 1995, 1996). From studies of severely degraded sites, we see that some alterations to ecosystems take them beyond the ecological conditions that they have experienced in their evolutionary history. This leads to the dominance of nonforest or nonnative plant species in some systems in the early stages of their recovery. Although there are many examples of the negative effects of nonnative species, in some cases their presence accelerates the recovery of ecosystems, and therefore the dominance of introduced species in the early **(p.28)** stages of recovery need not always cause alarm (Lugo and Helmer 2004; Lugo and Brandeis 2005), as their dominance at any location appears to be temporary (Wadsworth and Birdsey 1983; Lugo 2004). However, some introduced species have naturalized (Liogier 1990; Francis and Liogier 1991), and their dominance in certain sites is changing the trajectory of succession so that future forests will be different from what originally occupied the site (Lugo 1997, 2004; Lugo and Helmer 2004).

Figure 1.8 Changes in the structure and functioning of tabonuco stands (*Dacryodes excelsa*) for a period of over 60 y. This diagram is an updated version of the one in Lugo et al. (2000) and incorporates unpublished data available from the USDA Forest Service International Institute of Tropical Forestry and information from Smith (1970), Scatena et al. (1996), Lugo and Zimmerman (2002), and Lugo and Fu (2003). The data correspond to the El Verde-3 long-term plot of the USDA Forest Service (B., C., E., F) and other studies at El Verde in the immediate vicinity of the long-term plot (A., D.). This sector of the forest was on the leeward side of Hurricane Hugo and was not as affected as windward sectors of the Luquillo Mountains. The increase in the seedling density in the 1960s corresponds to a canopy opening experiment by Smith (1970). The diameter of the tree (dbh, in cm) with the mean basal area (BA, in $\mathrm{m}^2\ \mathrm{ha}^{-1}$) was estimated by the following formula: dbh in cm = √ (BA in $\mathrm{m}^2\ \mathrm{ha}^{-1}$) (12732.30)/tree density in trees ha^{-1}. The vertical arrows in 1932 and 1989 correspond to Hurricanes San Ciriaco and Hugo, respectively.

(p.29) Metaphors for Forest Complexity

The search for a holistic overview of the Luquillo Mountains has led us to perceive the Luquillo Mountains in terms of a series of heuristic metaphors and conceptual models (see chapter 2). These metaphors and models summarize our understanding of the Luquillo Mountains, which we pass to others much as the Taínos did millennia before us. One metaphor considers the Luquillo Mountains as a *tapestry*interwoven with elements of topography, water, geology, soil oxygen, and living organisms that is exposed continually to light, wind, rain, and periodic violent combinations of these elements. Such exposure usually nourishes and maintains the components of the tapestry, but occasionally it reorganizes them through large and infrequent disturbances, keeping the mountain in a continuous state of flux. Each event defines a new pattern in the tapestry, and the cumulative effects of these events leave an imprint on the genotypes, abundances, and distributions of the organisms that constitute the tapestry. In short, the tapestry metaphor implies that at any moment visible patterns are the result of a complex history of disruption and repair occurring through processes of either self-organization or management for conservation goals.

The metaphor of a tapestry evolved from field observations before and after Hurricane Hugo. Before the hurricane, studies documented the high diversity of algae (126 epiphytic algal species as reported by Foerster [1971]) and other aquatic organisms in specialized aquatic habitats (such tank bromeliads, as reviewed by Lugo [1986]) in the forests of the Luquillo Mountains. We surmised that saturated air and a continuous film of water (a tapestry of moisture) that periodically covers the Luquillo Mountains permit connections between bromeliads and the organisms they contain and other aquatic habitats, including communities in streams, rivers, and estuaries. After Hurricane Hugo, a dense mat of vines and climbers resulted in a continuous leaf cover that appeared like a green tapestry over the affected forests (figure 1-9).

The metaphor of a tapestry, however, is superficial with regard to the literal sense of the word. The tapestry that we see reveals only the surface details of the Luquillo Mountains while hiding the underlying dynamics of the forest. A more apt metaphor is that of a *palimpsest*, a manuscript page that has been written on more than once, with earlier messages only partially erased and still visible (Hubbell 1979). In ecological usage, a palimpsest is an area that reflects its history and highlights the notion of the changing organizational patterns that reflect the effects of contemporary, recent, and ancient disturbances. The geologic and topographic structure underlying the Luquillo Mountains results from a series of tectonic events that occurred eons ago and continue at a very slow pace. The biotic composition of the Luquillo Mountains arises from a series of relatively recent (in geological time scales) immigration and extinction events, each of which has left an evolutionary and paleontological record. Repeated contemporary disturbance events such as hurricanes or human land use are preserved as changes in the ecosystem characteristics that are visible through the examination of the forest’s composition and structure, including its soils. Each of these tectonic, biogeographic, or disturbance events is recorded in the biotic and abiotic structure of the Luquillo Mountains, and taken together they determine the composition of the palimpsest we see today.

(p.30)

Figure 1.9 A tapestry of leaves over a *Dacryodes excelsa* forest in the Luquillo Mountains. (Photo by A. E. Lugo.)

Our goal in this book is to elucidate the effects of recent disturbances on the Luquillo Mountains and to interpret them in the geologic, geographic, and climatic context of the mountains and Puerto Rico (chapter 3). In this context, we examine how disturbances restructure environmental gradients and affect ecosystem heterogeneity (chapter 4), how these changes interact with the biota (chapter 5), and how the biota affect environmental gradients. Each cycle of disturbance and response adds another layer to the historical record, partially obscuring previous patterns. The patterns that remain visible through the more recent layers (i.e., legacies) signal the importance of historical events and provide a better understanding of the ecosystems of the Luquillo Mountains. Our synthesis is another step in the development of the relationship between generations of people that care about and depend on nature, the Luquillo Mountains, and all tropical forests. Our hope is that our integrated and synthetic understanding of ecological dynamics in time and space will allow us to better appreciate and conserve the beauty of these mountains.

Summary

The forests of the Luquillo Mountains are representative of insular wet tropical forests subjected to frequent hurricane disturbances. Over 2,000 years of human activity have also affected the species composition and structure of forests in **(p.31)** parts of these mountains. We identify and discuss seven models of forest structure and functioning in these mountains as reflected in the views of indigenous people, conquistadors, early foresters, natural historians, modern foresters, government agencies, and modern ecologists. These models embody the outcomes of the history of human experience, including research, in the Luquillo Mountains and provide the foundation for a new long-term and disturbance-based research paradigm reported in this book. The paradigm shift from short-term studies leads to an improved understanding of the ecosystems of the Luquillo Mountains by focusing on the forest's response to natural and anthropogenic disturbances, with particular attention paid to hurricanes and land cover change. The information is the product of long-term ecological research involving collaboration between the National Science Foundation, the University of Puerto Rico, and the U.S. Forest Service.

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Figure 1.1 The global frost line defines the ecological space in which tropical forests occur. This map, prepared by R. P. Neilson, illustrates four levels of frost throughout the world. The tropics correspond to the area with a 12-month growing season and no frost. The long-term average monthly temperatures for all 12 months exceed the average monthly temperature associated with spring green-up (Neilson 1995). The other thermal zones are as follows: Boreal = supercooled freezing point (−40°C) reached annually; long-term minimum average monthly temperature < −16°C. Temperate = hard frosts annually (24 h < 0°C); long-term minimum average monthly temperature < −1.25°C. Subtropical = frequency of hard frosts ranging from less than annual to relatively rare; nearly zero days annually when the maximum temperature is < 0°C; long-term minimum average monthly temperature < 13°C. The definitions of "tropical" and "subtropical" in this system are different from the designations used by Holdridge (1967), who considers subtropical zones as also frost-free. Thus, "tropical" in this map coincides with "tropical" and "subtropical" in the Holdridge Life Zone System (figure 1-2).

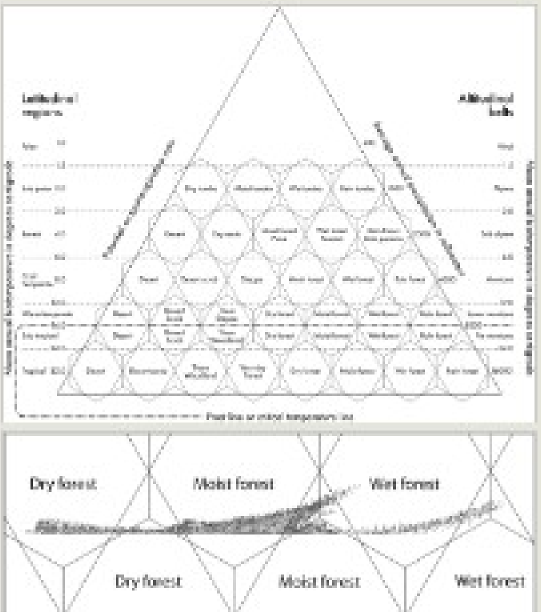

Figure 1.3 The Luquillo Mountains. (Photo by A. E. Lugo.)

n the Luquillo Mountains reveals the gradual tual models, as well as the punctuated development of ps of scientists. All of these investigations have their biotic and abiotic characteristics of the Luquillo ate in this chapter how our conceptualization of the to a general understanding of the dynamics of forested ally on research conducted by the Luquillo Long-Term to Hurricane Hugo, after which we launched a series of bances on forest dynamics, structure, and composition.

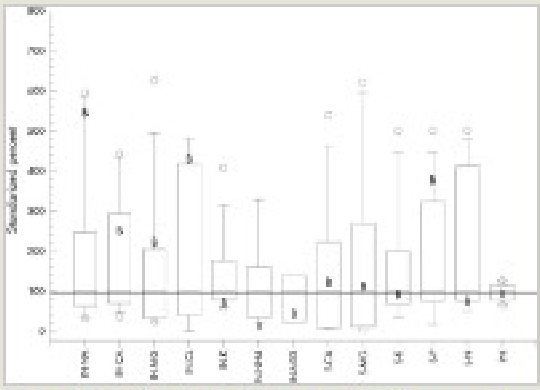

Figure 1.4 Box plots of standardized values of the bulk precipitation and soil pool size for various humid tropical forests (Scatena 1998). Values for Bisley (B), Luquillo Experimental Forest, are highlighted for comparison with other sites. Each box encompasses the 25th through 75th percentiles and has horizontal lines at the 10th and 90th percentiles. Circles represent data outside the range of the 10th and 90th percentiles. Dividing the value from a particular site by the meridian value of all the sites and then multiplying by 100 gives standardized values. The abbreviations IN-NA, IN-CA, IN-MG, IN-CL, IN-K, IN-NH_4, and IN-NO_3 denote the annual average inputs by bulk precipitation for sodium, Ca, Mg,

Figure 1.5 A Taino cemí illustrates the idea that the island of Puerto Rico is steadied by an anthropogenic being.

(Photo by Jerry Bauer.)

Figure 1.6 A mature artificial forest in the *Dacryodes excelsa* zone of the Luquillo Mountains. Dr. F. H. Wadsworth (right) was responsible for the management of this site.

(Photo by A. E. Lugo.)

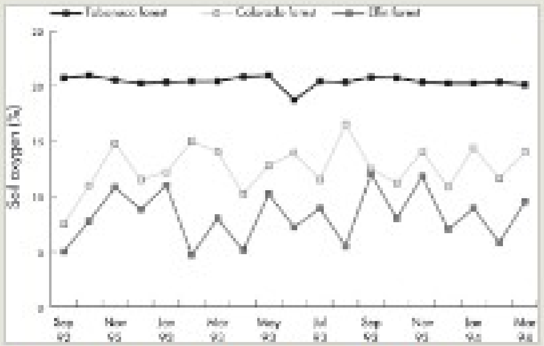

Figure 1.7 The soil oxygen gradient in the Luquillo Mountains (Silver et al. 1999).

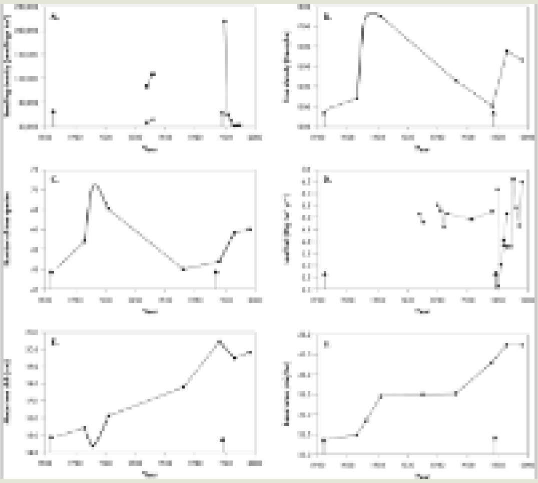

Figure 1.8 Changes in the structure and functioning of tabonuco stands (*Dacryodes excelsa*) for a period of over 60 y. This diagram is an updated version of the one in Lugo et al. (2000) and incorporates unpublished data available from the USDA Forest Service International Institute of Tropical Forestry and information from Smith (1970), Scatena et al. (1996), Lugo and Zimmerman (2002), and Lugo and Fu (2003). The data correspond to the El Verde-3 long-term plot of the USDA Forest Service (B., C., E., F) and other studies at El Verde in the immediate vicinity of the long-term plot (A., D.). This sector of the forest was on the leeward side of Hurricane Hugo and was not as affected as windward sectors of the Luquillo Mountains. The increase in the seedling density in the 1960s corresponds to a canopy opening experiment by Smith (1970). The diameter of the tree (dbh, in cm) with the mean basal area (BA, in m^2 ha^{-1}) was estimated by the following formula: dbh in cm = $\sqrt{}$ (BA in m^2 ha^{-1}) (12732.30)/tree density in trees ha^{-1}. The vertical arrows in 1932 and 1989 correspond to Hurricanes San Ciriaco and Hugo, respectively.

Figure 1.9 A tapestry of leaves over a *Dacryodes excelsa* forest in the Luquillo Mountains.

(Photo by A. E. Lugo.)