4

Disturbance Regime

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Key Points

- The Luquillo Mountains are affected by a wide array of environmental processes and disturbances. Events that concurrently alter the environmental space of several different areas of the Luquillo Mountains occur every 2 to 5 years. Events such as hurricanes that cause widespread environmental modification occur once every 20 to 60 years.
- The most common disturbance-generating weather systems that affect the Luquillo Mountains are (1) cyclonic systems, (2) noncyclonic intertropical systems, (3) extratropical frontal systems, and (4) large-scale coupled ocean-atmospheric events (e.g., North Atlantic Oscillation, El Niño-Southern Oscillation). Unlike some tropical forests, disturbances associated with the passage of the Inter-Tropical Convergence Zone or monsoonal rains do not occur.
- Hurricanes are considered the most important natural disturbance affecting the structure of forests in the Luquillo Mountains. Compared to other humid tropical forests, Luquillo has a high rate of canopy turnover caused by hurricanes but a relatively low rate caused by tree-fall gaps. Historically, pathogenic disturbances have not been common.
- Human-induced disturbances have historically included tree harvesting for timber and charcoal, agriculture, and agroforestry. In the past few decades, water diversions, fishing and hunting, and road building have been important disturbances. Present and future human-induced disturbances are related to regional land use change, the disruption of migratory corridors, and forest drying related to coastal plain deforestation and regional climate change.

- Hurricane-related storm discharges can cause significant geomorphic modifications to Luquillo stream channels, and stream water concentrations of sediments and nutrients can be elevated for months to years following a major hurricane. However, the largest floods are not necessarily associated with hurricanes, and the annual peak discharge can occur in any month of the year but is most common in the late summer and fall.
- Over the entire island of Puerto Rico, 1.2 landslide-producing storms occur each year. In the Luquillo Mountains, landslides are typically covered with herbaceous vegetation within 2 years, have closed canopies of woody vegetation in less than 20 years, and have aboveground biomass of the adjacent forest after several decades.

Introduction

The Luquillo Mountains, like many humid tropical environments, is a dynamic ecosystem that is affected by a wide array of environmental processes and disturbances (figures 4-1 and 4-2). Quantifying the magnitude, frequency, and impact of these natural disturbances on both geographical and ecological space is essential to understanding and managing these forests. This chapter reviews the causes, frequencies, and discrete and cumulative impacts of disturbances on

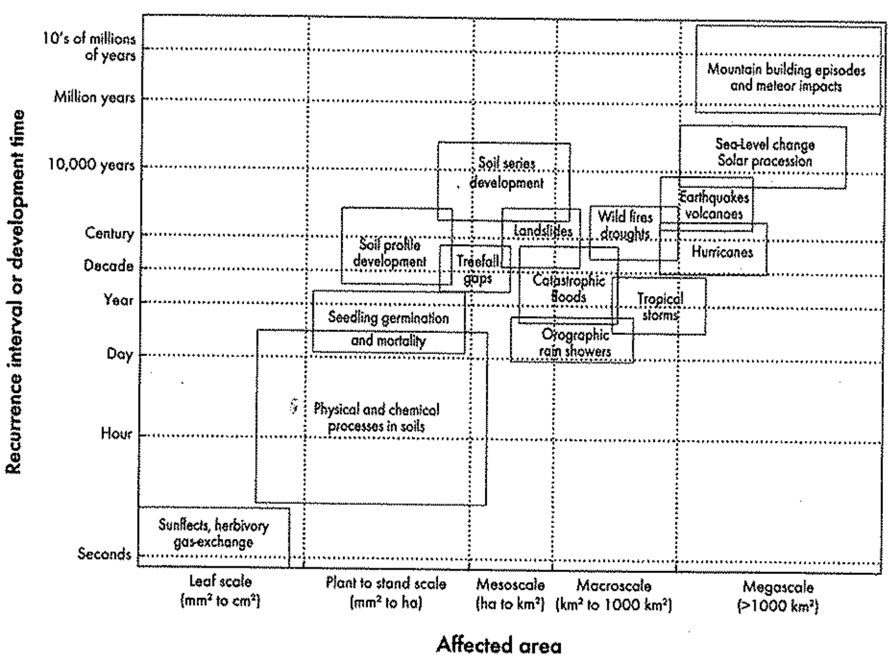

Figure 4.1 Spatial and temporal relationships of natural disturbances and processes affecting the Luquillo Mountains. (Modified from Scatena 1995.)

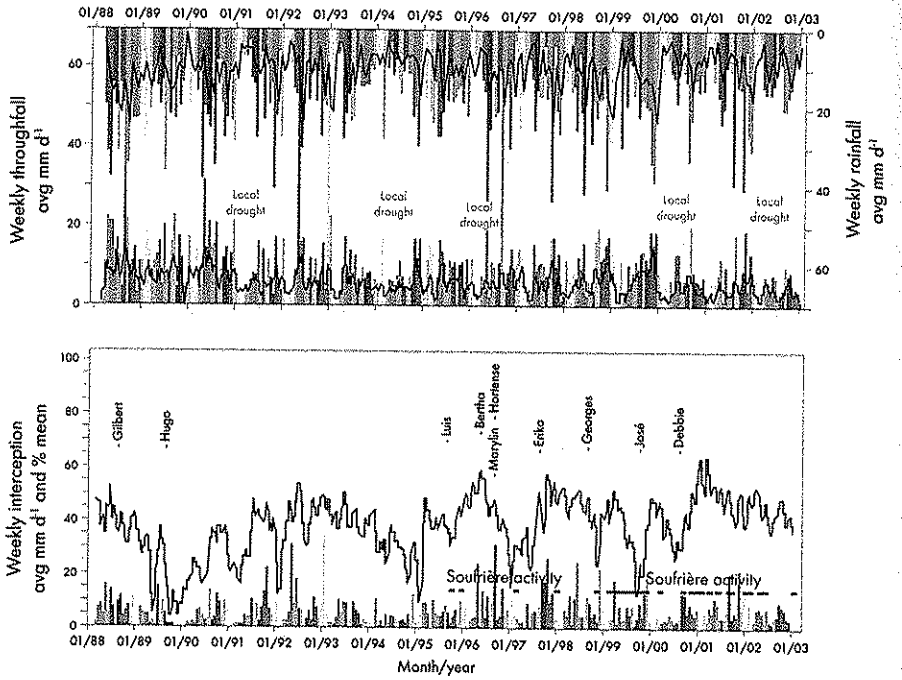

Figure 4.2 Weekly rainfall and throughfall and significant climatic events in the Bisley Research Watersheds, 1988 to 2003. (From Heartsill-Scalley et al. 2007.)

the Luquillo ecosystem. Subsequent chapters discuss the ecosystem's recovery after disturbance.

Disturbances can be defined as relatively discrete events that alter the structure of populations, communities, and ecosystems (see chapter 2) (White and Pickett 1985; Lugo and Scatena 1996; Walker and Willig 1999). "Disturbance regime" refers to the sum of disturbances acting on a particular location. The natural disturbances specified by the United Nations in the International Decade of Natural Disaster Reduction were earthquakes, windstorms, tsunamis, floods, landslides, volcanic eruptions, wildfires, insect infestations, drought, and desertification. Treefalls, pathogens, exotic invasions, and meteor impacts are also known to affect humid tropical forests. Of these 14 types of disturbances, 10 are known to have caused community-level impacts in northeastern Puerto Rico during the past century. These disturbances have also acted on a landscape that has undergone dramatic land use changes associated with forest harvesting and clearing, agriculture, urbanization, water diversions, and other modifications to hydrologic and nutrient cycles.

Quantifying the effects of disturbances on landform morphology and ecosystem development has been a traditional theme in geomorphology and ecology (Wolman and Miller 1960; Connell 1978). It is now generally recognized (Lugo and Scatena 1996) that the effect of a disturbance on the morphology of a landscape or the structure of an ecosystem depends on the following:

- The **type** of disturbance (i.e., flood, fire, landslide, biologic, anthropogenic, etc.)
- The **intensity** of the force exerted (i.e., wind velocity and duration, rainfall magnitude and intensity, earthquake magnitude, etc.)
- The ecosystem **component** that is directly impacted by the forces exerted (i.e., soil, biomass, leaf area, etc.)
- The spatial extent and the spatial distribution of impacts
- The return period or **frequency** of the event
- The **initial condition** and **resistance** (see chapter 2) of the system
- The **resilience** (see chapter 2) of the system and the magnitude of the constructive or restorative processes that occur between disturbances

Mortality is also a complex process that occurs over many spatial and temporal scales. Mortality events can range from "background events" to large-scale "catastrophic events" (Lugo and Scatena 1996). Background mortality is typically associated with senescence, competition, and succession. Catastrophic mortality occurs when a forest is mechanically or chemically impacted by an external force such as a hurricane, a landslide, or toxic waste. When expressed as percentage of stems or biomass per year, the background mortality is typically less than 3 percent per year. The median value of the background mortality in 68 pantropical moist, wet, and rain forest stands was 1.6 percent per year; this is similar to values reported from the Luquillo Mountains, as well as from temperate and boreal forests (Lugo and Scatena 1996). In contrast, catastrophic events can cause 100 percent mortality in small areas.

Tectonic Drivers of Disturbance

The Luquillo Mountains were formed from shallow marine deposits and the material produced by ancestral volcanoes that existed to the south of the present mountains (see chapter 3) (Scatena 1989a). This volcaniclastic bedrock formed from the debris of these volcanoes is of late to upper Cretaceous age (70 to 112 million years ago) and is intruded by a quartzdioritic batholith that underlies the Rio Blanco watershed (Seiders 1971a, 1971b). Existing geochronology suggests that the Rio Blanco batholith is 47 million years old and of Eocene age (Cox et al. 1977). It is also the only major Eocene addition of felsic magma to the Greater Antilles (Smith et al. 1998).

The island is currently located on the edge of a continental-type tectonic block that is rotating in a counter-clockwise fashion (Masson and Scanlon 1991). The tectonic forces associated with this block are ultimately responsible for the volcanic activity and mountain building that has formed the Luquillo Mountains. During its evolution, the island has also undergone considerable erosion and at one time might have had mountains tall enough to support a cold temperatelike flora (Graham and Jarzen 1969). During the Quaternary, uplift of the island has outpaced sea level rise and is estimated from subaerial coral reefs to have a rate of 0.055 mm y^{-1} (Taggart 1992). Over the Holocene, the net rate of uplift was probably higher and is estimated to have been between 0.125 and 0.25 mm y^{-1} (Clark and Wilcock 2000).

Although the origin of the Luquillo Mountains is closely linked to volcanic activity, presently volcanic activity is not an important disturbance in the area. Nevertheless, the Luquillo Mountains do receive occasional ash falls from volcanoes in the lower Caribbean. Between 1987 and 2003, at least two volcanic ash falls from the lower Caribbean island of Montserrat blanketed Puerto Rico with enough fine ash to be noticeable to the public and temporarily close the San Juan International Airport. Thick, catastrophic ash falls similar to those that have occurred in other tropical forests (Whittaker and Walden 1992) are unknown in the historical or recent geologic record of the Luquillo Mountains. Given Puerto Rico's distance from active volcanoes, such catastrophic ash falls are extremely rare, if not impossible, events. Nevertheless, volcanic events and Saharan dust deposition are detectable in Luquillo rainfall and throughfall and might account for up to 9 percent of the inputs of some constituents (McDowell et al. 1990; Heartsill-Scalley et al. 2007). Although there is no evidence that this dust is causing a major health problem in Puerto Rico, during intense events the concentrations of respirable dust do affect some island residents, and U.S. Environmental Protection Agency standards have probably been exceeded occasionally in the Caribbean (Prospero and Lamb 2004).

Although the Luquillo Mountains are not volcanically active, they are within a tectonically active zone, and multiple earthquakes are measured on the island each year. In 1918, an earthquake caused landslides throughout the mountainous regions of the island (Reid and Taber 1919). Devastating earthquake-generated tsunamis occurred in the northern Caribbean in 1867, 1918, and 1946 (Dillon and Brink 1999). However, owing to their elevation, the Luquillo Mountains have never been directly affected by tsunamis. The exact frequency of forest-modifying earthquake-induced disturbances in the Luquillo Mountains is unknown. However, based on these three historic events, a rate for the island can be conservatively estimated at one or two major events per century. Because the majority of the earthquake activity is located between Puerto Rico and the island of Hispaniola, the rate for northeast Puerto Rico and the Luquillo Mountains is probably less than that for the western part of the island. The residuals (see chapter 2) of these tectonic activities include landslides, fault scarps, and other topographic features. Their legacies (see chapter 2) include the location and morphology of stream channels (Ahmad et al. 1993), the location of palm brakes (Lugo et al. 1995), and the Luquillo Mountains themselves.

Meteor Impacts

Catastrophic meteor impacts are events that can have local, continental, and global consequences (Toon et al. 1997). The catastrophic disturbances associated with meteor impacts include earthquakes, blast waves, tsunamis, and fires. Effects from dust, smoke, and acid rain might have longer-term effects on the global climate and biota. Meteor impacts in the Luquillo Mountains have not been recorded in historical times. However, a meteor impact in the Caribbean basin has been implicated in the global Cretaceous-Tertiary age mass extinction of dinosaurs and apparently generated a free-standing ocean wave in the Caribbean that was over 500 m high (Hildebrand and Boynton 1990; Florentin et al. 1991) that would have impacted the ancestral Luquillo region. Because the flora of the Luquillo Mountains developed shortly after this impact (Graham and Jarzen 1969), the widespread extinction it caused might have had a fundamental, but yet unquantified, impact on the ecology of the Luquillo ecosystem.

Atmospheric Drivers of Disturbance in the Luquillo Mountains

The Luquillo Mountains have a humid tropical maritime climate that has rainfall and runoff every month of the year (see chapter 3 and figure 4-2). At mid-elevations, the median daily rainfall is low (3 mm/day), but rain events are numerous (267 rain days per year) and of relatively low intensity (<5 mm/h) (Schellekens et al. 2004). Nevertheless, individual storms with rainfall greater than 125 mm/day occur annually, and daily rainfalls greater than 600 mm have been recorded. The most common disturbance-generating weather systems that affect the Luquillo Mountains are (1) cyclonic systems, (2) noncyclonic intertropical systems, (3) extratropical frontal systems, and (4) large-scale coupled ocean-atmospheric events (e.g., North Atlantic Oscillation [NAO], El Niño-Southern Oscillation [ENSO]).

Unlike some tropical forests, the Luquillo Mountains do not commonly have disturbances associated with the annual passage of the Inter-Tropical Convergence Zone (ITCZ) or monsoonal rains (Walsh 1997). In general, Puerto Rico is too far north to directly experience the seasonal rainfalls that are associated with the ITCZ. Likewise, the relatively small size of Puerto Rico and its orientation relative to the prevailing winds prevent monsoonal systems from developing and sculpting the Luquillo landscape.

Cyclonic Systems

Cyclonic systems are large masses of air that rotate about a low-pressure center, and they include tropical waves and hurricanes. Tropical waves have incompletely closed circulations, whereas hurricanes have completely closed circulations. The occurrence of these systems is mainly confined to the period from May through November, when an average of two waves pass by the island every week (van der Molen 2002). Globally, approximately 82 hurricanes occur in a typical year, 12 percent of which pass through the Caribbean (table 4-1). However, the return period for a hurricane passing directly over the Luquillo Mountains is between 50 and 60 years (Scatena and Larsen 1991). In general, the frequency of hurricanes varies with the season (table 4-2, figure 4-3), decade (figure 4-4), and regional physiography (Boose et al. 1994). Multidecade variation in cyclone activity has been linked to variations in thermohaline oceanic circulation, global sea surface temperatures, West African monsoons, African droughts, and ENSO events (Gray et al. 1997).

Hurricanes are considered the most important natural disturbance affecting the structure of forests in the Luquillo Mountains (Crow 1980; Scatena and Lugo 1995). However, because cyclonic systems develop north and south of the ITCZ and travel poleward, many humid tropical forests are unaffected by hurricanes. In addition to the northern Caribbean, hurricanes are frequent disturbances in Madagascar,

Table 4.1 Mean annual named tropical storm and hurricane frequency for the Caribbean and other tropical regions. Adapted from Walsh (1997) and Planos Gutiérrez (1999)

Region	Tropical storms y^{-1}	Hurricanes y^{-1}	All named storms	Percentage of total	Principal humid tropical forests
North Indian Ocean	3.5	2.2	5.7	7.0	Andama Islands
North Atlantic/ Caribbean	4.2	5.2	9.4	11.5	Caribbean
Southwest Indian Ocean	7.4	3.8	11.2	13.7	Mauritius, Reunion, Madagascar
Southwest Pacific	10.9	3.8	14.8	18.1	Queensland, Fiji, Solomons, Vanuatu
Eastern North Pacific	9.3	5.8	15.2	18.6	None
Western North Pacific	7.5	17.8	25.3	31.0	Philippines, Taiwan, S. China, Borneo
Total	42.8	38.6	81.6	100.0	

Table 4.2 Monthly distribution of Atlantic cyclones between 1890 and 1990. (After Planos Gutiérrez 1999.)

	June	July	August	September	October	November	Other	Total
Percentage of total	6	8	25	34	20	5	2	100
Number for century	50	64	206	288	171	38	15	832
Maximum recorded in each month	3	4	7	7	6	2	2	NA

Mauritius, Reunion, the southwest Indian Ocean, the northern Philippines, Sabah, Taiwan, parts of Indo-China, the Pacific islands, and tropical Queensland (Walsh 1997). Hurricanes are rare to nonexistent in the humid tropical forests of South America, Africa, and northern Malaysia.

There is no simple, direct relationship between the magnitude and the destructive powers of Caribbean hurricanes (Planos Gutiérrez 1999). In general, windspeeds depend on the path of the hurricane and the local aspect and exposure. When hurricanes pass directly over the Luquillo Mountains, ground-level windspeeds can surpass 140 km h^{-1}. When hurricanes pass over or near other parts of the island, the Luquillo Mountains typically have sustained winds near canopy level of 60 km h^{-1} and gusts of over 150 km h^{-1} (table 4-3). The total amount of rain that falls in a given area for a given hurricane depends on (a) the intake of humid air into the

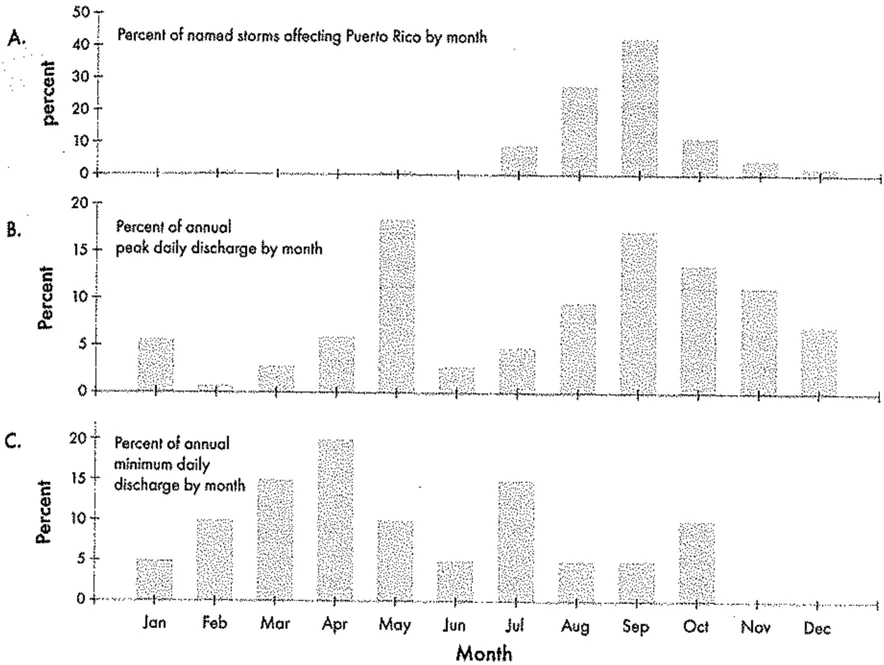

Figure 4.3 Named storms affecting Puerto Rico by month between 1899 and 1999 and percent occurrence of annual peaks and low flows by month for streams draining the Luquillo Mountains of Puerto Rico. (Modified from Scatena 2001.)

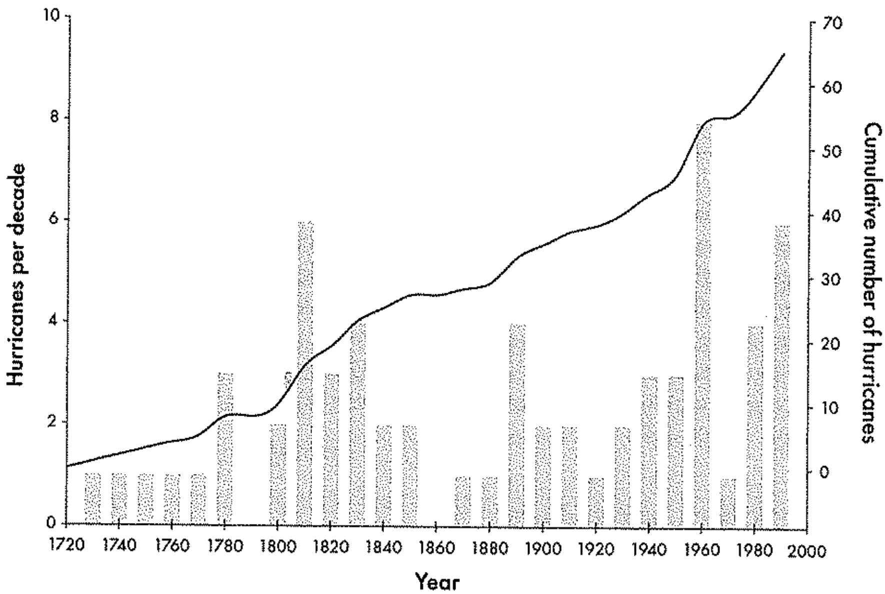

Figure 4.4 Number of hurricanes passing within 2 degrees of Puerto Rico between 1720 and 2000.

Table 4.3 Windspeeds at Roosevelt Roads and San Juan associated with named Puerto Rican storms since 1950. Based on data from the National Weather Service National Hurricane Center (http://www.nhc.noaa.gov), the National Climatic Data Center (http://ncdc.noaa.gov), and the USGS Caribbean Water Resources District (http://pr.water.usgs.gov)

Year	Date	Name	Landfall Y/N	Location of major impact	Roosevelt 2-minute gusts		San Juan 2-minute gusts		Storm duration over island
					Speed	*Direction*	*Speed*	*Direction*	
					km h^{-1}	deg	km h^{-1}	deg	h
1956	8/12/56	Betsy	Y	SE					3
1960	9/5/60	Donna	N	NE	93	210			
1963	9/26/63	Edith	N	SW	54	120	50	140	
1964	8/23/64	Cleo	N	S	56	50	63	50	
1966	8/26/66	Faith	N	NE	59	30	76	360	
1966	9/28/66	Inez	N	S	52	90	67	50	
1967	9/9/67	Beulah	N	SW	43	90	44	90	
1979	8/30/79	David	N	SW	74	100	76	50	
1979	2/17/79	Edith	N		24	70	30	90	
1987	9/22/87	Emily	N	SE	63	150	33	140	
1988	9/11/88	Gilbert	N	S	69	100	56	90	
1989	9/18/89	Hugo	Y	NE	nd	nd	148	320	4
1995	9/5/95	Luis	N	NE	64	350	65	360	
1996	9/15/96	Marilyn	N		37	90	nd	nd	
1996	7/9/96	Bertha	N	NE	37		nd	nd	
1996	9/10/96	Hortense	Y	SW	74	80	nd	nd	2
1997	9/5/97	Erika	N	NE	nd	nd	nd	nd	
1998	9/22/98	Georges	Y	SE	102	140	nd	nd	7
1999	10/20/99	Jose	N	NE	64	80	nd	nd	
2000	8/23/00	Debby	N	NE	60	180	nd	nd	
Average					60.3	120	64.4	158	4
Median					60.0	95	63.0	90	3.5
Maximum					102	350	148	360	7

circulating system, (b) the velocity of the winds within the hurricane, (c) the forward velocity of the eye, (d) the length of time for which the hurricane directly affects a particular area, and (e) the position of the storm and site relative to the ocean. Total storm rainfalls of 100 mm per event are common (table 4-4), and multiday hurricane totals of over 1500 mm are possible (Gupta 1975, 1988). Daily stream flows associated with hurricanes in Puerto Rico vary significantly but can be over 50 mm day^{-1} (table 4-5).

Noncyclonic Intertropical Systems

This group of atmospheric systems comprises those that originate and generally remain within the tropics and include micro- and meso-scale convective systems and orographic rains. Land-sea breezes that result from the differential heating of land and water surfaces are a dominant process that drives these systems, and they

Table 4.4 Daily maximum rainfall associated with named Puerto Rican storms since 1950. Based on data from the National Weather Service National Hurricane Center (http://www.nhc.noaa.gov), the National Climatic Data Center (http://ncdc.noaa.gov), and the USGS Caribbean Water Resources District (http://pr.water.usgs.gov)

Year	Date	Name	San Juan	Fajardo	Roosevelt Roads	Canovanas	East Peak
			mm d^{-1}	mm d^{-1}	mm d^{-1}	mm d^{-1}	mm d^{-1}
1956	8/12/56	Betsy	81	104		135	
1960	9/5/60	Donna	40	209	188	nd	
1963	9/26/63	Edith	22	24	9	18	
1964	8/23/64	Cleo	18	31	nd	18	
1966	8/26/66	Faith	13	19	17	10	
1966	9/28/66	Inez	30	27	28	23	
1967	9/9/67	Beulah	8	11	5	25	
1979	8/30/79	David	67	117	117	233	48
1979	2/17/79	Edith	3	9	28	152	68
1987	9/22/87	Emily	3	14		14	24
1988	9/11/88	Gilbert	47	33	40	36	91
1989	9/18/89	Hugo	225			79	
1995	9/5/95	Luis	54	51	28	46	97
1996	9/15/96	Marilyn	86		10	47	51
1996	7/9/96	Bertha	40		39	61	145
1996	9/10/96	Hortense	208		73	182	
1997	9/5/97	Erika	7		13	8	23
1998	9/22/98	Georges	103		90	215	
1999	10/20/99	Jose	18		15	46	68
2000	8/23/00	Debby	118		44	132	nd
Average			59.6	54.1	46.5	77.9	68.3
Median			40.0	29.0	28.0	46.0	68.0
Maximum			225	209	188	233	145

are responsible for many of the short rainfalls that are common throughout the day. Disturbances generated by these systems are most common in the summer months, when rainfalls of 100 mm in 24 h or less can occur (Planos Gutiérrez 1999). The most intense rains occur over relatively small areas, and rainfalls of greater than 200 mm per event are known to occur. Landslides, uprooted trees, and localized and coastal plain floods are often associated with these events.

Extratropical Frontal Systems

Disturbance-generating rainfalls that occur from November to April are typically associated with cold fronts that originate in extratropical areas to the north. Rains associated with these systems are usually of low intensity but can last for several days. Storm totals are usually less than 150 mm. Nevertheless, intense rainfalls can be associated with these frontal systems, and landslides and flooding are common when intense downpours follow several days of persistent, soil-saturating rain. The

Table 4.5 Peak stream flows associated with named Puerto Rican storms since 1950. Based on data from the National Weather Service National Hurricane Center (http://www.nhc.noaa.gov), the National Climatic Data Center (http://ncdc.noaa.gov), and the USGS Caribbean Water Resources District (http://pr.water.usgs.gov)

Year	Date of max. rain	Name	Mameyes daily peak	Espiritu Santo daily peak	Fajardo daily peak	Icacos daily peak
			mm d^{-1}	mm d^{-1}	mm d^{-1}	mm d^{-1}
1963	9/26/63	Edith			0.46	
1964	8/23/64	Cleo			0.51	
1966	8/26/66	Faith		1.35	0.46	
1966	9/28/66	Inez		3.66	0.95	
1967	9/9/67	Beulah	0.54	0.83	0.33	
1979	8/30/79	David		15.29	10.01	
1979	2/17/79	Edith		16.62	1.15	
1987	9/22/87	Emily	1.55	0.95	0.24	1.53
1988	9/11/88	Gilbert	3.16	4.49	1.58	4.46
1989	9/18/89	Hugo	35.90	22.23	51.84	32.74
1995	9/5/95	Luis	2.49	2.56	2.37	6.06
1996	9/15/96	Marilyn	1.87	1.12	1.21	4.32
1996	7/9/96	Bertha	5.84	7.58	3.71	14.84
1996	9/10/96	Hortense	27.64	20.39	15.37	25.0
1997	9/5/97	Erika	0.61	0.49	0.12	0.49
1998	9/22/98	Georges	19.11	24.3	4.49	17.70
1999	10/20/99	Jose	5.29	8.04	4.29	7.04
2000	8/23/00	Debby	9.09	12.64	8.36	10.38
Average			9.4	8.9	6.0	13.7
Median			4.2	6.0	1.4	7.0
Hurricane maximum			35.9	24.3	51.8	32.7
Record maximum			35.9	32.3	55.7	37.6
Date of record			9/18/89	8/13/90	1/5/92	4/21/93

record discharge and floods of the Río Fajardo were caused by a 1992 cold front. Similar extratropical fronts are important disturbance-generating systems in tropical forests in Central America, the South Pacific, the South Atlantic, South Africa, and Australia.

These systems might have had a larger influence in the past, as cooler tropical climates during the late Quaternary glacial period and the last glacial-interglacial transition have been linked to an increased frequency of polar air masses reaching the tropics (Servant et al. 1993).

Coupled Ocean-Atmospheric Systems

Large-scale ocean-atmospheric systems like the NAO and the ENSO are principal causes of global interannual climate variability and have been linked to disturbances in other tropical forests (Scatena et al. 2005). During El Niño events, the entire Caribbean region is relatively dry from September to October (Chen and Taylor 2002). During declining ENSO phases, the Caribbean is relatively wet during April and July. These ENSO events have also been linked to Caribbean Sea surface temperature anomalies (Spence et al. 2004) and to an increase in global hurricane activity and disturbances in other tropical forests. Nevertheless, the NAO has a stronger relationship with Puerto Rico's annual climate than the ENSO does (Malmgren and Winter 1998). This index is the normalized sea-level pressure difference between the Azores and Iceland and is significantly related to annual rainfall. In general, during years with a high winter NAO, the precipitation in Puerto Rico is lower than average. However, correlations between annual rainfall and NAO or ENSO indices are generally weak. Likewise, the relationships between these indices and the specific occurrence of hurricanes or other large-scale disturbances in Puerto Rico are poor.

Biotic Drivers of Disturbances in the Luquillo Mountains

Population and Land Use Change

Petroglyphs and scattered archeological remains suggest that Luquillo ecosystems were affected by indigenous populations (see chapter 1). The analysis of preserved plant parts from archeological sites also indicates that Pre-Columbian inhabitants had measurable impacts on the island's vegetation and were responsible for local extinctions and species introductions (Newsom 1993). Nevertheless, the two periods of the greatest human-induced transformations of the Luquillo landscape occurred immediately after European settlement in 1498 and after the Spanish Crown opened the island to immigration in the early 1800s (Scatena 1989a). Most of the Luquillo Mountains below 400 m have undergone the following sequence of land use: selective logging and agroforestry, clearing and agriculture, farm abandonment and reforestation, and construction and urban buildup of the surrounding areas (Thomlinson et al. 1996). Coincident with this change in land use was an increase in per capita energy use and a switch from internal (e.g., solar, biomass) to external (e.g., fossil fuel) sources of energy.

The municipal centers that surround the Luquillo Mountains, including Río Grande, Luquillo, Fajardo, and Ceiba, were incorporated between 1772 and 1840. By 1895, large parts of the coastal plain and foothills were planted with sugar cane (Thomlinson et al. 1996). During this period, most of the agricultural activity within the present Luquillo Experimental Forest (LEF) consisted of small subsistence farms and coffee plantations. Both of the areas that now encompass the El Verde and Bisley research areas supported shade coffee plantations at that time. However, most of the commercial coffee plantations in Luquillo were abandoned after a major hurricane in 1898 (Scatena 1989a). Overall, the Luquillo coffee industry could not compete with plantations in the interior of the island because of low yields related to hurricane damage, high rainfall, and relatively acidic and less productive soils. Nevertheless, both the El Verde and Bisley areas, like most of the lower LEF, supported small subsistence farms until they were purchased by the USDA Forest Service in the 1930s.

By the 1950s, the forest cover on Puerto Rico had reached its minimum level (figure 4-5). Since then, the island's economy has shifted from a rural, agricultural-based economy to an industrialized economy that is based on manufacturing and services. Coincident with this shift has been the migration to urban centers, the abandonment of agricultural lands, and an increase in forest cover as agricultural areas naturally reforest. In 1935, approximately 46.7 percent of northeastern Puerto Rico had agricultural land cover, but by 2003, 57 percent of the island was forested (Brandeis et al. 2007). When abandoned agricultural lands are allowed to reforest naturally, they can attain mature forest biodiversity and biomass in approximately 40 years (Aide et al. 1995; Zimmerman et al. 1995a; Silver et al. 2004). Nevertheless, past land management can leave legacies in the forest composition and soil resources that can last for decades, if not centuries.

Pathogens and Insects

Pathogens and insects, like the chestnut blight of New England or the pine beetles of Central America, can result in such rapid and dramatic changes to forest structure and composition that they are often considered landscape-level disturbances (Holdenrieder et al. 2004). In Luquillo, short-term but forest-wide defoliation of *Piper* was observed following Hurricane Hugo. European bees are also considered a threat to the endangered Puerto Rican Parrot (*Amazona vittata*), and since 1970 these bees have been manually removed from cavities in important breeding areas (Snyder et al. 1987). Although other pests and pathogens are present, no large-scale pathogenic disturbance is known to have affected the LEF in recent centuries. In fact, an important unanswered question regarding the disturbance ecology of the Luquillo Mountains is why pathogenic disturbances are not more common or apparent.

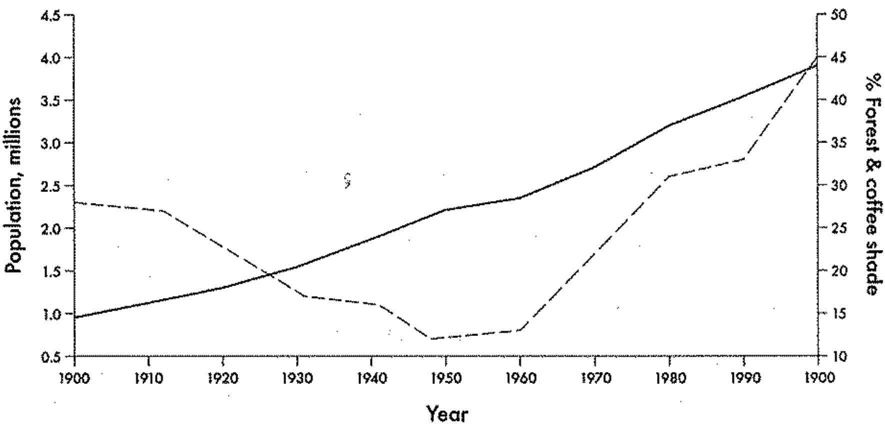

Figure 4.5 Island-wide population and forest cover (dashed line) by decade from 1900 to 2000.

Natural Disturbances in the Luquillo Mountains

Tree Mortality and Treefall Gaps

The creation of canopy gaps by individual or multiple treefalls is a common process involved in maintaining the structure and diversity of many tropical forests (Denslow 1987). The size of treefall gaps can range considerably but is typically between 50 and 100 m^2 (Hartshorn 1990). The rate of gap formation in mature tropical forests is typically around 1 gap ha^{-1} y^{-1}, and the turnover periods of forest canopy by tree fall gaps range from 50 to 165 years (table 4-6). Compared to other humid tropical forests, Luquillo has a high rate of canopy turnover due to hurricanes but a relatively low rate due to treefall gaps. The size and frequency of Luquillo gaps also varies with the topography, aspect, soil type, and forest age (Scatena and Lugo 1995). Only in riparian areas is the turnover by treefall gaps and slope failures faster than the turnover by hurricanes (table 4-7). Canopy throughfall in the center of a recent single-tree gap can be 30 to 50 percent higher than in the

Table 4.6 Canopy turnover periods by treefall gaps and hurricanes for some Neotropical forests

Location	Years	Source
Bisley, Puerto Rico: hurricane-induced defoliation; treefall, gap-induced	57–165	Scatena and Lugo 1995
Treefall gaps, Barro Colorado, Panama	62–159	Foster and Brokaw 1982
Treefall gaps, La Selva, Costa Rica	79–137	Hartshorn 1990
Treefall gaps, Tierra Firme, Amazonia	100	Uhl and Murphy 1981
Treefall gaps, Central America	62–155	Brokaw 1985
Treefall gaps, Los Tuxtlas, Mexico	61–138	Bongers et al. 1988

Table 4.7 Turnover periods in years by disturbance type and geomorphic setting for the Bisley watersheds between 1932 and 1989. (From Scatena and Lugo 1995.) Gaps = treefall gaps; Hurr = hurricanes; Slides = slope failures; Back = background, noncatastrophic mortality; dbh = diameter at breast height. Slope failures include those associated with hurricane and nonhurricane events

	Canopy area			Biomass				Stems > 10 cm dbh			
	Gaps yr	Hurr yr	Slides yr	Gaps yr	Hurr yr	Slides yr	Back yr	Gaps yr	Hurr yr	Slides yr	Back yr
Ridges	200	57	∞	250	110	∞	80	430	380	∞	75
Slopes	350	57	980	185	95	2,000	50	560	190	2,070	55
Valleys	60	57	430	40	105	680	30	110	145	400	50
Drainage	165	57	1,300	150	105	3,350	55	380	220	3,300	55

adjacent forest (Scatena 1989b). However, because the area in gaps is limited, their overall contribution to throughfall at the watershed scale is also limited (e.g., 3 percent).

The percentage of treefall gaps created by uprooted trees relative to snapped trees typically ranges between 20 and 50 percent in humid tropical forests and can be greater in steep land areas like Luquillo than in lowland tropical forests (Putz 1983; Scatena and Lugo 1995). The soil erosion associated with tree uproots contributes between 2.5 and 15 percent of the hillslope erosion in steep forested Luquillo watersheds (Larsen 1997; Larsen et al. 1999). In nearby agricultural and suburban watersheds, tree uproots account for less than 5 percent of soil erosion. The pit and mound features caused by these uproots typically occupy less than 0.1 percent of the Luquillo ground surface, whereas they can occupy as much as 60 percent in some temperate environments (Lenart et al. 2010). These differences are due in part to the dynamic surface erosion in tropical forests, which acts to remove rather than preserve the pit and mound features. Nevertheless, the pit and mound topography that results from treefalls does increase the surface storage of water and promotes the development of subsurface pipes and macropores.

The residuals of treefall gaps include an open canopy and associated microclimatic changes, coarse woody debris, and pit and mound topography. Microclimatic changes typically return to background levels within a year (Scatena 1989b). The pits and mounds created by treefalls can last for decades (Lenart et al. 2010) and are important microhabitats for certain Luquillo plants (Walker 2000).

Mass Earth Movements

Mass movements of earth are a common landform-scale disturbance in many upland humid tropical forests. In Luquillo, the velocity of downslope movement can range from the continuous downslope creep of soil profiles that occur on the order of millimeters per year (Lewis 1974) to debris flows that move tens of kilometers per hour. The frequency of Luquillo landslides and the rate of revegetation in mature forest stands have been related to bedrock geology, elevation, mean annual rainfall, and land use (Larsen and Simon 1993; Myster et al. 1997; Larsen et al. 1999). Within areas of similar geology and mean annual rainfall, mass wasting is five to eight times more frequent along roads than elsewhere and is most common on hillslopes that (1) have been anthropogenically modified, (2) have slopes greater than 12 degrees, and (3) face the prevailing trade winds.

Over the entire island of Puerto Rico, 1.2 landslide-producing storms occur each year (Larsen and Simon 1993). Storms with a total duration of 10 h or less typically require average rainfall intensities of nearly 14 mm h^{-1} in order to trigger landslides. In contrast, storms of 100 h or more can trigger landslides with an average rainfall intensity of 2 to 3 mm h^{-1}. A comparison of the Puerto Rican landslide threshold's relationship with rainfall intensities from the nearby island of Cuba indicates that all the common atmospheric systems in the Caribbean can produce landslide-generating storms (figure 4-6).

In the Luquillo Mountains, landslides are typically covered with herbaceous vegetation within 1 or 2 years, have closed canopies of woody vegetation in less

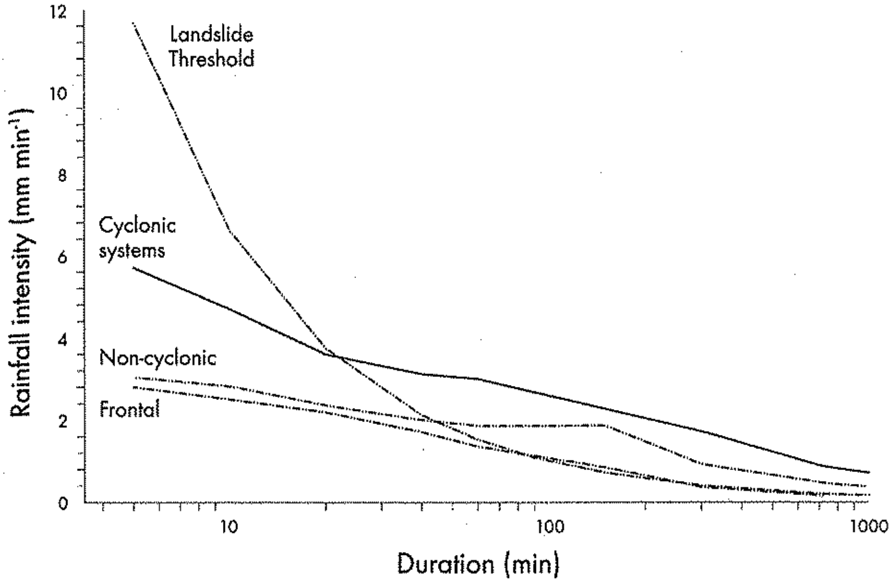

Figure 4.6 Rainfall intensity–duration curves by Caribbean storm type and a landslide rainfall intensity–duration threshold curve for Puerto Rico. (From Scatena et al. 2005.)

than 20 years, and have aboveground biomass equal to that of the adjacent forest after several decades (see chapter 5). Slope wash erosion and surface runoff from landslide scars also tend to approach adjacent forest values after a few years. After 4 years, the movement of surface soil on landslide scars can be reduced from 100 to 349 g m^{-2} y^{-1} to 3 to 4 g m^{-2} y^{-1} (Larsen et al. 1999). At the watershed scale, landslides can be major sources of stream sediment in upland humid tropical environments. They also disrupt roads and water conveyance systems and can be so chronic that certain roads in the forest need continual maintenance (Ahmad et al. 1993; Olander et al. 1998).

In summary, the changes in ecological space created by mass movements include the complete removal of above- and belowground biomass and changes in the local microclimate and soil resources. The residuals of mass movement include debris piles, unstable slopes, exposed soils, and pit and mound topography (Lenart et al. 2010). Their legacies include poor soil horizon development and the amphitheater-shaped valleys and narrow ridges that characterize much of the landscape (Scatena 1989a).

Floods and Fluvial Processes

Two general types of flood disturbances are commonly distinguished in the humid tropics: (1) seasonal inundation-type floods in which extensive areas are covered with lakelike water for extended periods (i.e., weeks to months) each year, and (2) event floods that are of relatively short duration (i.e., hours to days) and which have high-velocity stream flows (Scatena et al. 2005). In the steep Luquillo Mountains region, runoff is so rapid that only short-duration, high-intensity floods occur. However, standing floodwaters cover large parts of the surrounding coastal plain several times each century (Torres-Sierra 1996). Other areas of the tropics that have the physiographic and climatic conditions necessary to create flood disturbances and fluvial landforms similar to Luquillo and mountainous areas of the Caribbean and Central America include the following (Gupta 1988):

- river valleys of East Asia, especially Taiwan and the Philippines
- upland areas of Vietnam, Sumatra, Java, and Burma
- humid areas of the Indian subcontinent
- Madagascar and neighboring parts of coastal East Africa
- north and northeast Australia

Regression models of event-type flooding in the Luquillo Mountains indicate that both climatic and morphologic factors influence the magnitudes of peak flood discharge. Drainage area, mean annual rainfall, the 2-year 24-hour rainfall, the length of the main channel, and the total length of tributaries have been positively related to peak flood discharge and annual peak discharges (Ramos-Gines 1999; Rivera-Ramírez 1999). Likewise, the depth to bedrock and the watershed shape have been negatively correlated with peak discharge.

In the Luquillo region, the largest floods are not necessarily associated with hurricanes (table 4-5). The annual peak can occur in any month of the year but is most common in the late summer and fall (figure 4-3). In the lower Río Mameyes, flash floods (i.e., instantaneous discharge > 3.5 $m^3 s^{-1}$) occur at least once a month, and larger floods (instantaneous discharge > 18 $m^3 s^{-1}$) produced by cold fronts, tropical depressions, storms, and hurricanes occur several times per year on average (Blanco and Scatena 2005). These sudden increases in water depth and velocity increase water turbidity and flush particulate organic matter from the channels. If large enough, they can remove submerged aquatic vegetation, reduce periphyton, move bedload sediment, and rearrange aquatic habitats. Mass upstream migrations of juvenile freshwater snails can also be triggered by floods (figure 4-7).

Because of abundant bedrock and large boulders, the morphologies of the Luquillo stream channels are relatively stable and do not change dramatically following storm events. The stream hydraulic geometry is also considered relatively well developed, even in boulder-lined channels, and there are distinct longitudinal patterns in channel processes (Pike 2008; Pike et al. 2010). Floods also leave residuals, including the removal of periphyton and riparian vegetation, the addition of coarse woody debris, and the modification of aquatic habitats (Blanco and Scatena 2005, 2007). The sediments that fill the coastal plain and near-shore environments are the legacies of these processes.

Hurricanes

Hurricanes bring intense winds and rain that affect different parts of the landscape in different ways. At the scale of individual trees, winds in excess of about 100 to 130 km h^{-1} lethally damage trees within a few hours (figure 4-8). Winds in excess

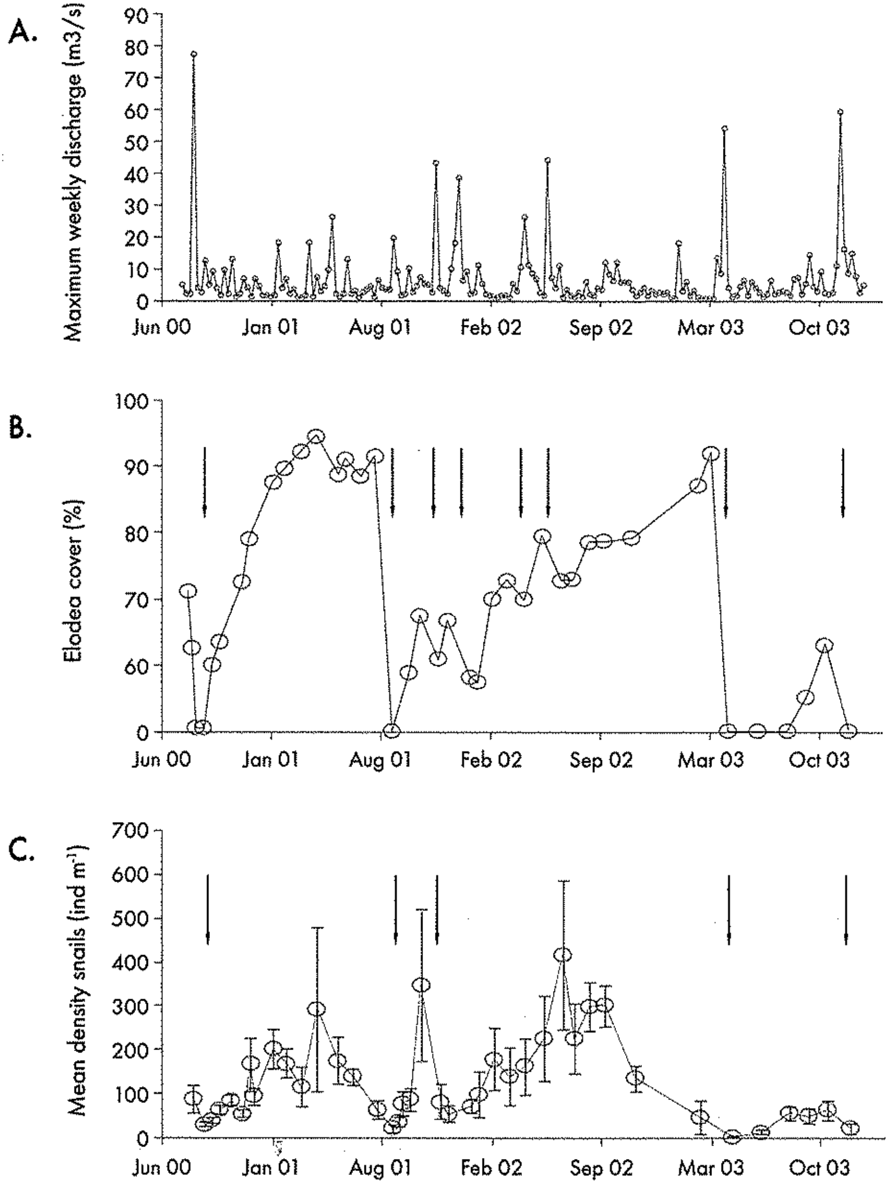

Figure 4.7 Stream discharge, cover of submerged aquatics, and density of freshwater snails in the lower Rio Mameyes between 2000 and 2002. Arrows indicate events of massive upstream snail migrations. (From Blanco and Scatena 2005.)

of 60 km h^{-1} cause large-scale defoliation and litterfall. At this scale, damage is related to the tree species, morphology, age, size, form, health, and rooting conditions. In general, fast-growing low-density woods are more susceptible to wind damage than high-density, late-successional species (Aide et al. 1995; Zimmerman et al. 1995b).

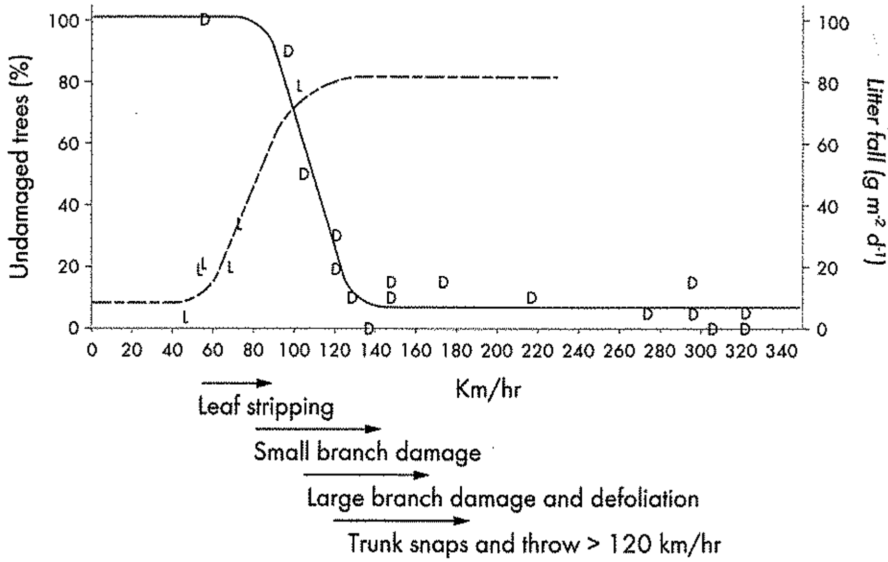

Figure 4.8 Maximum wind gusts versus percent of tree damage (D) and amount of litterfall (L) for the Luquillo Mountains. The types of canopy damage commonly observed for a given range of wind gusts are depicted by the arrows below the diagram. (After Scatena et al. 2005.)

At the landform scale, variations in wind damage result from differences in exposure and the modification of wind velocity caused by the landforms themselves. For example, valleys oriented parallel to the direction of dominant winds will receive more damage than nearby valleys that are perpendicular to the hurricane-force winds. Defoliation and the transfer of nutrients from the canopy to the forest floor can also cause major shifts in nutrient cycling pathways at the stand and landform scales (Lodge et al. 1991; Ostertag et al. 2003). Simulations of the hydrologic responses to daily rainfall following canopy defoliation suggest that significant changes in evapotranspiration, soil moisture, and stream flow occur when the forest is defoliated by 90 percent (figure 4-9). Moreover, although a 50 percent reduction in canopy leaf area does modify evapotranspiration, soil moisture, and stream flow, a 90 percent reduction in canopy leaf area can increase stream flow by over 300 percent relative to undisturbed conditions.

At the scale of the Luquillo Mountains, the spatial pattern of hurricane-induced damage can be complex and is strongly correlated with both aspect relative to the prevailing winds and forest type (Boose et al. 1994). In general, damage is spatially uniform in low-lying, uniform landscapes and more complex in dissected mountainous terrain. At the regional scale, the configuration of coastlines and mountains relative to the storm track determines how a storm will weaken when it crosses land. Factors controlling forest damage at this scale include gradients in wind velocity that are related to the size and intensity of the hurricane and large topographic features. In Puerto Rico, the Luquillo Mountains apparently influence the path of hurricanes across the island and create what is locally called the "Puerto Rican Split"—that is, the tendency for hurricanes approaching the Luquillo Mountains to be deflected to the north or south of the mountains. Apparently the 1,000 m Luquillo Mountains create enough resistance and friction to deflect the trajectory of approaching hurricanes to either the north or the south of the island.

At all scales, hurricanes create patches of survivors and new regeneration that change in structure and composition over decades (see Crow [1980] and chapter 5 for details). Nevertheless, hurricanes do not erase the signature of past land use on the species composition, and the composition of posthurricane regeneration can be directly related to the prior land use (García-Montiel and Scatena 1994; Zimmerman et al. 1995a; Thompson et al. 2002). In some stands, the forest composition still reflects the prior composition of shade coffee plantations after 100 years of abandonment and the direct impacts of several hurricanes.

Hurricane-related storm discharges can cause significant geomorphic modifications to stream channels (Scatena and Johnson 2001). Posthurricane stream-water concentrations of sediments and nutrients can also be elevated for months to years

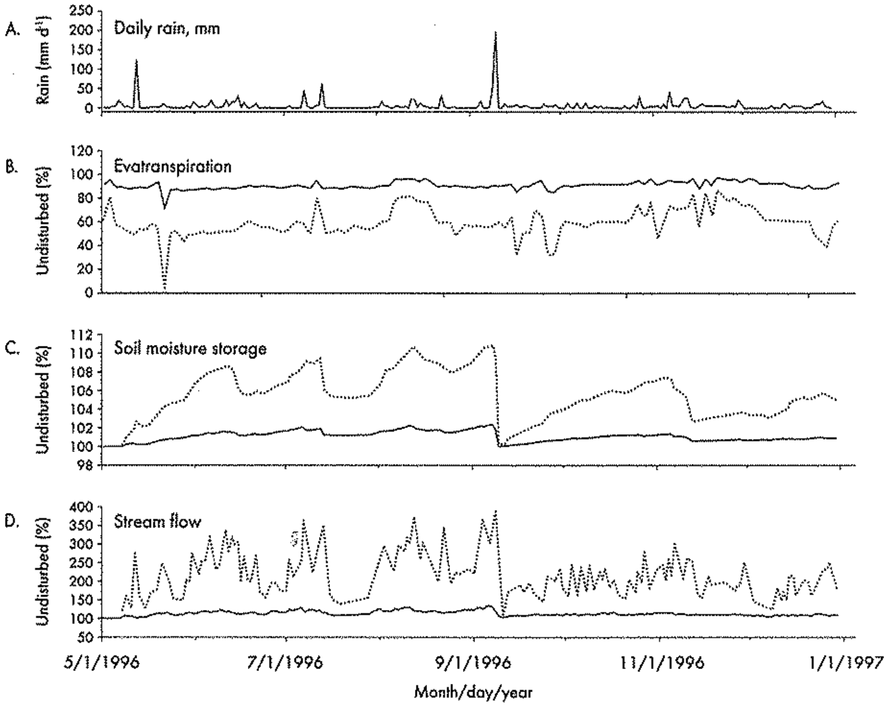

Figure 4.9 Daily rainfall and corresponding simulations of evapotranspiration, soil moisture storage, and stream flow in the Bisley Research Watersheds following simulated reductions in canopy leaf area of 50 and 90 percent. Simulations are expressed as a percent of undisturbed conditions for the same daily rainfall sequence and are represented by solid lines for a 50 percent reduction in canopy leaf area and dashed lines for a 90 percent reduction. (From Scatena et al. 2005.)

(Schaefer et al. 2000). However, suspended sediment concentrations can be lower than predicted from concentration-discharge relationships derived from nonhurricane storms of similar magnitudes (Gellis 1993). Apparently the defoliation caused by the hurricane-force winds creates residual debris dams that trap sediment and reduce suspended sediment concentrations. Nevertheless, because high stream flow can last for several days, the total sediment transported during the passage of a hurricane can be significant.

Hurricane winds also result in immediate changes in the canopy cover and aboveground biomass, the microclimate (Fernández and Fetcher 1991), and throughfall (Heartsill et al. 2007). In most tropical forest understories, the daily photosynthetic photon flux density (PPFD) is 1 to 2 percent of the value above the canopy (see, e.g., Denslow and Hartshorn 1994); at El Verde, the solar irradiance at the forest floor was 5 to 47 percent of full sunlight after Hurricane Hugo (Petty 1993; Scatena et al. 1996), a huge increase in this crucial environmental factor. For the 10 months after Hurricane Hugo, levels of understory PPFD were highly variable at a scale of 1 m, but the median was 7.7 to 10.8 mol m^{-2} d^{-1}, which is comparable to PPFD levels in a 400 m^2 treefall gap (Fernández and Fetcher 1991; Turton 1992; Bellingham et al. 1996; Fetcher et al. 1996). Values had fallen to 0.8 mol m^{-2} d^{-1} by 14 months, at which point rapid growth of *Cecropia schreberiana* overtopped the light sensors in the study. This is a clear example of how ecological space shifts rapidly over points in geographic space owing to disturbance and biotic response (see chapter 2).

In addition to these immediate changes to the forest's structure and ecological space, hurricanes also leave residuals on the landscape. These include landslides,

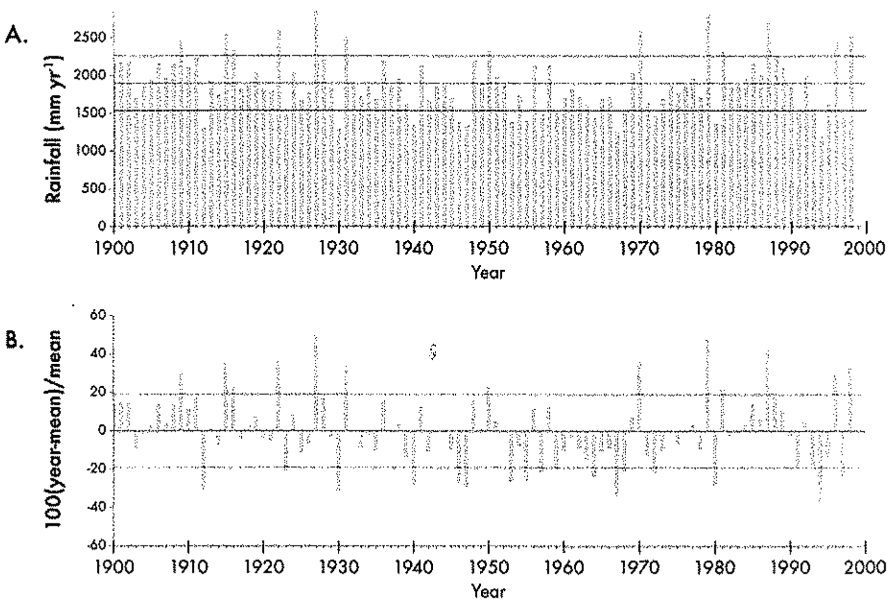

Figure 4.10 Annual rainfall series from the base of the Luquillo Mountains, Canovanas, Puerto Rico.

tip-up mounds, accumulations of coarse woody debris and litter, and large patches of defoliated or fallen trees. In turn, these residuals create opportunities for the regenerating forest and leave legacies that include cohorts of even-age stands that are distributed in patches across the mountain (see chapter 5).

Droughts

Droughts have historically been important disturbances to both the natural and human-dominated ecosystems of Puerto Rico. Rainfall records (figure 4-10) and interviews with long-term residents suggest that the 2-year drought of 1946 and 1947 was the worst drought on record. During the second year of this drought, headwater streams near El Verde were dry, crops failed, and Luquillo Mountain farmers were forced to travel to the other side of the island to find work (Alejo Estrada, University of Puerto Rico Research Technician, personal communication, 1994).

Although droughts have always been an important disturbance in the Luquillo Mountains, long-term precipitation records suggest that they might be becoming more frequent. During the 20th century, the annual precipitation had negative trends in all eight of the precipitation stations on the island, with records starting around 1900 (van der Molen 2002). The negative trends were significant in six of the eight stations and ranged from −1.59 to −4.90 mm y^{-1}. Another detailed trend analysis of 24 stations found that between 1931and 1996, 71 percent of the stations had significant decreases in monthly precipitation between May and October (Bisselink 2003). These decreases ranged between 0.6 and 2.3 mm y^{-1}. The same study also found that winter precipitation increased by 0.3 to 1.7 mm y^{-1}. Since 1987 and the initiation of the Luquillo Long-Term Ecological Research (LTER) project, the mean weekly rainfall has also decreased significantly at both the Bisley and El Verde research sites (Heartsill-Scally et al. 2007). In Bisley, the mean daily rainfall and throughfall had an average decline of 0.2 and 0.23 mm y^{-1}, respectively. Although significant, these declines are less than the average variation between years and between days. Nevertheless, islandwide, 1997, 1994, and 1991 were the second, third, and sixth driest years in the 20th century (Larsen 2002). Widespread mandatory water rationings also occurred six times on the island in the 1990s. The most severe drought, which occurred in 1994, resulted in an economic loss of $165 million (Lugo and García-Martinó 1996).

At the watershed level, the drainage density (the ratio of the length of tributaries to the length of the main channel), the percentage of the drainage basin with a northeast aspect, and the average weighted slope of the drainage basin have been used to estimate low stream flows (García-Martinó et al. 1996). At the scale of forest stands, short-term dry periods lasting weeks to months are common and have been linked to declines in the abundance of common lizards, spiders, exotic earthworms, and palaemonid river shrimp (Reagan and Waide 1996; Zou and González 1997; Covich et al. 2006). Prolonged dry periods can result in increased litterfall and decreased root biomass (Beard et al. 2005), whereas wet and drying cycles can stimulate microbial biomass growth, enhance microbial nitrogen immobilization, and impact detrital food chains (Lodge et al. 1994; Ruan et al. 2004). However,

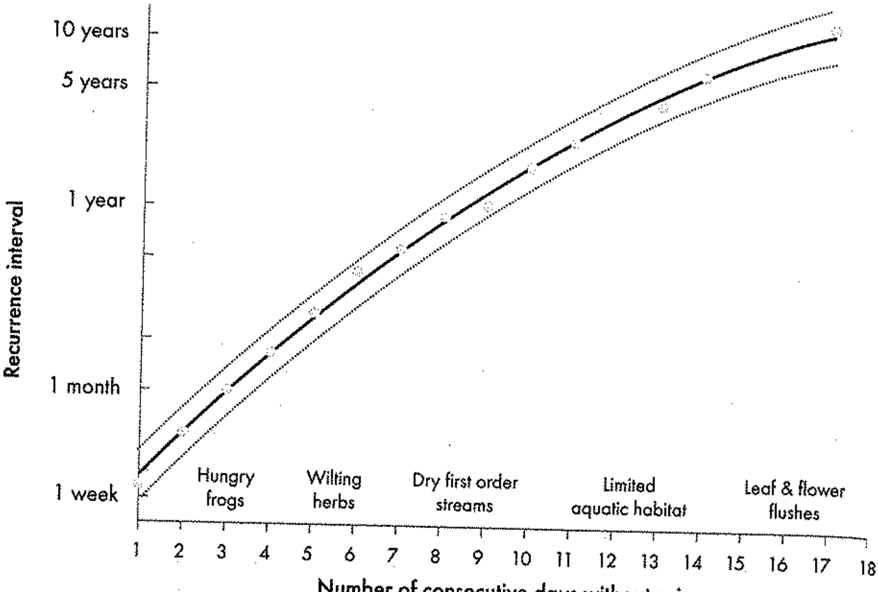

Figure 4.11 Ecological response to the number of consecutive days without rain in the tabonuco forest of the Luquillo Mountains of Puerto Rico. (Modified from Covich et al. 2006.)

these responses can be asynchronous and lag behind dry periods by weeks to months (Ruan et al. 2004). Responses to dry periods are also more apparent in well-drained ridges than in the wetter riparian valleys (Silver et al. 1999). In general, after 3 days without rain, the abundant tree frogs have empty stomachs because of the lack of insects that normally occur in wet forest litter (figure 4-11). One week without rain or canopy throughfall occurs nearly every year and causes the wilting of herbaceous vegetation in open areas such as gaps and roadways. Once every 10 to 20 years, there are enough consecutive rainless days that small headwater streams become dry and aquatic habitat becomes limiting. Unlike other disturbances, droughts cause residuals that are relatively short-lived (Beard et al. 2005), but their long-term legacies are not yet understood.

Wildfire and Lightning

Paleoclimatic evidence from the Caribbean, Amazonia, and Central America indicates that most Neotropical humid tropical forests have experienced fires and extended droughts during the past 10,000 years (Hodel et al. 1991; Servant et al. 1993). Deep ground fires have also been shown to cause massive above- and belowground biomass losses in tropical montane cloud forests in Mexico (Asbjornsen et al. 2005). Holocene charcoal stratigraphy from the north-central coast of Puerto Rico also indicates that fire frequency greatly increased at the time of human arrival to the island (Burney and Burney 1994). Nevertheless, interviews with long-time Luquillo residents indicate that there have been no extensive wildfires in the tabonuco or upper elevation forests in the past 80 years. Small patches (<0.5 ha) of roadside ferns and shrubs do burn nearly every year at lower elevations. However, the forest is generally considered too wet to sustain large wildfires.

Lightning-induced fires and tree mortality have been identified as important natural disturbances in many humid and dry tropical forests (Whitmore 1984; Horn 1991; Richards 1996; Middleton et al. 1997). In 15 years of observation in 13 ha of the Bisley watershed area, lightning strikes have killed three canopy trees (Scatena personal observation). None of these events caused fires, treefalls, or damage to multiple trees. Over a 10-year period, lightning has also damaged two of seven exposed LTER climate stations. At these rates, lightning-induced tree mortality is conservatively, and crudely, estimated at a relatively low rate of one or two trees per hectare per century. This relatively low rate of lightning might be due to the trade winds shearing the tops of developing convective clouds before they develop to the lightning-producing stage. When lightning strikes do occur, they leave isolated individual standing dead trees.

Human-Induced Disturbances in the Luquillo Mountains

The most commonly cited disturbance-generating activities that are currently operating in the Luquillo Mountains are water resource extraction, road development, and recreation (Scatena et al. 2002; Ortiz-Zayas and Scatena 2004). Long-term studies have shown that historical selective harvesting for timber and charcoal, agriculture, agroforestry, hunting, road building, water diversions, and two airplane wrecks have all caused measurable and documented changes in the ecological space of the Luquillo Mountains (see chapter 6). Unlike many of the natural disturbances, most human-induced disturbances in the Luquillo Mountains were not discrete events and instead have been cumulative and progressive in nature.

Selective Harvesting for Timber and Charcoal

The Luquillo Mountains have historically been an important source of timber and charcoal for the island. Because of the relative inaccessibility of the steeply sloping mountains, tree harvesting prior to the late 1880s was initially limited to valuable timber species, namely, ausubo (*Manilkara bidentata*) and laurel (*Magnolia splendens*) (García-Montiel and Scatena 1994). However, with increasing demand for fuelwood, tree harvesting for charcoal production became important throughout the first half of the 1900s. Today the legacy of this activity can be seen in cut tree stumps, remnant charcoal pits, and skidtrails that are scattered throughout the lower elevation areas of the forest. Comparisons of the forest structure and composition around abandoned charcoal pits and cut stumps indicate that these activities can change the local species composition. However, single-tree harvesting leaves a smaller legacy than the production of charcoal (García-Montiel and Scatena 1994). Moreover, neither disturbance creates uproot pits and mounds that facilitate regeneration, nor do they provide biomass for decomposition and nutrient recycling.

Agriculture and Agroforestry

In general, the type and magnitude of agricultural practices in the Luquillo Mountains have varied with topographic, geomorphic, and pedologic conditions. Within the Bisley watersheds, the major land use and impacts on ridges were associated with selective logging and silviculture (García-Montiel and Scatena 1994). In contrast, valleys and slopes tended to be used for agroforestry. At El Verde, areas with rocky soils were left to forest, whereas adjacent areas were cleared for pasture and cropland. Coffee cultivation, which involved liming of the soil and the cultivation of nitrogen-fixing shade trees, might have left detectable legacies in the soil pH and nitrogen following 70 years of abandonment (Beard et al. 2005). Agricultural land uses also left legacies in the species composition (see chapter 5), nutrient cycles (Silver et al. 2004), the spatial distributions of soil bacterial activity (Willig and Moorehead 1996), and the distribution of the tailless whip scorpion spider *Phrynus longipes* (Arachnida: Amblypygi) (Bloch and Weiss 2002).

Water Diversions

Water that is diverted for domestic and municipal uses is one of the major economic products of the Luquillo Mountains and accounts for about 10 percent of the total water deliveries on the island (Ortiz-Zayas and Scatena 2004). These water withdrawals have been directly linked to the reduction in the area of aquatic habitat and in the migratory routes of common aquatic species (Benstead et al. 1999; Scatena 2001; Blanco and Scatena 2005).

For decades, the standard practice has been to build small (<3 m high) dams in upland streams of the Luquillo Mountains. Water is then diverted by gravity for human uses at lower elevations. The resulting wastewater is then returned to the rivers near their estuary. This water use has been shown to alter water chemistry (Santos-Román et al. 2003) and impact the abundance and composition of aquatic life. Large dams on the island can be complete barriers to migration (Holmquist et al. 1998), and smaller diversions act as filters (Benstead et al. 1999). Since the early 1990s, the Luquillo LTER program has made significant progress in understanding the ecology and instream requirements of aquatic organisms in the Luquillo Mountains. Much of this research has been used to develop more ecologically based water management practices (see chapter 7).

Fishing and Hunting

Although poorly quantified, fishing and hunting have been, and continue to be, important community-level disturbances affecting the Luquillo Mountains. The declines of both the Puerto Rican Parrot and the plain pigeon (*Columba inornata*) have been partly attributed to hunting. Although bird hunting is not allowed within the Experimental Forest, every year birds are hunted in the region, and shell casings are commonly found near the forest boundary.

Fishing in Luquillo streams is a more common practice than hunting. Freshwater shrimp, fish, and snails are all caught on a daily basis from Luquillo Mountain streams and used for local consumption. Although historical rates of fishing are not known, interviews with long-term residents indicate that the fishing pressure on aquatic organisms is greater now than in the recent past. Moreover, during the agrarian period, local residents did not have time to fish and fished only on special occasions. When they did fish, they used the traditional hand and gig methods. The increase in free time since the late 1950s has apparently increased the fishing pressure on Luquillo Mountain streams. In addition, harvesters now use baited traps, large nets, and poison or chemical approaches to harvesting fish and shrimp. Harvest-related poisoning events cause massive mortality of shrimps and aquatic life and leave legacies that are apparent for months after an event (Greathouse et al. 2005).

Recreation

Recreational visits by island and nonisland residents are the greatest direct use of the Luquillo Mountains. In fact, the Luquillo Mountains have one of the highest visitor uses per area of any forest or grassland in the National Forest system (Scatena et al. 2002). Between 1980 and 1990, this tourism generated approximately US$5.2 million per year in economic activity. Most of the visitation occurs in the summer months and during weekdays (figure 4-12). However, most of this recreation is relatively passive and includes picnicking, swimming, and hiking in designated areas. Therefore, the direct impacts of recreation on the ecosystems of the Luquillo Mountains are considered limited and restricted to designated recreation areas and roadways. Nevertheless, where recreation is intense, it does leave residuals of trash and trampled riparian vegetation.

Road Building

All of the major roads in the Luquillo Mountains were constructed prior to 1970. Although some off-road vehicles occasionally enter the forest, this activity is currently limited to annexed lands near the community of Cubuy. The vast majority of vehicle use is on paved or maintained roads. Nevertheless, it has been shown that roads greatly increase the magnitude and frequency of landslides and promote the establishment of alien species within the forest. Mass wasting is five to eight times more frequent along roads and can affect an area that is several times the width of the road itself (Larsen and Parks 1997). The legacies left by road building include the expansion of nonnative species (Olander et al. 1998), landslides, and changes in slope morphology (Larsen and Parks 1997). Because of the aging road network, a greater frequency of landslides and road-related disturbances is expected in the future.

Future Disturbance Regimes

Although the Luquillo Mountains have had a dynamic and resilient history, past performance is not a guarantee of future behavior. In the next 100 years, the magnitude and frequency of the disturbances affecting the Luquillo Mountain forests

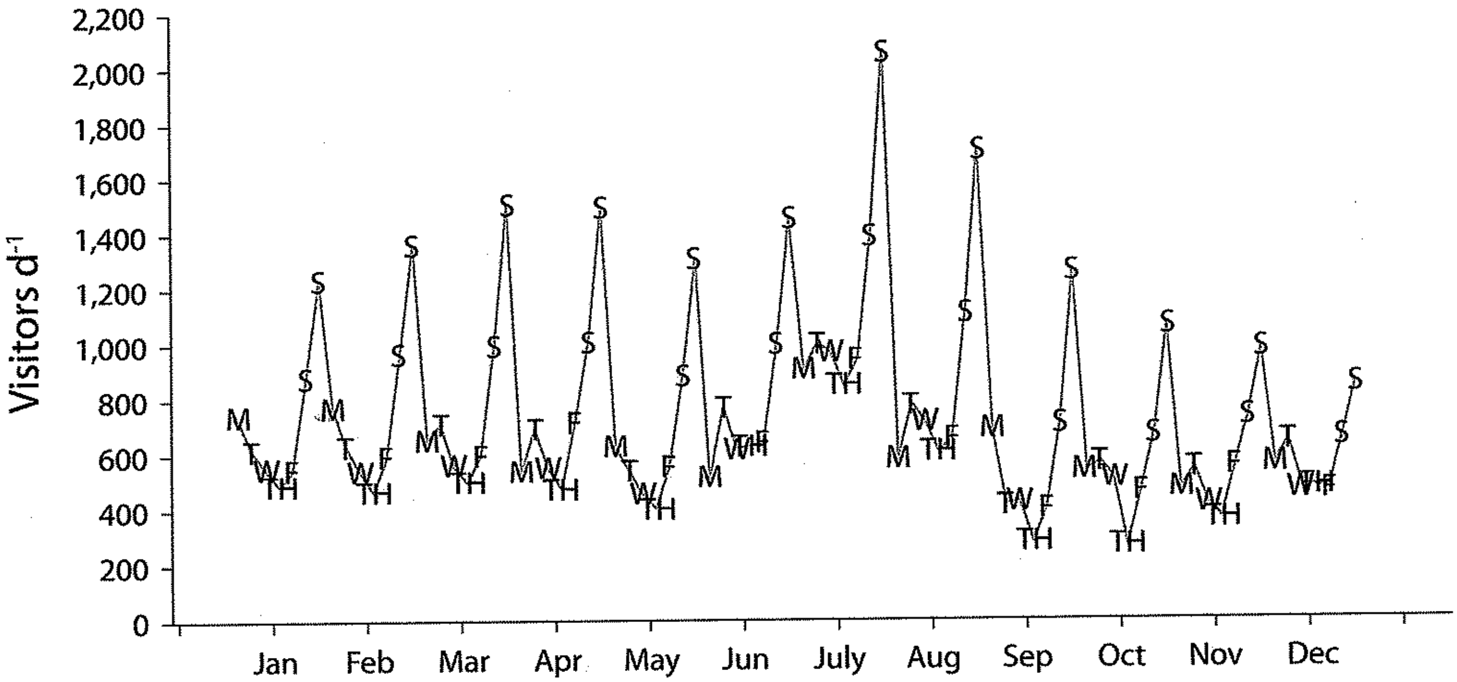

Figure 4.12 Average number of visits to the Yokahu Recreational Center in the Caribbean National Forest by day of week and month. Based on daily recreational surveys from 1980 to 1995.

can be expected to change as a result of changing local, regional, and global stressors.

Model simulation of future global-scale carbon dioxide (CO_2)-induced climate change indicates that over the next few decades, Puerto Rico might experience increases in hurricane activity (Emanuel 1987), increases in the length of the dry season, and decreases in soil moisture (Hulme and Viner 1995). Recent empirical and simulation studies also indicate that deforestation of the coastal plain reduces cloud moisture and rainfall over the island (van der Molen 2002). Increases in water diversions, land use change (Wu et al. 2007), and urban heat island effects (González et al. 2005) will also act to dry the landscape. All of these activities imply that droughts, and possible fires, will also become more common.

Although hurricane activity is expected to increase, the magnitude of the resulting hurricane-induced changes is uncertain. High-resolution computer simulations of 51 western Pacific storms under present-day and high-CO_2 conditions indicate that windspeeds will increase 3 to 7 m s^{-1} (5 to 12 percent) with a 2.2°C increase in the sea surface temperature (Knutson et al. 1998). Given the magnitude of the expected increase in windspeeds and the resilience of the Luquillo forests to wind (figures 4-8 and 4-9), increases in hurricane frequency might be more important than increases in the magnitude of hurricane winds. Simulations of the response of Luquillo Mountain forests to changes in hurricane frequency indicate that a range of forest compositions can occur with different hurricane regimes (O'Brien et al. 1992). In general, a decrease in hurricane frequency will result in mature forest with large trees, whereas an increase in frequency will result in forests that are shorter, are younger, and have a greater abundance of pioneer species and lower aboveground biomass.

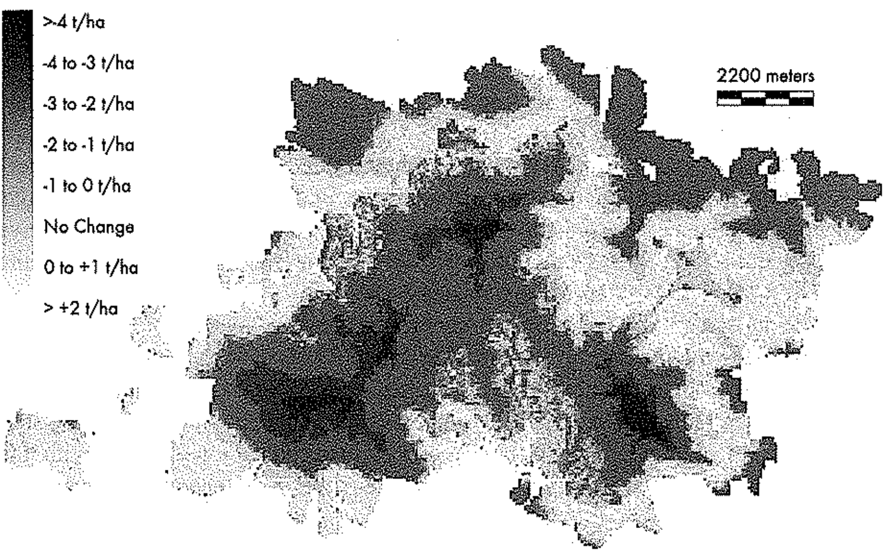

Figure 4.13 Simulated changes in soil organic carbon in response to an increase in temperature. (From Wang et al. 2002a.)

The absolute magnitudes of historical and future changes in the climate of the Luquillo Mountains are unknown. Nevertheless, the precipitation records and the presence at lower elevations of isolated large upper elevation trees does suggest that the Luquillo Mountains are drying and that the drier forest types are migrating to higher elevations (see chapter 3 for a description of forest types). Based on existing climate–elevation relationships, a change in the air temperature of 1.5°C to 2.5°C and changes in precipitation of −11 to +33 percent would drastically alter the distribution of forest types in the Luquillo Mountains (Scatena 1998). Simulations indicate that a warming of 2.0°C is likely to result in losses in soil organic carbon in the lower and higher elevations, but increased storage in the middle elevations, of the Luquillo Mountains (figure 4-13) (Wang et al. 2002a). Simulations also suggest that both gross and net primary productivity would decrease under a doubling of atmospheric CO_2 (Wang et al. 2002b).

Regardless of climate changes, changes in land use and land cover are also expected to change the hydrologic budgets of the Luquillo Mountains. Comparisons of rainfall and stream flow between the "agricultural" period of 1973–1980 and the "urbanized/reforested" period of 1988–1995 indicate that a smaller proportion of rainfall became stream flow in the urbanized/forested period because of reforestation (Wu et al. 2007). Simulations in the same study indicate that annual stream flow in northeastern Puerto Rico would decrease by 3.6 percent in a total reforestation scenario, and it would decrease by 1.1 percent if both reforestation and urbanization continue at their present rates until 2020.

Summary

- Like many humid tropical environments, the Luquillo Mountains is a dynamic ecosystem that is affected by a wide array of environmental processes and disturbances. Events that concurrently alter the environmental space of several different areas of the Luquillo Mountains occur every 2 to 5 years. Events such as hurricanes that cause widespread environmental modification occur once every 20 to 50 years.
- Although the Luquillo Mountains are the product of ancient igneous and tectonic activity, they are not as tectonically active as many tropical mountains and have been subaerial for millions of years. Nevertheless, they do receive occasional ash falls from volcanoes in the lower Caribbean, and multiple earthquakes are measured on the island each year.
- The most common disturbance-generating weather systems that affect the Luquillo Mountains are (1) cyclonic systems, (2) noncyclonic intertropical systems, (3) extratropical frontal systems, and (4) large-scale coupled ocean-atmospheric events (e.g., North Atlantic Oscillation, El Niño-Southern Oscillation). Unlike in some tropical forests, disturbances associated with the passage of the Inter-Tropical Convergence Zone or monsoonal rains are not common.
- Hurricanes are considered the most important natural disturbance affecting the structure of forests in the Luquillo Mountains. Compared to other humid tropical forests, Luquillo has a high rate of canopy turnover by hurricanes but a

relatively low rate by tree-fall gaps. Historically, pathogenic disturbances have not been uncommon.

- Hurricane-related storm discharges can cause significant geomorphic modifications to Luquillo stream channels, and stream water concentrations of sediments and nutrients can be elevated for months to years following a major hurricane. However, the largest floods are not necessarily associated with hurricanes, and the annual peak discharge can occur in any month of the year but is most common in the late summer and fall.
- Over the entire island of Puerto Rico, 1.2 landslide-producing storms occur each year. In the Luquillo Mountains, landslides are typically covered with herbaceous vegetation within 1 or 2 years, have closed canopies of woody vegetation in less than 20 years, and have an aboveground biomass equivalent to that of the adjacent forest after several decades.
- Human-induced disturbances have historically included tree harvesting for timber and charcoal, agriculture, and agroforestry. In the past few decades, water diversions, fishing and hunting, and road building have been important disturbances. Present and future human-induced disturbances are related to regional land use change, the disruption of migratory corridors, and forest drying related to coastal plain deforestation and regional climate change.

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Edited by

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