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## Geographic and Ecological Setting of the Luquillo Mountains

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### Key Points

- The Luquillo Mountains in northeastern Puerto Rico are geologically dynamic, with recurrent hurricanes, landslides, and earthquakes.
- Puerto Rico has never been physically connected to continents by land bridges, which, together with the island's long distance from North and South America, contributes to its relatively low numbers of native plant and animal species for a tropical location and its high rate of endemism.
- The climate is warm, wet, and relatively aseasonal but shows strong gradients with elevation.
- Soils are deep and highly weathered, with carbon and nutrient concentrations and standing stocks similar to those in many other tropical forests. Soils contain much to most of the available nutrients and total carbon, but plant biomass is a particularly important pool of potassium.
- Nutrient inputs in precipitation are dominated by marine aerosols; these aerosols and rapid weathering contribute to a substantial export of base cations in streams.
- Nitrogen budgets are unbalanced at the watershed scale, suggesting that significant amounts of N fixation are occurring.
- The Luquillo Mountains contain many types of forest, but four are common and particularly well studied: tabonuco, colorado, palm, and elfin.

- Aboveground net primary productivity is high, as it is in many other tropical sites, and aboveground biomass, productivity, and forest stature decrease with elevation.
- Large mammalian herbivores and predators are absent; lizards, frogs, snakes, and a few birds are the top terrestrial predators.
- Stream and river food webs are dominated by freshwater shrimp and fish species that migrate to the estuary; nonmigratory freshwater crabs are also important, but aquatic insects are neither diverse nor abundant.
- Leaf litter decomposition is rapid in both the forest and streams, and detrital pathways provide a major energy source to higher trophic levels.

## Introduction

In this chapter, we describe the geologic, geographic, and ecological context in which the Luquillo Mountains (figure 3-1) are situated, with particular emphasis on factors that potentially influence the response of terrestrial and aquatic ecosystems to disturbance. We start with the physical and chemical environment and then discuss the biota. Whenever possible, we address the whole of the Luquillo Mountains, although we know the most about the mid-elevation forests. We address long-term results and ambient conditions as a prelude to our detailed descriptions



Figure 3.1 The Luquillo Mountains of Puerto Rico. (Photograph by William McDowell.)

of disturbances and the biotic response to disturbance in chapters 4, 5, and 8. It is difficult to discuss the Luquillo Mountains without considering the role that previous disturbances have played in shaping the mountains as we know them today (see chapter 1). Consequently, we synthesize the results of several decades of research and reflect on the lessons learned from our research as we place the Luquillo Mountains in the context of other tropical ecosystems, and of forest and stream ecosystems globally.

## Geology

### *Regional Geology*

Puerto Rico is located in one of the most dynamic regions on the planet, with severe hurricanes, landslides, tsunamis, and earthquakes all occurring with significant frequency (see chapter 4 for details). Much of this dynamism is related to Puerto Rico's location at the junction of the American and Caribbean crustal plates (Mason and Scanlon 1991; ten Brink et al. 2006). Puerto Rico is the smallest island (figure 3-2) of a large volcanic island-arc (the Greater Antilles) that developed during the Cretaceous, about 100 million years ago (mya), along a broad strike-slip zone between these crustal plates. The Puerto Rico Trench, the deepest spot in the Atlantic, lies about 150 km north of Puerto Rico. Although the islands are primarily volcanic in origin, only dormant volcanoes are currently found in the Greater Antilles. The Lesser Antilles is a younger (created ~35 to 24 mya), predominantly volcanic island arc with active volcanoes lying south and east of Puerto Rico and stretching south to the coast of Venezuela.

Although it is possible to see from one island to the next all the way from Florida to Venezuela, the islands are not thought to have formed continuous land bridges between North and South America (Graham 2003a; Hedges 2006). The geologic history of the Caribbean that is relevant for biogeography is still uncertain and controversial (Graham 2003b). Previously, most of the smaller Caribbean islands, including Puerto Rico, were not thought to have been physically connected to their neighbors (Heatwole and MacKenzie 1967). However, the Virgin Islands, which are part of the Puerto Rico Bank, were contiguous with Puerto Rico during glacial maxima, most recently during the Pleistocene. Furthermore, geologic evidence indicates that the proto-Antilles were once connected below the sea surface, and more recently Heinicke et al. (2007) suggested that Cuba, Hispaniola, and Puerto Rico were connected above sea level during the late Eocene (35 mya) and that subsidence during the Oligocene (~23 to 34 mya) broke these connections. Others have proposed, however, that the emergence of the proto-Antilles above sea level did not occur until the middle Eocene (~47 mya) (Iturralde-Vinent and MacPhee 1999; Graham 2003b), and that Puerto Rico did not emerge until the middle Miocene (~23 to 17 mya), after its separation from Hispaniola in the late Oligocene to early Miocene (~24 mya) had already occurred (Graham 2003b).

Puerto Rico has undergone a full cycle of mountain development subsequent to its emergence in the Miocene and is now relatively stable in terms of volcanic

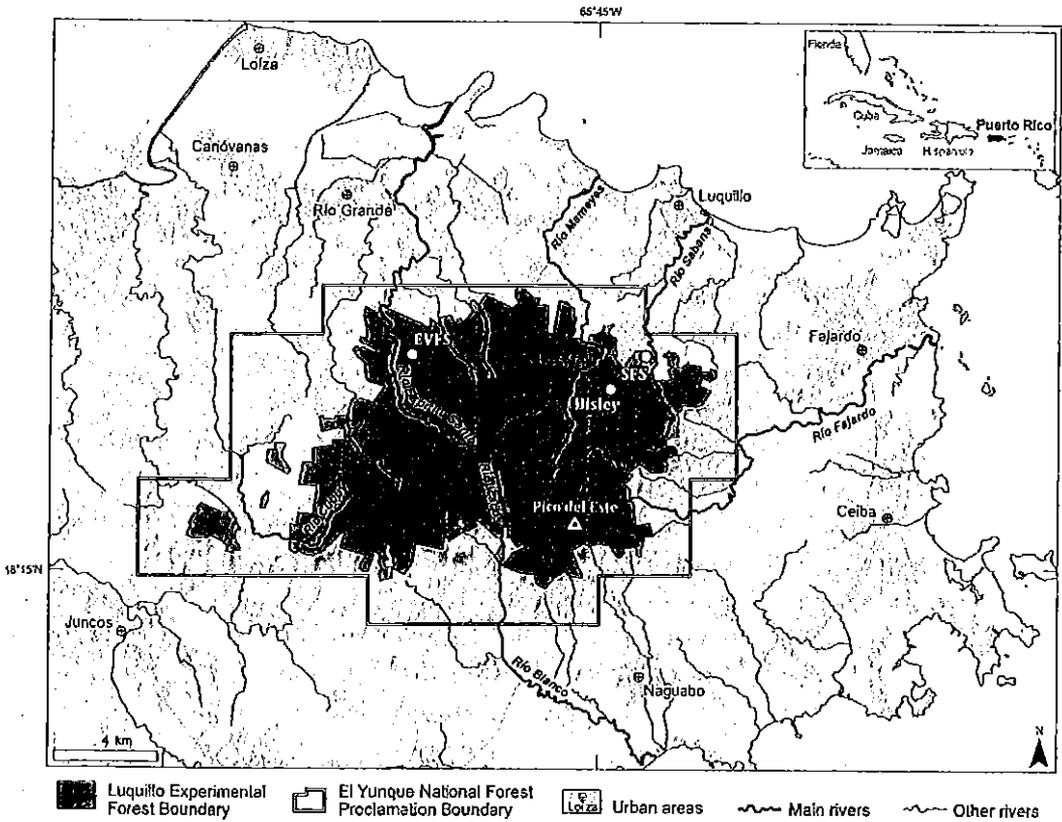


Figure 3.2 Map of northeastern Puerto Rico and the Luquillo Mountains. The dark gray area is the Luquillo Experimental Forest (coterminous with El Yunque National Forest), administered by the U.S. Forest Service. EVFS = El Verde Field Station; SFS = Sabana Field Station (U.S. Forest Service); Bisley = Bisley Experimental Watersheds. (Map by Olga Ramos.)

activity, as the most recent volcanic eruption occurred at least 30 mya (Seiders 1971). There is still, however, considerable seismic activity in the area. The largest earthquake in the past century (7.5 on the Richter scale) occurred in 1918 and originated in the Mona Passage (López-Venegas et al. 2008). This and a subsequent tsunami caused 116 deaths. Earthquakes of magnitude 3.0 or above are common in Puerto Rico.

### Local Geology

The island of Puerto Rico is a rugged mountain mass that has been described as a “heap of volcanic debris” (Hodge 1920; Mitchell 1954). The core of Puerto Rico is an east-west trending body that was formed in association with Cretaceous and Tertiary volcanoes. Tilted beds of clastic and carbonate sediments flank this volcanic core and form an apronlike structure that is progressively younger toward both the Caribbean and the Atlantic coasts. The Luquillo Mountains are the eastern terminus of the volcanic core of Puerto Rico and are the dominant geologic feature on the eastern end of the island. Geologically, they are best described as a tilted fault block dominated by northwest-trending faults and northeast-trending folds (Scatena 1989).

The Luquillo Mountains are underlain by volcanoclastic rocks, plutonic quartz diorite intrusions, and contact metamorphic rocks that were all derived from a similar andesitic magma during the Cretaceous and lower Tertiary, about 50 to 100 mya (Seiders 1971) (figure 3-3[B]). The source of the volcanoclastic sediments was an active volcanic complex that was standing at or near sea level. Debris from these volcanoes was deposited in moderately deep water after being transported and reworked by submarine slides, turbidity currents, ash flows, and ash falls. During this period of active volcanism in Puerto Rico, the Caribbean basin experienced a large meteor impact that defines the Cretaceous–Tertiary boundary and which has been implicated in massive regional and global extinctions (Hildebrand and Boynton 1990; Florentin et al. 1991).

Following the accumulation of volcanoclastic debris in the marine environment, late Eocene or early Oligocene tectonic activity about 30 to 40 mya uplifted this material. The subsequent intrusion of plutonic rock (the quartz-rich dioritic Rio Blanco complex) (figure 3-3[B]) marked the last phase of igneous activity in the area and caused the formation of contact metamorphic rocks when the hot igneous intrusion contacted the existing volcanoclastic rock. This contact metamorphism produced the erosion-resistant rocks that now underlie the major peaks of the Luquillo Mountains. This period of tectonic activity was followed by a period of stability until the middle Miocene, about 10 mya, when the Caribbean plate drifted eastward and the Greater and Lesser Antilles began to assume their present configuration. Since the end of the Eocene 34 mya, the regional tectonics of Puerto Rico and the Virgin Islands have been dominated by left-lateral slip between the North American and Caribbean plates (Masson and Scanlon 1991).

### ***Local Topography and Land Forms***

The Luquillo Mountains rise to an elevation of 1,074 m and are flanked by a coastal plain to the north, east, and south that is 8 to 16 km wide. Within the Luquillo Mountains, the rugged landscape has three major peaks (El Yunque Peak, East Peak, and El Toro Peak) and four main valleys that correspond to the four major rivers (the Espíritu Santo, the Mameyes, the Fajardo, and the Icacos/Blanco) (figure 3-2). Important research stations are located in several of these major watersheds, including the El Verde Field station in the Espíritu Santo, the Bisley Experimental Watersheds in the Mameyes, and the Sabana Field Station in to the Río Sabana watershed.

Hillslopes in the Luquillo Mountains are steep and form well-defined convex-concave catenas. Ridgetops are typically well-defined *cuchillo* or knife-like divides. Lower hillslope segments are generally concave where they pass into first-order valleys and straight where they join perennial channels. The major physical processes acting on these hillslopes include landslides, slope creep, debris flows, and tree throws (Scatena and Lugo 1995). These processes occur throughout the Luquillo Mountains, but their frequency, magnitude, and ecological significance vary with the bedrock geology, elevation, and forest type (Larsen and Torres Sánchez 1996; Larsen 1997).

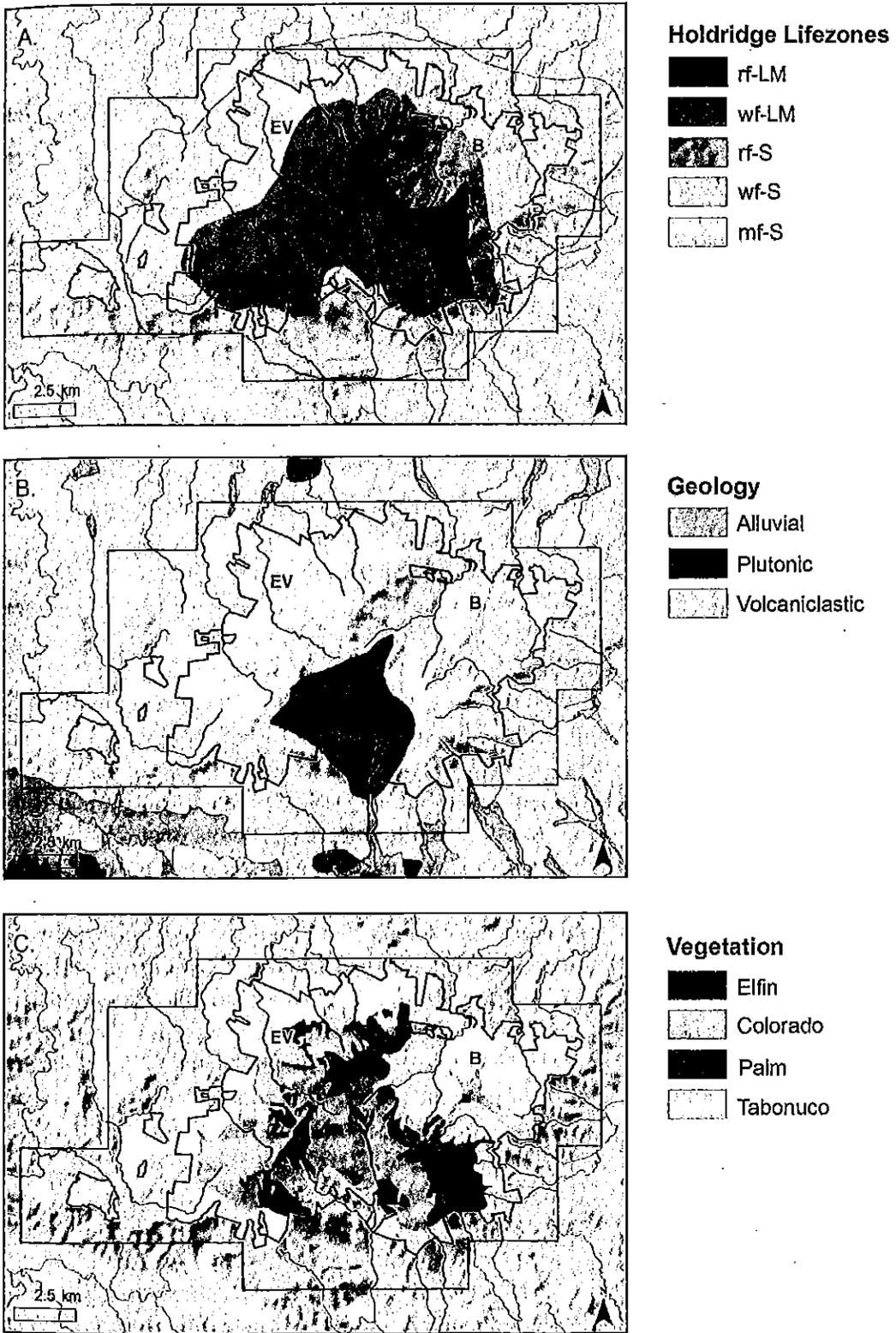


Figure 3.3 Life zones, geology, and vegetation of the Luquillo Mountains. (A) Holdridge Life Zones. rf-LM = lower montane rain forest; wf-LM = lower montane wet forest; rf-S = subtropical rain forest; wf-S = subtropical wet forest; mf-S = subtropical moist forest. (B) Surficial bedrock geology (see text). (C) Vegetation (see text). (Map by Olga Ramos.)

Bedrock under the Icacos Valley is quartz diorite, and volcanoclastic rocks underlie most of the Mameyes and Espiritu Santo valleys, where the Bisley Experimental Watersheds and El Verde Field Station are located (figure 3-3[B]). Bedrock underlying the Bisley Experimental Watersheds is mapped as the Fajardo formation (Briggs and Aquilar-Cortés 1980), whereas the El Verde Field Station research area is underlain by the Hato Puerco formation (Seiders 1971). The two formations have a similar chemistry and origin, but the Hato Puerco formation tends to produce larger boulders when weathered.

Weathering rates on the two bedrock types are rapid, resulting in large hydrologic exports of both dissolved and particulate matter to the sea (McDowell and Asbury 1994). Geochemical techniques suggest that the quartz diorite Río Blanco formation in the Icacos Valley is weathering at the rate of 0.58 cm per millennium, making it one of the fastest weathering granitic terrains that has ever been measured (White and Blum 1995; White et al. 1998). The rate of export of sediment from the Icacos basin is  $3,200 \text{ kg ha}^{-1} \text{ y}^{-1}$ , and silica ( $\text{SiO}_2$ ) loss occurs at a rate of  $487 \text{ kg ha}^{-1} \text{ y}^{-1}$  (McDowell and Asbury 1994). Work on the chemistry of tributaries to the Icacos suggests that a primary driver of this rapid weathering rate is the rapid physical denudation associated with landslides, which expose fresh mineral surfaces to weathering (Bhatt and McDowell 2007). Landslides occur frequently throughout the Luquillo Mountains, but they are largest and most common in higher-elevation areas where slopes are steep and in areas underlain by quartz diorite bedrock such as the Río Icacos valley (Larsen and Torres-Sanchez 1996). Weathering in the volcanoclastic terrain is also high, with sediment losses of 150 to  $330 \text{ kg ha}^{-1} \text{ y}^{-1}$  and  $\text{SiO}_2$  losses of 180 to  $400 \text{ kg ha}^{-1} \text{ y}^{-1}$  (McDowell and Asbury 1994). The Icacos and Espiritu Santo valleys are U.S. Geological Survey (USGS) Water, Energy, and Biogeochemical Budgets sites that focus on weathering rates (Peters et al. 2006).

The drainage network of the Luquillo Mountains consists of concave valleys and a dense network of intermittent, zero-order swales and gullies draining into first-order channels with steep gradients. Most channels are boulder- and bedrock-lined, with steep sides that tightly confine and structure them. Channels of the upper Icacos valley and some reaches of the Mameyes (Baño de Oro) are notable exceptions, as the quartz diorite bedrock (Río Blanco formation) of the Icacos valley weathers to produce large amounts of quartz sand and broad, sand-filled channels. Waterfalls are common throughout the Luquillo Mountains, and high falls (>3 m) represent an important barrier to the upstream passage of aquatic organisms (figure 3-4) (Covich et al. 2006, 2009; Kikkert et al. 2009; Hein et al. 2011).

## Biogeography

The Caribbean Basin is a biogeographically complex region, owing to its complex, and still uncertain, geologic history, described earlier in this chapter. About 100 mya, Puerto Rico and other islands of the proto-Antilles were part of an island arc (Donnelly 1992; Pindell and Kennan 2002) that might have served as a conduit for biotic interchange between North America and South America (Donnelly 1990; Hedges 2006). By the end of the Cretaceous, the island arc had moved 1,000 km to



Figure 3.4 A stream in the The Luquillo Mountains of Puerto Rico. Waterfalls such as this are barriers to the upstream passage of aquatic organisms. (Photograph by William McDowell.)

the northeast and could no longer have served as a conduit between North and South America (Graham 2003b). There were various periods of island emergence and submergence in the period between 50 and 100 mya, but the principal period of sustained emergence began with the compression of the Caribbean Plate against the Bahamas Platform in the middle Eocene, ~49 mya (Iturralde-Vinent and MacPhee 1999; Graham 2003b). The Antilles are only about 1 to 3 crater diameters away from the site of the bolide impact in the Yucatán that defines the Cretaceous–Tertiary boundary (65 mya) (Pindell 1994). The resulting impact waves were hundreds to thousands of meters in height (Maurrassee 1991) and are thought to have extinguished most life in the Caribbean at that time (Hedges et al. 1994; Hedges 2006).

Detailed studies of the flora of Puerto Rico, although extensive, are confined principally to the 20th century. Because the ecosystems of the island had been widely disturbed by at least four hundred years of active human intervention by the time of these studies (Figueroa Colón 1996), the composition of the original flora prior to human presence is not well known. The most recent assessment suggests that a large fraction of species (672 of 3,032) are naturalized or of uncertain origin. Ten percent of the original flora of the island is now extinct, and 38 percent is critically imperiled (Gann and Bradley 2006). Approximately 10 percent of the flora consists of endemics (Liogier and Martorell 1982). Within the remaining areas of native forest, the Luquillo Mountains represent an area of high species richness and endemism, with at least 830 plant species and more than 250 tree species. Nearly

half of all of the endemic trees of Puerto Rico (67 of 139) are found in the Luquillo Mountains (Figuerola Colón 1996). A significant number of nonendemic species found in the Luquillo Mountains are endemic to the West Indies, and the remaining trees are widespread in Central and South America. In addition to native species, a large number of species have been introduced. The most significant introductions to the Luquillo Mountains are described later in this chapter ("Effects of Recent Invasions") and in chapter 6.

Puerto Rico's Luquillo Mountains contain fewer tree species than other well-studied tropical sites that bracket the Puerto Rican site in elevation and rainfall (table 3-1). In addition to insularity, many other factors such as life zone, age of the flora, climate, habitat heterogeneity, and disturbance regime can contribute to species richness (Whitmore 1974; Lugo 1987; Lugo et al. 2002). Thus, it is difficult to ascribe these differences in tree species richness among tropical sites to any single causative factor.

In studies of orchid biogeography, Ackerman et al. (2007) found that area (for islands  $> 750 \text{ km}^2$  in size) and maximum elevation were good predictors of species diversity and endemism in the West Indies. This pattern was primarily driven by the effect of elevation on montane islands, as the species richness of low islands was not associated with land area. Orchid species richness apparently results from an interaction between area and topographic (habitat) diversity (Ackerman et al. 2007). The majority of the 728 species of orchid had a high vagility of seed dispersal, and their occurrence was primarily determined by habitat characteristics (Trejo-Torres and Ackerman 2001). However, the occurrence of 300 single-island endemics, nearly all on high islands, indicates very limited seed dispersal in these species (Ackerman et al. 2007).

Biogeographic patterns in some families of fungi most closely resemble those of the orchid island endemics studied by Ackerman et al. (2007). Two families of agaric (mushroom) fungi that grow primarily on soil, the Hygrophoraceae and Entolomataceae, were analyzed for biogeographic patterns in the Caribbean Basin (Baroni et al. 1997; Lodge et al. 2002). Species in these families were most abundant in moist and wet habitats and were thus most abundant and diverse on high-elevation islands in the Caribbean. One-third to one-half of the species of Hygrophoraceae and Entolomataceae in the Greater Antilles do not occur in the Lesser Antilles (Lodge et al. 2002). Some Greater Antillean species (or their closest relatives) do occur in South or North America, and a few are found in Africa, but pantropical species are very rare (Baroni et al. 1997; Lodge et al. 2002). Long-distance spore dispersal followed by successful colonization appears to be limited in these two families of mushrooms, and speciation appears to be rapid (Lodge et al. 2002).

Compared to tropical mainland areas of similar size and habitat diversity, the biota of Puerto Rico is depauperate for many animal groups (Garrison and Willig 1996; Reagan 1996; Thomas and Kessler 1996), and currently there are no native mammals except bats (Anthony 1918; Reagan and Waide 1996). The islands of the West Indies, including Puerto Rico, lack many families characteristic of mainland avifaunas (Waide 1996). For example, the widespread and diverse avian families of motmots, jacamars, puffbirds, barbets, toucans, woodcreepers, ovenbirds, and manakins are absent from the West Indies. The absence of these groups coupled

Table 3.1 Environmental and stand data for trees  $\geq 10$  cm dbh in various tropical forest plots with environmental characteristics that span the range of environmental conditions found at the LFDP at El Verde in the Luquillo Mountains

| Location                             | Area (ha) | Latitude (°N) | Elevation (masl) | Temperature (°C) | Rain (mm y <sup>-1</sup> ) | Trees (stems ha <sup>-1</sup> ) | Basal area (m <sup>2</sup> ha <sup>-1</sup> ) | Species (no. ha <sup>-1</sup> ) | Spp. stem <sup>-1</sup> | $\alpha$ | Reference             |
|--------------------------------------|-----------|---------------|------------------|------------------|----------------------------|---------------------------------|---|---------------------------------|-------------------------|----------|-----------------------|
| <b>CTFS plots</b>                    |           |               |                  |                  |                            |                                 |   |                                 |                         |          |                       |
| LFDP, subtropical wet                | 16        | 18            | 381              | 22.8             | 3500                       | 876                             | 34.3  | 42                              | 0.048                   | 9        | Thompson et al. 2004  |
| Thailand, Doi Inthanon               | 15        | 18            | 1700             | 20.9             | 1908                       | 519                             | 36.1  | 67                              | 0.129                   | 21       | Kanzaki et al. 2004   |
| Philippines, Palanan                 | 16        | 17            | 113              | 26.1             | 5000                       | 537                             | 36.1  | 100                             | 0.186                   | 37       | Co et al. 2004        |
| Panama, Barro Colorado Island        | 50        | 9             | 140              | 26.9             | 2551                       | 429                             | 27.8  | 91                              | 0.212                   | 36       | Leigh et al. 2004     |
| Colombia, La Planada                 | 25        | 1             | 1840             | 18.3             | 4087                       | 586                             | 23.8  | 88                              | 0.150                   | 29       | Vallejo et al. 2004   |
| Ecuador, Yasuní                      | 25        | 0             | 230              | 28.4             | 3081                       | 702                             | 27.3  | 251                             | 0.358                   | 142      | Valencia et al. 2004  |
| <b>One-hectare plots</b>             |           |               |                  |                  |                            |                                 |   |                                 |                         |          |                       |
| Puerto Rico, Bisley, subtropical wet | 1         | 18            | 301              | -                | 3500                       | 434                             | 28.2  | 33                              | 0.076                   | -        | Dallmeier et al. 1998 |
| Mexico, Los Tuxtlas, Veracruz        | 1         | 18            | 150              | 24.6             | 4639                       | 348                             | 34.9  | 76                              | 0.218                   | -        | Bongers et al. 1987   |
| Belize, Bladen, subtropical wet      | 1         | 16            | 45               | 26.7             | 2490                       | 358                             | 31.5  | 89                              | 0.249                   | 38       | Brewer and Webb 2002  |
| <b>Other plots</b>                   |           |               |                  |                  |                            |                                 |   |                                 |                         |          |                       |
| Puerto Rico, subtropical wet         | 0.81      | 18            | c. 380           | c. 22.8          | -                          | 936                             | 39.7  | 45                              | 0.048                   | -        | Wadsworth 1987        |
| Costa Rica, premontane wet           | 0.80      | c. 10         | -                | -                | -                          | 528                             | 33.2  | 42                              | 0.080                   | -        | Wadsworth 1987        |

CTFS = Center for Tropical Forest Science, a network of large tropical forest study plots (Condit 1995). The Holdridge Life Zone is given to facilitate comparison of the LFDP with other Neotropical sites and is included in the location description. Holdridge life zone determinations for Puerto Rican sites are from Ewel and Whitmore (1973); those for Costa Rica are from Wadsworth (1987), and those for Belize are from Hartshorn et al. (1984). The low density of stems  $\geq 10$  cm dbh at Los Tuxtlas, Mexico, and Bladen, Belize, is partly due to the heavy understory dominance of 5 to 8 cm dbh palms (*Astrocaryum mexicanum*). The Palanan site, in the Philippines, is on a continental (formerly part of the mainland) island and is damaged by strong storms (winds speeds  $> 100$  km h<sup>-1</sup>) about every 10 years (Co et al. 2004). Stem and species data in the Puerto Rican and Costa Rican sites described by Wadsworth (1987), and calculated per hectare, are means of two c. 0.4 ha plots at each site.  $\alpha$  is Fisher's  $\alpha$ , which measures species diversity independently of sample size (Condit et al. 1998). Temperature is mean annual.

with the high frequency of natural disturbance in the West Indies promotes the occurrence of a high proportion of habitat generalists in West Indian avifaunas (Waide 1996).

The depauperate nature of the fauna found in Puerto Rico might be in part a consequence of typical island-biogeographic processes related to the size of the island and its distance from pools of colonists. Even compared to other islands in the Greater Antilles, however, Puerto Rico's animal species richness is well below the equilibrium level predicted by its area (MacArthur and Wilson 1967), at least for some taxa such as the bats (Griffiths and Klingener 1988). This is thought to result from Puerto Rico's long isolation from other larger islands and the continents (Hedges 2006), as well as the combined effects of frequent and widespread natural and human disturbances, which likely have extirpated species throughout the Caribbean (Turvey et al. 2007). The effects of disturbance might be especially important in Puerto Rico, which is the only island in the Greater Antilles to have lost all of its native land mammals (six), with some losses occurring following Amerindian or European colonization (Turvey et al. 2007). The concept of "equilibrium" numbers of species as embodied in the MacArthur and Wilson (1967) paradigm is thus difficult to apply to the biota of Puerto Rico (Lazell 2005; Covich 2006).

## Climate

### *Caribbean Paleoclimate and Long-Term Trends*

The climate of the Caribbean is warm, has slight but highly predictable seasonal temperature variations, and is subject to a variety of atmospheric systems that influence levels of precipitation. Paleoclimatic data suggest that Puerto Rico's climate, and that of most of the Caribbean, has been relatively stable for many millions of years compared to those of temperate and boreal regions. Studies of flora preserved in sediments from the Oligocene (34 to 24 mya) indicate that in coastal and upland sites, Puerto Rico had a range of tropical to subtropical plant communities similar to those of today (Graham and Jarzen 1969). Of the 44 genera of plants identified by Graham and Jarzen (1969), 31 presently occur in Puerto Rico, 3 occur on other Caribbean islands, and 7 are found in ecologically comparable environments in Latin America. Only three of the genera found were temperate tree species that require a habitat that is not presently available on the island or in the immediate region, suggesting a relatively stable climate for the region over the past 20 million to 30 million years.

There is some evidence that the Caribbean is currently warmer and wetter than it was during the Pleistocene. In the Pleistocene, a permanent snowline might have existed between 2,300 and 2,600 meters above sea level (masl) in Hispaniola, and parts of the Caribbean were more arid than they are today (Schubert and Medina 1982; Schubert 1988). Data from corals in Barbados indicate that temperatures in shallow Caribbean waters were 4°C to 6°C lower during Pleistocene glacial advances to the north (Guilderson et al. 1994). Climatic reconstruction from records of oxygen isotopes in Yucatán (Covich and Stuiver 1974) and Haitian lake sediments

(Hodell et al. 1991) suggests that relatively dry conditions occurred during the early Holocene. This was followed by a wetter mid-Holocene and a return to drier conditions during the late Holocene, several thousand years ago.

Climatic reconstruction in Puerto Rico from flood plain sediments in the coastal plain of the Río Fajardo suggests that the climate of the Luquillo region was humid during the Pleistocene but has become progressively drier during the Holocene (Mellon 2000). Although widespread fires are indicated in the stratigraphy of Holocene charcoal from Laguna Tortuguero on the north-central coast of Puerto Rico, they probably correspond to a peak of human activity around 5,300 years ago, and not to dramatic shifts in climate (Burney and Burney 1994). The Puerto Rican climate has thus been relatively unchanged since the geologic development of the island 30 mya and has not undergone the large shifts from glaciated to unglaciated conditions seen in many other regions.

Climatic data collected over the past 100 years suggest that the region is currently undergoing a period of minor drying and warming. A detailed study of precipitation trends at 24 stations throughout Puerto Rico from 1931 to 1966 shows a statistically significant decrease for most stations of  $-0.6$  to  $-2.3$  mm  $y^{-1}$  for the period of May–October (Bisselink 2003). In contrast, precipitation increased by  $0.3$  to  $1.7$  mm  $y^{-1}$  from November through April (see also chapter 4). The eight stations with the longest monitoring records (approximately one hundred years) all have negative trends in total annual precipitation, with decreases ranging between  $1.59$  and  $4.90$  mm  $y^{-1}$ . Furthermore, 1997, 1994, and 1991 were the second, third, and sixth driest years in the 20th century (Larsen 2000). These data suggest a trend of decreasing precipitation over most of Puerto Rico during the past century.

Regional temperatures have also changed over time in the Caribbean. In Cuban soils, changes in vertical temperature profiles indicate that climatic warming has increased surface temperatures at a rate of  $1.0^{\circ}\text{C}$  to  $1.2^{\circ}\text{C}$  per century over the past 200 to 300 years. In the past 100 to 200 years, deforestation has also contributed to the recorded increases in soil temperature (Cermak et al. 1992).

### *Large-Scale Climate Drivers*

Four major types of atmospheric systems affect the Luquillo Mountains: (1) intratropical systems; (2) extratropical frontal systems; (3) cyclonic systems; and (4) large scale, coupled ocean-atmospheric events (North Atlantic Oscillation [NAO], El Niño-Southern Oscillation [ENSO]). All of these systems can result in large-scale disturbances that generate significant rain and wind (see chapter 4). Neither monsoonal rains nor the Inter-Tropical Convergence Zone, however, affect the climate of the Luquillo Mountains.

Intratropical atmospheric systems are those that originate and generally remain within the tropics and include micro- and meso-scale convective systems and orographic rains. Owing to pronounced orographic effects, rainfall is unevenly distributed over Puerto Rico and ranges from less than  $1,000$  mm  $y^{-1}$  on the southwest (leeward) side of the island to  $1,400$  mm  $y^{-1}$  in the coastal plains on the northeastern (windward) side of the island, and up to  $5,000$  mm  $y^{-1}$  in the mountains (see

figure 2-4). These orographic effects on rainfall are largely responsible for the steep environmental gradients that occur in the Luquillo Mountains (García-Martínó et al. 1996). Environmental gradients in the Luquillo Mountains are discussed in detail later in this chapter.

Extratropical frontal systems, locally known as cold fronts, occur during the temperate zone winter and spring with the arrival of polar lows from the northeastern United States. Cyclonic systems (large masses of air that rotate about a low-pressure center) occur from May to November. When the closure of a cyclonic system is incomplete, it is known as a tropical wave; when it is complete, it is termed a tropical storm or a hurricane. During the peak months of cyclonic activity (June–September), an average of two tropical waves pass by the Luquillo Mountains weekly (van der Molen 2002). Rainfall intensities and wind regimes associated with different atmospheric systems are described in more detail in chapter 4.

Large-scale ocean-atmospheric systems like the NAO and the ENSO are a principal cause of global interannual climate variability and have been linked to ecological processes in other tropical forests (Scatena et al. 2005). Although ENSO events have been linked to an increase in hurricane activity in Puerto Rico (Donnelly and Woodruff 2007), the NAO, rather than the ENSO, has the strongest relationship to the Puerto Rican climate (Malmgren et al. 1998). The NAO index is the normalized sea level difference in barometric pressure between the Azores and Iceland. It is significantly related to variations in annual rainfall in Puerto Rico; during years with a high northern winter NAO index, precipitation is generally lower than average. Annual rainfall in the Luquillo Mountains is only weakly correlated with either NAO or ENSO indices (Schaefer 2003), but Greenland (1999) did find a correlation between ENSO events and temperature in the Luquillo Mountains.

### *Climate of the Luquillo Mountains*

The Luquillo Mountains have a humid tropical maritime climate. Water enters the ecosystem as rain and cloud drip, and on rare occasions as hail; snow and frost have never been recorded in the Luquillo Mountains. There is no pronounced dry season as found in monsoonal climates. The regular and predictable seasonal droughts (<50 mm monthly precipitation) or dry periods (<100 mm monthly precipitation) that are found in other tropical sites such as those in Barro Colorado Island, Panama (Zimmerman et al. 2007), or in a variety of Asian forests (Richards 1996) do not occur in the Luquillo Mountains. Episodic drought and rainy periods do occur throughout the year in the Luquillo Mountains, however.

The amount of rainfall increases with elevation, but during a 2-year study it showed similar patterns throughout the year at low, middle, and high elevations (figure 3-5). Long-term records from a mid-elevation site (El Verde Field Station, 365 masl; figure 3-2) show little seasonal variation over a 30-year record (figure 3-6). The highest rainfall tends to occur in May or September through December, but any month can be very wet (over 400 mm) or relatively dry (below 125 mm; figure 3-6). No month averages below 200 mm of precipitation. In general, more rain falls during the day than during the night (in terms of the total precipitation depth), but the frequency of

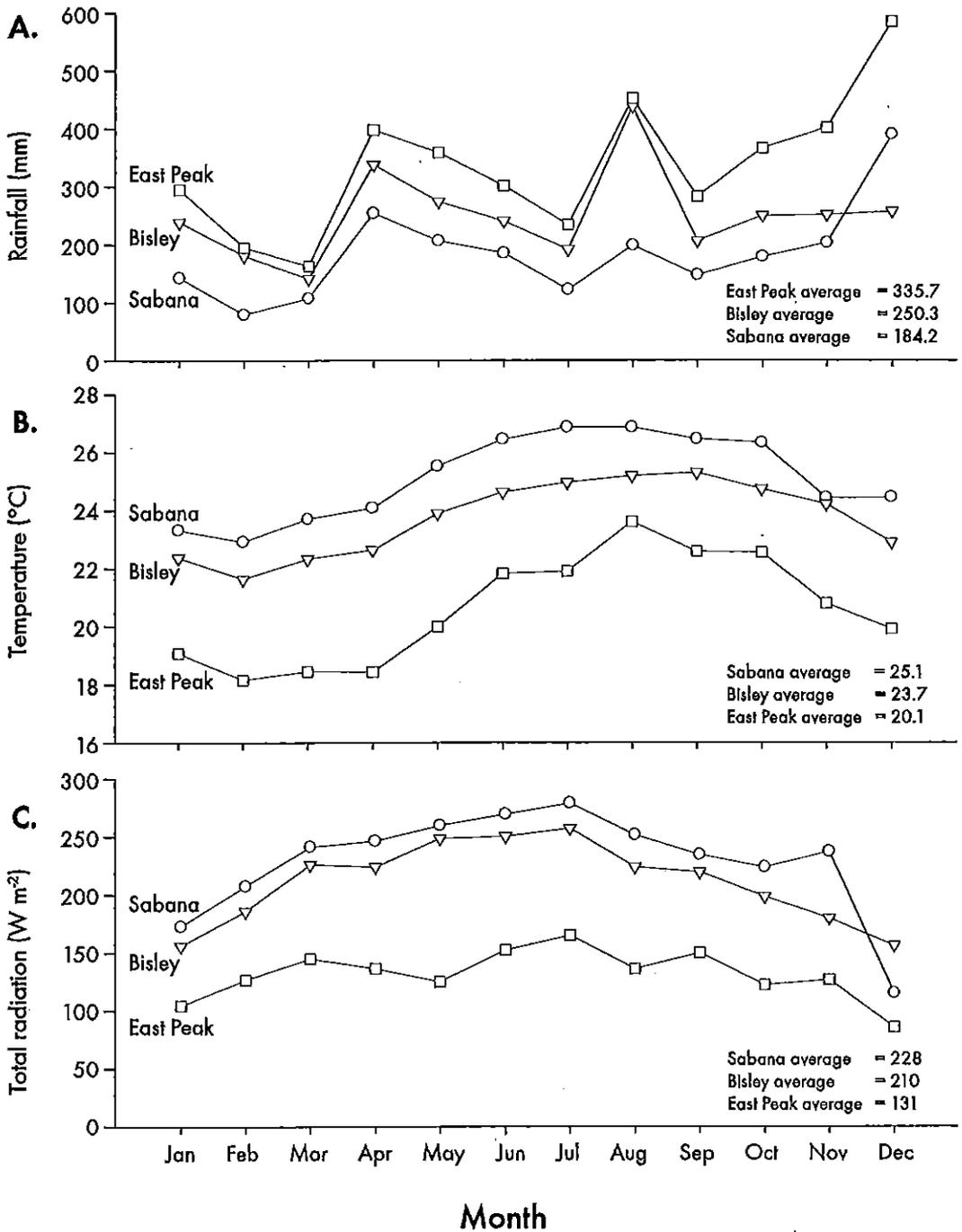


Figure 3.5 Variation in climatic conditions from 2000 to 2002 at three sites spanning the elevation gradient in the Luquillo Mountains: Sabana Field Station (100 masl), Bisley Experimental Watersheds (359 masl), and East Peak (Pico del Este) (1051 masl). (A) Average monthly precipitation (mm). (B) Average hourly air temperature by month (°C). (C) Average monthly total radiation (W m<sup>-2</sup>).

rainfall events is highest at night and in the early morning (Schellekens et al. 1999). This pattern reflects the occurrence of smaller, low-intensity events at night and in the early morning, and larger events during the day.

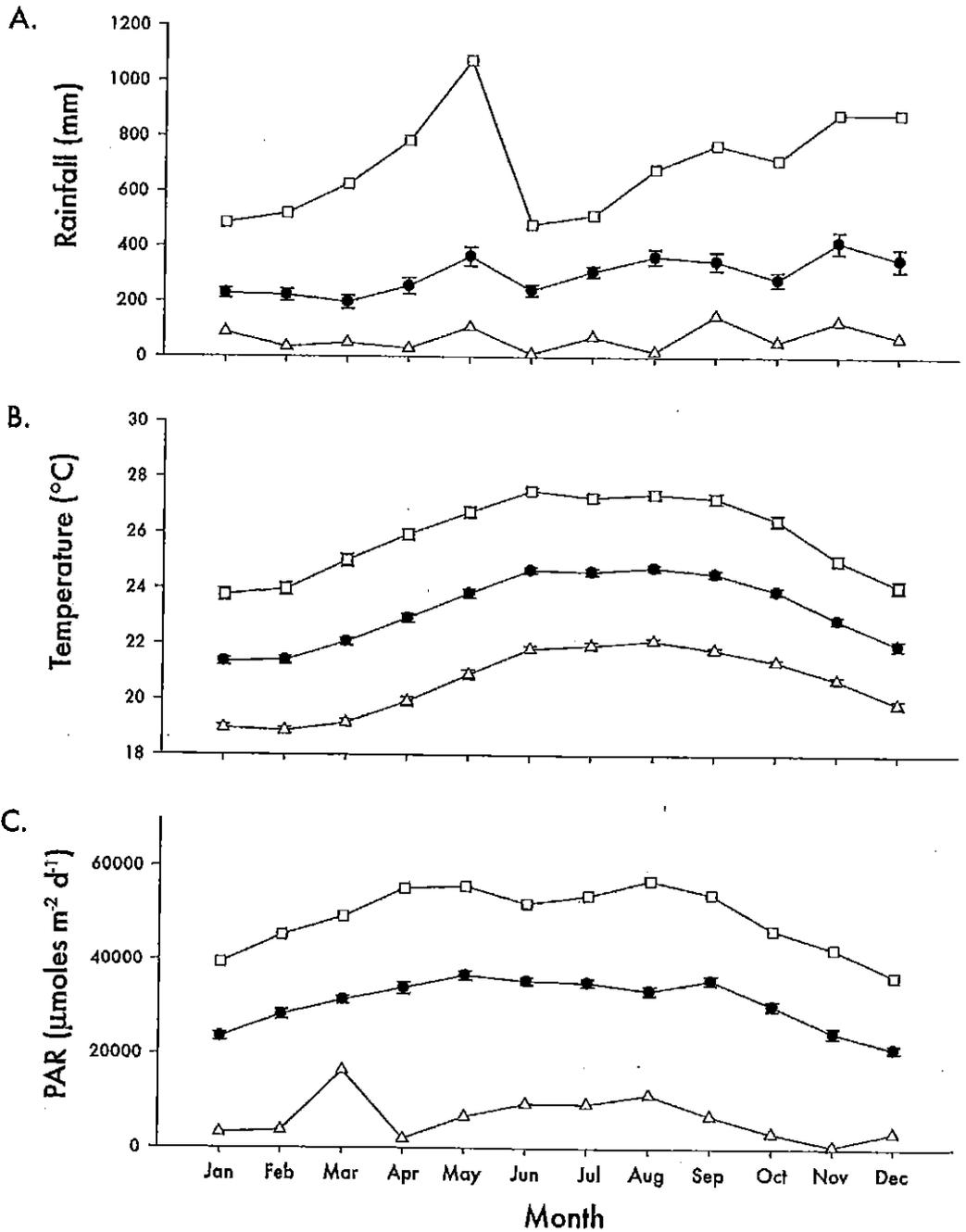


Figure 3.6 Long-term seasonal variation in climatic conditions at the El Verde Field Station in the Luquillo Mountains (350 masl). (A) Monthly precipitation in 1975–2004 (● = mean  $\pm$  SEM; □ = maximum for 1975–2004; △ = minimum for 1975–2004). (B) Mean daily air temperature ( $\pm$  SEM) by month in 1975–2004 (● = monthly mean; □ = hottest day of the month; △ = coolest day of the month). (C) Monthly photosynthetically available radiation (PAR =  $\mu\text{mol m}^{-2} \text{day}^{-1}$ ) at canopy level at the El Verde Field Station (350 masl). ● = mean daily values  $\pm$  SEM; □ = maximum light level recorded during a day, by month (mean  $\pm$  SEM); △ = minimum light level recorded during a day, by month (mean  $\pm$  SEM), in 2000–2004.

Daily average air temperatures at all elevations in the Luquillo Mountains show small (3°C to 4°C) but highly predictable seasonal patterns, with the highest temperatures in June–July and the lowest temperatures in January (figures 3-5 and 3-6). The average annual air temperature varies with location and elevation in the Luquillo Mountains, with a difference of about 5°C between the temperature measured at the base of the mountains at Sabana Field Station (100 masl) and that at the weather station on East Peak (1,051 masl). Similar results were reported earlier by Briscoe (1966). Over the course of an average day, the temperature changes by 5°C at the base of the mountain but by only about 1°C at East Peak (figure 3-7), which is almost constantly bathed in cloud and fog. Humidity is high throughout the year in the Luquillo Mountains, with monthly minima (65 to 70 percent) and maxima (95 percent) showing no strong seasonal patterns (figure 3-8). Changes in the relative humidity over the course of a day strongly mirror changes in the air temperature at all elevations in the Luquillo Mountains, with humidity decreasing as air temperatures increase (figure 3-7). Windspeed is constant throughout the year, at about 1.3 m s<sup>-1</sup> at the El Verde Field Station and 1.2 m s<sup>-1</sup> at the Bisley Experimental Watersheds (figure 3-9). The average daily maximum wind speed is 6.4 m s<sup>-1</sup> at the Bisley Experimental Watersheds and shows no seasonal patterns (figure 3-9). The average monthly total radiation shows strong seasonal patterns at lower elevations in the Luquillo Mountains, peaking in July, but seasonal patterns are much less distinct and the average total radiation is about 40 percent lower at East Peak than at lower elevations (figure 3-5). Photosynthetically active radiation (PAR) shows broad maxima during the period from June to August and has its lowest values in January (figure 3-6). Meteorological data for the Bisley Experimental Watersheds are available online from USGS National Weather Information Service Meteorological Station 50065549. Additional summary data on the climate of the Luquillo Mountains can be found at <http://luq.lternet.edu/data/lterdb90/metadata/BisleyTowergraphs-Rad.htm> for the Bisley Experimental Watersheds, and raw data files can be found for data throughout the Luquillo Mountains at <http://luq.lternet.edu/data/databasesbycategory.html#Meteorology>.

### *Climatic Gradients*

Rainfall, humidity, wind, and cloudiness all tend to increase with elevation, whereas irradiance, air temperature, and soil temperature decrease (figures 3-5 and 3-7) (Briscoe 1966; Brown et al. 1983; García-Martínó et al. 1996). Rainfall shows a particularly strong pattern with elevation (figure 3-10). Taken together, these climatic variables all contribute to the decreased evapotranspiration and higher runoff observed at higher elevations (García-Martínó et al. 1996). The highest elevations of the Luquillo Mountains are covered in clouds for weeks at a time, resulting in significant interception of cloud moisture. Cloud cover is estimated to occur at least 75 percent of the time at East Peak, with an average cloud water deposition of 1 to 4 mm day<sup>-1</sup>, which is higher than the deposition at most other sites globally where significant cloud inputs occur (Asbury et al. 1994; Eugster et al. 2006; Holwerda et al. 2006). Because rainfall is also very high at East Peak (15 to 30 mm day<sup>-1</sup>), however, cloud water inputs represent a small part of the total hydrologic input.

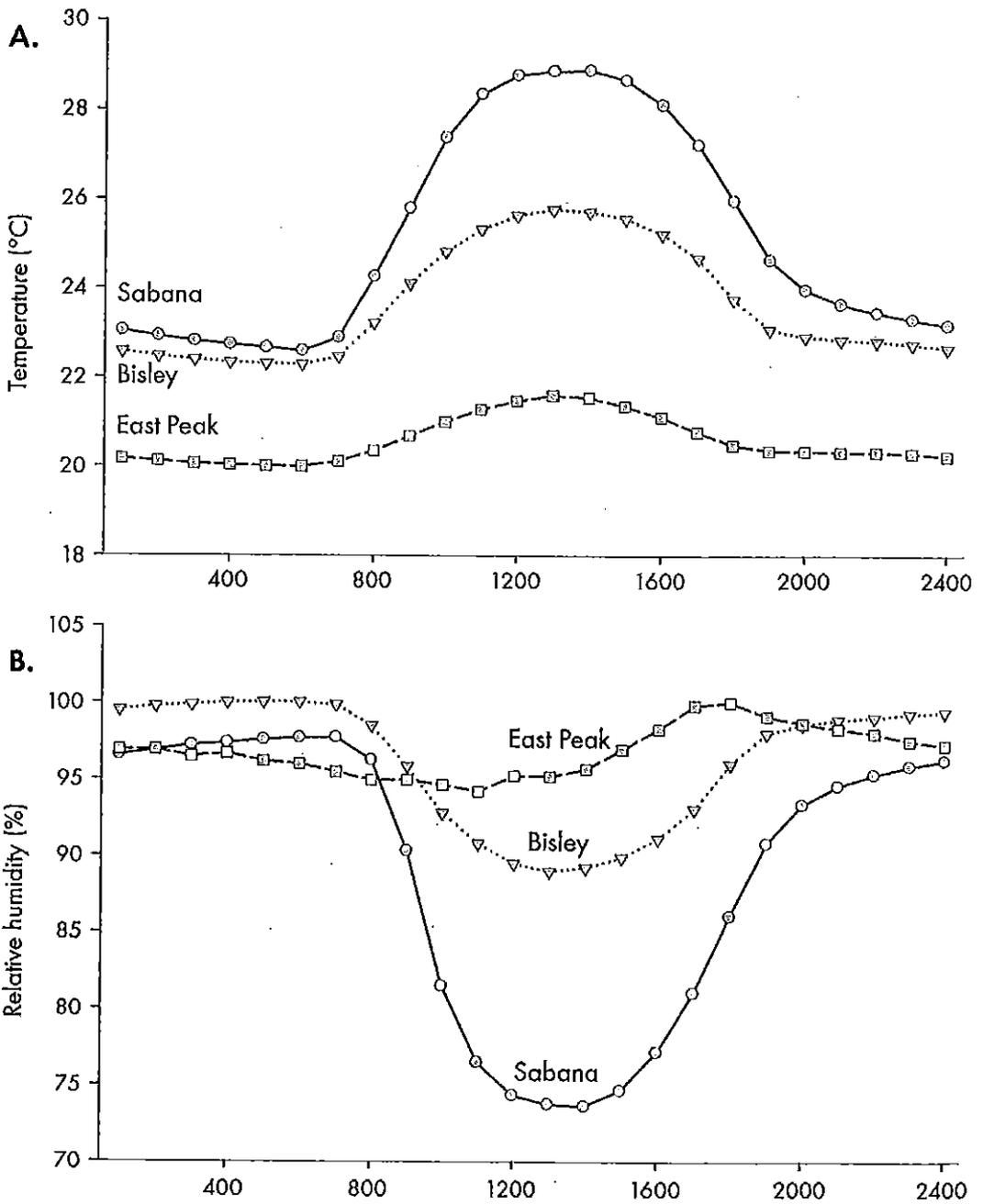


Figure 3.7 (A) Diel variation in mean hourly temperature (°C) and (B) relative humidity (percent) during 2000–2002 at three sites spanning the elevation gradient in the Luquillo Mountains: Sabana Field Station (100 masl), Bisley Experimental Watersheds (359 masl), and East Peak (1051 masl).

Local geographic position is particularly important in determining environmental conditions in the Luquillo Mountains, owing to the strong and steady trade winds. Seasonal patterns in rainfall, for example, vary spatially. The Luquillo summit casts a moderate rain shadow on its downwind flank, and the location of this shadow varies seasonally with the prevailing wind direction. Rainfall at the

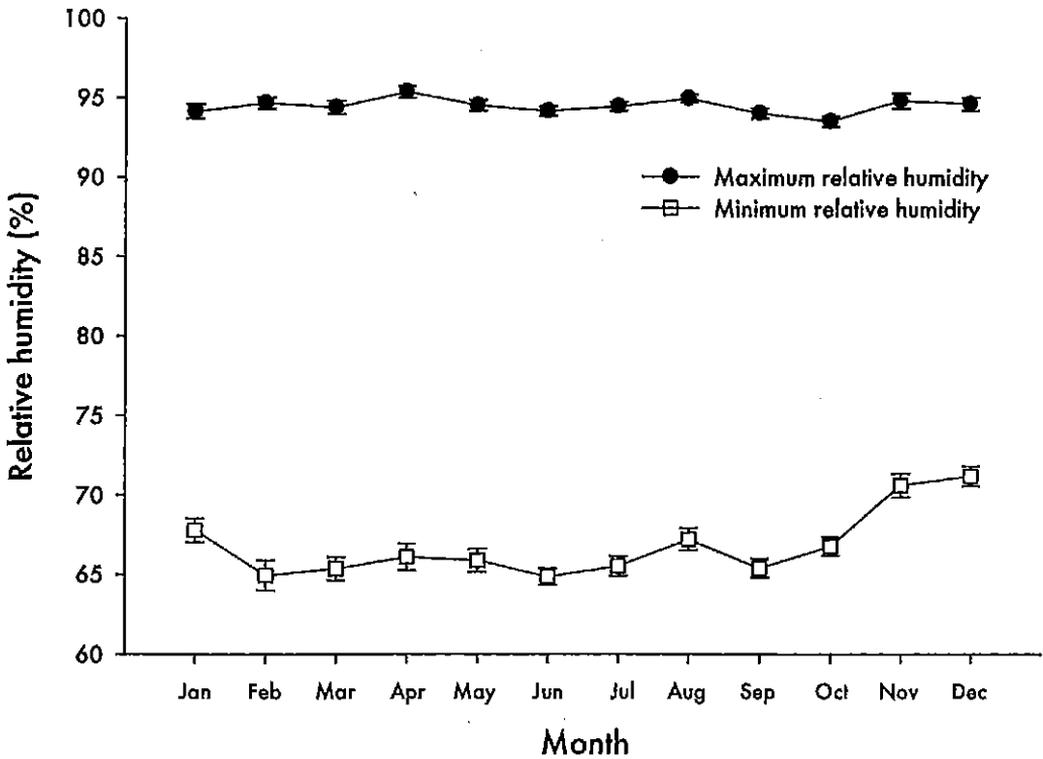


Figure 3.8 Variation in relative humidity by month during 2000–2004 at the El Verde Field Station (350 masl). □ = mean daily maximum humidity ± SEM; △ = mean daily minimum relative humidity ± SEM.

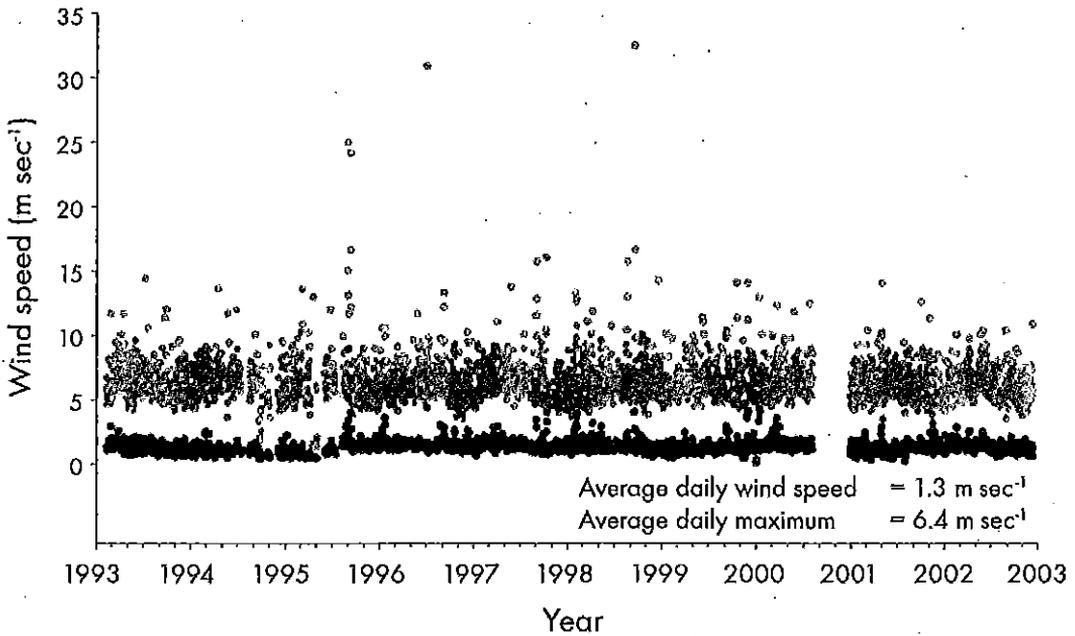


Figure 3.9 Long-term variation in wind velocity (m s<sup>-1</sup>) at the Bisley Experimental Watersheds (359 masl) for the period of 1993–2002. ● = daily average wind velocity; ○ = daily maximum wind velocity. For the period of record, the mean daily wind velocity averaged 1.3 m s<sup>-1</sup>, and the daily maximum wind velocity averaged 6.4 m s<sup>-1</sup>.

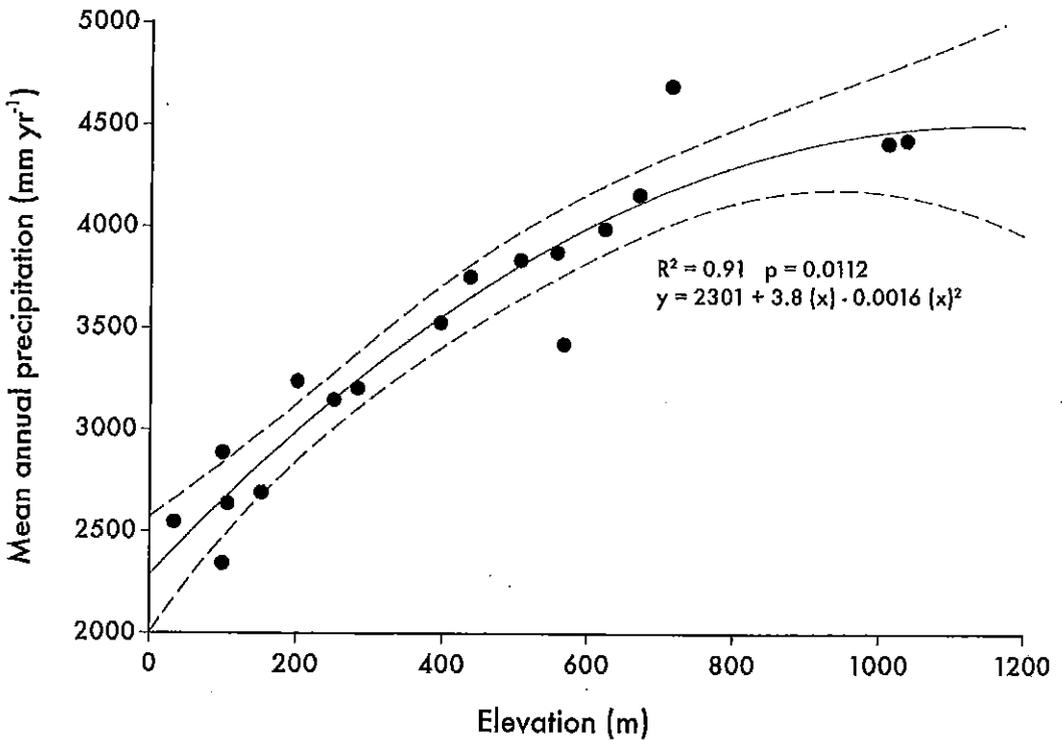


Figure 3.10 Variation in annual precipitation with elevation in the Luquillo Mountains. Redrawn from data presented in García-Martínó et al. (1996).

Bisley Experimental Watersheds and the El Verde Field Station, which are at similar elevations, is comparable throughout much of the year but is up to 30 percent lower at El Verde in May and June (Heartsill-Scalley et al. 2007). Wang et al. (2003) modeled the spatial and temporal variability of air temperature, solar insolation, rainfall, and transpiration (see figure 2.8) within the Luquillo Mountains. Their results show a complex pattern of spatial variability in climatic variables. The combined effects of elevation and geographic position on rainfall and temperature result in five different subtropical Holdridge life zones in the Luquillo Mountains: moist forest, wet forest, lower montane wet forest, lower montane rain forest, and rain forest (figure 3-3) (Ewel and Whitmore 1973).

## Nutrient Cycling

### *Atmospheric Inputs*

In the Luquillo Mountains, the biogeochemical cycles of most elements are driven by high rainfall, rapid river runoff, and the proximity of the mountains to the sea. Rains are intense and frequent, averaging three showers daily, and they bring large amounts of sea salt aerosols with them. Marine aerosols are the source of nearly all the sodium, chloride, magnesium, and potassium in rain (McDowell et al. 1990), and because of this, inputs of sodium are much higher than those typically seen in

other humid tropical forests (figure 3-11). Calcium (Ca), nitrogen (N), and phosphorus (P) in rain come from predominantly nonmarine sources. For calcium, dust from the Sahara is a likely source of non-sea salt inputs (McDowell et al. 1990; Heartsill-Scalley et al. 2007). Because rain chemistry changes relatively little with elevation, the wet deposition of various elements is proportional to the increases in rainfall with elevation (Asbury et al. 1994). Cloud deposition also adds to nutrient deposition at high elevations (Asbury et al. 1994).

Saharan dust is a common occurrence throughout the Caribbean (Prospero and Nees 1986; Shinn et al. 2000; Muhs et al. 2007). It is found most often from June to August, when it can cause atmospheric haze, is readily visible as orange particles in rain collectors, and is the subject of local newspaper articles because of its nuisance value for residents of Puerto Rico. Dust inputs to the Caribbean coincide with North African droughts and are correlated with the NAO (Moulin et al. 1997). Beyond the effects of Saharan dust on soluble Ca concentrations in rainfall, little is known of its ecological significance in Puerto Rico, although recent work suggests that it might be a significant source of P to watersheds of the Luquillo Mountains (Pett-Ridge 2009). Evidence from the Hawaiian Islands, where dust from Asian deserts is important, suggests that atmospherically transported dust can be a major

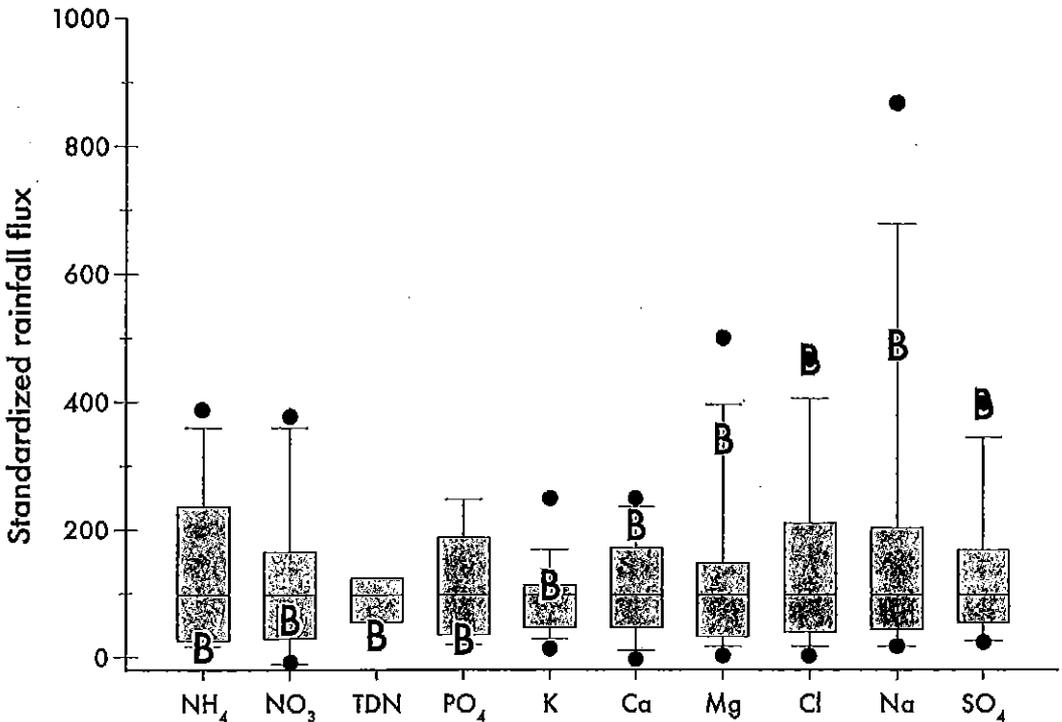


Figure 3.11 Box plots of standardized values for input of ammonium, nitrate, phosphate, potassium, calcium, magnesium, chloride, sodium, and sulfate (NH<sub>4</sub>, NO<sub>3</sub>, PO<sub>4</sub>, K, Ca, Mg, Cl, Na, and SO<sub>4</sub>) in rainfall at the Bisley Experimental Watersheds (B) compared to other humid tropical forests. Standardization is done by expressing the values from each site as a percentage of the median for all sites. Sample size ranges from 7 to 23, with most being at least 14. Box shows 25th through 75th percentiles; error bars show 10th and 90th percentiles; solid circles are outliers. Adapted and redrawn from Scatena (1998).

source of elements such as Ca and P in highly weathered landscapes (Chadwick et al. 1999). On some Caribbean islands (Barbados and the Florida Keys), Saharan dust plays an important role in soil formation (Muhs et al. 2007), but its significance for elemental cycles in the Luquillo Mountains is not as well understood. Atmospheric deposition can be a critical source of growth-limiting nutrients for the reestablishment of vegetation following disturbance. Zarin and Johnson (1995) found that rainfall inputs were sufficient to provide nearly all of the Ca required for the growth of vegetation on landslide scars in the Luquillo Mountains, and that they provided significant quantities of other nutrients needed for regrowth.

With regard to elements not found in significant quantities in sea salt (e.g., N, P, and potassium [K]), the chemistry of rain in the Luquillo Mountains is relatively dilute, making the overall deposition rates of these elements modest and at or below levels recorded at other tropical sites (figure 3-11). The rates of inorganic N deposition are typical of those found throughout rural Central and South America (Sanhueza and Santana 1994). In comparison with rain from remote areas of the world, Puerto Rican rainfall was only slightly enriched in non-sea-salt sulfate and nitrate in the period from 1984 to 1987, indicating that there was little anthropogenic influence on the precipitation chemistry (McDowell et al. 1990). Since then, however, nitrate deposition in wet-only precipitation samples analyzed as part of the National Atmospheric Deposition Program has steadily increased (Ortiz-Zayas et al. 2006).

The sources of this increase in nitrate deposition are unknown. Urbanization has increased in all directions around the Luquillo Mountains, and this might be contributing to the observed increases in nitrate deposition. Increased volcanic activity since 1995 in the Soufrière Hills, Montserrat, has increased the deposition of total dissolved N, but not nitrate, in bulk precipitation collected at the Bisley Experimental Watersheds during periods of volcanic activity (Heartsill-Scalley et al. 2007). There are few anthropogenic pollution sources to the northeast of Puerto Rico, the direction from which the dominant trade winds originate. Because air masses from North America do reach the island, they might also be contributing to nitrate and sulfate inputs above global background levels (McDowell et al. 1990). Air masses from North America can reach Puerto Rico throughout the year, but most of the North American air reaching Puerto Rico arrives in early spring, when the rainfall pH is somewhat reduced, dropping from its typical pH of 5.5 to values around 5.0.

## ***Soils and Nutrient Pools***

### **Soil Characteristics**

Soils in the Luquillo Mountains are deep, highly weathered iron (Fe) and aluminum (Al) clay soils with nutrient concentrations that are typical for the tropics (Sánchez 1976; Silver et al. 1994). The surface organic layer, or forest floor, above the clayey soil is generally poorly developed or intermittent, so it represents a relatively minor pool of nutrients at most locations in the Luquillo Mountains. Nonetheless, most of the carbon flowing through the food web passes through the detrital system on the forest floor (Lodge 1996), where it is processed rapidly (Ostertag et al. 2003).

Soils of the Luquillo Mountains are primarily classified as Ultisols. Less commonly found, but present in small areas, are other soil orders (Oxisols, Entisols, and Inceptisols). Oxisols are mostly found in the well-drained upland areas in the tabonuco forest, whereas Inceptisols and Entisols are located in the drainage areas along streams and in the upper elevations near quartz diorite intrusions. Detailed descriptions of soils have been published by Silver et al. (1994, 1996), Scatena and Lugo (1995), the Soil Survey Staff (1995), and Cox et al. (2002). Ultisols of the Luquillo Mountains have a clay content that ranges from 35 percent to 88 percent; the average clay content is  $(52 \pm 5)$  percent (McGroddy and Silver 2000). Unlike the riparian Inceptisols of the Icacos basin, where clay concentrations (ranging from 49 percent to 15 percent) tend to decrease with depth, the Ultisols of the Bisley Experimental Watersheds have higher concentrations of clay (51 percent to 54 percent), and clay concentrations do not vary with depth (McDowell et al. 1992).

Soil carbon (C) concentrations are typically 2 percent to 4 percent in surface soils (0–10 cm) of the Luquillo Mountains, and they decline to less than 1 percent at depths of 35 to 60 cm. Soil N is typically found in concentrations of 0.1 percent to 0.4 percent in surface soils and declines to 0.1 percent or less at depth (Fox 1982; McDowell et al. 1992; Silver et al. 1994; Scatena and Lugo 1995). In the tabonuco forest, soil C and N concentrations can be as high as 7.6 percent and 0.67 percent, respectively, in surface soils (0–10 cm) and up to 4.1 percent and 0.29 percent in subsurface (10–25 cm) soils (Li 1998). Light-fraction C and N, which are thought to represent more biologically available material than the denser fractions, was measured as 2.9 and 0.17 mg g<sup>-1</sup>, respectively, in the surface soils studied by Li (1998). Light-fraction C shows large increases with elevation in the Luquillo Mountains and accounts for almost all C storage in soils above 900 m elevation (McGroddy and Silver 2000). The soil N concentration (averaging 0.31 percent in surface soils) is somewhat lower in the Bisley Experimental Watersheds than in soils found in other tropical montane sites (figure 3-12). Soil C is higher under decaying logs than elsewhere (Zalamea et al. 2007).

The amount of extractable phosphorus typically decreases sharply with depth in the soil profile (Silver et al. 1994). Soils from mid-elevation tabonuco forests have levels of potassium chloride-extractable P averaging  $(26 \pm 2)$  μg g<sup>-1</sup> in surface soils (0–10 cm), and these levels declined to 3 μg g<sup>-1</sup> at depths of 35 to 60 cm. In samples from colorado forests, at higher elevations, Frizano et al. (2002) found that concentrated hydrochloric acid extraction recovered 27 μg g<sup>-1</sup> P at both the surface and depths of 35 to 60 cm. They also examined a wide range of extractants and found very high variability in the patterns of extractable P with depth. Extractable nutrient cations from mid-elevation soils in the Bisley Experimental Watersheds average 0.42, 1.83, and 1.37 cmol kg<sup>-1</sup> for K<sup>+</sup>, Ca<sup>2+</sup>, and magnesium (Mg<sup>2+</sup>), respectively (Scatena and Lugo 1995) (table 3-2).

The soil chemistry shows strong variation with topographic position in tabonuco and colorado forests, but the patterns vary. In the volcanoclastic soils associated with tabonuco forests, organic matter and nitrogen levels are highest on the ridges and upper slopes, but in the colorado forest soils the pattern is reversed, with the highest C and N levels in riparian soils (tables 3-2 and 3-3). In both forest types, greater amounts of extractable Ca, Mg, and P are found in riparian than in upland

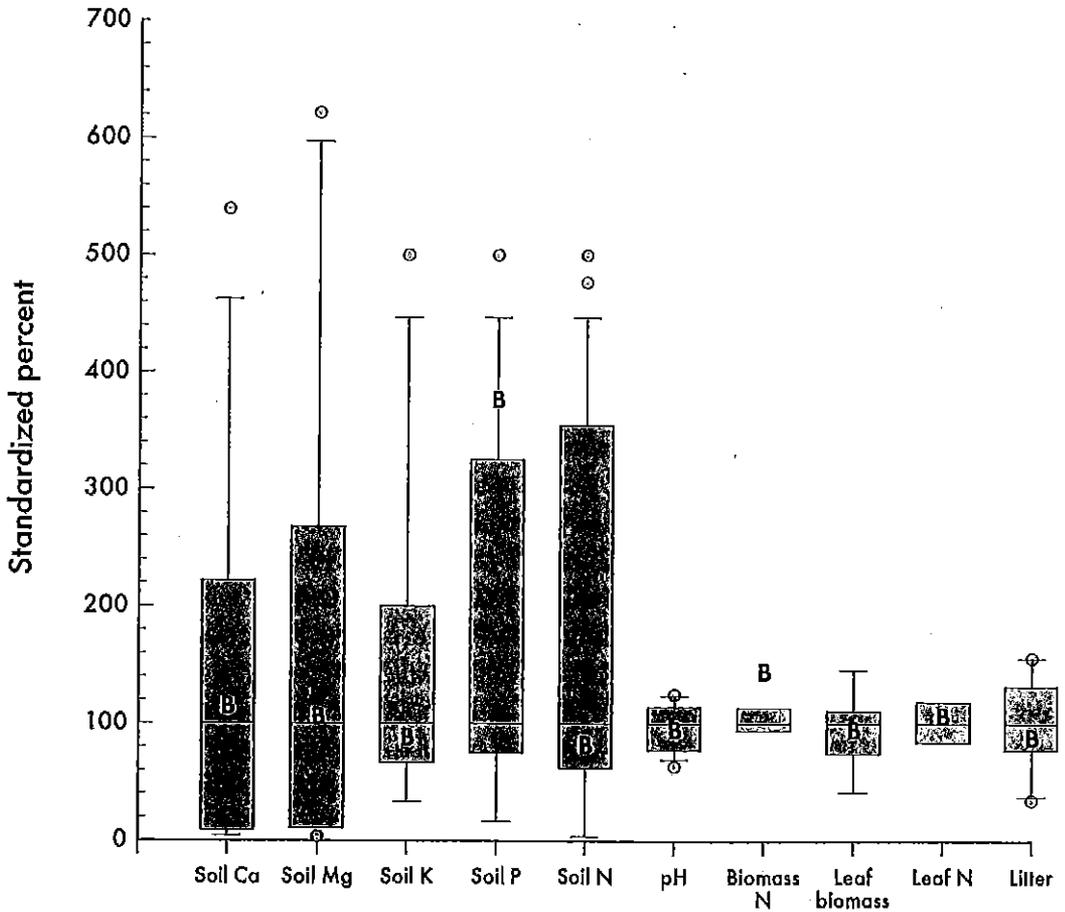


Figure 3.12 Box plots of soil chemistry, biomass, and chemistry of leaf and total biomass in the Bisley Experimental Watersheds (B) of the Luquillo Mountains compared to other humid tropical forests. Box plots show standardized percentage values for soil chemistry (Soil Ca, Mg, K, P, N, and pH), aboveground biomass nitrogen stock (Biomass N), leaf biomass, leaf nitrogen concentration (Leaf N), and litterfall (Litter). Standardization is done by expressing the values from each site as a percentage of the median for all sites. Sample size ranges from 7 to 23 tropical forest sites, with at least 14 sites for most parameters. Box shows 25th through 75th percentiles; error bars show 10th and 90th percentiles; solid circles are outliers. Adapted and redrawn from Scatena (1998).

soils (tables 3-2 and 3-3). Organic matter tends to accumulate on mid-elevation ridges and slopes dominated by *Dacryodes excelsa* (figure 3-13), a tree that produces thick surface root mats, but the exact mechanisms of soil carbon accumulation on ridges are not known. The higher organic matter content leads to greater exchangeable acidity and lower soil pH on ridges (4.8) as compared to riparian valleys (5.4) (table 3-2). High densities of basidiomycete litter mats on slopes contribute to the retention of leaf litter and the protection of surface soil from the erosive effects of rain and overland flow, thereby conserving soil carbon on slopes (Lodge and Asbury 1988; Lodge et al. 2008).

The patterns in soil chemical properties along the catena can be partially explained by redox processes and their effects on the amount and form of Fe in the

Table 3.2 Variation of soil chemistry (organic matter, nutrients, exchangeable cations, and pH) in the Bisley Experimental Watersheds by topographic position and for the entire watershed

| Group            | <i>n</i> | SOM                 | N                   | P               | K                | Ca              | Mg                    | Na              | Fe               | Mn               | pH             |
|------------------|----------|---------------------|---------------------|-----------------|------------------|-----------------|-----------------------|-----------------|------------------|------------------|----------------|
|                  |          | Mg ha <sup>-1</sup> | kg ha <sup>-1</sup> |                 |                  |                 | cmol kg <sup>-1</sup> |                 |                  |                  |                |
| Ridge            | 22       | 210a<br>(23)        | 9.0a<br>(0.7)       | 42.0a<br>(4.8)  | 0.39ab<br>(0.04) | 0.88a<br>(0.28) | 0.76a<br>(0.26)       | 0.31a<br>(0.03) | 4.74a<br>(0.76)  | 0.29a<br>(0.09)  | 4.8a<br>(0.1)  |
| Slope            | 40       | 163a<br>(11)        | 7.7a<br>(0.5)       | 39.8a<br>(3.8)  | 0.44a<br>(0.05)  | 1.56a<br>(0.40) | 1.51ab<br>(0.44)      | 0.29a<br>(0.03) | 2.83ab<br>(0.31) | 0.52ab<br>(0.09) | 5.0ab<br>(0.1) |
| Upland valley    | 12       | 143ab<br>(18)       | 7.0ab<br>(0.7)      | 47.1a<br>(5.6)  | 0.36b<br>(0.04)  | 3.18a<br>(1.93) | 1.93b<br>(0.75)       | 0.31a<br>(0.05) | 2.68b<br>(0.72)  | 0.97b<br>(0.16)  | 5.2bc<br>(0.1) |
| Riparian valley  | 9        | 131b<br>(9)         | 7.2b<br>(1)         | 71.7b<br>(10.3) | 0.48a<br>(0.04)  | 3.33b<br>(0.64) | 1.59b<br>(0.35)       | 0.24a<br>(0.47) | 2.65b<br>(0.4)   | 0.91ab<br>(0.2)  | 5.4c<br>(0.1)  |
| Entire watershed | 83       | 170<br>(9)          | 8.5<br>(0.3)        | 45.4<br>(2.7)   | 0.42<br>(0.03)   | 1.83<br>(0.37)  | 1.37<br>(0.24)        | 0.29<br>(0.02)  | 3.33<br>(0.3)    | 0.572<br>(0.06)  | 5<br>(0)       |

Modified from Scatena and Lugo 1995. Mean chemistry of surface soils (0 to 60 cm) for individual geomorphic settings (ridge, slope, upland valley, and riparian valley) is shown with the standard deviation on the line below. The estimation of the average nutrient standing stocks for the combined Bisley watersheds 1 and 2 is based on the frequency of each geomorphic setting within the combined watersheds. Sample *n* refers to the number of sites sampled within the watershed or the geomorphic setting. SOM = soil organic matter plus forest floor. For each column, means with the same letters are not different at the 0.05 level according to Duncan's multiple range test.

soil. In well-aerated soils, oxidized Fe (Fe<sup>3+</sup>) can coat exchange sites, essentially blocking the retention of other base cations that are normally associated with mineral exchange complexes (Abruna and Smith 1953; Fox 1982). Ridges and slopes are generally well aerated, whereas upland valleys and riparian zones experience frequent low-oxygen events associated with rainfall and high stream flow (Silver et al. 1999). Soil exchange sites become available for other base cations such as Ca and Mg when Fe becomes reduced, resulting in higher levels of extractable cations in riparian soils (table 3-2). Conversely, scouring of riparian valleys in tabonuco forest during overland flow events leads to lower carbon stocks (Weaver et al. 1987; Lodge et al. 2008).

### Soil Carbon and Nutrient Pools

Nutrient pools in soils of the Luquillo Mountains are similar to those reported for other lower montane wet tropical forests (Silver et al. 1994; Scatena 1998). Soil organic matter averages 170 Mg ha<sup>-1</sup> to a depth of 60 cm in the Bisley Experimental Watersheds (table 3-4). Soil P is found at somewhat higher standing stocks in the Luquillo Mountains (45 kg ha<sup>-1</sup>) than at other tropical forests (Scatena and Lugo 1995; Scatena 1998).

Pools of available nutrients in the soils of the Luquillo Mountains are typically as great as or greater than those in the aboveground biomass (table 3-4). The exception is K, with up to an order of magnitude more K being stored in the plant biomass than in the labile soil pool (Scatena et al. 1993; Silver et al. 1994).

Table 3.3 Variation of soil chemistry (organic matter, nutrients, exchangeable cations, and pH) and bulk density (BD) in the leacos watershed by topographic position and depth

| Position        | SOM          | C           | N           | P                   | K                  | Ca          | Mg           | Na           | Fe          | Mn                  | BD                 |
|-----------------|--------------|-------------|-------------|---------------------|--------------------|-------------|--------------|--------------|-------------|---------------------|--------------------|
|                 |              | %           |             | mg kg <sup>-1</sup> | mg g <sup>-1</sup> |             |              |              |             | mg kg <sup>-1</sup> | g cm <sup>-3</sup> |
| <b>Ridge</b>    |              |             |             |                     |                    |             |              |              |             |                     |                    |
| 0-10 cm         | 13.62 (1.12) | 5.19 (0.51) | 0.23 (0.02) | 6.70 (0.53)         | 0.06 (0.003)       | 0.12 (0.03) | 0.06 (0.07)  | 0.04 (0.003) | 2.06 (0.15) | 5.32 (0.88)         | 0.69 (0.02)        |
| 10-25 cm        | 9.13 (0.51)  | 2.88 (0.25) | 0.14 (0.01) | 3.78 (0.54)         | 0.04 (0.003)       | 0.02 (0.00) | 0.02 (0.002) | 0.03 (0.004) | 1.54 (0.11) | 1.93 (0.16)         | 0.86 (0.03)        |
| 25-50 cm        | 7.15 (0.41)  | 1.18 (0.09) | 0.07 (0.01) | 0.68 (0.21)         | 0.01 (0.002)       | 0.01 (0.00) | 0.01 (0.001) | 0.01 (0.001) | 0.55 (0.07) | 0.76 (0.1)          | 1.3 (0.05)         |
| <b>Slope</b>    |              |             |             |                     |                    |             |              |              |             |                     |                    |
| 0-10 cm         | 12.15 (0.56) | 4.75 (0.37) | 0.23 (0.02) | 8.18 (0.71)         | 0.05 (0.002)       | 0.06 (0.01) | 0.03 (0.003) | 0.04 (0.003) | 1.92 (0.17) | 3.61 (0.41)         | 0.67 (0.03)        |
| 10-25 cm        | 9.64 (0.48)  | 3.53 (0.30) | 0.17 (0.01) | 6.24 (0.68)         | 0.04 (0.003)       | 0.02 (0.00) | 0.02 (0.002) | 0.03 (0.002) | 1.58 (0.11) | 2.17 (0.18)         | 0.9 (0.03)         |
| 25-50           | 6.37 (0.33)  | 1.33 (0.15) | 0.06 (0.01) | 1.30 (0.33)         | 0.01 (0.002)       | 0.01 (0.00) | 0.01 (0.001) | 0.01 (0.001) | 0.70 (0.09) | 1.52 (0.4)          | 1.25 (0.04)        |
| <b>Riparian</b> |              |             |             |                     |                    |             |              |              |             |                     |                    |
| 0-10 cm         | 21.46 (0.94) | 7.33 (0.65) | 0.33 (0.02) | 14.57 (0.95)        | 0.08 (0.005)       | 0.26 (0.05) | 0.08 (0.009) | 0.05 (0.004) | 1.00 (0.11) | 41.80 (11.2)        | 0.58 (0.02)        |
| 10-25 cm        | 20.07 (0.77) | 6.39 (0.57) | 0.29 (0.02) | 11.90 (0.87)        | 0.06 (0.004)       | 0.23 (0.09) | 0.05 (0.006) | 0.03 (0.003) | 0.83 (0.08) | 35.78 (10.7)        | 0.62 (0.02)        |
| 25-50 cm        | 18.79 (1.85) | 5.46 (0.65) | 0.20 (0.02) | 8.04 (0.78)         | 0.04 (0.006)       | 0.18 (0.07) | 0.05 (0.009) | 0.04 (0.004) | 0.67 (0.09) | 29.24 (8.99)        | 0.65 (0.04)        |

Modified from McSwiney (1999). Chemistry of surface soils by depth for individual geomorphic settings (ridge, slope, and riparian zone) is shown with standard deviation on the line below. Three different catenas were sampled at lower-elevation sites (approx 725 m) in the Rio Leacos, and three samples were taken at each position and depth in each catena. SOM = soil organic matter plus forest floor.



Figure 3.13 Group of tabonuco trees (*Dacryodes excelsa*), which dominate especially on ridge tops, with individuals usually interconnected by roots. (Photograph by Jerry Bauer.)

Table 3.4 Variation in nutrient capital and organic matter (OM) in plant biomass and soils of the tabonuco forest type.

|   | OM Mg ha <sup>-1</sup> | N     | P    | K    | Ca   | Mg    |
|---|------------------------|-------|------|------|------|-------|
|   | kg ha <sup>-1</sup>    |       |      |      |      |       |
| Overstory                               | 221                    | 614   | 33.4 | 514  | 464  | 126   |
| Roots (C)                               | 72.4                   | 203   | 10.9 | 79.6 | 156  | 50.7  |
| Roots (F)                               | 2.20                   | 34.6  | 1.2  | 2.4  | 17.0 | 2.2   |
| Understory                              | 4.31                   | 55.8  | 3.4  | 48.6 | 16.0 | 13.8  |
| Total biomass                           | 300                    | 907   | 48.9 | 644  | 653  | 192   |
| Soil                                    | 170                    | 8,500 | 45.4 | 70   | 600  | 1,100 |
| Percent total standing stock as biomass | 64                     | 10    | 52   | 90   | 52   | 15    |

Values represent watershed mean values of the Bisley Experimental Watersheds, tabonuco forest type. In soils, total N is reported, but other nutrients represent the extractable fraction only. Plant biomass is divided into overstory trees with dbh > 2.5 cm (including boles, leaves, and bark), coarse roots (C), fine roots (F), and understory plants. Data from Scatena et al. (1993), Silver et al. (1994), and Scatena and Lugo (1995).

Nutrient pools in aboveground biomass are similar to those in other montane tropical forests in New Guinea (Grubb and Edwards 1982) and Venezuela (Grimm and Fassbender 1981), but they are higher than those in upper montane forest sites in Jamaica (Tanner 1985) and Hawaii (Mueller-Dombois et al. 1984). A comparison with a broad range of montane tropical sites shows that soils in Bisley are typical for base cations, elevated in extractable P, and lower than the median in N (figure 3-12).

Although mineral nutrients are present in soils, they are not necessarily available to plants. The soils of the Luquillo Mountains, as in many tropical areas, have phosphorus-fixing clays dominated by iron and aluminum oxides that bind tightly to phosphorus and make it less available to plants and microbes. Oxygen levels in soils can also affect the nutrient availability through a number of mechanisms. Low oxygen (O<sub>2</sub>) availability in the flooded soils of high-elevation elfin forests in the Luquillo Mountains (Silver et al. 1999) might result in decreased decomposition rates and the decreased efficiency of nutrient uptake by roots or their mycorrhizal fungi. On the other hand, low O<sub>2</sub> concentrations can also increase the availability of P, as periods of soil anoxia result in the reduction of Fe<sup>3+</sup> to Fe<sup>2+</sup>, which releases the P held in FePO<sub>4</sub> bonds (Silver et al. 1999). Oxygen concentrations in soils decrease significantly as the annual rainfall at a location increases, and they can reach very low levels (<3 percent) at individual sampling points for periods of up to 25 consecutive weeks (Silver et al. 1999). Soil O<sub>2</sub> concentrations of <3 percent are frequently cited as being below the critical threshold for the survival of some herbs and wetland plants (Drew 1990).

### Variation in Soils with Elevation

Soils of the Luquillo Mountains show considerable variation in C, N, and P with elevation and vegetation type (table 3-5). Carbon and nitrogen are highest in high-elevation soils, and the C:N ratio (mass:mass) increases from 12 to 24 along the elevational

Table 3.5 Variation in nutrient pools of surface soils (0–10 cm depth) from pasture and three forest types in the Luquillo Mountains.

| Vegetation<br>(elevation,<br>masl) | C                   | N              | P                   | K              | Ca            | Mg           | Na             | Fe           | Mn             | pH             |
|------------------------------------|---------------------|----------------|---------------------|----------------|---------------|--------------|----------------|--------------|----------------|----------------|
|                                    | Mg ha <sup>-1</sup> |                | kg ha <sup>-1</sup> |                |               |              |                |              |                |                |
| Pasture<br>(100)                   | 34.9<br>(6.54)      | 2.78<br>(0.62) | 6.34<br>(3.11)      | 60.0<br>(14.0) | 217<br>(47.4) | 136<br>(57)  | 30.3<br>(6.1)  | 482<br>(146) | 65.1<br>(23.7) | 3.72<br>(0.07) |
| Tabonuco<br>(300)                  | 47.1<br>(11.3)      | 3.51<br>(0.53) | 7.49<br>(1.28)      | 75.3<br>(31.3) | 472<br>(499)  | 242<br>(151) | 49.7<br>(19.0) | 676<br>(304) | 41.2<br>(28.5) | 3.81<br>(0.28) |
| Palo colorado<br>(650)             | 67.3<br>(23.7)      | 3.49<br>(1.40) | 4.92<br>(2.08)      | 46.5<br>(6.12) | 293<br>(212)  | 95<br>(33)   | 38.5<br>(8.96) | 813<br>(114) | 24.9<br>(21.7) | 3.87<br>(0.23) |
| Elfin<br>(950)                     | 220<br>(54.7)       | 9.30<br>(2.68) | 6.01<br>(1.59)      | 37.3<br>(12.4) | 202<br>(134)  | 67<br>(14)   | 43.6<br>(6.04) | 501<br>(171) | 14.2<br>(15.6) | 3.79<br>(0.22) |

Data from Cox et al. (2002). Each sample represents the mean (SD) of two ridge sites and two valley sites per forest type, with multiple auger samples composited from each site.

gradient (table 3-5) (Cox et al. 2002). Available cations tend to be highest in the mid-elevation tabonuco forest, but wide variability in elemental contents and in the interactions between elevation and topographic position within each forest type results in few statistically significant differences for individual elements (Cox et al. 2002).

### Internal Nutrient Fluxes

Litterfall, throughfall, and the movement of soil solution and groundwater represent large internal transfers of nutrients within the forest ecosystems of the Luquillo Mountains. The importance of each pathway differs by element. Throughfall, for example, provides more than twice the flux of K to the forest floor than does litterfall (McDowell 1998). For nitrogen, however, the opposite situation occurs, with 20 times as much N transferred in litterfall as in throughfall (figure 3-14).

Internal nitrogen dynamics have been particularly well studied in tabonuco forests (see the summary by Chestnut et al. [1999]). In the forests of the Luquillo Mountains, the sum of N export and net biomass N accumulation exceeds N inputs

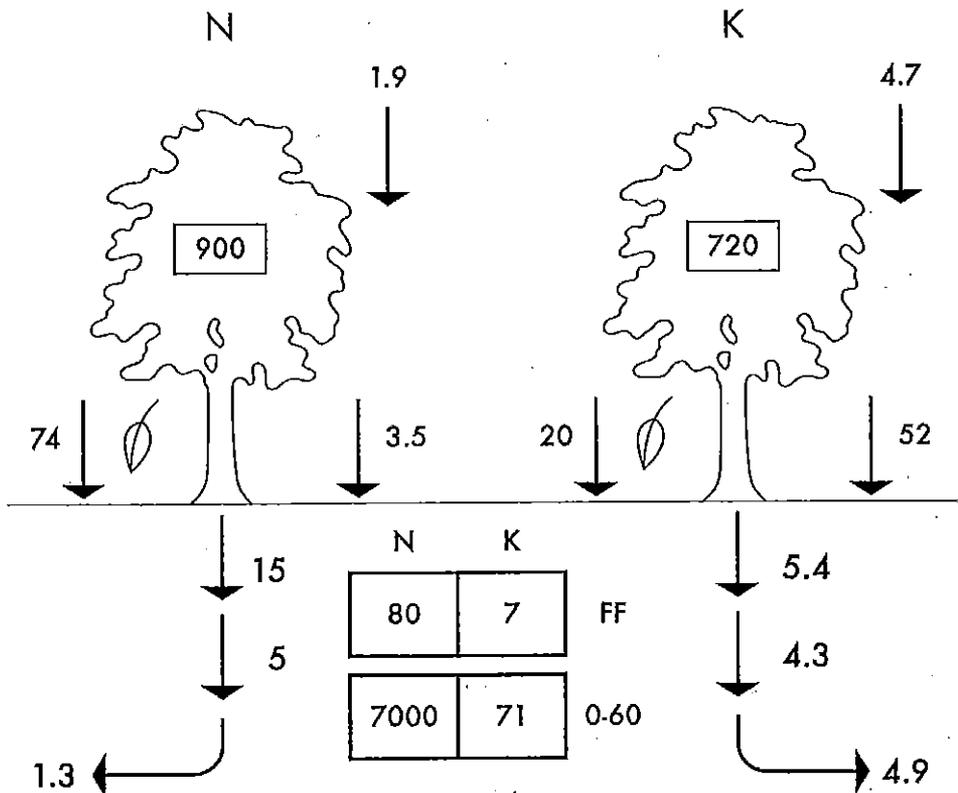


Figure 3.14 Standing stocks and internal fluxes of nitrogen (N) and potassium (K) in the tabonuco forest type, Luquillo Experimental Forest, Puerto Rico. Standing stocks (boxes) are kg ha<sup>-1</sup>; fluxes (arrows) are kg ha<sup>-1</sup> y<sup>-1</sup>. Fluxes shown include precipitation, throughfall, litterfall, soil solution at 40 and 80 cm, and streamflow. FF = forest floor; 0-60 = soil pools from 0 to 60 cm in depth. Standing stock of potassium in soil is the exchangeable pool only. Modified from McDowell (1998). Reprinted with permission from Cambridge University Press.

in rainfall (McDowell and Asbury 1994). This imbalance in the nitrogen budget might be due to unmeasured inputs from biological nitrogen fixation or unmeasured changes in the total standing stock of soil N. Because standing stocks are very large relative to inputs and outputs, it is hard to rule out changes in soil N storage as a potential explanation for the imbalance in the N budget (Chestnut et al. 1999). Nitrogen fixation is also very likely to occur, as it is typically high in tropical environments (Cleveland et al. 1999), and various N fixers are known to occur in the Luquillo Mountains (Edmisten 1970). Some variability in the rates of N fixation appears to be associated with patterns of past land use. Trees planted with coffee (e.g., *Inga*) are common at many sites in the Luquillo Mountains, and in the Bisley Experimental Watersheds soils under *Inga* have a higher N content than those under other species (Beard et al. 2005). Free-living soil microbes in the Luquillo Mountains contribute the most to N-fixation rates on an areal basis, but nitrogenase activity is highest on a per-gram basis in mosses (Cusack et al. 2009). An estimate of the rate of N fixation in watershed-scale studies of N inputs and outputs (McDowell and Asbury 1994; Chestnut et al. 1999) suggests that it might be up to  $16 \text{ kg ha}^{-1} \text{ y}^{-1}$ . No systematic survey of N fixation has been conducted in the Luquillo Mountains.

The aquatic habitat within bromeliad tanks is particularly nutrient rich, with the concentrations of many elements being orders of magnitude higher than those found in rain or streamwater (Richardson et al. 2000). These tanks serve as spatially distributed, high-nutrient aquatic microcosms in the terrestrial ecosystem. Depending on the elevation, the average total dissolved N (TDN) and phosphate ( $\text{PO}_4^{3-}$ ) concentrations can exceed 3 and  $0.4 \text{ mg l}^{-1}$ , respectively, and dissolved organic carbon (DOC) concentrations can exceed  $50 \text{ mg l}^{-1}$ . In contrast, the average concentrations of TDN,  $\text{PO}_4^{3-}$ , and DOC in stream water rarely exceed 0.25, 0.02, and  $3 \text{ mg l}^{-1}$ , respectively (McDowell et al. 1990; McDowell and Asbury 1994). Annual nutrient budgets indicate that these bromeliad microcosms are nutrient rich because of their high inputs of both throughfall and litter from canopy trees. In general, tank bromeliads in all forest types accumulate <5 percent of the nutrients that pass through them; the exception is in high-elevation elfin forest, where bromeliads accumulate about 25 percent of P and K inputs (Richardson et al. 2000). The relative importance of bromeliad phytotelmata (tanks) as storage compartments increases with elevation, as the bromeliad density increases, along with their efficiency of nutrient retention (Richardson et al. 2000).

### *Interfaces as Biogeochemical Hot Spots*

Interfaces where two distinct parts of an ecosystem meet are often important in defining ecological processes at multiple spatial and temporal scales. Interfaces play an important role in biogeochemical transformations because the transformations often occur at higher rates per surface area or volume at interfaces than at adjacent, homogeneous units of the landscape. McClain et al. (2003) have summarized the situations in which interfaces are more active, and they have proposed a formal set of definitions, including “hot spots” and “hot moments,” which often occur at interfaces. Hot spots are points in the landscape at which the rates of biogeochemical processes are disproportionately high relative to the surrounding area.

They are often the result of converging hydrologic flowpaths, where the reactants needed for a reaction (e.g., the low-oxygen water, nitrate, and organic matter needed for denitrification) are delivered to a point in the landscape. Hot moments occur when the same confluence of reactants and conditions are present for a specific moment in time, generating intense biological activity.

Drought-induced crashes in microbial populations result in pulses of nutrient availability when the forest floor is rewetted and the microbial biomass killed off by the drought is mineralized (Lodge et al. 1994), representing an excellent example of the "hot moment" concept. Local weather systems such as large storms and prolonged droughts (see chapter 4) can have a significant effect on the short-term variation in internal nutrient cycling rates in tropical forests (Lodge et al. 1994). These pulses are often quantitatively significant, because microbes represent a significant fraction of the total labile nutrient pool. Mean fungal biomass accounted for 22 percent of the total phosphorus in the litter layer at El Verde, and for between 3 percent and 85 percent of the litter P at different sites (Lodge 1993, 1996). In soil at El Verde, fungal biomass accounted for 0.8 percent to 20 percent of the labile (Olson extractable) P and 24 percent of the Ca (Lodge 1993, 1996). The rapid growth and nutrient immobilization by microbes under favorable moisture conditions helps to retain nutrients against leaching loss; crashes in fungal populations in response to drying release nutrients from the microbial biomass, making them available to plants (Lodge 1993; Lodge et al. 1994).

In the Luquillo Mountains, the oxic-anoxic interface and the stream-groundwater interface represent two hot spots for biogeochemical transformations. These two can be related; changes in oxygen status are often associated with the groundwater-streamwater interface in the Luquillo Mountains (see, e.g., McDowell et al. 1992). But oxic-anoxic interfaces can also be found in upland soils, far from the stream's edge (Silver et al. 1999). In these soils, the maintenance of low-oxygen conditions is typically related to inputs of rainfall that drive the metabolic processes that deplete molecular oxygen in the soil matrix and prevent the resupply of atmospheric oxygen by reducing open pore space.

The low soil O<sub>2</sub> concentrations that can occur in Luquillo Mountain soils affect a variety of biogeochemical processes in upland soils, in addition to having effects on riparian biogeochemistry. Elfin forest soils, for example, have extremely high soil methane (CH<sub>4</sub>) concentrations (3 percent to 24 percent), indicating the strong influence of anaerobic processes. These high soil CH<sub>4</sub> concentrations result in net CH<sub>4</sub> emission into the atmosphere in the elfin forest ( $[98 \pm 50] \text{ mg m}^{-2} \text{ d}^{-1}$ ), and net emission is also seen in lower elevation valleys ( $[5 \pm 1] \text{ mg m}^{-2} \text{ d}^{-1}$ ), but soils in other parts of the forest are net CH<sub>4</sub> consumers (McSwiney 1999; Silver et al. 1999). Nitrous oxide (N<sub>2</sub>O) flux responds little to rainfall in chronically wet soils but appears to be related to differences in oxygen concentrations across topographic gradients, with maximal N<sub>2</sub>O production occurring at intermediate oxygen levels (McSwiney et al. 2001).

At the stream-water interface, or riparian zone, the interplay between oxygen, carbon, and nitrogen drives most biogeochemical processes (see, e.g., Hedin et al. 1998). The riparian zone, as a topographic low point, tends to have high C inputs that are often stored in layers of buried organic matter along the banks of larger

streams. These high C inputs often result in the O<sub>2</sub> depletion of riparian groundwater and increased rates of dissimilatory pathways in the nitrogen cycle. These potential pathways include the dissimilatory reduction of nitrate to ammonium (Silver et al. 2001) and denitrification, which results in the conversion of nitrate to gaseous end products (N<sub>2</sub>O or N<sub>2</sub>) that eventually leave the soil and return to the atmosphere.

The importance of the riparian zone in regulating losses of N from the Luquillo Mountains was first examined by McDowell et al. (1992) and Bowden et al. (1992), and their two companion papers were the first to examine the significance of the riparian zone for N biogeochemistry in a tropical environment. They compared riparian zone function in the two bedrock types and found that the differences in bedrock resulted in geomorphological differences in riparian zones that had major impacts on N retention and loss. In soils derived from volcanoclastic parent material (as in the Bisley Experimental Watersheds), groundwater flow paths were shallow, oxygen status varied along the flow path (e.g., patches of oxidized and reduced soils), and little nitrogen in any form was delivered to the riparian zone (McDowell et al. 1992; Schellekens et al. 2004). In contrast, in soils derived from igneous parent material (e.g., the quartz diorite of the Icacos watershed), flow paths were much deeper, and the nitrogen dynamics were characterized by sharp transitions along the flow path. Upslope groundwater was entirely oxic and showed a significant accumulation of nitrate (up to 1 mg l<sup>-1</sup> as N). This nitrate was lost, in part to N<sub>2</sub>O production at the slope–floodplain interface (Bowden et al. 1992; McSwiney et al. 2001), and ammonium (NH<sub>4</sub>) accumulated in the extremely reduced groundwater of the floodplain. The amounts of ammonium and total dissolved N subsequently decreased as groundwater passed through the stream bank and into the stream, suggesting the importance of coupled nitrification-denitrification in the variably oxygenated soils of the stream's edge (McSwiney et al. 2001).

Subsequent work has examined the importance of riparian processes in regulating N flux at the reach and basin scale in the Ríó Icacos valley. Chestnut and McDowell (2000) intensively monitored groundwater inputs along a 100 m reach of a tributary to the Ríó Icacos. By directly measuring the groundwater inputs and groundwater chemistry, they determined that the N export would be 6 to 10 times greater in the absence of riparian and hyporheic N retention or denitrification. Madden (2004) expanded this approach to the main stem of the Ríó Icacos, using a variety of direct and indirect measurements of groundwater inputs to the main stem. She estimated that the hydrologic losses of N from the entire Icacos valley would be double or triple the observed values if not for denitrification in the riparian zone.

### ***Stream and Atmospheric Outputs***

The export of nutrients from Luquillo Mountain watersheds in stream flow is comparable to that reported from other humid tropical watersheds (table 3-6). One of the most detailed comparisons among tropical watersheds was published by Lewis et al. (1999), who synthesized data on the export of nitrogen in organic, inorganic, and particulate forms from large and small basins throughout South America and the Caribbean. They found that losses of N as dissolved organic and particulate N

were significant, and that Luquillo Mountain sites were typical of those found throughout the Neotropics. They also found that nitrogen export in tropical streams and rivers is greater than nitrogen export from temperate watersheds with a similar degree of human effects. Phosphorus and K losses are moderate and typical of those from humid tropical forests (table 3-6). The hydrologic export of DOC from watersheds of the Luquillo Mountains is within the range reported for other tropical forests (25 to 100 kg ha<sup>-1</sup> y<sup>-1</sup>) (McDowell and Asbury 1994). The adsorption of DOC on mineral soil appears to limit the loss of DOC in runoff, as it does in temperate forests (McDowell 1998). Losses of base cations in stream water show clear variation with bedrock geology. In the quartz diorite lithology (Río Icacos), K concentrations and fluxes are at least double those from the volcanoclastic lithology, but the opposite is true for Mg (McDowell and Asbury 1994). Losses of N show no clear patterns in relation to the watershed size or forest type (McDowell and Asbury 1994; Schaefer et al. 2000).

Instream processes, as well as watershed processes, can be important in regulating nutrient losses. Studies with stable isotopic tracers show that the rates of nitrification are very high in Bisley (stream 3) relative to temperate streams. The fraction of total NH<sub>4</sub> uptake converted to nitrate (NO<sub>3</sub>) is 60 percent, higher than at any other site studied by Webster et al. (2003), and the uptake length (the distance an average molecule travels before uptake or assimilation) is only 26 m (Merriam et al. 2002). Nitrate uptake is relatively slow in comparison, occurring over many hundreds of meters (Merriam et al. 2002).

The flashy nature of stream flow in the Luquillo Mountains produces high temporal variability in the rates of watershed nutrient output. Streams in the Luquillo Mountains respond quickly to rainfall (figure 3-15), and discharge can change a hundred-fold in a few hours. In a comparison of Long Term Ecological Research (LTER) sites, Post and Jones (2001) found that streams of the Luquillo Mountains are among the quickest to respond to rainfall, owing to their shallow flow paths through macropores in the dense clay soils. To use the terminology of Olden and Poff (2003), stream flows in the Luquillo Mountains are typically “perennial flashy or runoff.” Flow paths and stream base flow differ considerably between the two bedrock types in the Luquillo Mountains, with the quartz diorite bedrock of the Icacos basin producing deeper flow paths and more stable base flows than the volcanoclastic bedrock (McDowell et al. 1992; McDowell and Asbury 1994; Schellekens et al. 2004). The mass of dissolved and particulate matter exported from watersheds in stream water typically increases with increased stream discharge, and streams in the Luquillo Mountains are no exception. The export of sediments is particularly sensitive to discharge, because sediment concentrations increase with increased flow (figure 3-16). The export of dissolved nutrients is less sensitive to increases in stream flow, as the concentrations of most elements decrease with increased flow (e.g., Shanley et al. 2011; figure 3-16). There is little evidence of seasonality in stream chemistry, and long-term trends appear to be driven by hurricanes (figure 3-17).

For carbon, nitrogen, and sulfur, trace gas fluxes can be an important watershed-scale export term. In their synthesis of the nitrogen budget for tabonuco forests, for example, Chestnut et al. (1999) estimated that losses of N resulting

Table 3.6 Nutrient flux from tropical and temperate forested watersheds with relatively little anthropogenic disturbance.

| Name                                | Location                        | NO <sub>3</sub> -N | NH <sub>4</sub> -N | DON  | TDP  | Na   | K    | Ca   | Mg   | DOC | SiO <sub>2</sub> | Runoff |
|-------------------------------------|---------------------------------|--------------------|--------------------|------|------|------|------|------|------|-----|------------------|--------|
| kg ha <sup>-1</sup> y <sup>-1</sup> |                                 |                    |                    |      |      |      |      |      |      |     |                  |        |
| cm                                  |                                 |                    |                    |      |      |      |      |      |      |     |                  |        |
| W3                                  | Malaysia <sup>a</sup>           | 0.38               | 0.29               | 1.93 | 0.19 | 30.7 | 12.4 | 19.7 | 17.3 | 86  | 104              | 196    |
| W6                                  | Malaysia <sup>a</sup>           | 0.10               | 0.22               | 4.15 | 0.07 | 7.1  | 3.2  | 3.1  | 3.2  | 194 | 13               | 195    |
| Kali Mondo                          | Indonesia <sup>b</sup>          |                    |                    |      | 0.70 | 27.4 | 22.0 | 29   | 30.5 |     | 538              | 359    |
| Pedra Preta                         | Anapa, BR <sup>c</sup>          | 0.71               | 0.24               |      |      | 15.1 | 4.7  | 22.1 | 7.5  |     |                  | 135    |
| Calado                              | Manaus, BR <sup>d</sup>         | 2.67               | 0.18               | 0.76 | 0.05 | 2.6  | 0.5  | 0.5  | 0.3  |     |                  | 165    |
| Tempisquito                         | Costa Rica <sup>e</sup>         | 6.10               |                    | 3.00 | 0.57 | 114  | 26   | 192  | 70   | 37  |                  | 290    |
| Temp. Sur                           | Costa Rica <sup>e</sup>         | 4.90               |                    | 2.10 | 0.33 | 339  | 64   | 442  | 137  | 27  |                  | 430    |
| Kathia                              | Costa Rica <sup>e</sup>         | 5.60               |                    | 1.50 | 0.34 | 110  | 21   | 151  | 57   | 19  |                  | 310    |
| Marilin                             | Costa Rica <sup>e</sup>         | 4.00               |                    | 1.90 | 0.46 | 123  | 41   | 174  | 67   | 24  |                  | 160    |
| El Jobo                             | Costa Rica <sup>e</sup>         | 4.30               |                    | 2.00 | 0.34 | 104  | 35   | 133  | 53   | 26  |                  | 140    |
| Zompopa                             | Costa Rica <sup>e</sup>         | 6.00               |                    | 3.40 | 0.43 | 164  | 31.0 | 199  | 73   | 43  |                  | 280    |
| Icaos                               | Puerto Rico <sup>f</sup>        | 2.54               | 0.68               | 4.79 | 0.08 | 161  | 17.3 | 96   | 35   | 94  | 486              | 368    |
| Sonadora                            | Puerto Rico <sup>f</sup>        | 1.39               | 0.30               | 3.74 | 0.05 | 96   | 5.5  | 44.1 | 28.1 | 74  | 180              | 438    |
| Toronja                             | Puerto Rico <sup>f</sup>        | 0.90               | 0.26               | 2.80 | 0.03 | 113  | 4.9  | 87.6 | 62.7 | 33  | 325              | 175    |
| Orinoco                             | Venezuela <sup>g</sup>          | 0.95               | 0.41               | 1.92 | 0.24 | 17.5 | 7.8  | 30.9 | 7.9  | 52  | 70               | 119    |
| Hubbard Bdk.                        | New Hampshire, USA <sup>h</sup> | 0.60               | 0.10               | 1.30 | 0.02 | 7.2  | 1.9  | 13.7 | 3.1  | 29  | 38               | 83     |
| Coweeta                             | N. Carolina, USA <sup>i</sup>   | 0.05               | 0.04               |      | 0.02 | 8.7  | 4.1  | 5.3  | 3.3  | 15  | 59               | 119    |
| HI Andrews                          | Oregon, USA <sup>j</sup>        | 0.81               |                    | 0.69 | 0.70 | 52.8 | 9.5  | 123  | 8.6  |     | 114              | 237    |

From McDowell (2002). DON = dissolved organic nitrogen; TDP = total dissolved phosphorus; DOC = dissolved organic carbon.

<sup>a</sup> Grip et al. 1994.

<sup>b</sup> Bruijzeel 1983.

<sup>c</sup> Forti et al. 2000.

<sup>d</sup> Williams and Melack 1997.

<sup>e</sup> Newbold et al. 1995.

<sup>f</sup> Lewis and Saunders 1989.

<sup>g</sup> Campbell et al. 2000; Likens et al. 1977.

<sup>h</sup> Swank and Waide 1988.

<sup>i</sup> Solkins et al. 1980.

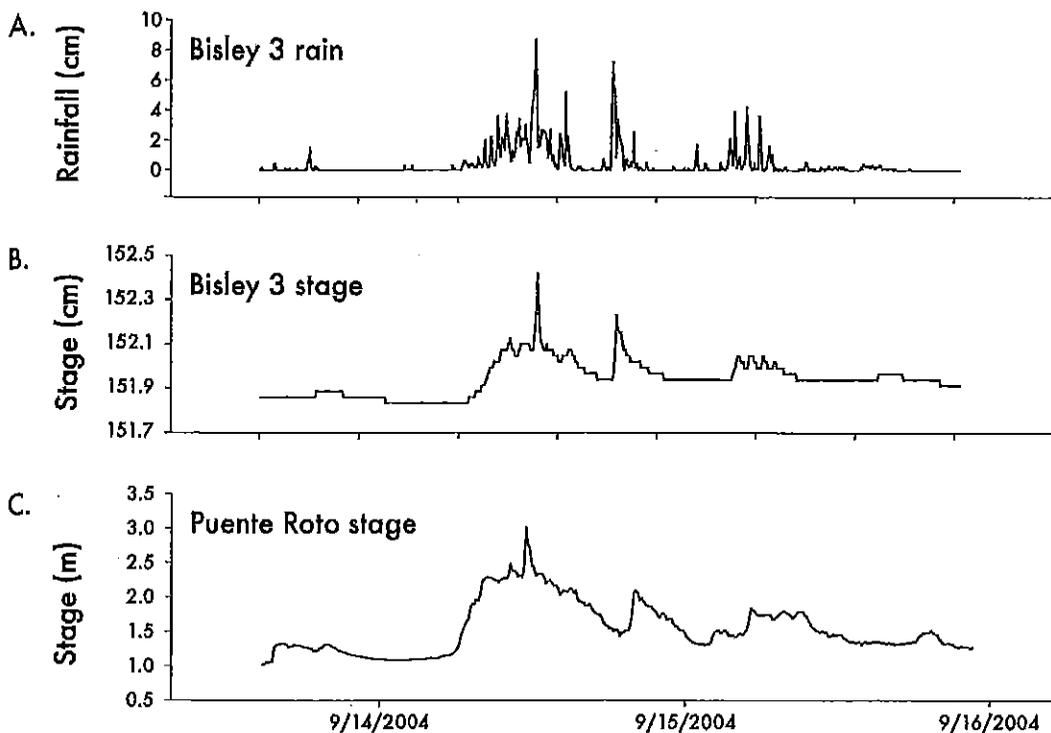


Figure 3.15 Response of stream stage height to rainfall in Bisley Experimental Watershed (BEW) 3 during several days in September 2004. Stream discharge typically increases as the cube of the stage height. (A) Rainfall in BEW 3 ( $\text{mm day}^{-1}$ ) collected during a 2-week sampling period. (B) Stage height at the gauge on BEW 3 (cm above an arbitrary datum). (C) Stage height (m above an arbitrary datum) on the Río Mameyes at Puente Roto, near the edge of the Luquillo Experimental Forest.

from denitrification accounted for 1 to 4  $\text{kg ha}^{-1} \text{y}^{-1}$ ; the upper end of this range is equal to inputs of nitrogen in rainfall. Trace gas fluxes and trace gas concentrations tend to be highly sensitive to the topographic position. Nitrous oxide fluxes tend to be highest at topographic breaks in the colorado forest (Bowden et al. 1992; McSwiney et al. 2001). In a year-long study of soils from ridgetops to the stream bank, McSwiney et al. (2001) found that highest fluxes of  $\text{N}_2\text{O}$  were typically found in the topographic break where the ridge meets the riparian floodplain, and that available manganese (Mn) was a good predictor of high  $\text{N}_2\text{O}$  flux. Only soils containing available Mn produced significant  $\text{N}_2\text{O}$  fluxes. In contrast,  $\text{CH}_4$  flux was less clearly related to the topography, with significant rates of  $\text{CH}_4$  consumption found at all topographic positions (McSwiney et al. 2001). Concentrations of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  at depths of 10 to 80 cm in the colorado forest are also sensitive to topographic position, with the highest concentrations in riparian and streambank soils and the lowest in ridge soils (McSwiney 1999; Silver et al. 1999). The response of biogeochemical conditions to an environmental variable such as rainfall also can vary with topographic position. For example, soil  $\text{O}_2$  concentrations in valley soils are correlated with rainfall from the previous day, but at ridge sites they are correlated with cumulative rainfall inputs over the previous 4 weeks.

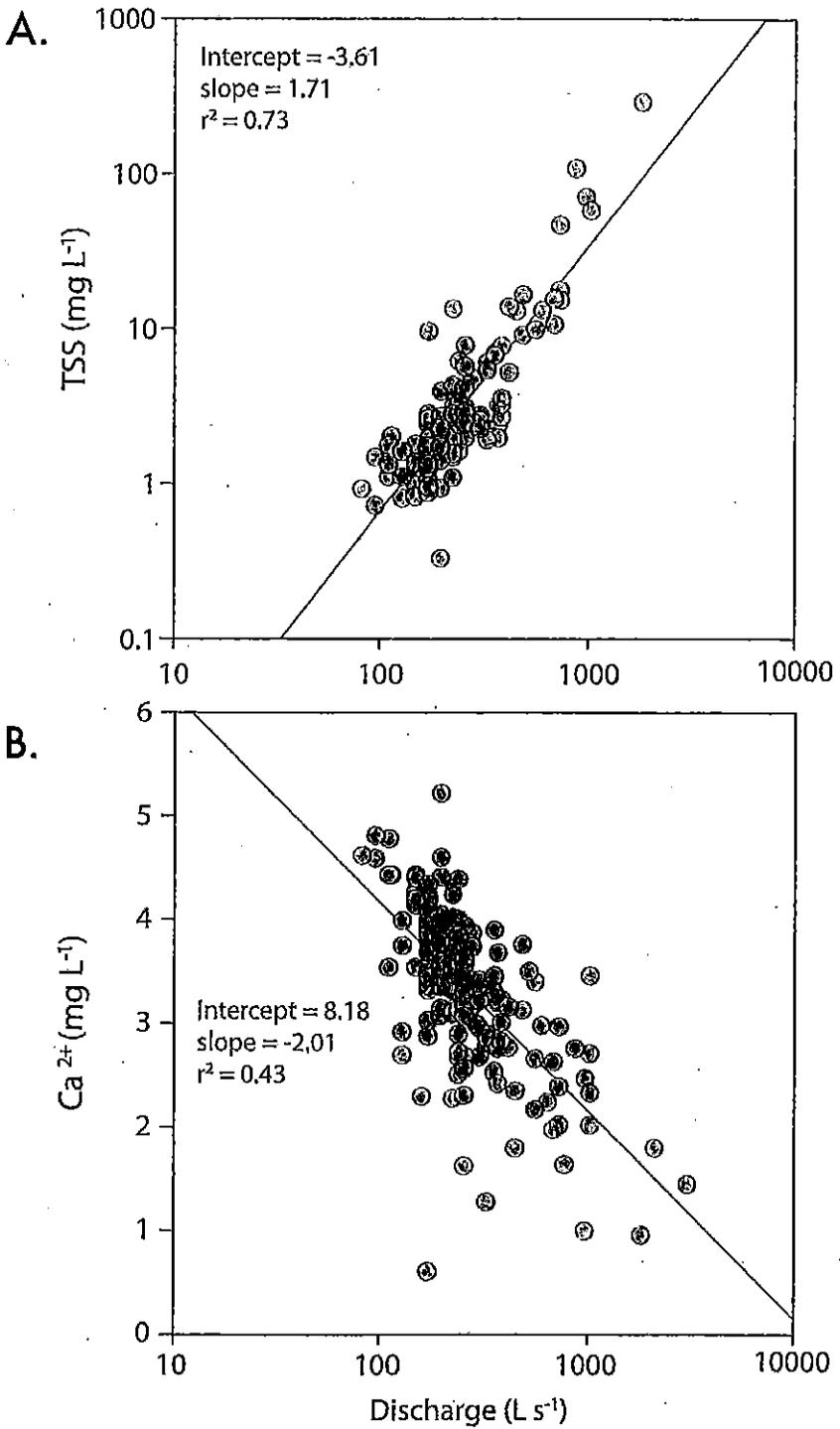


Figure 3.16 Variation in the concentration of (A) total suspended sediments (TSS) and (B) calcium (Ca<sup>2+</sup>) with stream flow in the Río Icacos in the Luquillo Mountains in 1983–1986. Data from McDowell and Asbury (1994).

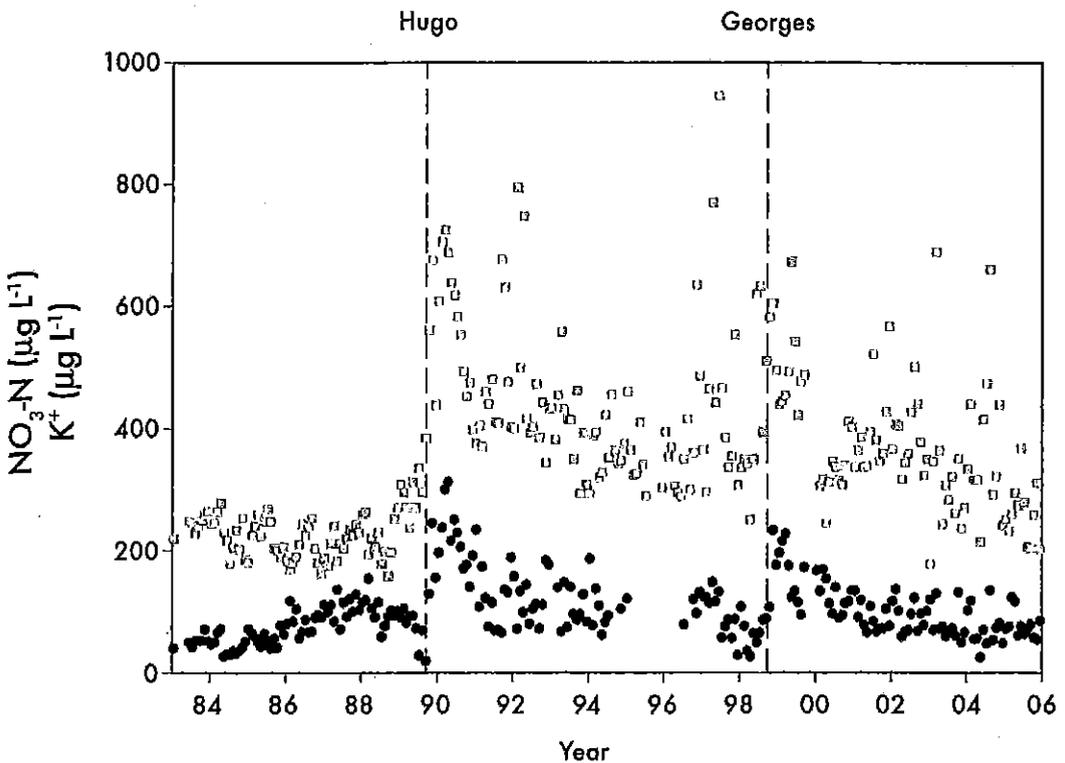


Figure 3.17 Long-term variation in monthly average concentrations of nitrate ( $\text{NO}_3\text{-N}$ ; solid circles) and potassium ( $\text{K}^+$ ; boxes) in water in Quebrada Sonadora in the Luquillo Mountains in relation to major hurricanes Hugo and Georges. Data from McDowell and Asbury (1994), Schaefer et al. (2000), and unpublished work of the authors.

## Terrestrial Biota and Ecosystem Processes

### Primary Producers

#### Species Composition

Forests in the Luquillo Mountains have been classified into four major forest types: tabonuco, colorado, elfin, and palm brake forests (Gleason and Cook 1927; Wadsworth 1987). Other minor forest types include *Pterocarpus* forest, palm floodplain forests, palm brakes, and bogs (Brown et al. 1983). The tabonuco forest type (occurring in the subtropical moist forest and subtropical wet forest life zones) (Ewel and Whitmore 1973) is named for the tabonuco (*Dacryodes excelsa*), which is the dominant tree species growing from the lower slopes near sea level to elevations of about 600 m. In well-developed stands of this forest type, the taller trees exceed 30 m in height, there is a fairly continuous canopy at 20 m, and the shaded understory is moderately dense (figure 3-18). The shape of the canopy profile varies following hurricane disturbance, with reduced cover at the highest points in the profile. The most common tree species in this forest type are *Casearia arborea*, *Dacryodes excelsa*, *Manilkara bidentata*, *Inga laurina*, and *Sloanea berteriana* (Thompson et al. 2002). These tree species and the sierra palm *Prestoea montana* (previously

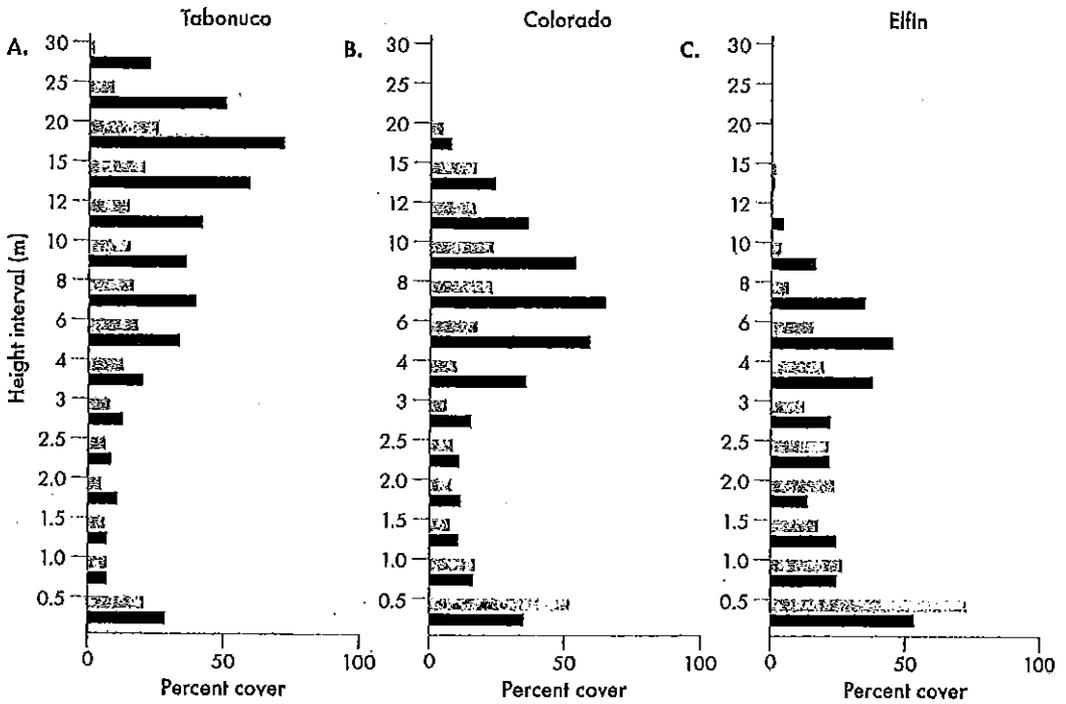


Figure 3.18 Vegetation height profiles in 1 ha plots in (A) tabonuco (350 m elevation, 475 sample points), (B) colorado (750 m, 451 points), and (C) elfin (900 m, 451 points) forest plots in the Luquillo Mountains in 1989, before (dark bars) and after (light bars) Hurricane Hugo. Horizontal scale shows total points with cover as a percentage of the total number of grid points in each plot. Vertical scale is graduated and shows the upper limit for each height interval. From Brokaw and Grear (1991). Reprinted with permission of the Association for Tropical Biology and Conservation.

*Euterpe globosa* and named *P. acuminata* in Henderson et al. [1995]; figure 3-19) account for 65 percent of all stems  $\geq 10$  cm diameter at a breast height of 1.3 m from the ground (dbh) in the intensively studied Luquillo Forest Dynamics Plot (LFDP) near El Verde Field Station (figure 3-2). *Prestoea montana* contributes the greatest number of stems to the total stem count in the LFDP. The most common shrubs in the tabonuco forest are *Palicourea riparia*, *Psychotria berteriana*, and *Piper glabrescens*. Grasses, ferns, and forbs are frequent on the ground, especially in canopy gaps. Epiphytes are common, but vines are uncommon (Rice et al. 2004). Both the El Verde Field Station and the Bisley Experimental Watersheds, principal research sites for the Luquillo LTER Program, are in tabonuco forest (see Lugo and Scatena [1995] for a synthesis).

Biomass in the tabonuco forest type ranges from 122 to 300 Mg ha<sup>-1</sup> on average (Ovington and Olson 1970; Scatena et al. 1993; Beard et al. 2005). Live fine root biomass ranges from 1.5 to 8.0 Mg ha<sup>-1</sup>, and total live fine and structural root biomass totals 20 to 74 Mg ha<sup>-1</sup> (Parrotta and Lodge 1991; Kangas 1992; Lugo 1992; Scatena et al. 1993; Silver and Vogt 1993; Vogt et al. 1995, 1997). Fine root biomass changed significantly with weather events (Parrotta and Lodge 1991), with the higher biomasses recorded before Hurricane Hugo and the lowest recorded during the 1994 drought (see chapter 5; Beard et al. 2005). These fine root biomass



Figure 3.19 Wind in a palm (*Prestoea montana*) forest, Luquillo Mountains of Puerto Rico. (Photograph by Jerry Bauer.)

levels are about one-third of those recorded in tropical lowland forests in South America (Cuevas et al. 1991; Vogt et al. 1997) but are similar to those in other montane tropical forests (see, e.g., Grubb 1977). Much of the tabonuco forest type in the Luquillo Mountains was logged for valuable tree species such as tabonuco or partially cleared for coffee or other crops prior to the purchase of most of the Luquillo Mountains by the United States Forest Service in the 1930s (García-Montiel and Scatena 1994). The impacts of past land use on the distribution and abundance of trees were still evident in 1989 (Thompson et al. 2002).

The structure of tabonuco forest shows clear variation with topography. Tabonuco trees are most common on ridges and least common in riparian valleys, where sierra palms are common (Basnet 1992; Johnston 1992; Thompson et al. 2002). Root biomass also varies by topographic position in the tabonuco forest type, with higher fine root biomass on ridges than on slopes or valleys (Vogt et al. 1995, 1997). This might be due to differences in species composition, with shallow-rooted palms found growing most commonly in riparian areas and deeper-rooted dicots being more common on ridges.

Higher in elevation, extending up to about 900 m in the subtropical rain forest and lower montane wet forest life zones (Ewel and Whitmore 1973), is the colorado forest type, named for the dominant tree, palo colorado (*Cyrilla racemiflora*). Species also found in this forest type include *Magnolia splendens*, *Matayba domingensis*, *Micropholis garciniaefolia*, *M. chrysophylloides*, *Calycogonium squamulosum*,

*Ocotea moschata*, and *Croton poecilanthus* (Brown et al. 1983). Most of the colorado forest type is found growing on quartz diorite bedrock; it is not known to what extent this bedrock favors a shift to colorado forest type at higher elevations, although changing environmental conditions alone drive the shift to colorado forest in the Sonadora watershed of the Río Espíritu Santo drainage (Barone et al. 2008), which does not contain quartz diorite. In the colorado forest type, soils are often saturated, and root mats on the soil surface are common. The canopy of the colorado forest type reaches about 15 m in height (figure 3-18), and its biomass is 130 Mg ha<sup>-1</sup> (table 3-7) (Weaver and Murphy 1990).

Sierra palms (*Prestoea montana*) are frequently found at the same elevation and in the same life zones as tabonuco and palo colorado forests, but they achieve maximum dominance as palm brakes in especially steep and wet areas (Lugo et al. 1995). Depending on the degree of soil saturation and aspect, the number of associated tree species can vary between 24 and 35 species per 0.4 ha. Like palo colorado forest, palm forest is about 15 m in height. The aboveground biomass in palm-dominated floodplain forest can be as high as 223 Mg ha<sup>-1</sup>, with 54 Mg ha<sup>-1</sup> of palm biomass alone (Frangi and Lugo 1985). Palms are also found in riparian forest (palm floodplain forest) and on very steep slopes at low elevation (palm brakes) (Frangi 1983; Lugo et al. 1995). Because individual palm trees are found throughout the forest, and because patches of palm forest are found in a variety of wet or steep environments at most elevations in the Luquillo Mountains, it is difficult to make generalizations about the palm forest type, although palms are usually associated with saturated soils and disturbance.

Elfin forest type, a dense forest growing on saturated soils derived from bedrock formed by contact metamorphism, is found above 900 masl (Weaver 1995) in the subtropical rain forest life zone as defined by Ewel and Whitmore (1973). The canopy height is typically 3 to 5 m (figure 3-18), although a variant of elfin forest growing in more protected sites such as small valleys near mountain peaks can

Table 3.7 Aboveground biomass, litterfall, and net primary productivity from four forest types of the Luquillo Mountains found in three subtropical life zones.

|   | Subtropical wet forest (Tabonuco) | Lower montane wet forest |            | Lower montane rain forest (Elfin) |
|---|-----------------------------------|--------------------------|------------|-----------------------------------|
|   |                                   | (Palm)                   | (Colorado) |                                   |
| Biomass (Mg ha <sup>-1</sup> )                    | 190                               | 174                      | 130        | 80                                |
| Litterfall (Mg ha <sup>-1</sup> y <sup>-1</sup> ) |                                   |                          |            |                                   |
| Leaf  | 4.94                              | 6.26                     | 5.05       | 2.45                              |
| Wood  | 1.38                              | 0.86                     | 1.22       | 0.28                              |
| Flower  | 0.17                              | 0.18                     | [0.23]     | —                                 |
| Fruit   | 0.34                              | 1.14                     |            | —                                 |
| Miscellaneous                                     | 1.78                              | 0.36                     | 0.30       | 0.37                              |
| Total litterfall                                  | 8.6                               | 8.8                      | 6.8        | 3.1                               |
| Total aboveground                                 | 10.5                              | 19.5                     | 7.60       | 3.70                              |
| NPP (Mg ha <sup>-1</sup> y <sup>-1</sup> )        |                                   |                          |            |                                   |

From Weaver and Murphy (1990). Aboveground net primary productivity is estimated as the sum of annual litterfall plus stem increment.

reach a height of 10 m. In elfin forest, the trees and ground are covered with mosses and epiphytes, and the sierra palm can be common in some areas. The dominant species of tree in the elfin forest is *Tabebuia rigida*, and the community also includes *Calycogonium squamulosum*, *Ocotea spathulata*, *Calyptranthes krugii*, and *Miconia pachyphylla* (Brown et al. 1983; Weaver and Murphy 1990). The biomass in the elfin forest is 80 Mg ha<sup>-1</sup> (table 3-7) (Weaver et al. 1986; Olander et al. 1998). The elfin forest has also been referred to as cloud forest, because it typically occurs at elevations with persistent cloud cover, or as dwarf forest. We prefer the term “elfin forest” to describe the particularly small-stature forest growing on peaks and high ridges (Boynton 1968; Howard 1968) over “cloud forest,” because the cloud level frequently is as low as 600 m elevation in the Luquillo Mountains and thus enshrouds both colorado and palm forest types in addition to the elfin forest. Other studies in the Caribbean (e.g., Tanner 1977) have used the term “cloud forest” to describe forests that we refer to as colorado forest type.

For fuller descriptions of the species composition in the forest types, see Wadsworth (1951), Odum and Pigeon (1970), Brown et al. (1983), Lugo and Scatena (1995), Lugo et al. (1995), Weaver (1995), and Thompson et al. (2002, 2004). All of these forest communities continue to be dominated by native species while existing in a variable matrix of human and natural disturbance, species invasion, and forest regeneration following agricultural abandonment at lower elevations (Gould et al. 2006).

Tank bromeliads (mainly *Vriesia* and *Guzmania* spp.) are important components of lower canopy and understory plant communities throughout the Luquillo Mountains. They are most abundant at the highest elevations, where the forest canopy becomes more open and rainfall increases, and the same species can be both epiphytic and saxicolous (ground living). In the elfin forest on East Peak, the dominant bromeliad is *Vriesea sintenisii*, which can have a density of up to 3.2 plants m<sup>-2</sup> (Richardson et al. 2000).

The phenology of vascular plants in the Luquillo Mountains follows patterns in annual solar insolation, as has been suggested for other tropical forests (van Schaik et al. 1993). Seasonal drought has most often been assumed to be the primary abiotic factor controlling the timing of leaf flush and reproduction in tropical forests, but van Schaik et al. (1993) and Wright and van Schaik (1994) questioned that conclusion for all but the driest forests. Results from ever-wet tabonuco forest support the conclusion that leaf flush and flowering are driven by light levels in the absence of seasonal drought (figure 3-20). Leaf flush is highly synchronous in eight dominant species of understory trees and shrubs and is highest in June, when light levels are highest (figure 3-20) (Angulo-Sandoval and Aide 2000). Zimmerman et al. (2007) showed that seasonal patterns in flowering are also tied to periods of maximal light levels, with highest flowering in June, July, and August (figure 3-20). In general, flowering peaks are broad in most tabonuco forest species, with 75 percent of flowering observations in a given species spread over a 3- to 6-month period (summary of 10 years of data on flower parts falling into litter traps) (Zimmerman et al. 2007). Summed over all species, peak flowering occurs during the period of June through August, and relatively few species have peak flowering in October through March (figure 3-20). In palo colorado forest, peak flower and fruit

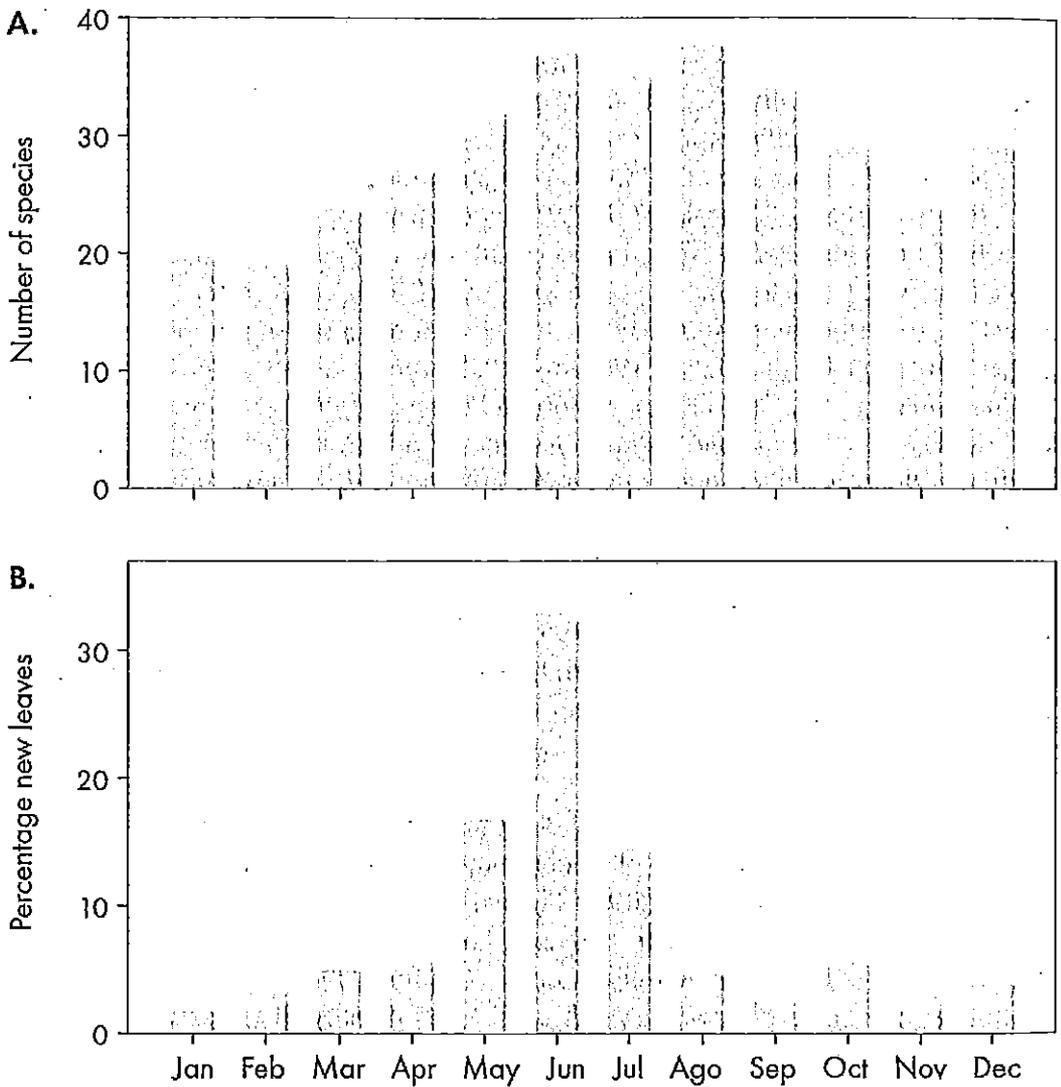


Figure 3.20 Seasonal variation in (A) flowering and (B) leaf production in the tabonuco forest type. The extent of flowering is shown as the monthly sum of the number of species in peak flower, with peak flowering for a species defined by the months containing 75 percent of all observations (Zimmerman et al. 2007). Leaf production is the mean percentage of leaf area sampled that is newly produced when sampled each month, averaged over eight understorey species (Angulo-Sandoval and Aide 2000).

production also occurs in June (Weaver and Murphy 1990). Biotic factors such as herbivory and seed predation might also play a role in promoting leaf flushing and peaks of reproductive effort (Angulo-Sandoval and Aide 2000; Angulo-Sandoval et al. 2004).

### Primary Productivity

In forests of the Luquillo Mountains, the measurement of primary productivity is complicated by frequent disturbance, leading to a mosaic of forest patches at different successional stages. A synthesis of early data across forest types collected

before Hurricane Hugo struck the Luquillo Mountains in 1989 indicates that the aboveground net primary productivity (ANPP) ranged from 2.7 to 19.5 Mg ha<sup>-1</sup> y<sup>-1</sup> (table 3-7) (Weaver and Murphy 1990; Lugo 1992). Net primary productivity peaks at mid-elevation in the Luquillo Mountains (Waide et al. 1998; Harris 2006). Forest-wide, ANPP has been estimated at 9.4 Mg ha<sup>-1</sup> y<sup>-1</sup> (Wang et al. 2003). The primary productivity of bromeliads increases with elevation and makes up 12.8 percent of ANPP in the elfin forest (Richardson et al. 2000).

The production of leaves, fruit, flowers, and small wood in litterfall often represents the majority of aboveground primary productivity (table 3-7), and thus can be used as an indicator of patterns in productivity. Litterfall in the Luquillo Mountains follows a pattern similar to that for the ANPP, declining with elevation except for the mid-elevation palm stand. In the tabonuco forest type, there is an extensive data set on leaf fall (e.g., Wiegert and Murphy 1970; Lodge et al. 1991; Zou et al. 1995; Vogt et al. 1996; Zalamea and González 2008), which averages about 57 to 80 percent of total litterfall (table 3-7). Values for annual leaf fall were consistent (ranging from 1.29 to 1.38 g m<sup>-2</sup> d<sup>-1</sup>) in measurements taken over several decades before Hurricane Hugo and among stands with different disturbance histories (Odum 1970a; Lodge et al. 1991; Zou et al. 1995). The total litterfall has varied dramatically following major named storms and hurricanes, however, with litterfall equivalent to a year or more of daily background rates occurring as a result of single hurricanes (figure 3-21). In the absence of major storms, leaf fall patterns in the tabonuco forest are correlated primarily with solar radiation, day length, and air temperature (Zalamea and González 2008). Litterfall also increases from the riparian zones to ridgetops in the tabonuco forest (Vogt et al. 1996; Beard et al. 2005).

The control of primary productivity in forests of the Luquillo Mountains is a complicated and still-unresolved issue (Waide et al. 1998). In general, wet tropical forests are thought to be limited by phosphorus or trace elements rather than nitrogen (Vitousek 1982, 1984; Martinelli et al. 1999). In the Luquillo Mountains, limitation by phosphorus or nitrogen seems unlikely, as soil phosphorus and the nitrogen concentration of the foliage are as high as or higher than in other tropical sites (figure 3-12). However, following Hurricane Hugo, the experimental addition of nutrients resulted in increased productivity in tabonuco and elfin forest plots (Zimmerman et al. 1995; Waide et al. 1998). The control of primary productivity might be more complicated than a single-factor limitation, especially at higher elevations. Episodic water shortage, frequent inundation in clouds, root inhibition because of low oxygen levels in periodically waterlogged soil, exposure to strong winds, and reduced leaf temperatures and photosynthesis at higher elevations (as discussed in other sections of this chapter) can all contribute to a limiting of the primary productivity.

### *Herbivores and Herbivory*

Herbivorous insects and a wide range of invertebrates living near the forest floor are the dominant primary consumers, as there are no large mammalian herbivores in the Luquillo Mountains. Small animals, including many birds and the omnivorous

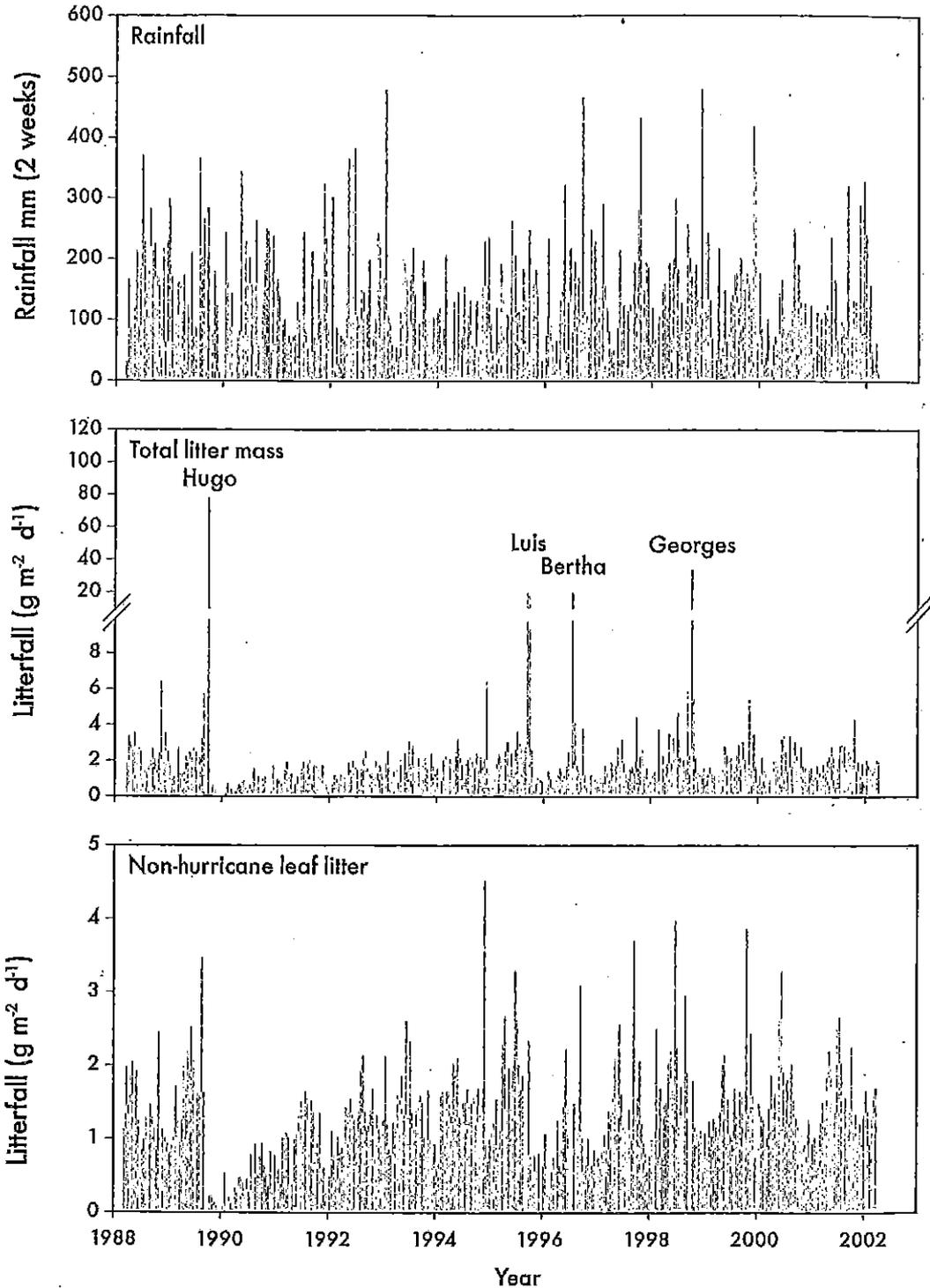


Figure 3.21 Long-term variation in (A) rainfall, (B) total litterfall, and (C) nonhurricane leaf fall collected every 2 weeks in the Bisley Experimental Watersheds of the Luquillo Mountains. Hurricanes are shown by name above the associated litterfall. Litterfall is total (leaf litter plus fruits and woody material collected in litter traps). Nonhurricane leaf fall excludes collection periods immediately following major hurricanes and does not include wood or fruits. From Scatena et al. (1996) and unpublished data.

black or roof rat (*Rattus rattus*) and Indian mongoose (*Herpestes auropunctatus*), also consume fruits and seeds (Willig and Gannon 1996). In the colorado forest type, herbivory ranges from 0.6 to 11 percent of leaf area, depending on tree species (Weaver and Murphy 1990). Canopy herbivory in the tabonuco forest type, measured as the frequency of herbivore-caused damage (6 percent) (Odum and Ruiz-Reyes 1970), is comparable to rates in other forest ecosystems (Pfeiffer 1996) and is highly correlated with the density of roaches and orthopterans (Dial and Roughgarden 1995). Schowalter and Ganio (1999) showed that canopy herbivory increased with greater canopy closure.

Many of the herbivores in the tabonuco forest type are polyphagous, eating a variety of plant species. Bark beetles (Scolytidae) are relatively common, and some are known to eat seed pods of the tree *Inga vera*, as well as dead and decaying wood; a few are known to eat live trees (Garrison and Willig 1996). Several species of grasshoppers are common in the tabonuco forest and can reach lengths of 45 mm (Garrison and Willig 1996). Synchronous leaf production among plant species in the Luquillo Mountains appears to significantly lower rates of herbivory during maximal leaf production in June (Angulo-Sandoval and Aide 2000; Angulo-Sandoval et al. 2004).

Snails and walking sticks are two well-studied groups of herbivores that are found primarily in the understory and on the forest floor in the Luquillo Mountains. Seventeen species of gastropods representing 14 genera, 12 families, and 3 subclasses have been identified (Willig et al. 1998; Bloch 2004). Eight species are arboreal grazers, six are forest floor grazers (or detritivores), and three are carnivores. Three grazer/detritivores (*Caracolus caracolla*, *Nenia tridens*, and *Gaeotis nigrolineatus*) are the most abundant snails, with mean densities in 1994–2003 (mean  $\pm$  SD) of  $0.20 \pm 0.06$ ,  $0.19 \pm 0.12$ , and  $0.07 \pm 0.04$  individuals  $m^{-2}$ , respectively. They can reach local densities of up to one to three individuals  $m^{-2}$ , depending on the extent of the disturbance and microhabitat characteristics (Willig et al. 1998; Bloch 2004). In general, *N. tridens* is most often associated with treefall gaps, whereas *C. caracolla* (figure 3-22) is more often found in undisturbed forest (Alvarez and Willig 1993). The slug *G. nigrolineatus* is one of the few species that are strongly associated with a particular plant species; it is commonly found on the leaflets of the sierra palm *Prestoea montana*. Because snails and slugs are not particularly mobile, they can be affected strongly by disturbances that affect microclimate (especially temperature and humidity) and the availability of detritus (see chapter 5). Crabs of the genus *Epilobocera* (figure 3-23) eat fruits and flowers on the forest floor. Although these crabs have an obligate freshwater life-history phase, they forage widely on the forest floor (Covich and McDowell 1996). More details on crabs are given further on in the section “Aquatic Biota and Ecosystem Processes.”

The Luquillo Mountains harbor five species of walking stick, but only one (*Lamponius portoricensis*) is common (Garrison and Willig 1996; Tilgner et al. 2000; Van Den Bussche et al. 1988). *Lamponius* is found primarily in the forest understory and is most common in areas containing one of its important food plants, *Piper glabrescens* (Willig et al. 1993). Prior to Hurricane Hugo, the density of *L. portoricensis* in a 100  $m^2$  area dominated by a treefall gap was between 0.4 and 1 individual  $m^{-2}$  (Willig et al. 1986). Because of its size, habitat associations, and

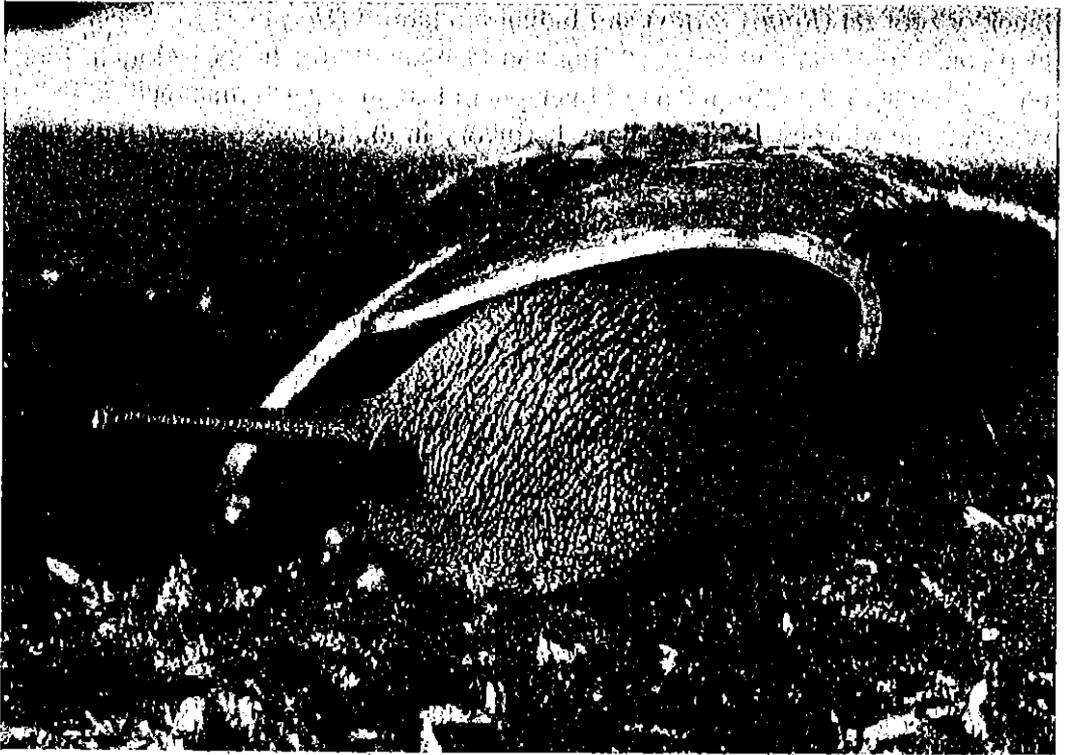


Figure 3.22 Terrestrial snails, such as *Caracolus caracolla*, are abundant generalist consumers in the Luquillo Mountains, eating fresh leaves, leaf litter, fruits, fungi, and bacteria. (Photograph by Paul Klawinski.)

food preferences, *L. portoricensis* might act as a keystone species by affecting species survivorship and nutrient cycling within light gaps (Willig et al. 1986).

Birds and bats consume fruit, seeds, and nectar, as do some insects. Birds ranging in size by over two orders of magnitude (3 to 300 g) consume a variety of plant parts. The most notable frugivorous specialists are the Scaly-naped Pigeon (*Columba tagioenas squamosa*), the Puerto Rican Spindalis (*Spindalis portoricensis*), the Puerto Rican Parrot (*Amazona vittata*), and the Antillean Euphonia (*Euphonia musica*), but fruit is an important element of the diet of many other species (e.g., the Red-legged Thrush [*Turdus plumbeus*], the Black-whiskered Vireo [*Vireo altiloquus*], the Pearly-eyed Thrasher [*Margarops fuscatus*], and the Puerto Rican Bullfinch [*Loxigilla portoricensis*]). The range of food types consumed differs among species; the Puerto Rican Parrot feeds on at least 58 plant species (Snyder et al. 1987), and the Antillean Euphonia is a mistletoe specialist (Waide 1996). Species whose diet consists primarily of seeds include the Ruddy Quail-Dove (*Geotrygon montana*), the Zenaida Dove (*Zenaida aurita*), and the Black-faced Grassquit (*Tiaris bicolor*). Nectarivores include two hummingbirds (Puerto Rican Emerald [*Chlorostilbon maugaeus*] and Green Mango [*Anthracothorax viridis*]) and the Bananaquit (*Coereba flaveola*), which forages among flowers for nectar and insects.

Bats appear to be an important part of the nocturnal food web in the tabonuco forest, although their ecological functions are not well known (Willig and Gannon

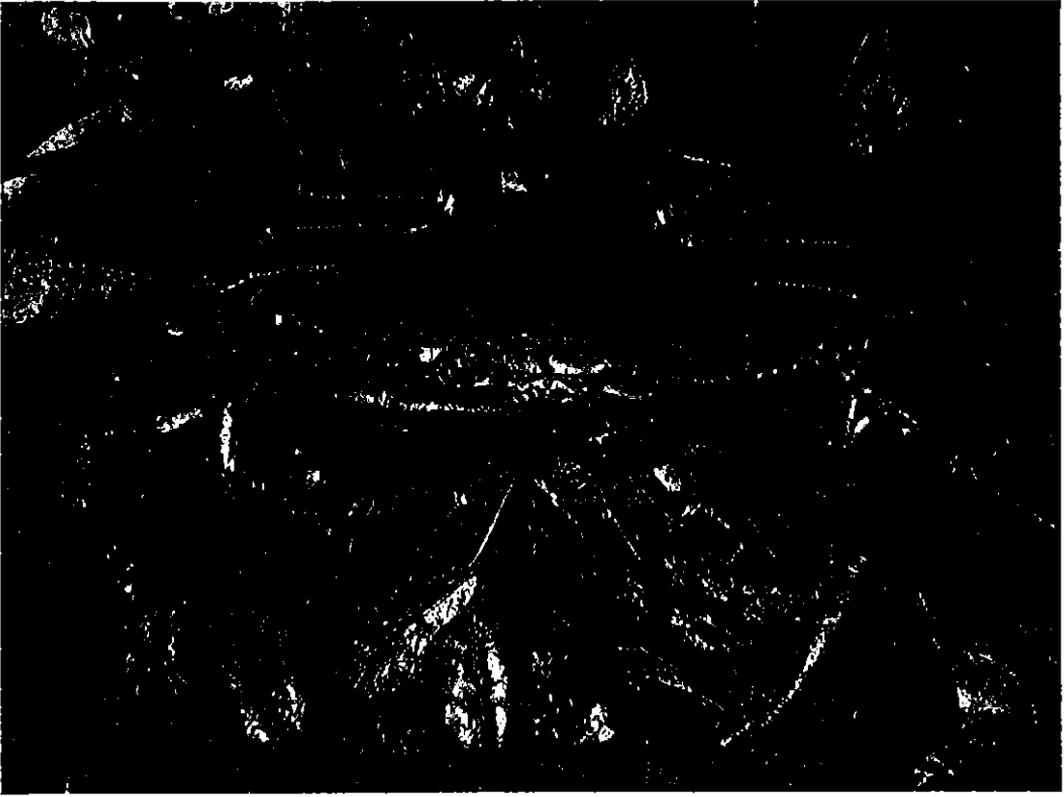


Figure 3.23 The freshwater crab *Epilobocera sinuatifrons* (Pseudothelphusidae) on the forest floor with a palm seed (*Prestoea montana*) in its left chela. (Photograph by Paul Klawinski.)

1996). Thirteen species of bats occur on the island of Puerto Rico. Of the species found in the Luquillo Mountains, one (*Monophyllus redmani*) is a nectarivore, and four (*Brachyphylla cavernarum*, *Artibeus jamaicensis*, *Stenoderma rufum*, and *Erophylla sezekorni*) are frugivores. Densities are not known for any bat species in the Luquillo Mountains, but relative abundances suggest that *A. jamaicensis* and *S. rufum* are numerically the most important species (Willig and Gannon 1996).

### **Detritivores**

Detritivores found in the litter layer of Luquillo Mountain soils include mites, millipedes, centipedes, collembolans, ants, flies, beetles, isopods, termites, and earthworms. Faunal inventories at the El Verde Field Station demonstrated that about half of the total faunal biomass was concentrated in a relatively thin layer of soil and litter (Odum 1970a; Pfeiffer 1996). Mites are the numerically dominant taxon in the litter layer of the tabonuco forest, accounting for 33 to 69 percent of all arthropods extracted from litter samples, with densities of 1,000 to 2,700 individuals  $m^{-2}$  (Pfeiffer 1996; Richardson et al. 2005). The dominance of litter invertebrates by mites is typical for tropical sites (Pfeiffer 1996). Because of their small size, however, mites account for only 1 percent of the total invertebrate biomass

(6.4 mg m<sup>-2</sup>) (Richardson et al. 2005). Larger, less common taxa such as Isoptera (termites) and Diplopoda (millipedes) are found at densities of a few hundred m<sup>-2</sup>, but they account for nearly 40 percent of the total invertebrate biomass in the litter layer of the Luquillo Mountains (table 3-8) (Richardson et al. 2005). Ants are also an important component of the litter invertebrate community, with densities of 500 to 1,200 m<sup>-2</sup> (Pfeiffer 1996; Richardson et al. 2005), but the army and leaf cutter ants found in many other tropical regions are not present in Puerto Rico. The densities of macroarthropods (such as millipedes, isopods, cockroaches, and crickets) are higher than those found in other tropical sites (Pfeiffer 1996). The population levels of various taxa found in the litter layer vary over the course of the year but do not show synchronous or strong seasonal variations. In a detailed study of monthly changes in forest floor leaf litter invertebrates at El Verde, Pfeiffer (1996) found that the numbers of Diptera and Lepidoptera increased 5- or 10-fold in June, and isopod numbers declined 4-fold. No long-term studies have been conducted to determine whether these variations in abundance represent robust seasonal trends or the response to a particular event that occurred during the study year.

Litter invertebrates are thought to be particularly important as agents of litter decomposition in tropical relative to temperate forests (Heneghan et al. 1999). Experimental manipulations restricting invertebrate access to litter suggest that up to 66 percent of litter decomposition in the Luquillo Mountains is due to forest floor invertebrates (González and Seastedt 2001). Most oribatid mites and collembolans have well-developed mouth parts capable of fragmenting organic matter while feeding on the microflora adhering to this detritus (Seastedt 1984), and they are thought to be one of the key invertebrate groups responsible for litter decomposition in the forest floor (González and Seastedt 2001).

Termites are specialist consumers of cellulose in litter and wood. There are four species of termites in the tabonuco forest (McMahan 1996), and all are xylophagous on dead standing wood, downed boles, or smaller twigs and branches. In Puerto Rico, there are no termites that cultivate fungi and their reproductive structures (i.e., mushrooms) or feed on soil, and the termite species richness is much lower in the Luquillo Mountains than the 40 to 85 species reported in Malaysia, Cameroon, or Guiana (McMahan 1996). Thus, the overall contribution of termites to plant decomposition is thought to be less in the Luquillo Mountains than in other tropical forests (McMahan 1996).

*Nasutitermes costalis* is the most evident and most widely studied termite in the Luquillo Mountains. Nests constructed by the worker caste can be up to 40 cm in diameter, have a half-life of about 4 y, and occur at a density of approximately 4.5 ha<sup>-1</sup>. The density of *N. costalis* individuals in tabonuco forest litter ranges from 86 to 95 m<sup>-2</sup>, with a dry mass biomass of 74 to 207 mg m<sup>-2</sup> (Wiegert 1970; Richardson et al. 2005). The polymorphism of workers (which are found as distinctive large and small lines; McMahan 1996) might account for the similar densities but wide differences in total biomass reported in the two studies.

Earthworms are a key component of the soil fauna and play an important role in litter decomposition, as well as in the maintenance of the physical structure and porosity of soils in the Luquillo Mountain (Lyford 1969; Camilo and Zou 1999;

Table 3.8 Average abundance and biomass of major taxonomic groups of invertebrates in the litter layer of the forest floor collected from both palm and nonpalm forests at elevations ranging from 350 to 1000 masl in the Luquillo Mountains.

| Abundance                   |                  |      | Biomass                     |                  |      |
|-----------------------------|------------------|------|-----------------------------|------------------|------|
| Individuals m <sup>-2</sup> | Percent of total |      | mg m <sup>-2</sup>          | Percent of total |      |
| Acari                       | 979              | 33.9 | Isoptera                    | 130.9            | 23.3 |
| Formicidae                  | 525              | 18.2 | Diplopoda                   | 82.0             | 14.6 |
| Collembola                  | 285              | 9.9  | Coleoptera (adults)         | 60.3             | 10.7 |
| Isoptera                    | 247              | 8.6  | Mollusca                    | 55.7             | 9.9  |
| Coleoptera (adults)         | 180              | 6.2  | Araneae                     | 39.5             | 7.0  |
| Hemiptera and Homoptera     | 112              | 3.9  | Onychophora                 | 33.3             | 5.9  |
| Diptera (adults)            | 105              | 3.6  | Formicidae                  | 30.9             | 5.5  |
| Diptera (immature)          | 99               | 3.4  | Isopoda                     | 23.6             | 4.2  |
| Isopoda                     | 79               | 2.7  | Chilopoda                   | 20.9             | 3.7  |
| Coleoptera (immature)       | 73               | 2.5  | Hemiptera and Homoptera     | 19.8             | 3.5  |
| Diplopoda                   | 67               | 2.3  | Diptera (adults)            | 13.1             | 2.3  |
| Pseudoscorpiones            | 51               | 1.8  | Lepidoptera (adults)        | 9.8              | 1.7  |
| Araneae                     | 29               | 1.0  | Blattodea                   | 8.0              | 1.4  |
| All other taxa <sup>a</sup> | 27               | 0.9  | All other taxa <sup>a</sup> | 7.6              | 1.3  |
| Chilopoda                   | 8                | 0.3  | Collembola                  | 6.9              | 1.2  |
| Lepidoptera (adults)        | 7                | 0.3  | Acari                       | 6.4              | 1.1  |
| Lepidoptera (larvae)        | 6                | 0.2  | Coleoptera (immature)       | 5.2              | 0.9  |
| Opiliones                   | 4                | 0.2  | Pseudoscorpiones            | 4.9              | 0.9  |
| Blattodea                   | 4                | 0.1  | Diptera (immature)          | 4.6              | 0.8  |
| Mollusca                    | 1                | <0.1 | Opiliones                   | 2.9              | 0.5  |
| Onchophora                  | 0                | <0.1 | Lepidoptera (larvae)        | 2.6              | 0.5  |
| Total                       | 2,889            |      | Total                       | 562.9            |      |

Modified from Richardson et al. (2005).

<sup>a</sup>"All other taxa" combines those individual taxa that either occurred more infrequently than those in the table or made up only a small biomass.

Liu and Zou 2002). Approximately 30 species of terrestrial oligochaetes have been described in Puerto Rico, and about half of them are present in the Luquillo Mountains (González et al. 2007). At least two species of Puerto Rican earthworms are endemic: *Estherella montana* (figure 3-24) and *Neotrigaster complutensis* (Borges 1996). González et al. (2007) described earthworm communities along an elevation gradient of eight forest types in northeastern Puerto Rico and

found that the density, biomass, and diversity of worms varied significantly among forest types, with the highest earthworm density in the *Pterocarpus* forest. The total earthworm biomass is highest in the elfin and *Pterocarpus* forest types. The number of earthworm species increases with elevation and is predicted by soil pH and fine root density.

In tabonuco forest, the introduced *Pontoscolex corethrurus* dominates the total earthworm density and biomass. The average density and biomass of *Pontoscolex corethrurus* in the tabonuco forest type is 95 individuals and 21.6 g of fresh biomass  $m^{-2}$  (González et al. 1996; González and Zou 1999b). This earthworm increases N availability and rates of N mineralization in soils (González and Zou 1999a). The introduced *Ocnerodrilus parki* dominates the total earthworm density in the colorado, palm, and elfin forest types (Borges and Alfaro 1997), with unknown effects on the soil structure or biogeochemical processes. Earthworm abundance in the Luquillo Mountains varies with plant species composition and soil properties. Densities and biomass are nearly twice as high in soil beneath *Dacryodes excelsa*, for example (109 worms  $m^{-2}$  and 31 g of fresh biomass  $m^{-2}$ ), than beneath *Heliconia caribea* (64 individuals and 17 g of fresh biomass  $m^{-2}$ ; González et al. 1999). Carbon and nitrogen concentrations in the top 25 cm of the soil profile also vary with the two plant communities, suggesting interactions among earthworms, vegetation, and soil carbon and nutrient status.



Figure 3.24 *Estherella* sp. is a native earthworm commonly found in the Luquillo Mountains of Puerto Rico. (Photograph by Grizelle González.)

### *Microbes and Litter Decomposition*

Much of the carbon in the food web of the tabonuco forest passes directly from plants through the detrital system rather than through herbivores (Lodge 1996). Fungi, bacteria, and a variety of invertebrates are important decomposers of detrital inputs to the forest floor (figure 3-25). Terrestrial fungi in the Luquillo Mountains typically prefer particular types of substrates, such as roots, leaves, petioles, twigs, branches, and logs (Holler and Cowley 1970; Lodge and Cantrell 1995; Lodge 1996, 1997). Furthermore, most terrestrial wood decomposers and other wood-inhabiting fungi in the Luquillo Mountains have preferences for a particular diameter of branch or bole, and sometimes for whether the bole lies on the ground or is suspended above it (Lodge and Cantrell 1995; Lodge 1996, 1997; Huhndorf and Lodge 1997). Basidiomycetes and slime molds also have preferences for whether the decomposing leaves are on the ground or suspended in the understory (Lodge and Cantrell 1995; Stephenson et al. 1999). Likewise, the majority of microfungi in decomposing leaves have strong preferences for a particular leaf species or leaf type, resulting in low similarities in microfungi communities on different leaf species that are located on the same patch of forest floor (Cowley 1970; Polishook et al. 1996; Lodge 1997; Santana et al. 2005). Microfungi that were dominant in a particular leaf species decomposed their preferred substrate faster than did microfungi feeding on "nonpreferred" leaves (Santana et al. 2005). In contrast, very few of the fungi that inhabit decaying wood show strong host preferences or specificity (Huhndorf and Lodge 1997; Lodge 1997). Microbial biomass in soil tracks litterfall, with peak microbial biomass occurring one month prior to peak litterfall (Ruan et al. 2004).

Rates of leaf, wood, and fine root decomposition are rapid in the Luquillo Mountains, as they are in many other tropical forests (La Caro and Rudd 1985; Bloomfield et al. 1993; Zou et al. 1995; Vogt et al. 1996; Sullivan et al. 1999). Leaves decompose rapidly, with 75 to 80 percent mass loss of mixed litter assemblages (tabonuco forest type) in 1 year (Zou et al. 1995). Turnover rates vary approximately twofold among species, with the sierra palm having the slowest decomposition rate among species that have been tested (La Caro and Rudd 1985; Vogt et al. 1996). In the Luquillo Mountains, as is typical elsewhere, a high lignin content is associated with slow leaf decomposition (La Caro and Rudd 1985; Bloomfield et al. 1993; Sullivan et al. 1999; Santana et al. 2005). Rates of mass loss in leaves with a high lignin content were increased by about 20 percent when the leaves were decomposed on litter mats formed by ligninolytic basidiomycete fungi (Lodge et al. 2008). Although the litter mat density is highest on steep slopes, especially in tabonuco forest (Lodge et al. 2008), leaf litter decomposition does not vary with topographic position in either the tabonuco forest type (Wiegert and Murphy 1970; Bloomfield et al. 1993; Sullivan et al. 1999; Ruan et al. 2005) or the colorado forest type (Sullivan et al. 1999).

The decomposition of plant materials is controlled by climatic conditions on a global scale (Meentemeyer 1978; Coûteaux et al. 1995; Parton et al. 2007). At the local scale, under similar climatic conditions, the litter chemistry can also regulate decomposition rates (Melillo 1982). Studies from the tabonuco forest show that although the litter chemistry clearly affects rates of decomposition, soil arthropods

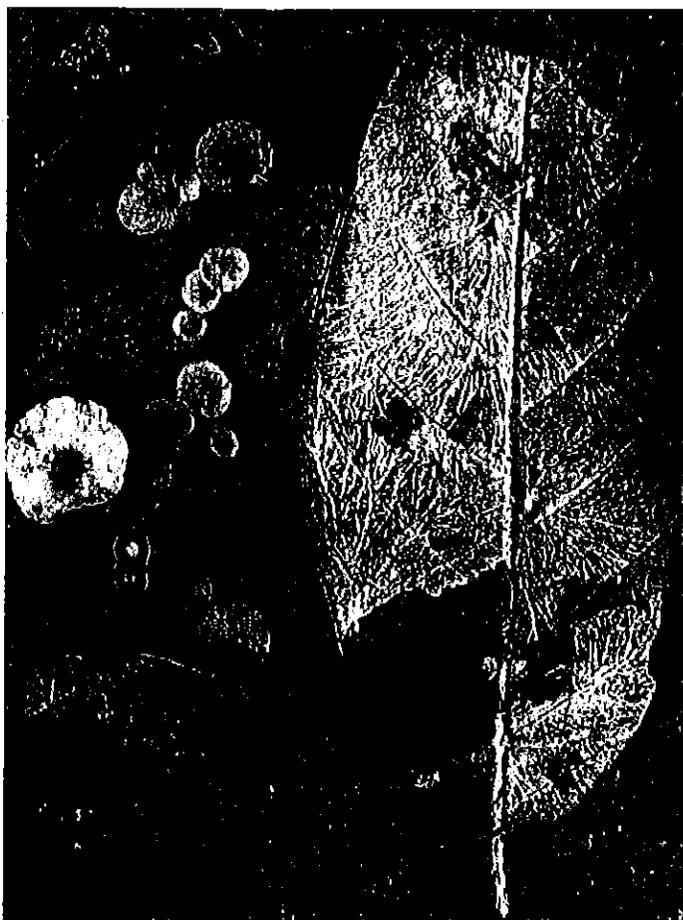


Figure 3.25 *Collybia johnstonii* is a litter decomposer fungus that binds fresh litterfall into mats; thereby reducing erosion on steep slopes; translocates phosphorus from decomposing leaves into freshly fallen leaves to build biomass; uses lignin-degrading enzymes that accelerate decomposition; alters subsequent microbial communities and processes; and is abundant in tabonuco forest under closed canopy but is sensitive to canopy opening from disturbance. (Photograph by Jean Lodge.)

and earthworms have particularly strong influences on the rates of litter decomposition in the Luquillo Mountains. González and Seastedt (2001) reported that soil arthropods were responsible for up to 66 percent of the total decomposition of *Cecropia schreberiana*. Earthworms also accelerated the decomposition of mixed-species litterbags that represented the natural species composition of the tabonuco forest (Liu and Zou 2002), and the addition of debris that facilitated fungal and invertebrate colonization resulted in increased rates of leaf decomposition (Ruan et al. 2005). Especially after hurricanes, when the number of habitats available for the amphibian *Eleutherodactylus coqui* increases, decomposition rates of litter increase within the 1 m<sup>2</sup> area used by coqui to call for mates at night, because of nutrient inputs from their feces (Beard et al. 2003).

During the decomposition process, leaf litter of all but the highest N concentration tends to increase in N concentration during the early stages of decomposition; often twofold (Lodge 1993; Parton et al. 2007). This global tendency has also been

observed in the tabonuco forest in mixed-species litterbags by Zou et al. (1995), who found that an initial 1.1 percent N concentration in leaf litter increased to a final value of 2.2 percent after 300 days of decomposition. The total N mass in absolute terms can also increase during the early stages of leaf decomposition (Zou et al. 1995) due to N immobilization by microorganisms active in the decomposition process. Absolute increases in the N content can also occur during the decomposition of wood, and this N accumulation in decaying wood and leaves is thought to be important in whole-ecosystem C and N dynamics in tabonuco forest (Lodge et al. 1994; Zimmerman et al. 1995; Walker et al. 1996; Miller and Lodge 1997; Beard et al. 2005). Similar to N, other nutrients such as P, Mg, and Ca can also increase in concentration, especially when the nutrient is in short supply in the substrate that is being decomposed. As is typical of tropical forests, phosphorus appears to be highly conserved and is translocated by basidiomycete fungi that decompose leaf litter in tabonuco forest, resulting in P contents that exceed initials during the early stages of leaf decomposition, whereas nitrogen contents only rarely exceed 100 percent of the initial amount (Lodge 1993, 1996; Lodge et al. 1994, 2008).

### *Predators*

Frogs and anoline lizards are the dominant predators in the canopy and understory of the tabonuco forest (Garrison and Willig 1996; Reagan et al. 1996), with lizards dominating the daytime food web and frogs dominating the nocturnal food web. The densities of frogs are among the highest recorded anywhere (Stewart and Woolbright 1996). Frogs are generalist predators that take mainly invertebrate prey, and they are prey to numerous vertebrate and invertebrate predators (Stewart and Woolbright 1996). Most of the frogs in the Luquillo Mountains are terrestrial breeding members of the genus *Eleutherodactylus* (family Leptodactylidae) that range throughout the forest and are generally not restricted to the vicinity of standing water. The most common is *E. coqui* (figure 3-26), which occurs across the island from lowlands to mountain tops, and which attains very high densities of two frogs  $m^{-2}$  in the mid-elevations of the Luquillo Mountains (Stewart and Woolbright 1996). Reproduction in *E. coqui* is highest in the summer, and the total population numbers peak with high juvenile densities in the winter. *Eleutherodactylus coqui* is limited by retreat and nest sites (Stewart and Pough 1983). Locally high densities are associated with concentrations of suitable retreat sites including fallen leaves of *Prestoea montana* and *Cecropia schreberiana*, and density within the forest can be patchy because of changes in the plant community following disturbances such as treefalls (Woolbright 1996).

Of the other 15 species of Puerto Rican *Eleutherodactylus*, 12 were historically found in the vicinity of the Luquillo Mountains, although all were less numerous and more restricted in range than *E. coqui* (Rivero 1978). At least four of these have undergone widespread local extinctions in the past 40 years, consistent with the global pattern of amphibian declines, and at least two of these species are probably extirpated from the Luquillo Mountains (Woolbright 1997). The remaining frog community generally varies with elevation and cover type (Drewry 1970; Rivero

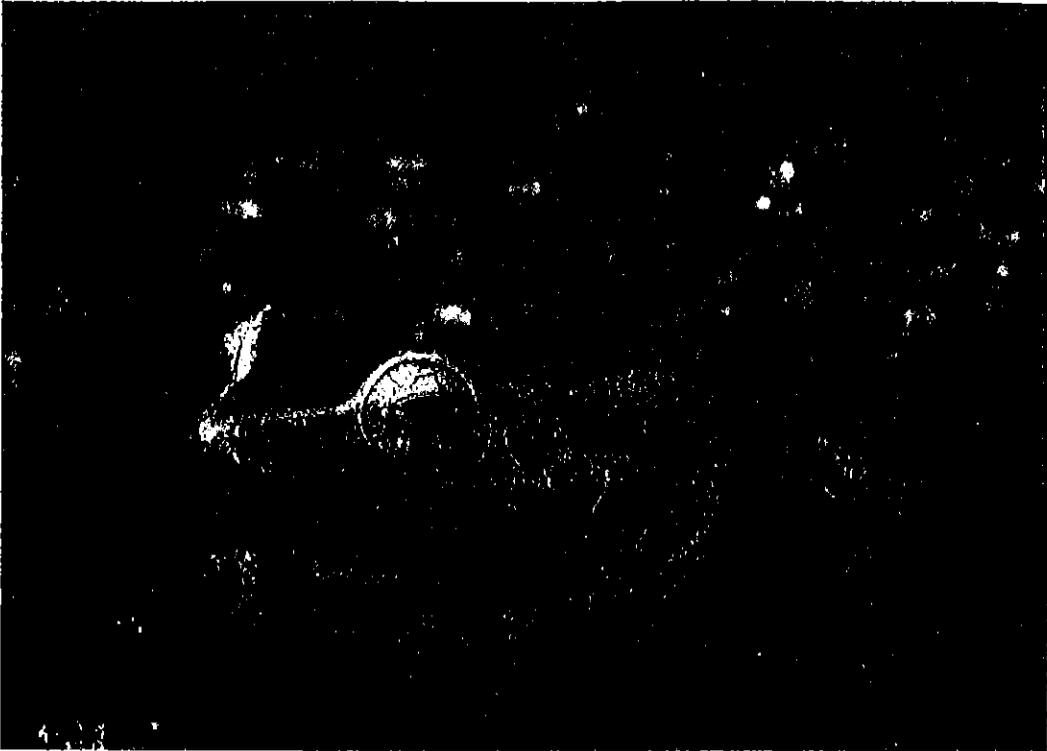


Figure 3.26 A coquí (*Eleutherodactylus coqui*), the abundant tree frog in the Luquillo Mountains of Puerto Rico. (Photograph by Jerry Bauer.)

1978). One aquatic breeding native, *Leptodactylus albilabris*, is also common in the Luquillo Mountains, building bubble nests in puddles. The only nonnative amphibian commonly seen in the Luquillo Mountains is the cane toad, *Bufo marinus*, which moves into the forest along roads.

Anoline lizards are conspicuous, abundant, and well-studied predators of insects on Caribbean islands, and they are particularly important in daytime food webs in the Luquillo Mountains. Seven species of anole are found in the Luquillo Mountains, three of which (*Anolis occultus*, *A. krugi*, and *A. cristatellus*) inhabit edges and openings in the forest (Reagan 1996). The Puerto Rican giant anole (*A. cuvieri*) is a rare, canopy-dwelling species that feeds on snails, butterfly and moth larvae, beetles, walking sticks, plant material, and other anoles (Reagan 1996). Three other species are common within tabonuco forest and are specialized foragers found on small branches and twigs (*A. stratulus*), tree trunks into the crown (*A. evermanni*), and tree trunks and the ground (*A. gundlachi*). On Caribbean islands where insectivorous mammals and birds are more rare than in continental sites, anoles are among the most important higher-order consumers and have significant effects on the structure of terrestrial food webs (Schoener and Toft 1983; Schoener and Spiller 1987; Reagan 1996).

Surveys from canopy towers at El Verde found that *A. stratulus* was extremely abundant in the forest canopy and *A. evermanni* used the canopy frequently (Reagan 1996). Individual *A. stratulus* occupy small ellipsoidal home ranges/territories (males only) layered within the forest canopy. This three-dimensional

habitat partitioning is unique among terrestrial vertebrates and allows *A. stratulus* to achieve the highest population densities of any lizard species (Reagan 1992). *Anolis gundlachi* was most abundant near the ground (Reagan 1992). The combined abundance of these three species is approximately 2.5 individuals  $m^{-2}$  (Reagan 1996), with *A. stratulus* contributing more than 80 percent of the individuals. Repeated population estimates of *A. stratulus* in different seasons and years found relatively stable population numbers, consistent with data for other West Indian anoles (Schoener 1985).

The diets of the four common forest anoles included 34 animal orders, 20 of which were insects (Reagan 1996). The most common prey in *A. gundlachi* stomachs were ants, but Lepidoptera larvae, crickets, and earthworms constituted the largest volume of prey consumed. *Anolis gundlachi* consumed several taxa of arthropods inhabiting soil litter that were not eaten by the other two species. *Anolis evermanni* is a generalist, foraging on tree trunks, in the canopy, and on rocks in streams beds. All *A. evermanni* consumed ants, Homoptera, and spiders regardless of where they foraged, but individuals foraging in streams also ate significant numbers of seeds, as well as insects that dwell on the surface of water. Ants were also the most common prey for *A. stratulus*, followed by Homoptera and Diptera, but, by volume, planthoppers (Homoptera) constituted nearly 50 percent of their stomach contents. Stomachs of *A. stratulus* held fewer insects during the drier part of the year (February–May), suggesting the possibility of food limitation for this species (Reagan 1996; see also Licht 1974; Andrews 1976; Sexton et al. 1976; Lister 1981). Reagan (1996) estimated the total daily intake of insects for these three species at around 450,000 individuals  $ha^{-1}$ .

Nine nonanoline reptile species are found throughout Puerto Rico in moist forest at elevations of up to about 600 m (Thomas and Kessler 1996). This assemblage includes two typhlopoid blind snakes (*Typhlops platycephalus* and *T. rostellatus*), one amphisbaenian (*Amphisbaenia caeca*), an anguid lizard (*Diploglossus pleei*), two geckos (*Sphaerodactylus macrolepis* and *S. klauberi*), the Puerto Rican boa (*Epicrates inornatus*), and two colubrid snakes (*Alsophis portoricensis* and *Arrhyton exiguum*; see Thomas and Kessler [1996] for photographs). Except for the boa and one of the colubrids (*Alsophis portoricensis*), which forage in trees, these species prey on arthropods in the soil and leaf litter. The effect of nonanoline reptiles on their prey species is unknown, as neither abundances nor foraging rates are known for these species (Thomas and Kessler 1996). However, information on their diet indicates some degree of specialization, especially for *Typhlops* (termites and ants), *Diploglossus* (millipedes), and *Alsophis* and *Arrhyton* (lizards).

Spiders are the dominant predators on the forest floor, with a mean annual density (356  $m^{-2}$ ) that is much higher than in most other temperate or tropical forests (Pfeiffer 1996). Predaceous beetles, bugs, and centipedes are also found on the forest floor (table 3-8), but relatively little is known of their densities or feeding habits.

By their diversity and abundance, birds are among the most important consumers in the Luquillo Mountains. The avifauna of Puerto Rico, including on the islands of Vieques, Culebra, Mona, Monito, and Desecheo and on smaller cays and islands, includes a total of 275 extant species, 36 of which are introduced (Raffaele et al.

1998). Approximately 136 bird species, including 14 endemics and 31 introduced species, breed in Puerto Rico. Sixty-six species of land birds occur in the Luquillo Mountains, and two extinct (*Aratinga chloroptera*, Psittacidae; *Corvus leucognaphalus*, Corvidae) and three fossil (*Tyto cavatica*, Tytonidae; *Geotrygon larva*, Columbidae *Corvus nasicus*, Corvidae) species might also have occurred there (Waide 1996).

In the tabonuco forest type of the Luquillo Mountains, long-term studies at the El Verde Field Station provide information about the structure and dynamics of the avian community and about the importance of birds as consumers (Waide 1996). The most common species in mature tabonuco forest include the Bananaquit, the Black-whiskered Vireo, the Ruddy Quail-Dove, the Scaly-naped Pigeon, the Puerto Rican Tanager (*Nesospingus speculiferus*), the Puerto Rican Tody (*Todus mexicanus*; figure 3-27), and the Puerto Rican Emerald (Waide 1996). Seven of the fifteen most common species are endemic to Puerto Rico. Comparisons of counts conducted in 1964–1966 and 1981–1982 found both increases (Black-whiskered Vireo,

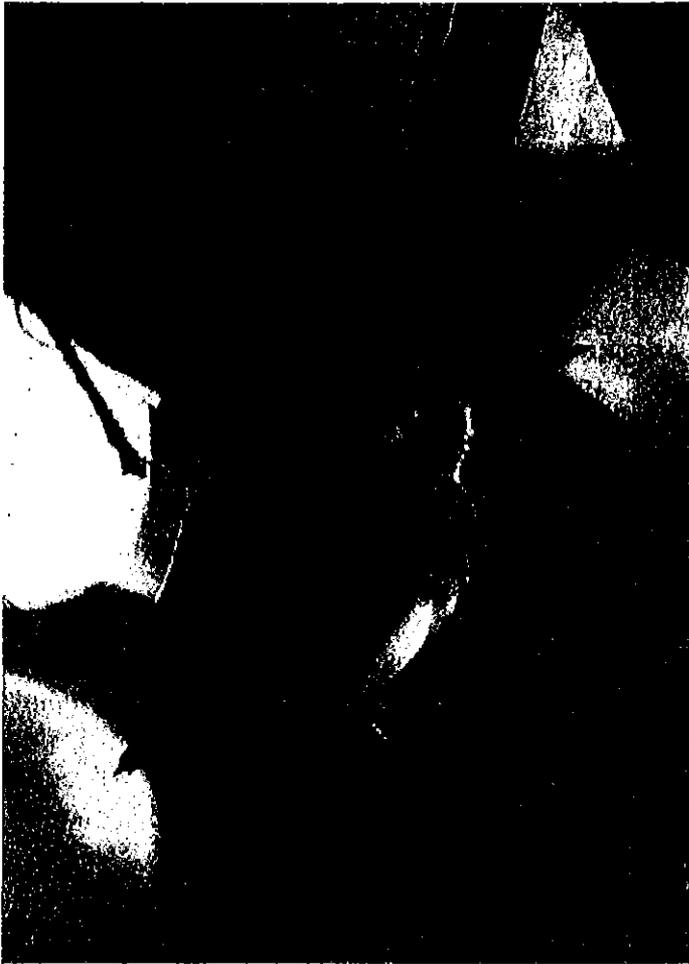


Figure 3.27 The Puerto Rican tody (*Todus mexicanus*), an understory insectivore and representative of the family Todidae, endemic to the West Indies. (Photograph by Jerry Bauer.)

Ruddy Quail-Dove, Scaly-naped Pigeon, Puerto Rican Spindalis) and decreases (Pearly-eyed Thrasher) in abundance during a period of relatively stable forest composition and structure. The distribution of species among feeding guilds differs from continental tropical avifaunas by having a smaller proportion of insectivores (16.7 percent) and a larger proportion of frugivores (33.3 percent) (Waide 1996). The reduced number of insectivorous species might reflect competition from abundant frogs and lizards in tabonuco forest. High numbers of lizards also lead to the occurrence in the Luquillo Mountains of an endemic predatory bird specializing on lizards as prey (the Puerto Rican Lizard Cuckoo [*Coccyzus vieilloti*]).

In tabonuco forest, the introduced black rat is common and can reach densities of up to 40 individuals  $\text{ha}^{-1}$  (Snyder et al. 1987). This contrasts with data from the palo colorado forest type, where rats can attain densities of 281 individuals  $\text{ha}^{-1}$  (Willig and Gannon 1996). Black rats feed on the forest floor as well as in the trees, consuming fruits from a variety of early (e.g., *Cecropia*) and late (e.g., *Dacryodes*) successional trees, and they also eat snails, fungi, insects, lizards, and frogs. Although more rare than the black rat, the small Indian mongoose is similarly omnivorous (Willig and Gannon 1996). Because of their abundance, size, metabolic rate, and omnivorous food habits, both of these introduced mammals likely have altered the structure and dynamics of food webs and are now integral components of the animal community in the Luquillo Mountains and the entire island of Puerto Rico.

### ***Bromeliads as Specialized Terrestrial Habitats***

In the terrestrial environment, bromeliads act as widely dispersed aquatic microcosms with both terrestrial and aquatic animal communities. Within a single bromeliad, habitats range from accumulations of dry leaf litter to the truly aquatic phytotelmata at the base of the bromeliad leaves. Bromeliads are colonized by a variety of detritivorous animals, including isopods, millipedes, cockroaches, and beetles. Dipteran larvae such as crane flies and mosquitoes are found in the pools of water trapped by the bromeliads. Some of the animals found in bromeliads, such as the pseudoscorpion *Macrochernes attenuatus* and the hydrophilid beetle *Omicrus ingens*, are endemic to bromeliads and to Puerto Rico (Hansen and Richardson 1998; Richardson 1999). Bromeliads and their associated fauna are tightly linked to atmospheric processes and thus can be particularly sensitive to climate change (Lugo and Scatena 1992).

### ***Terrestrial Food Web***

Trophic interactions among terrestrial species are best understood for the tabonuco forest, about which Reagan and Waide (1996) summarized 4 decades of research at El Verde Field Station. More than 2,600 animal species are known from El Verde, and more than 2,500 of these are invertebrates (Garrison and Willig 1996; Pfeiffer 1996). This number of invertebrates is likely an underestimate, as not all species have been described. Five interrelated features characterize the terrestrial food web at El Verde (figure 3-28) and distinguish it from food webs in similar, continental tropical forests. These features are the absence of large herbivores and predators, low faunal richness, a superabundance of frogs and lizards, discontinuities within

the food web, and frequent disturbances. The first three of these distinctive features arise either directly or indirectly from Puerto Rico's geographic position as an island in the Caribbean basin and its past history of isolation.

Because most animal species occurring in Puerto Rico arrived through the process of overwater dispersal from South America, the present fauna of the island lacks those groups that have poor dispersal capabilities, including large mammalian herbivores (e.g., deer, tapirs) and predators (e.g., jaguar) and large frugivorous birds (e.g., toucans, guans, curassows, chachalacas, and turkeys). The absence of these taxa has significant effects on the structure of the food web, in which the largest predators are relatively small and include birds, introduced mammals, and a reptile (figure 3-28). The proportion of top predators is smaller than in continental food webs, which might reduce the top-down control of consumer populations.

The Luquillo Mountains have fewer animal species overall than mainland tropical forests do (Waide 1987; Reagan et al. 1996). Precise comparisons are difficult because of the lack of data from mainland sites representing the same life zones as in the Luquillo Mountains. The relatively small number of species affects the structure of the terrestrial food web in at least two ways. Reduced interspecific competition leads to habitat generalization in the existing species (Waide 1996). Moreover, the relatively small number of species limits the number of possible feeding interactions within the food web, with potential effects on food chain length and connectivity that would not be found in more species-rich communities.

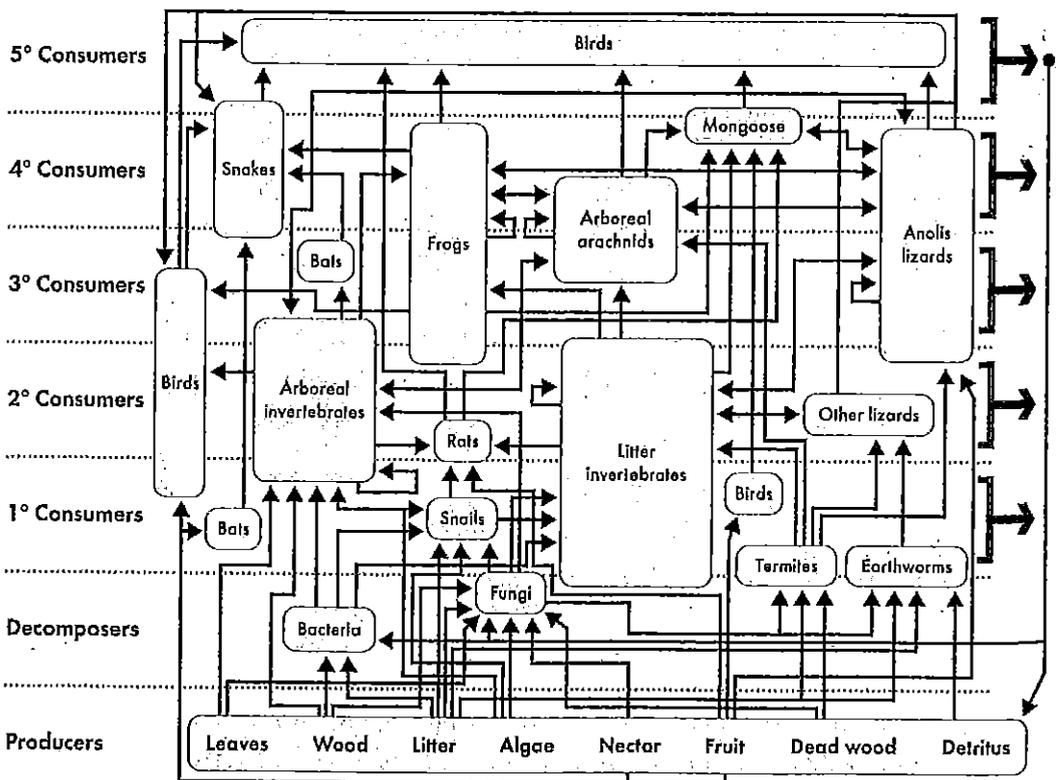


Figure 3.28 Terrestrial food web of the subtropical wet forest in the Luquillo Mountains. Redrawn from Reagan and Waide (1996).

The absence of large predators in Puerto Rico is thought to be responsible for the extremely high densities of small frog (*Eleutherodactylus*) and lizard (*Anolis*) predators that are found in tabonuco forest (Reagan et al. 1996). The abundance of these small predators has a number of potential consequences for the structure of the animal community and for functional attributes of these forest ecosystems such as rates of herbivory and nutrient cycling. Small, ectothermic predators have higher conversion efficiencies, can potentially support longer food chains and more levels of predators, and can potentially promote reciprocal predation (feeding loops) (Formanowicz et al. 1981; Reagan et al. 1996). Angulo-Sandoval et al. (2004) have also proposed that the high densities of frogs and lizards in the tabonuco forest type have led to a suppression of invertebrate herbivores and lower rates of herbivory than in continental communities where larger predators occur (e.g., Panama). Dial and Roughgarden (1995) provided support for this hypothesis by showing that the exclusion of lizards increased the density of invertebrate herbivores and the frequency of herbivory. Similarly, Beard et al. (2002, 2003) showed that the experimental manipulation of coqui populations directly affects herbivory rates by invertebrates.

Both spatial and temporal discontinuities in the animal community lead to compartmentalization of the food web. Distinct groups of animals inhabit aquatic (see below) and terrestrial habitats, which minimizes consumption between groups. The vertical stratification of foraging by species in the terrestrial community structures connections within the food web. The dependence on live or dead sources of energy separates the food web into predatory and detrital compartments, with the vast majority of carbon flowing through the detrital compartment and mycorrhizal fungi (Lodge 1996; Pfeiffer 1996). The food web at El Verde is distinguished by differences in the activity times of the most abundant predatory taxa that separate the roles that they each play within the food web. *Eleutherodactylus* are primarily nocturnal, and *Anolis* are diurnal (Reagan et al. 1996; Stewart and Woolbright 1996). This is reflected in their respective diets and, to an even greater degree, in the diets of the bird and snake predators that feed on them. This separation in activity times divides the food web into compartments (subwebs) and increases the complexity of the trophic structure in tabonuco forest.

Frequent disturbance in the Luquillo Mountains might also structure the food web. The relative scarcity of large predators (which are more likely to go extinct than small predators in a dynamic disturbance environment [Pimm 1982]), the prevalence of omnivory, and the tendency toward donor-controlled predator-prey systems are all characteristics of the El Verde food web that might be affected by frequent disturbance (Reagan et al. 1996). Frequent disturbance-driven changes in the habitat structure and microenvironment work in favor of habitat generalists. All of these factors suggest a strong relationship between the disturbance regime of the Luquillo Mountains and the structure of the food web.

### ***Terrestrial Elevational Gradient***

One of the most striking features of the elevational gradient in the Luquillo Mountains is the sharp decline in tree stature from the base of the mountain to the summit. In the elfin forest of the Luquillo Mountains, trees seldom exceed 5 m in height, but

they are commonly 25 m or taller at lower elevations (figure 3-18) (Waide et al. 1998). Aboveground biomass also tends to decrease with elevation in dicotyledonous communities in the Luquillo Mountains, as does net primary productivity (see the section "Terrestrial Primary Producers" above; table 3-7).

The underlying mechanisms that reduce forest stature with elevation have been the subject of considerable debate but little consensus (Bruijnzeel and Veneklaas 1998). Mineral nutrient deficiencies, low rates of transpiration, waterlogged soils, wind stress, and reduced nutrient uptake and root damage from polyphenolic inhibition at the soil-root interface have all been suggested as possible causes (Odum 1970b; Grubb 1977; Tamer 1977; Lawton 1982; Weaver and Murphy 1990; Bruijnzeel et al. 1993). Grubb (1977) suggested that although anoxia can affect tropical montane forest plant communities, the primary stress would be induced by the low pH and low soil nutrient levels caused by high rates of nutrient leaching.

Our data do not provide a convincing explanation for the stunted vegetation on the peaks of the Luquillo Mountains. There is no compelling evidence of direct nutrient or pH limitation in the elfin forest. Levels of N and P in the soil are somewhat higher than at lower elevations, the pH is unchanged, and base cation levels are only marginally lower (table 3-5). Even though standing stocks of N are higher in the elfin forest soils, concentrations ( $\text{mg g}^{-1}$ ) of N and Ca in foliage are significantly lower in the elfin forest than in the colorado forest type. When expressed on a unit area basis, however, the nutrient levels are comparable. Understanding the extent to which nutrient availability limits the productivity and stature of elfin vegetation is further complicated by the fact that there can be significant foliar uptake of nutrients from precipitation or uptake by fine roots found in the canopy (Nadkarni 1981).

The number of tree species decreases with increasing elevation, with about 170 species in the tabonuco forest type, 90 in the colorado forest type, and 40 in elfin forest (Weaver and Murphy 1990). The mean height, dbh, and basal area per hectare also tend to decrease with increasing elevation, whereas the stem density increases (White 1963; Weaver and Murphy 1990).

The composition of tree communities along the elevational gradient in the Luquillo Mountains suggests that they have a complicated origin and do not match either continuous or community unit distributional models. A recent study examined changes in the vegetation community structure with elevation by sampling along three transects (0.1 ha plots every 50 m in elevation) in different watersheds of the Luquillo Mountains (Barone et al. 2008). Based on an analysis of the clustering of the elevational ranges and modes of tree species, the data showed that the upper boundaries of species ranges were significantly clustered on the two longest transects, whereas lower boundaries were not. These changes in the community structure corresponded roughly to the broad forest types discussed above (tabonuco, palo colorado, palm, and elfin), but there was also significant nestedness among the plots because some species had broad elevational ranges. These patterns thus do not match either continuous or community unit distributional models along the elevational gradient, as has been seen in other tropical mountains (Ashton 2003).

Elevation has a marked indirect effect on termite abundance in the Luquillo Mountains through its effects on plant communities and litter type. Termites are absent from the thinly distributed litter of the high-elevation elfin forest, but they are abundant ( $442 \text{ m}^{-2}$ ) in litter under palm stands at all elevations (Richardson et al. 2005). Termites are vulnerable to predation and dehydration, and the physical conditions in moist layers of palm litter might provide the necessary protection. Ants and most other taxonomic groups show similar patterns of decline in abundance with increasing elevation, but they consistently have their highest densities in palm litter in all forests. These comparisons of palm and nonpalm litter invertebrate communities up the elevation gradient suggest that community composition is determined more by the forest type than by the direct climatic effects of decreasing temperature and increasing rainfall (Richardson et al. 2005).

The distribution of birds with elevation in the Luquillo Mountains has not been studied systematically. However, some species, such as the Puerto Rican Parrot and the Elfin Woods Warbler (*Dendroica angelae*), do favor higher-elevation forests.

The species richness and abundance of decomposer basidiomycetes and pyrenomycetes decline at higher elevations. The few basidiomycete species that are found at high elevations show an interesting biogeographic affinity with North American taxa, and in some cases the same species is found in both the Luquillo Mountains and North America (Baroni et al. 1997). As noted above, the overall tree species richness also declines with elevation, and the decline in fungal diversity might be a reflection of the declining numbers of potential hosts. Many ascomycetous fungi and their asexual stages are restricted to colonization of the dead leaves of particular trees (Laessøe and Lodge 1994; Lodge et al. 1995; Polishook et al. 1996; Lodge 1997; Santana et al. 2005). Although some decomposer basidiomycetes are widespread among the ecological zones of the Luquillo Mountains, many species are largely restricted to a particular life zone, as confirmed by terminal restriction fragment length polymorphism analysis (Lodge et al. 2008; Cantrell et al., in press). In contrast, a greater proportion of bacteria are shared among forest types (Cantrell et al., in press). Although total soil microbial C does not differ between the elfin and tabonuco forests (Zou et al. 2005), the total soil C does increase with elevation (Wang et al. 2002), and soil microbial communities also differ significantly among forest types along the elevation gradient (Cantrell et al., in press).

The invertebrate community living in the phytotelmata of bromeliads shows striking shifts in diversity with elevation, with the highest diversity at mid-elevation in the palo colorado forest type (Richardson 1999; Richardson et al. 2000). Species richness is high in tabonuco forest (167 species), peaks in mid-elevation colorado forest (198), and is significantly lower in elfin forest (97) (Richardson et al. 2000). Typical litter detritivores, such as isopods, millipedes, and cockroaches, were reduced in abundance in the elfin forest, as were larvae of the tipulid fly *Trentepohlia dominicana*. Scirtid beetle larvae (*Scirtes* sp.), the most abundant species in the two lower-elevation forest types, were absent from the elfin forest, as were hydrophilid beetles, *Omicrus ingens*, the nauidid worm *Aulophorus superterrenus*, and larvae of the large predatory elaterid beetle *Platycrepidius* sp. In general, invertebrate predators were absent or few in number in

the elfin forest (Richardson 1999). Changes in microclimate and nutrient conditions in the bromeliad phytotelmata are probably responsible for the changes in animal diversity with elevation. The colorado forest might provide the most favorable conditions for the survival of both larval and adult invertebrates, as it has lower wind velocities than the elfin forest, higher rainfall than the tabonuco forest, and an intermediate level of anoxia in the phytotelmata. Bromeliads in the colorado forest type are thus less likely to dry out, allowing species with lower abundance and drought intolerance a greater chance of persistence during dry periods.

## Aquatic Biota and Ecosystem Processes

### *Primary Producers and Stream Energy Budgets*

Primary production by benthic algae and inputs of leaves, fruits, and other material from the terrestrial landscape form the basis of stream food webs in the Luquillo Mountains. Where light limits primary productivity, as is often the case, organic matter of terrestrial origin (e.g., dissolved organic carbon in groundwater, leaf litter from the adjoining forest) fuels much of the stream metabolism (Ortiz-Zayas et al. 2005). Algae present in streams of the Luquillo Mountains most commonly include diatoms, green algae, and blue-green algae (Pringle 1996). Macrophytes are typically absent, except *Elodea*, which is found at low elevations. Long strands of filamentous green and blue-green algae are observed periodically, but typically few algae are visible in the streambed (Pringle 1996; Pringle et al. 1999). Frequent high-discharge events scour the streambed and remove algae from rock surfaces. In between high-discharge events, herbivory by atyid shrimps (middle- to high-elevation streams) or snails (lower-elevation streams) plays a key role in maintaining the algal standing crop at low levels (Pringle and Blake 1994; Pringle et al. 1999; March et al. 2002).

The net primary productivity is low in small streams of the Luquillo Mountains, and it is often undetectable with whole-stream measures of respiration and productivity (Buzby 1998; Merriam et al. 2002; Ortiz-Zayas et al. 2005). Ortiz-Zayas et al. (2005) conducted an extensive study of the primary productivity and respiration in the Río Mameyes, with 8 to 10 measurements at each of multiple sites over 2 years. They found that the rates of oxygen production were low in headwaters of the Río Mameyes ( $<70 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ) throughout the year, but they were higher (453 to  $634 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ) in the middle and lower reaches. Ratios of productivity:respiration (P/R) were typically about 0.2, with only one station exceeding a P/R of 1 for only a few of the dates sampled (Ortiz-Zayas et al. 2005). The Río Icacos and other streams in areas with quartz diorite bedrock support particularly few attached algae, owing to the very sandy and unstable streambed, but throughout the Luquillo Mountains there is little evidence of significant primary production in streams.

Atyid shrimps are key grazers in stream ecosystems of the Luquillo Mountains, significantly affecting the algal standing crop, the community structure, and the spatial heterogeneity of algal communities (Pringle 1996; Pringle et al. 1999).

Because of their size relative to insects, shrimp can affect the algal standing crop and community structure on spatial and temporal scales that are quite different from those of smaller invertebrates. Algal biovolumes can be as high as  $26 \text{ cm}^3 \text{ m}^{-2}$  in sunny spots where consumption rates by atyid shrimp are low or in streams with few *Atya*, but they are typically  $0.03$  to  $0.18 \text{ cm}^3 \text{ m}^{-2}$  in other environments (Pringle 1996). Grazing by shrimp and light levels interact to determine this heterogeneity in the algal biovolume. In Quebrada Toronja, a stream with high shrimp densities near the El Verde Field Station, the algal standing crop in the margins of pools with direct sunlight was 140-fold greater than that in deeper areas where atyids foraged; in shaded pools, the standing crop in pool margins was only five times that in deeper areas (Pringle 1996). Shrimps also influence the algal community composition, maintaining low-diversity diatom-dominated communities where they graze; ungrazed pool margins have significantly greater taxonomic richness and structural complexity (figure 3-29).

Different phenological patterns of leaf fall among native and nonnative riparian species provide a spatially and temporally heterogeneous series of alternative energy sources for stream microbes and detritivores. Relatively little is known about how qualitative differences in the nutrient content and leaf chemistry might drive variability in the food quality of different species of riparian leaves. In the Luquillo Mountains, more than 40 species of riparian trees can supply leaf litter at various times (Reed 1998). Native riparian species such as tabonuco, *Cecropia schreberiana*, and sierra palm are commonly distributed along stream banks in the Luquillo Mountains.

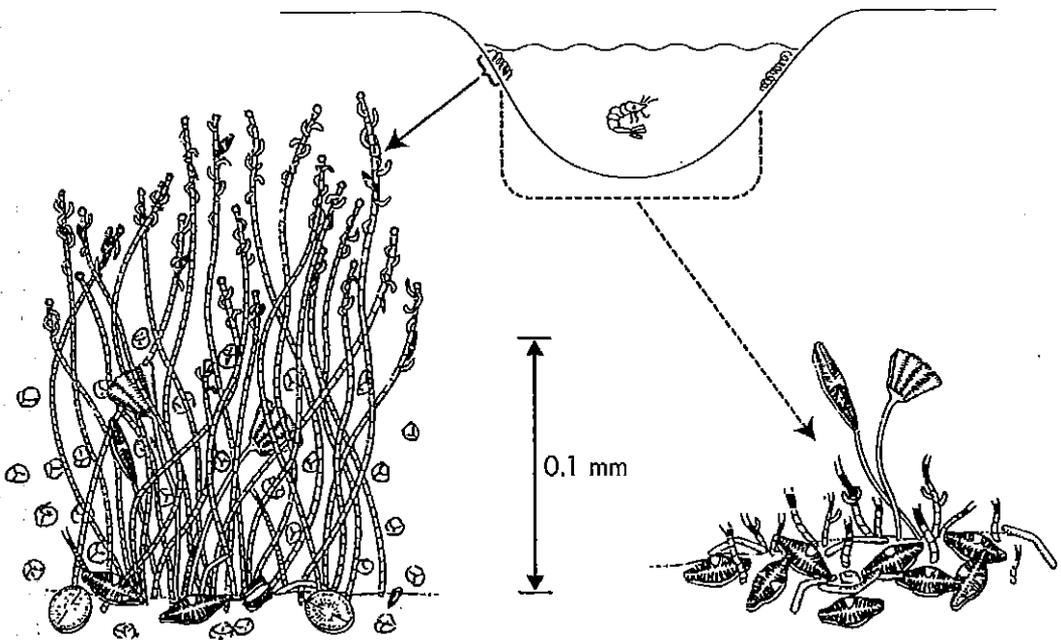


Figure 3.29 Effects of shrimp on benthic algal community composition. Where shrimp have access to the streambed, most of the algal flora is small prostrate diatoms. On pool edges where shrimp do not forage, filamentous algae dominate. Modified and redrawn from Pringle (1996).

### *Aquatic Consumers and Decomposers*

Decapod crustaceans (shrimps and crabs) are the most important group of consumers in streams of the Luquillo Mountains. They include four atyid shrimps (including the common *Atya lanipes*), the common xiphocaridid (*Xiphocaris elongata*), various predatory palaemonid shrimp of the genus *Macrobrachium*, and the crab *Epilobocera sinuatifrons* (Covich and McDowell 1996; Zimmerman and Covich 2003). Each of these crustaceans is omnivorous and displays multiple methods of feeding as an adult. For example, *Atya lanipes* switches between filtering fine particles from flowing water and scraping/gathering benthic algae and fine particulate organic matter (FPOM), and *Xiphocaris elongata* shreds coarse organic matter and also scrapes and gathers benthic algae and FPOM (Pringle et al. 1993; Pringle 1996; Cowl et al. 2001; March et al. 2001). The feeding habits of atyid and xiphocaridid juveniles are poorly known but are thought to be similar to those of adults. Stable isotopic analysis indicates that algal-based resources, as well as detrital food sources, are important to stream consumers, even in small forested headwater streams (March and Pringle 2003). The results of a two-source mixing model suggest that shrimps relied more on algal-based carbon resources than terrestrially derived resources at three sites along the Río Espíritu Santo (March and Pringle 2003).

Fishes and snails are also important consumers in many of the streams of the Luquillo Mountains, particularly the algivorous goby (*Sicydium plumeri*), the predatory mountain mullet (*Agonostomus monticola*), and herbivorous neritid snails (*Neritina* spp.) (Erdman 1986; Nieves 1998; Blanco 2005). Aquatic invertebrates other than decapods and snails include a low diversity of aquatic insects (e.g., baetid and leptophlebiid mayflies, hydroptilid caddisflies, and libellulid dragonflies), as well as miscellaneous invertebrates such as aquatic worms, copepods, and mites (Buzby 1998; Greathouse and Pringle 2006). There are no species of stoneflies in the streams of the Luquillo Mountains, and the total known richness of aquatic insects is approximately 60 to 70 species (Covich and McDowell 1996).

Typical mean densities and biomass of aquatic invertebrates within the Luquillo Mountains range from ~200 to 6,000 individuals  $m^{-2}$  and ~0.3 to 10 g ash-free dry mass  $m^{-2}$  (Greathouse and Pringle 2006). Densities and biomass reach higher values (~25,000 individuals  $m^{-2}$  and ~25 g ash-free dry mass  $m^{-2}$ ) when streams draining the Luquillo Mountain enter the lowlands of the coastal plain (Greathouse and Pringle 2006). Typically, aquatic invertebrate biomass is dominated by shrimps, crabs, and snails. Insects and other invertebrates generally account for only a few percent of the total standing stock of aquatic invertebrates, although particular habitats, such as riffles, sometimes have high densities of nondecapod, nongastropod invertebrates (Merriam et al. 2002; Greathouse and Pringle 2006).

All of the native shrimps, fishes, and neritid snails of the Luquillo Mountains have a marine stage in their life cycle, and thus migrations up and down the drainage basin are an important feature of the stream community (Pringle 1997; Holmquist et al. 1998; March et al. 1998; Nieves 1998; Benstead et al. 2000; Pyron and Covich 2003; Blanco and Scatena 2005). The life cycles of shrimps, neritid snails, and *Sicydium* (gobies) are categorized as freshwater amphidromous (adults breed in

freshwater, larvae passively drift to estuary before returning to freshwater as juveniles). The American eel (*Anguilla rostrata*) is catadromous (migratory to the sea for breeding). Detailed life cycles of other fishes, such as mountain mullet, are poorly known, but they are thought to be freshwater amphidromous (Nieves 1998). Other invertebrates (e.g., *Epilobocera*, aquatic insects) lack a marine stage but "migrate" between freshwater and land. The semiaquatic crab (*Epilobocera*) has direct development in fresh water. Juveniles then feed and develop in fresh water, and adults move between fresh water and the forest floor (Covich and McDowell 1996; Zimmerman and Covich 2003).

### Effects of Shrimp Foraging

The foraging activities of atyid and *Xiphocaris* shrimps have large effects on benthic sediment, algae, and insects. Field observations and numerous experimental studies using enclosure/enclosure techniques have documented that shrimp reduce benthic algal biomass, reduce the standing stock of benthic organic matter and nitrogen, and alter algal and insect communities (Pringle et al. 1993; Pringle and Blake 1994; Pringle 1996; Pringle et al. 1999; March et al. 2002; Greathouse et al. 2006b; see also chapter 6). When shrimp were excluded from Quebrada Sonadora, a shrimp-rich river, for example, benthic organic material increased 10-fold (from 1.1 to 10.6 g ash-free dry mass m<sup>-2</sup>), and benthic nitrogen increased 5-fold (from 0.04 g m<sup>-2</sup> to 0.2 g m<sup>-2</sup>) (Pringle et al. 1999). Pringle et al. (1993) suggested that the differences in the abundance of atyid shrimp seen among streams of the Luquillo Mountains result in changes in the distribution and abundance of relatively sessile benthic invertebrates. Their hypothesis is supported by several lines of evidence. Enclosure/enclosure experiments show that foraging by atyid shrimp and *Xiphocaris* reduces the numbers of retreat-dwelling chironomid (midge) larvae (e.g., Pringle et al. 1993; March et al. 2002), and field observations indicate that particle-feeding benthic insects such as black flies are restricted to fast-flowing riffles and pool margins outside of shrimp foraging areas (Pringle et al. 1993; Buzby 1998). Other benthic invertebrates that are negatively affected by shrimp include odonate dragonflies, caenid mayflies, ceratopogonid midges, limpets, and aquatic worms (Greathouse et al. 2006b). Shrimp can have positive effects on motile mayflies such as Baetidae (Buzby 1998; Greathouse et al. 2006b).

### Leaf Decomposition

Leaf decomposition in the streams of the Luquillo Mountains is rapid, with most species of leaves fully decomposed in less than 9 months (Padgett 1976; Vogt et al. 1996). Shrimp and fungi dominate the decomposition process. The aquatic hyphomycetes *Campylospora chaetoclada*, *Triscelophorus monosporus*, and *Pyramidospora casuarinae* were the most abundant of 16 fungal species found to colonize leaves during an experimental study of leaf decomposition (Padgett 1976). Whole-pool manipulations of shrimp abundance suggest that the presence of both *Xiphocaris elongata* and *Atya* species is necessary for the efficient processing of leaf material. *Xiphocaris* shred the leaves, and *Atya* filter the resulting particles from the

water column (Crowl et al. 2001; also see chapter 6). Changes in shrimp communities along the elevational gradient are reflected in changes in the rates of litter decomposition (March et al. 2001). Leaf-shredding insects are uncommon; only *Phanocerus* elmid beetles and *Phyllocius pulchrus* (a calamoceratid caddisfly) are present, and they exist in low numbers (Buzby 1998). Leaf-mining Chironomidae also occur in Puerto Rican streams (Greathouse and Pringle 2006; Greathouse et al. 2006c).

### *Food Webs along the Aquatic Elevational Gradient*

Because of the nature of streams and flowing waters, stream communities at a point in geographic space are inextricably linked to upstream and downstream communities. This is particularly so in the Luquillo Mountains, where many stream biota have direct connections to the sea at some point in their life cycle. The species composition of aquatic communities and the influence of aquatic consumers on ecosystem-level processes (e.g., decomposition) in the Luquillo Mountains vary with elevation and the position of natural and anthropogenic barriers such as waterfalls and dams (Greathouse et al. 2006a, 2006c; Covich et al. 2009). Longitudinal distributions of shrimps, fishes, and snails are particularly influenced by their migratory life cycles between fresh and salt water and by variation among taxa in their abilities to migrate past barriers (Covich and McDowell 1996; Covich et al. 1996).

Geomorphic breaks are central to understanding the community structure and food webs in streams of the Luquillo Mountains. Predatory fishes such as mountain mullet are typically limited to elevations below 400 m, because waterfalls limit their passage upstream. Although neritid snails can climb steep slopes, they also are limited to lower elevations below waterfalls. Their distribution is thought to represent the tradeoffs among predation risk, the energetic demands of migrating upstream, and life span (Pyron and Covich 2003). Gobies are found at elevations of up to ~700 m because they have the ability to move upstream against high-velocity currents using sucking discs evolved from pectoral fins (Erdman 1961, 1986). Shrimp reach the highest-elevation headwater streams, beyond the upstream limits of *Sicydium*. Xiphocaridid and atyid shrimps also occur at much higher abundances upstream from waterfalls. These high abundances above waterfalls are thought to be due to the release from predation by fish and/or competition from neritid snails (Covich 1988; March et al. 2002; Greathouse and Pringle 2006; Covich et al. 2009; Hein et al. 2011).

Distributions of functional feeding groups along the elevational gradient have been well studied in the Río Mameyes and Río Espíritu Santo (figure 3-2). In the Río Mameyes drainage, from the headwaters of the Río de La Mina (720 masl) to within 2.5 km of the Río Mameyes mouth (5 masl), several patterns are observed with increasing catchment area/decreasing elevation (Greathouse and Pringle 2006). Xiphocaridid and atyid shrimps reach their highest densities and standing stocks upstream from the upper limit of predatory fishes (figure 3-30). In contrast, high densities and standing stocks of gastropods (primarily neritid snails) occur at sites where predatory fishes are present (figure 3-30). *Macrobrachium* shrimps have high densities of small juveniles at lower-elevation sites, but no clear patterns in

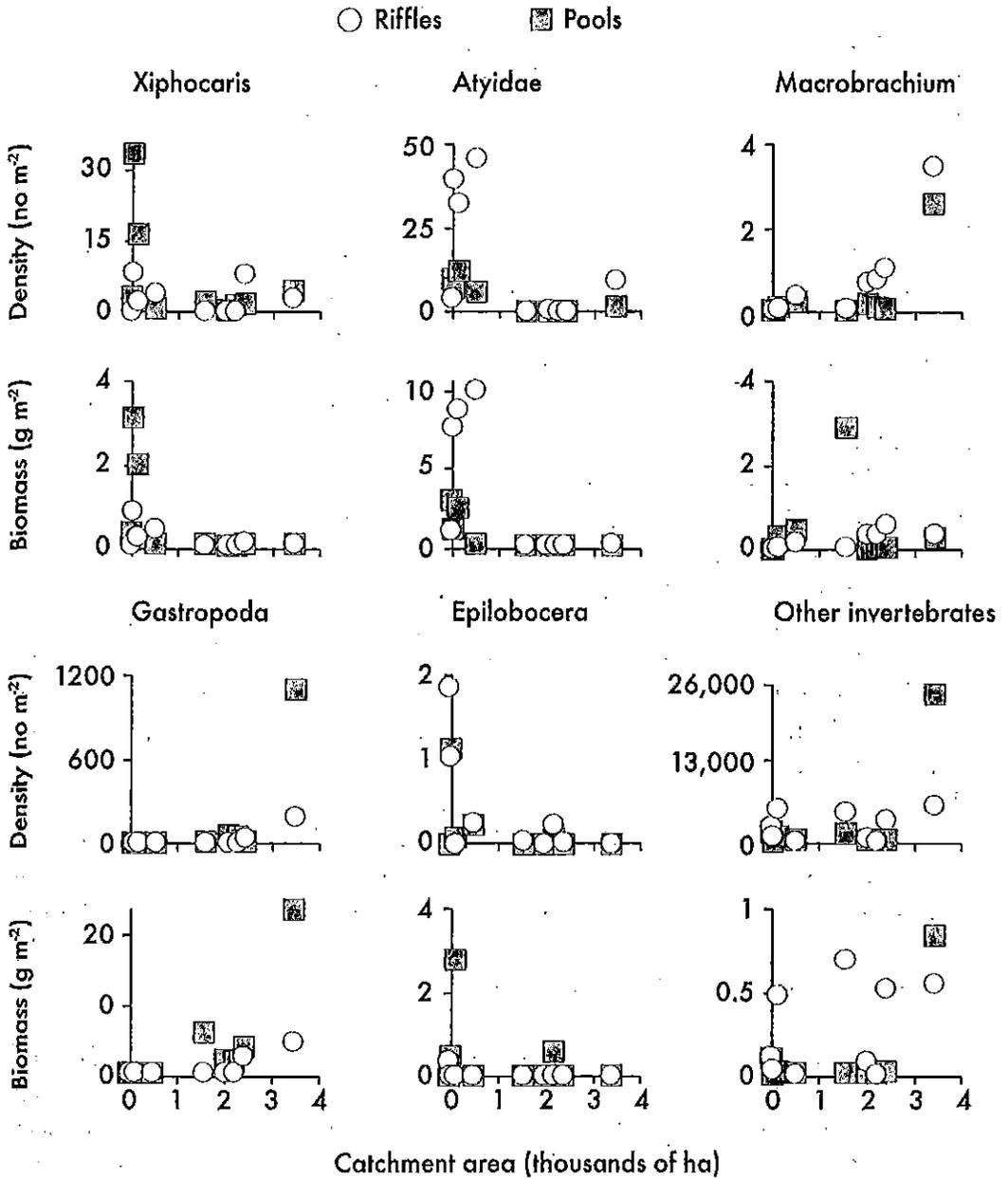


Figure 3.30 Densities and standing stocks (biomass as ash-free dry mass) of aquatic invertebrates in riffles and pools along a stream continuum from the headwaters of the Río de La Mina to within 2.5 km of the mouth of the Río Mameyes. Data from Greathouse and Pringle (2006). Invertebrate groups are shrimps (*Xiphocaris elongata*, Atyidae, *Macrobrachium*), Gastropoda (primarily neritid snails, but also the snail *Thiara granifera*, and limpets), crabs (*Epilobocera sinuatifrons*), and other invertebrates (e.g., aquatic insects, Oligochaeta, Copepoda). Shrimps and crabs were sampled via depletion electroshocking over a known area. Gastropods and other invertebrates were sampled using standard quantitative methods appropriate to each habitat (e.g., Surber net in riffles, cores in pools). Horizontal black bars below the bottom x-axes indicate sites at which predatory fishes (e.g., *Agonostomus monticola*, *Anguilla rostrata*, *Eleotris pisonis*) are present. Samples taken from riffles are represented by open circles, and those taken from pools by solid squares. Note axes of different scales.

biomass. Crabs reach their highest densities and biomass at high-elevation sites (figure 3-30) above high (>10 m), steep waterfalls (Covich et al. 2006; Covich et al. 2009; Hein et al. 2011). The remaining invertebrates (including insects) are grouped into a single “other” category that shows the highest density and biomass in low-elevation pools where abundant *Elodea* provides a complex habitat (figure 3-30).

Similar elevational patterns in shrimp and snail densities in the neighboring Espiritu Santo drainage drive variation in leaf decomposition rates (March et al. 2001) and algal biomass (March et al. 2002). When shrimp were excluded from a mid-elevation site lacking predatory fishes (at ~300 masl), leaf decomposition rates decreased by almost 50 percent ( $k = 0.067 \text{ day}^{-1}$  vs.  $0.036 \text{ day}^{-1}$ ,  $p = 0.019$ ; March et al. 2001). In contrast, at both mid- and low-elevation sites where predatory fishes were present (~90 and 10 masl, respectively), the exclusion of macrobiota had no significant effect on rates of leaf breakdown. Subsequent laboratory experiments confirmed that the shrimp *Xiphocaris elongata* was the dominant consumer of leaf material but that it consumed significantly less when in the presence of predatory shrimps (*Macrobrachium* spp.). The combined results of laboratory and field experiments indicate that interference competition/predation between these two taxa accounts for the differences in leaf breakdown rates observed between sites. The role of *X. elongata* in detrital processing is context dependent, with strong effects occurring only in stream headwaters, where predatory fishes and *Macrobrachium* spp. are less abundant, and where *Macrobrachium* spp. make up a smaller proportion of the shrimp biomass.

The effects of shrimp exclusion on epilithic communities in the Espiritu Santo drainage also varied with elevation (March et al. 2002). At two mid-elevation sites (300 and 90 masl) where snails were absent or low in abundance, shrimp exclusion had strong effects on the accrual of inorganic and organic material, chlorophyll *a*, algal biovolume, and biomass of Chironomidae. At the low-elevation site (10 masl), snails were abundant, and shrimp exclusion had no effect on benthic organic matter, algae, or Chironomidae.

Algae appear to be important food resources for shrimp along the elevational gradient despite the relatively low primary productivity of these streams. Shrimp appear to rely primarily on algal carbon for growth in larger streams with sufficient sunlight, with no strong patterns in the importance of terrestrial versus algal food sources along the elevational gradient (March and Pringle 2003).

Understanding the context-dependent effects of stream biota along river continua is critical, owing to the migratory life cycle of shrimps and fishes of streams draining the Luquillo Mountains (Covich and McDowell 1996; March et al. 1998; Greathouse and Pringle 2006). With the increasing number of large man-made dams limiting the access of shrimps and fishes to upper-elevation sites, changes in a variety of ecological processes are likely (Pringle 1997; Holmquist et al. 1998; Benstead et al. 1999), and these changes are expected to vary with elevation (March et al. 2001, 2002; Greathouse et al. 2006c) (see chapter 7).

Migration patterns also differ with elevation and stream size. During base flows, the densities of larval shrimp drifting downstream to the estuary increase exponentially with increasing stream size (as measured by cumulative stream length) (March et al. 1998; Kikkert et al. 2009). Whether this relationship holds true during storm

flows is unknown. The diel periodicity of larval shrimp drift also appears to vary with elevation in response to the risk of predation. Larval shrimp drift was strongly nocturnal at five low- and mid-elevation sites where predatory fishes were present but showed no diel periodicity at a mid-elevation site lacking predatory fishes due to its position above a waterfall. Upstream migration by juvenile shrimp and neritid snails also shows elevational patterns (see, e.g., Pyron and Covich 2003).

The River Continuum Concept (RCC) formalizes predicted changes in stream food webs with stream order and position in the drainage network (Vannote et al. 1980; Minshall et al. 1985). At high elevations, streams are small and shaded. Coarse particulate organic matter (CPOM) from terrestrial sources is predicted to dominate basal resources, and functional feeding groups that rely on this CPOM (shredders, collector-gatherers, and collector-filterers) are predicted to dominate macroinvertebrate biomass. As the elevation decreases and streams widen, these medium-sized streams with higher light levels are predicted to support more algae and the functional feeding groups (scrapers, collector-gatherers, and collector-filterers) that feed on algae and benthic biofilms. At the lowest-elevation sites in a large river system, high turbidity is predicted to result in low light levels and low algal productivity, and thus a macroinvertebrate community dominated by collector-filterers, which utilize transported FPOM. Macroinvertebrate predators are predicted to show no consistent change with stream order.

These RCC predictions for temperate streams largely hold true for the Río Mameyes, a system that spans small headwater streams to medium-sized channels within the Luquillo Mountains before entering the ocean as a fourth-order stream in the urbanized lowland floodplain downstream of the Luquillo Mountains (Ortiz-Zayas et al. 2005; Greathouse and Pringle 2006). The P/R in the Río Mameyes increases from headwaters to lowlands, as predicted (Ortiz-Zayas et al. 2005). The relative dominance of macroinvertebrate biomass also follows predictions for most functional groups: shredders decreased, scrapers increased, collector-gatherers decreased, and predators showed no change from headwaters to lowlands (Greathouse and Pringle 2006). Filterers, represented by shrimp of the genus *Aitya*, decreased with distance downstream, rather than increasing as predicted by the RCC.

Stream chemistry reflects both terrestrial and aquatic biogeochemical processes, and thus the changes in terrestrial and aquatic ecosystems documented in the preceding paragraphs might be expected to cause changes in the stream chemistry and nutrient export with elevation. Contrary to this expectation, however, data published to date show no striking differences in the stream chemistry among watersheds with different mean elevations. McDowell and Asbury (1994), for example, found that nitrate-N concentrations in the high-elevation Río Icacos (700 to 1,000 masl;  $66 \mu\text{g l}^{-1}$ ) were similar to those in the low-elevation Toronja watershed ( $62 \mu\text{g l}^{-1}$ ). Fluxes of  $\text{NO}_3\text{-N}$  from the Icacos ( $2.5 \text{ kg ha}^{-1} \text{ y}^{-1}$ ) were much greater, however, than those from the Toronja ( $0.9 \text{ kg ha}^{-1} \text{ y}^{-1}$ ), owing to the much higher runoff at higher elevations (McDowell and Asbury 1994). Temporal variation in N flux is greater than the spatial variation alone, as  $\text{NO}_3\text{-N}$  export varied from 0.7 to  $8 \text{ kg ha}^{-1} \text{ y}^{-1}$  among six watersheds in the years before and after Hurricane Hugo (Schaefer et al. 2000).

## Effects of Recent Invasions

Although the biotic assemblage in a given locale or region is frequently thought of as resulting from ecological and evolutionary processes occurring over thousands to millions of years, the rapid pace of biotic introductions and successful invasions in the past few centuries have resulted in significant changes in the biota of many regions. The flora and fauna of Puerto Rico have been affected in many ways: by introduced species. Bamboos (*Bambusa vulgaris*, *B. longispiculata*, *B. tulda*, *B. tuldoides*, *Dendrocalamus strictus*) are common along the roads of the Luquillo Mountains, where they were originally planted by the U.S. Forest Service to assist in erosion control. Bamboos have spread along stream channels (O'Connor et al. 2000) but are not widespread in the Luquillo Mountains. Pomarrosa (*Syzygium jambos*) is another nonnative species common in riparian zones, but it too is not common elsewhere in the tabonuco forest type. Nonnative plants are common in lower-elevation forests that have undergone extensive human modification or suffered significant hurricane effects, but as the native overstory returns, these introduced trees lessen in importance (Lugo 2004; Thompson et al. 2007). Black rats are not native to Puerto Rico and likely reached the island with Ponce de León in 1508 (Snyder et al. 1987). Rats and the Indian mongoose (intentionally introduced to control the rats) threaten a variety of native fauna, including four bird species (Puerto Rican Parrot, Short-eared Owl [*Asio flammeus*], Puerto Rican Whip-poor-will [*Caprimulgus noctitherus*], and Key West Quail Dove [*Geotrygon chrysis*]) and two snake species (Puerto Rican boa and Puerto Rican racer [*Alsophis portoricensis*]) (Raffaele et al. 1973). The endangered birds construct nests in which eggs and nestlings are vulnerable to predation by rats and mongooses. The cane toad (*Bufo marinus*) was introduced in order to control pests in sugar cane and is now found in much of the Luquillo Mountains. Disturbance due to anthropogenic practices seems to be the major factor causing the spread of introduced earthworms in the tropics (González et al. 2006). Introduced earthworms can establish their populations in sites modified after deforestation (e.g., forest-pasture conversion), tree plantations, and cultivation activities, and also follow human migrations (González et al. 1996; Zou and González 2002). Conversely, native species can return upon the regrowth of forest in abandoned pastures (Sánchez et al. 2003).

Most major functional groups of plants and animals have one or more important introduced species that play a significant role in community dynamics and ecosystem processes. Introduced earthworms, rats, mongooses, and the cane toad each play an important role in terrestrial food webs, and introduced bamboo and pomarrosa are plant species that have a significant role in stream food webs.

Aquatic invasions have occurred in lowland Puerto Rican streams, including those that originate in the Luquillo Mountains. The freshwater snail *Thiara granifera* is a conspicuous introduced species. In the main stem of the Río Mameyes, *T. granifera* reaches standing stocks of  $\sim 2 \text{ g m}^{-2}$ , but its biomass is generally one to two orders of magnitude lower than the biomass of native *Neritina* snails (Greathouse and Pringle 2006). *Thiara granifera* occurs only at lower elevations (its island-wide upstream limit is  $\sim 480 \text{ masl}$ ) (Chanotis et al. 1980) and is low in biomass in most streams of the Luquillo Mountains. Competition from *T. granifera*

is thought to have caused an island-wide decline in lotic populations of *Biomphalaria glabrata*, the native snail that serves as host to the liver fluke that causes schistosomiasis (Butler et al. 1980; DeJong et al. 2001). The invasion of *T. granifera* in the 1950s appears to have been accidental (Butler et al. 1980; Chaniotis et al. 1980), and its impact on native snails thus represents a positive unintended impact on human health. In contrast, the snail *Marisa cornuarietis* was introduced intentionally for the biological control of *B. glabrata* in standing waters such as farm ponds (Butler et al. 1980). The prevalence of schistosomiasis is now very low in the streams of Puerto Rico, as are densities of *B. glabrata* (Giboda et al. 1997).

Although fisheries introductions across the island have primarily focused on reservoirs, introduced reservoir fishes do invade running waters. The abundance of these introduced fishes is high in streams above large reservoirs but low in streams below reservoirs and in streams with no reservoirs. These patterns indicate that the near extirpation of native fishes and shrimps from streams above dams that are large enough to block migrations results in stream communities with reduced biotic resistance to invasion (Holmquist et al. 1998). This biotic resistance of the native fauna might explain why the aquatic fauna of the Luquillo Mountains is remarkably lacking in introduced species.

Aquatic habitats across the island, including those in the Luquillo Mountains, are at risk for future invasions by a variety of aquarium and aquaculture species that are poorly regulated (Williams et al. 2001). Australian redclaw (*Cherax quadricarinatus*) is a particular threat to the Luquillo Mountains. A population of this crayfish has become established in the Carraizo Reservoir on the Río Grande de Loíza, a river that drains the Luquillo Mountains, and this species appears to be capable of outcompeting native shrimps (Williams et al. 2001).

Introduced plants appear to be altering or supplementing stream food webs in the Luquillo Mountains in ways that are not necessarily negative. Asian species such as bamboo and pomarrosa provide some of the ecosystem functions provided by native species (e.g., leaf litter food sources, woody debris, and shade) (Covich et al. 1999). More freshwater shrimp (both *Atya* and *Macrobrachium*) were found in pools with riparian bamboo than in adjacent pools of similar size that lacked bamboo, and laboratory studies showed that shrimp prefer nonnative bamboo when offered either bamboo or native leaves as cover (O'Connor 1998). The microhabitat created by bamboo litter in streams thus appears to be very well suited for use by these shrimp.

### Luquillo Mountains from a Tropical Perspective

Understanding the drivers of spatial and temporal variability in ecosystem structure and function is a long-standing goal in ecology. Within the Luquillo Mountains, one of our primary research foci has been to examine the importance of gradients in driving spatial variability in community structure and ecosystem processes. The broad gradients in rainfall and temperature associated with elevation provide the primary abiotic drivers of variation in community structure and ecosystem processes in the Luquillo Mountains. Patches of different bedrock and the disturbance history (landslide, hurricane damage, intensive past land use) provide complexity

along the elevational gradient. With the high rainfall and runoff found in the Luquillo Mountains, aquatic–terrestrial interfaces occur frequently and are “hot spots” of biogeochemical activity (McDowell et al. 1992; McDowell 2001). With such spatial and temporal variation in abiotic drivers and ecosystem properties across the Luquillo Mountains, it is difficult to describe the variation across the landscape in purely spatial terms; a more dynamic temporal component is also needed in order to capture the ways in which a site varies depending on the legacy of past disturbance events and the biotic responses to them.

The concept of ecological space (see chapter 2) provides a useful way to organize our understanding of how environmental characteristics change over time in response to underlying landscape features and the disturbance regime. The heterogeneity of ecological characteristics in geographical space is dictated by a combination of geographic circumstances (e.g., leeward/windward vs. elevation to drive rainfall; elevation/cloudiness vs. aspect to drive PAR at the canopy), the underlying geologic substrate (quartz diorite vs. volcanoclastic bedrock), and the legacies of past disturbances. The biota both respond to ecological space and help create it. Seedling germination and growth, for example, require specific conditions for various species (Guzmán-Grajales and Walker 1991), and successful recruitment of the seedling causes changes in the light and moisture characteristics that are important elements in the ecological space at the site.

Soils provide important nutrient pools in terrestrial ecosystems, and their chemical and physical properties are highly variable in tropical forests (figure 3-12). Wet tropical forests were once thought to have soils containing low concentrations of mineral nutrients. Unfortunately this concept has become embedded in the popular and scientific literature, even though it is not generally applicable (Sánchez 1976; Richter and Babbar 1991; Lal and Sánchez 1992). Although some tropical forests, such as those on Amazonian white sands, conform to this model, many areas of wet tropical forest have soils with considerable mineral pools, including the Luquillo Mountains (Silver et al. 1994). Many tropical forests also have large nitrogen pools, which are presumably the result of high rates of nitrogen fixation (Cleveland et al. 1999; Cusack et al. 2009) and the legacies of past land uses (Beard et al. 2005).

A corollary to this general misconception regarding the nutrient content of tropical soils is that plant biomass is the primary nutrient store in tropical rainforests. For many years, tropical forests were characterized as nutrient-poor ecosystems with low nutrient-holding capacity, with the nutrient content of the aboveground biomass greatly exceeding that of labile nutrient storage in soils (see Whitmore [1989] for an overview of the genesis of this concept). Such characterizations led many to believe that tropical forests were extremely fragile ecosystems, and that plant biomass was much more important than soils for nutrient cycling and conservation. These generalizations were derived from many sources, but the strongest empirical evidence for this view came from studies on forest C and nutrient distribution and cycling in San Carlos de Río Negro in the Venezuelan Amazon (see the review by Jordan [1985]). Although these studies represented some of the most careful and complete early ecosystem research conducted in the tropics, the results were not necessarily generalizable to a wide range of tropical environments because of the unusual soil mineralogy. The soils of the San Carlos site, white sands or

psamments, are a relatively rare tropical soil type with some of the lowest cation and P availability of any tropical environment (Jordan 1985; Cuevas and Medina 1986, 1988; Medina and Cuevas 1989). Results from the Luquillo Mountains and other tropical forests suggest that a low nutrient content is not particularly characteristic of tropical forests, as many sites are rich in nutrients owing to their geologic history and soil depth. This has important implications for ecosystem behavior following a disturbance, which is addressed in chapter 5.

## Summary

The Luquillo Mountains contain insular ecosystems that have never been connected to a continental land mass and which are subject to severe disturbances, including hurricanes, landslides, and earthquakes. Soils are deep, weathered, and not particularly nutrient poor, and they support a moderately diverse flora and fauna with high endemism. Strong gradients in rainfall, temperature, and insolation, driven by elevation and aspect, help structure the forests found at different elevations and topographic positions in the Luquillo Mountains. Forest productivity does not appear to be limited by nitrogen and declines with increasing elevation. Soil carbon and nitrogen concentrations in surface horizons increase with increasing elevation, and the topographic position also causes substantial variation in the soil chemistry. Concentrations of inorganic nitrogen in streams are high relative to those in montane temperate sites and are stable over time, except for brief periods following hurricanes. One of the greatest ecological distinctions between Puerto Rico and mainland tropical forests is the complete lack of large mammals and the absence of many families of birds, reptiles, and amphibians, which are the result of Puerto Rico's biogeographic insularity and disturbance history. The low species richness for several vertebrate taxa relative to that in otherwise similar continental montane forests is typical of Caribbean islands. No large mammalian herbivores are found, and herbivory is dominated by insects and birds. Top predators in the forest include lizards, frogs, and a few species of birds; large mammalian predators are absent. Stream food webs are dominated by shrimps and crabs, with food webs being fueled by both detrital and algal resources. Shrimps play a key role in stream ecosystems by maintaining a low algal standing crop and benthic insect abundance, altering the algal species composition, regulating benthic inorganic sediments and the quality and quantity of benthic organic matter, and driving rates of litter decomposition. Invasive plants and animals are prominent in both aquatic and terrestrial ecosystems and appear to be most successful following disturbance.

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# A Caribbean Forest Tapestry

*The Multidimensional Nature of  
Disturbance and Response*

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