

CHAPTER

## 5 Response to Disturbance

Nicholas Brokaw, Jess K. Zimmerman, Michael R. Willig, Gerardo R. Camilo, Alan P. Covich, Todd A. Crowl, Ned Fetcher, Bruce L. Haines, D. Jean Lodge, Ariel E. Lugo ... [more](#)

<https://doi.org/10.1093/acprof:osobl/9780195334692.003.0005> Pages 201–271

**Published:** June 2012

### Abstract

This chapter describes the responses of the organisms, communities, and ecosystems to the variety of disturbances by utilizing the conceptual model discussed in Chapter 2. It also dwells on the concepts of residuals, legacies, and ecological space in the understanding of disturbances such as background treefalls, hurricanes, floods, drought, landslides, and other human-induced disturbances. Finally, it outlines the variations caused by disturbances and the interactions among these disturbances.

**Keywords:** [variety of disturbances](#), [conceptual model](#), [residuals](#), [legacies](#), [ecological space](#), [background treefalls](#)

**Subject:** [Plant Sciences and Forestry](#)

**Collection:** [Oxford Scholarship Online](#)

## Key Points

- Background treefall gaps (not caused by hurricanes) are filled with plant regrowth as in other tropical forests. There is limited response by animals to treefall gaps, probably because background treefall gaps are relatively less important in these forests, which are dominated by chronic, widespread hurricane effects.
  - Despite substantial effects on trees, the tree species composition changed little in the tabonuco forest after two recent hurricanes.
  - Animal species show various responses to the changes in forest architecture and food resources caused by hurricanes. Bird species tend to be plastic in habitat and dietary requirements, probably due to the large changes in forest structure caused by hurricanes and regrowth, which require birds to change their foraging locations and diets.
  - Although hurricane-produced debris is substantial (litterfall up to 400 times the average daily amount), decomposition, nutrient export, and trace gas emissions after hurricanes change only briefly, as rapid regrowth reasserts control over most ecosystem processes.
  - In general, terrestrial ecosystem functions recover faster than structure.
  - Hurricanes dump debris in streams, and floods redistribute inorganic and detrital material, as well as stream organisms, throughout the benthic environment along the stream continuum.
- p. 202
- ↳ Succession in landslides is slow and primarily limited by the availability of seed and by low nutrient availability, and early plant colonists, especially ferns, have a strong influence on later dynamics.
  - Past land use is the most important determinant of species composition in tabonuco forest, despite repeated hurricane effects and underlying environmental variation such as in soil and topography.
  - The native organisms of the Luquillo Mountains are more resilient after natural than human disturbances.

## Introduction

---

The Luquillo Mountains are a heterogeneous landscape, produced by environmental variation (chapter 3), a varied disturbance regime (chapter 4), and varied responses to disturbances in space and time. Background treefall gaps (gaps not caused by hurricanes) open up 0.24 to 1.8 percent of tabonuco forest per year (Scatena and Lugo 1995); landslides denude a minimum of 0.08 to 0.30 percent of the Luquillo Mountains each century (Guariguata 1990); and severe hurricanes strike the Luquillo Mountains every 50 to 60 years (Scatena and Larsen 1991) and cause treefall gaps, landslides, and floods. To these disturbances we can add thousands of lesser storms, floods, and droughts over the millennia. Moreover, various kinds of human disturbance have affected nearly all forest area below 600 meters above sea level (masl) (Foster et al. 1999). The Luquillo Mountains represent many other tropical landscapes in which disturbance produces heterogeneity (Foster 1980).

How do the organisms of the Luquillo Mountains respond to this great variety, high frequency, and long history of disturbances? To describe these responses, we use the conceptual approach outlined in chapter 2. The response depends on the predisturbance conditions and the disturbance severity, which determine the conditions at the onset of response, and on the characteristics of the responding species. The initial conditions created by a disturbance can be classified as abiotic (including structure) and biotic (see figure 2-2) and are thought of as “residuals,” or primary effects. Residuals are the physical manifestations of disturbance, that is, what remains of the abiotic, biotic, and structural features. These residuals shape the response to disturbance, creating secondary effects in the form of “legacies,” or the long-term subsequent behavior of the ecosystem as determined by the residuals. Residuals and legacies of disturbance help explain the present condition of ecosystems (Foster et al. 2003).

The conditions at any given time can be described in terms of ecological space (see figure 2-8). Ecological space may be visualized as a multidimensional hypervolume that reflects abiotic, biotic, and structural components of a system. Disturbance changes this hypervolume by modifying these components at points

located in geographical space. For instance, forest canopy changes can turn a previously shaded, cool, moist geographical point at ground level into a sunny, hot, dry point. In turn, biotic responses to disturbance, such as forest regrowth, can change conditions at that geographical point back to those of the earlier, shady, cool, moist ecological point. In such a situation, geographical space has not changed; ecological space has. The trajectory of response ↴ in ecological space depends on the intensity, duration, and extent of the disturbance, and then on the degree of resistance and resilience of biotic responses (see figure 2-9) (Lugo et al. 2002; see also chapter 4). Resistance is the degree to which a system is not affected by disturbance, as, for example, when trees are affected but not killed. Resilience is the time required for a system to return to a state that is similar to that before the disturbance, as when trees recover their predisturbance biomass.

With these concepts in mind, in this chapter we describe the responses of organisms, populations, communities, and ecosystems to the variety of disturbances in the Luquillo Mountains. We look at residuals and legacies, at resistance and resilience, and at mechanisms or processes of response. The chapter is organized according to descriptions of disturbances that act at stand to landscape scales, including background treefalls, hurricanes, floods, droughts, landslides, and various human disturbances. Most sections begin with a description of residuals—of how disturbance affects the biotic and structural environments (chapter 2)—and proceed to a discussion of legacies, or longer-term responses (abiotic effects are mainly covered in chapter 4). The chapter concludes with a discussion of the variation in responses to different disturbances and of interactions among disturbances. Variations and interactions among responses weave the tapestry of the Luquillo Mountains, encompassing landscape variation in space, and they also produce the layers of the palimpsest, encompassing persisting variations in time (chapter 1). (Chapter 6 continues the discussion of response to disturbance but emphasizes the role of key species and their control of ecosystem processes.)

## Response to Background Treefall Gaps

Background treefall gaps are gaps in the forest not caused by hurricanes. When a background treefall creates a forest gap (an opening through the canopy to near the ground), the gap is filled with the growth of adjacent trees, sprouts from affected trees, and seedling and sapling regeneration, and thus the gap area eventually returns to a mature phase, barring further disturbance (Hartshorn 1978; Whitmore 1978). From disturbance through recovery, this gap-phase regeneration adds diversity to the structure of the forest and to the structure of tree populations and tree communities (Brokaw and Busing 2000). Background treefalls are not a severe disturbance; there are many residuals that support response, such as mostly intact soil with nutrients and buried seeds, advance regeneration (surviving seedlings and saplings), and affected and bordering trees ready to sprout and fill the gap. Regrowth from these residuals is fast enough (cf. Fraver et al. 1998) that it reduces values of throughfall (rain reaching the forest floor) in gaps from post-treefall highs to pretreefall values in 1 year (Scatena 1990).

There have been three studies of plants in background treefall gaps in the Luquillo Mountains. The first study showed that the seedling gas exchange of the common tree species *Dacryodes excelsa* and *Sloanea berteriana* increases in gaps (Lugo 1970). The other two studies were on species composition in gaps. Both took place when the forest canopy had been developing for some 60 years without hurricane effects, and the relatively mature forest canopy had begun to open up with background gaps. In a study of 15 natural, recently formed gaps (34 to 322 m<sup>2</sup>) in tabonuco forest ↴ (chapter 3), soil temperatures were higher in gaps than in adjacent intact forest, probably because of the higher insolation in gaps (Pérez Viera 1986). Soil humidity did not differ between gap and intact forest, whereas in some other forests it is wetter in gaps (Becker et al. 1988). There was a high density of colonizing saplings in gaps, as in other gap studies (see Brokaw 1985). The species composition of colonizers differed among gaps but typically included saplings of light-demanding species (Smith 1970), especially in some larger gaps. The species richness of saplings was higher in gaps than in intact forest because gaps have more small stems and thus a larger sample of plants (the “density effect”) (Denslow 1995), and because a few gap specialists are, by definition, found mainly in gaps and are regenerating from seed. The second study in background treefall gaps was a rapid survey of all gaps in about 35 ha of tabonuco forest and aimed to record the number of seedlings and saplings of the disturbance-dependent species *Cecropia schreberiana* (Brokaw 1998). Only 34 *C. schreberiana* saplings were found, a number apparently insufficient to maintain the larger population of adults in the area, suggesting the importance of regeneration after hurricane, rather than gap, disturbance for this species (see below).

Gap-phase regeneration is less important for the tree community composition and dynamics in the tabonuco forest than in many other tropical forests because background treefall gaps are relatively few and small in this forest (Brokaw et al. 2004). Gaps are few (except in some riparian zones) (Scatena and Lugo 1995) because the periodic, simultaneous removal of many vulnerable trees by hurricanes reduces the number of treefalls between hurricanes (Lorimer 1989; Lugo and Scatena 1996; Whigham et al. 1999; Debski et al. 2000). Gaps are smaller in tabonuco forest than in some forests not affected by hurricanes because hurricanes tend to prevent trees from reaching large sizes and making large gaps when they fall (Odum 1970; Perez 1970).

Because gap creation and gap-phase regeneration are not the prevailing dynamics in the tabonuco forest, we expect little specialization by animals based on the environment of background treefall gaps. However, some species are found in higher densities in gaps than in the adjacent understory of intact forest. Community assemblages of birds differed between gaps and the understory of intact forest at El Verde, because species normally found in the canopy also frequented gaps (Wunderle 1995), but there were no species that specialized on gaps (i.e., that mainly occurred there), as found in other tropical forests (Schemske and Brokaw 1981; Wunderle et al. 2005). Coquí frogs (*Eleutherodactylus coqui*) move to gaps where debris provides the preferred humidity and shelter from predators (Stewart and Woolbright 1996; Woolbright 1996), but, as with the birds, they are not gap specialists.

Sixteen species of snails have been found in treefall gaps in tabonuco forest, but none were restricted to gaps, and community assemblages of snails did not differ between gap and nongap areas (Alvarez and Willig 1993). Five snail species were common enough for their habitat preferences to be assessed. The densities of *Austroselenites alticola*, *Megalomastoma croceum*, and *Subulina octana* did not differ between gap and intact forest; *Nenia tridens* was more abundant in gaps; and *Caracolus caracola* was more abundant in intact forest. *Nenia tridens* might gravitate toward gaps in order to eat dead plant material or the algae and fungi on dead plants. *Caracolus caracola* might avoid gaps due to its low tolerance for the heat and aridity in gaps, or because those factors reduce food quality (Alvarez and Willig 1993). Among insects, walking sticks (Phasmodidae) are herbivores that preferentially frequent treefall gaps, presumably to eat the new plant growth there (Willig et al. 1986, 1993; Sandlin and Willig 1993; Garrison and Willig 1996).

p. 205

The lack of striking differences in animal assemblages between treefall gaps and intact forest understory might be related to two factors. First, the generally small size of treefall gaps might reduce the environmental differences between gap and intact forest relative to differences found in other forests. Second, animals in the Luquillo Mountains have evolved in an environment that is strongly disturbed by hurricanes, which would favor generalist species that are adapted to both successional and mature forest stands (Waide 1991b), and so they are not especially responsive to background treefalls.

The accumulated ecosystem effects of frequent background tree mortality (not necessarily creating gaps) are comparable to the effects of less frequent but catastrophic tree mortality from hurricanes (Scatena and Lugo 1995; Lugo and Scatena 1996; see also chapter 4). For tabonuco forest, an estimated constant tree mortality of 2.0 percent  $y^{-1}$  for 100 years would release the biomass and nutrients of a forest stand two times per century, whereas two highly catastrophic events of 30 percent mortality, plus extensive effects to surviving trees (50 percent reduction of aboveground biomass) (Scatena et al. 1996), would also release nearly all tree biomass and nutrients about twice per century. Thus, although background tree mortality might not even disturb the canopy, over time it can equal some ecosystem effects of hurricanes that dramatically alter the forest structure.

# Terrestrial Response to Hurricanes

Unlike background treefalls, hurricanes create a range of terrestrial disturbances, including large areas of affected and defoliated trees, individual and multiple treefall gaps, and landslides, depending on the topography and location of a site relative to the storm trajectory (chapter 4) (Brokaw and Gear 1991; Walker 1991; Larsen and Torres-Sánchez 1992). The catastrophic, sudden tree mortality (Lugo and Scatena 1996) and the extensive effects on surviving trees caused by a strong hurricane have a major influence on the distribution and quantity of biomass and nutrients, on microclimates, and on populations (figure 5-1; Walker et al. 1991). Biomass and nutrients move from the canopy to the forest floor and soil. Light floods the understory over large areas. Fine root biomass drops sharply. Many plants and some animals die. In turn, responses are manifest at all levels, from individual to ecosystem, and it is striking how resistant and resilient the organisms and ecosystem processes in the Luquillo Mountains are. In fact, numerous features of the forest return to prehurricane levels within about 5 years (Zimmerman et al. 1996).

**Figure 5.1**



Structural effects in tabonuco forest at El Verde Research Area, Puerto Rico, resulting from Hurricane Hugo, 1989.

(Photograph by Nicholas Brokaw.)

## Hurricanes, Forest Canopy Structure, and Microclimate

The upper canopy of the tabonuco forest is lower and typically smoother than that in many other tropical forests in which background treefall gaps dominate the forest dynamics (Odum 1970; Brokaw et al. 2004).

p. 206 For example, the compositionally similar *Dacryodes-Sloanea* forest on the Lesser Antillean island of Dominica experiences fewer hurricanes and is much taller than tabonuco forest in the Luquillo Mountains (Perez 1970).

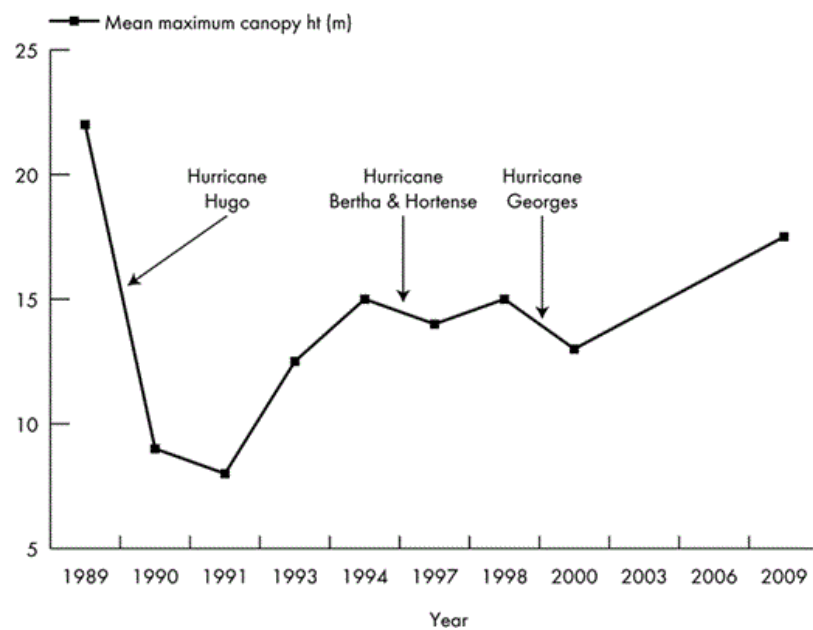
To account for the smooth canopy of tabonuco forest, Odum (1970) suggested that repeated hurricanes in Puerto Rican tabonuco forest have selected, evolutionarily, against the emergent habit among trees and for smaller crowns with reduced wind resistance, with both resulting in a smooth forest canopy. A more parsimonious explanation of this smooth canopy is simply that hurricanes and lesser storms repeatedly prune the extended tops and branches of trees that would otherwise grow tall and spread their canopies as in some hurricane-free forests. Thus, short trees with small crowns would be a phenotypic, not a genotypic,



feature (Fetcher et al. 2000; Myster and Fetcher 2005). Persistent trade winds probably help produce a smooth canopy at higher elevations in the Luquillo Mountains (cf. Lawton 1982), but these winds might not explain the relatively smooth-canopied tabonuco forest at lower elevations, such as El Verde. At El Verde, the mean annual windspeed above the canopy (Waide and Reagan 1996) is similar to the annual windspeed on Barro Colorado Island, Panama (Brokaw et al. 2004), which has a forest of large, spreading trees and a comparatively rough canopy punctured by treefall gaps. Other tropical forests subject to cyclonic storms are typically short (de Gouvenain and Silander 2003), but the canopy structure among hurricane-disturbed forests differs widely (Brokaw et al. 2004).

In a 1.08 ha plot at El Verde, the canopy was relatively smooth before Hurricane Hugo (Brokaw and Grear 1991). After the storm, the residual canopy surface was much rougher and lower in average height than before (figure 5-2). With the sprouting of surviving trees and new regeneration, the mean height of the canopy increased, and the coefficient of variation of the height, here a measure of roughness, declined, suggesting that the canopy was redeveloping its former smoothness. Hurricanes Hortense and Georges temporarily reversed this trend toward smoothness, but 18 years after Hurricane Hugo the canopy has returned to nearly the structure it had before that hurricane, and which it had been developing since the previous major hurricane passage in 1932. The small individual tree crowns in tabonuco forest (whether genetically or phenotypically determined) confer resistance to wind effects (Everham and Brokaw 1996), and the rapid sprouting of hurricane-trimmed trees (see below) provides resilience.

**Figure 5.2**



Mean height of upper surface of forest canopy before Hurricane Hugo and at points in time afterward, with effects of all hurricanes in the period indicated, at El Verde, Puerto Rico (N. Brokaw).

Data from measurements at 475 points in a 1.08 ha plot.

Hurricanes tend to affect older forests with large trees more than they do young forests with small trees (Everham and Brokaw 1996; Grove et al. 2000; Lomascolo and Aide 2001; but see Franklin et al. 2004). Hurricane Hugo affected a relatively mature forest in the Luquillo Mountains; it was the first hurricane to cross Puerto Rico since 1956, and it passed closer to the Luquillo Mountains than any hurricane since 1867 (Scatena and Larsen 1991). Hurricane Georges, on the other hand, struck the Luquillo Mountains only 9 years after Hurricane Hugo, and therefore affected a less structurally mature forest (figure 5-2). Due to this effect and to lower storm intensity, Hurricane Georges produced smaller canopy openings and deposited less debris than did Hurricane Hugo (Lugo and Frangi 2003; Ostertag et al. 2003).

Canopy openings increase the understory light climate (chapter 4), which apparently stimulates seed germination and plant growth (see below and chapter 6) that eventually return the understory structure and light to prehurricane conditions.

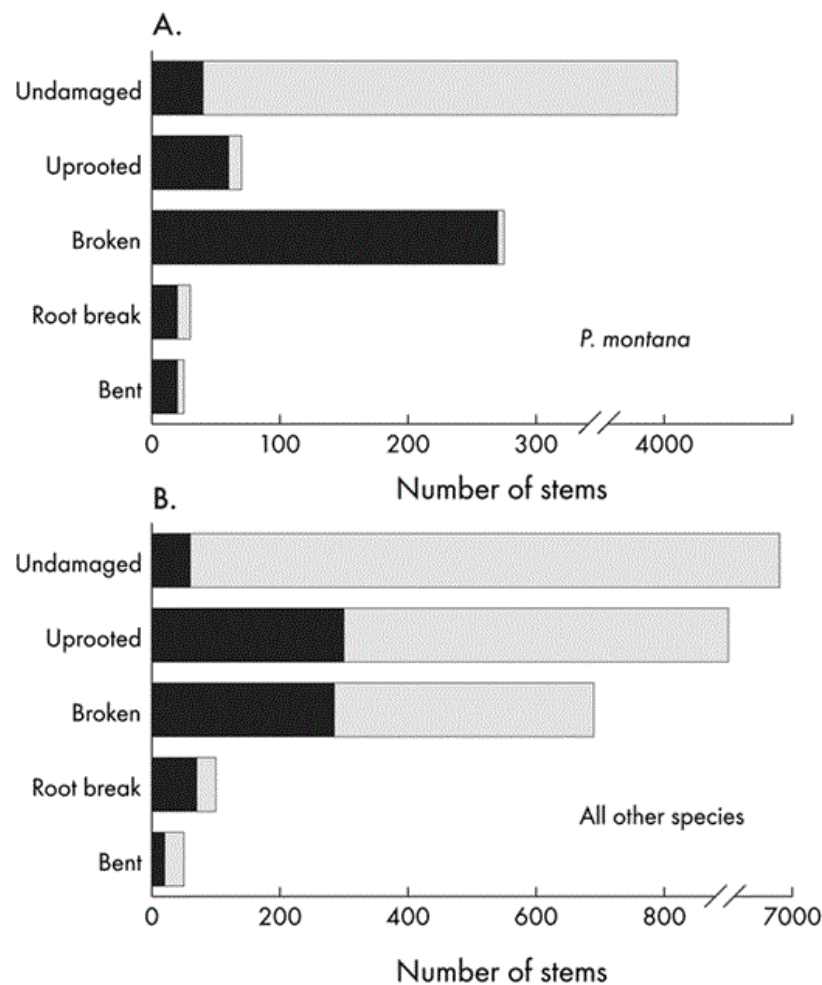
## Tree Response

### Effects and Mortality

p. 208

The effect on trees of Hurricanes Hugo (1989) and Georges (1998) varied across the landscape and among tree species (Walker 1991; Boose et al. 1994; Ostertag et al. 2005), but some patterns were evident (Brokaw and Walker 1991). In general, forests on slopes facing winds were more affected than those on lee slopes (e.g., Walker 1991). Ridges were more affected than slopes at a Colorado forest (chapter 3) site, whereas the reverse was true in a tabonuco site, probably due to the presence of stable (resistant) tabonuco trees (*Dacryodes excelsa*; see below) on ridges (Brokaw and Grear 1991; Basnet et al. 1992). Defoliation was the most common type of effect, followed by effects on small branches, the loss of large branches, and the snapping and uprooting of large stems (figure 5-3) (Brokaw and Walker 1991; Zimmerman et al. 1994). Tall trees were more likely to be defoliated, snapped, or uprooted, and tall trees with larger diameters were more likely to uproot than snap (Walker 1991; You and Petty 1991; Basnet et al. 1992; Ostertag et al. 2005). Size-specific effects varied greatly among species (Zimmerman et al. 1994). Generally, shade-tolerant species (Smith 1970) and species with dense wood lost many branches but suffered less uprooting and snapping than did light-wooded and shade-intolerant species (Zimmerman et al. 1994; Ostertag et al. 2005). Understory trees were more likely to be defoliated or snapped than uprooted (Walker et al. 1992). Direct effects on trees led to indirect effects when downed trees and limbs fell on other trees (accounting for 16 percent of all effects at one site) (Frangi and Lugo 1991) and in places where increased sunlight scalded understory juveniles and seedlings (You and Petty 1991). Effects on understory plants from falling debris are frequent in tropical forests, whether hurricane-related or not (Aide 1987; Clark and Clark 1991).

**Figure 5.3**



Frequency of hurricane-affected and unaffected main stems in the Luquillo Forest Dynamics Plot at El Verde, Puerto Rico (Zimmerman et al. 1994). Black portions of bars indicate tree mortality. (A) Effects on the sierra palm *Prestoea montana*. (B) Effects on all other tree species.

(Used with permission from the British Ecological Society.)

Hurricanes cause catastrophic sudden tree mortality, defined as sudden mortality greater than 5 percent (Lugo and Scatena 1996). Hurricane Hugo immediately killed 9.1 percent of trees  $\geq 10$  cm in diameter at breast height (dbh) in the 16 ha Luquillo Forest Dynamics Plot (LFDP), located in the tabonuco zone at El Verde (Zimmerman et al. 1994; Thompson et al. 2004). In another study, in twenty 300 m<sup>2</sup> plots in the tabonuco zone, the storm had killed 7.4 percent of trees after 54 weeks, and this number rose to 13.3 percent after 171 weeks (Walker 1995). At Bisley, a site in the tabonuco forest that was especially affected by Hurricane Hugo, mortality in a 1.0 ha plot was 16.8 percent just after Hurricane Hugo and had risen to 31.6 percent 5 years later (Dallmeier et al. 1998); by that time mortality probably included some background deaths not attributable to the hurricane. In a secondary forest, mortality 21 months after Hurricane Georges was 5.2 percent  $y^{-1}$ —seven times the background mortality (Ostertag et al. 2005). However, the immediate mortality from Hurricane Hugo was only 1.0 percent in a sheltered 0.25 ha riparian forest stand, whereas the annual mortality there over the following 5 years was 2.0 percent, mainly involving dicotyledonous trees, not palms (Frangi and Lugo 1991). At an elfin forest (see chapter 3) site, mortality was 21 percent of stems in the 5 years following the hurricane (Weaver 1999).

Mortality after Hurricane Hugo was greater among the more affected trees (Dallmeier et al. 1998), especially among uprooted and snapped trees in the LFDP (figure 5-3) (Zimmerman et al. 1994). Snapping and uprooting did not necessarily kill dicotyledonous trees but did kill the palm *Prestoea montana* (table 5-1) (previously *Euterpe globosa*, and named *P. acuminata* in Henderson et al. [1995]). Mortality differed among size classes in a population of the canopy tree *Manilkara bidentata*, in which 4 percent of large trees died from direct effects and 60 percent of seedlings died from burial by litter (You and Petty 1991). Elsewhere in the Caribbean, tree mortality from hurricanes also differs greatly among sites and species (Bellingham et al. 1992; Imbert et al. 1998; Whigham and Lynch 1998), and cyclone effects in Asia and Oceania can cause higher tree mortality than that recorded in these Caribbean studies (Dittus 1985; Elmqvist et al. 1994).

**Table 5.1** Types of effects on trees as a percentage of trees observed in various tabonuco forest stands after Hurricane Hugo

Total trees	Defoliation	Branch effects	Crown loss	Uprooted	Snapped	Mortality	Sprouting	Source
8,579 dicots <sup>1</sup>	–	24.9 <sup>2</sup>	–	9.8	8.3	9.1	64.8 <sup>3</sup>	Zimmerman et al. 1994
4,498 palms <sup>1</sup>	–	–	–	1.5 <sup>4</sup>	6.0	8.8	–	Zimmerman et al. 1994
2,278 <sup>5</sup>	–	–	25.5	2.4	2.2	1.0	98.0 <sup>6</sup>	Frangi and Lugo 1991
732	56 <sup>7</sup>	13 <sup>8</sup>	–	9	11	7.0 <sup>9</sup> 13.1 <sup>10</sup>	–	Walker 1991, 1995

1 Dicots and palms  $\geq 10$  cm dbh.

2 Percentage of trees with no affected stems with at least one broken branch  $> 10$  cm dbh.

3 Percentage of surviving trees.

4 Stem broken above ground level.

5 Dicots  $\geq 4.0$  cm dbh, palms  $\geq 0.7$  m tall.

6 Palms that lost all leaves.

7  $>75$  percent leaf loss, on trees not uprooted or snapped.

8 Branches  $> 5$  cm diameter, on trees not uprooted or snapped.

9 Assumed dead if no leaves at 54 wk.

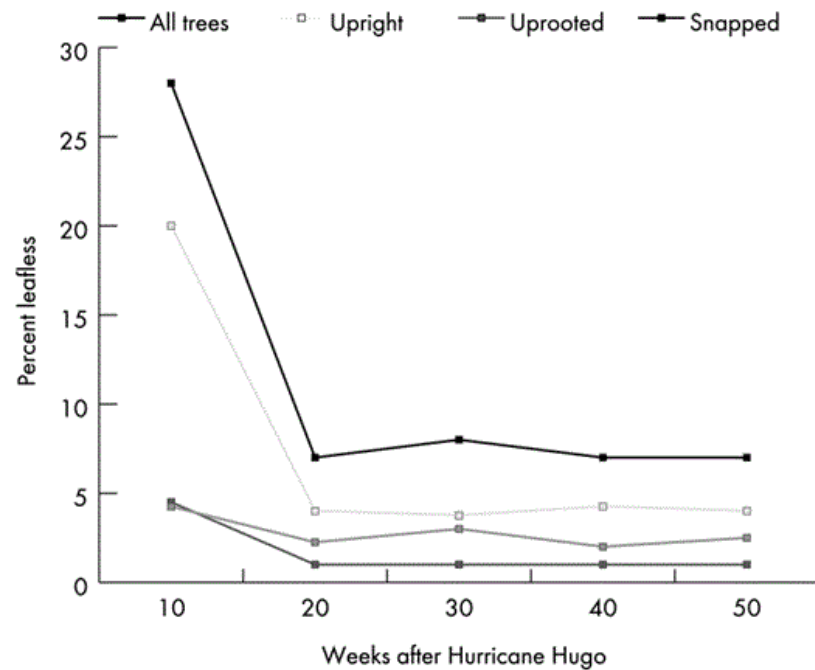
10 After 171 wk.



p. 211

Surviving trees respond to hurricane effects with refoliation and the sprouting of new branches; saplings (advance regeneration) respond with accelerated growth, and seedlings emerge and become established (Brokaw and Walker 1991; Everham and Brokaw 1996). In tabonuco forest, after Hurricane Hugo, leaves had regrown on some affected trees in 2 weeks and on most by 7 weeks; only 7 percent of all trees were leafless after 54 weeks (figure 5-4) (Walker 1991). In a palm forest (see chapter 3) site, 98.0 percent of defoliated palms had produced an average of 4.7 new leaves by 9 months after Hurricane Hugo (Frangi and Lugo 1991). In the high-elevation elfin forest, refoliation was slower than in tabonuco forest (Walker et al. 1996b). New branches in the tabonuco forest were common; in the LFDP, 64.8 percent of surviving trees sprouted new branches, especially those suffering branch loss (Zimmerman et al. 1994). Both uprooted and snapped stems were capable of sprouting new branches from main trunks or at the top of broken stems, but shade-tolerant species sprouted more abundantly than shade intolerant species (Zimmerman et al. 1994; but see Walker 1991). The refoliation and sprouting of affected trees after Hurricane Hugo has been commonly observed in other hurricane-affected forests (Brokaw and Walker 1991; Yih et al. 1991; Bellingham et al. 1992, 1994; Everham and Brokaw 1996).

Figure 5.4

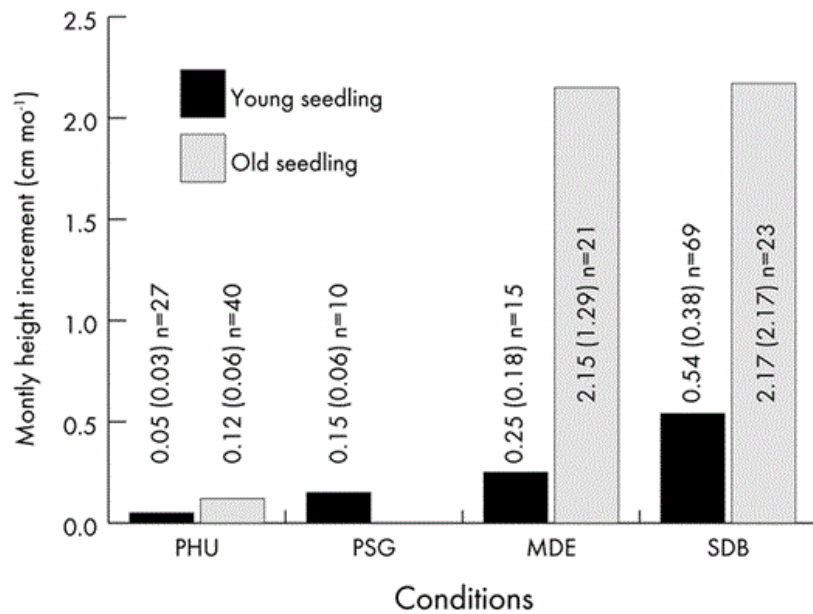


Percent of trees ( $\geq 5$  cm dbh, no palms) with leaves at intervals after Hurricane Hugo, as a function of the type of effect, at El Verde, Puerto Rico (Walker 1991).

(Used with permission from the Association for Tropical Biology and Conservation.)

p. 212

Advance regeneration is “released,” that is, grows faster, after canopy disturbance provides it with more light and perhaps a larger share of soil resources (Denslow and Hartshorn 1994; Fraver et al. 1998). As mentioned above, *Manilkara bidentata* seedlings suffered much mortality from Hurricane Hugo, but surviving seedlings grew 17 times faster than before the hurricane, presumably in response to higher light (figure 5-5) (You and Petty 1991). This accelerated growth reduced the transition period from seedling to sapling from 292 to 16 weeks, which suggests how important hurricane disturbance could be for the population dynamics of this and other tree species (You and Petty 1991).

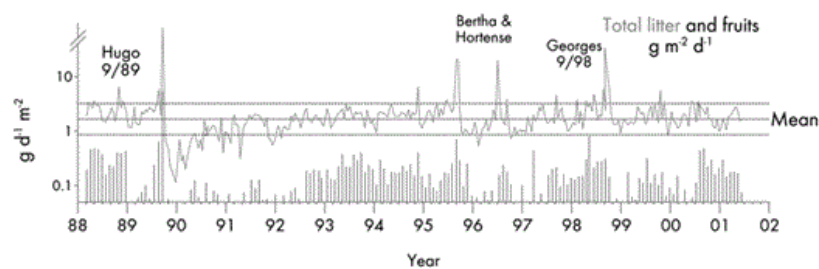
**Figure 5.5**

Seedling growth rates of *Manilkara bidentata* under pre- and posthurricane conditions. PHU = prehurricane understory conditions at El Verde, Puerto Rico, less than 5 percent of maximum potential photosynthetic photon flux density (MP); PSG = prehurricane small gap at El Verde, 5 to 15 percent of MP; MDE = moderately affected posthurricane site at El Verde, 45 percent of MP; SDB = severely damaged posthurricane site at the Bisley Experimental Watersheds, Puerto Rico, 64 percent of MP. Standard deviations of growth rates are in parentheses.  $n$  = sample size (You and Petty 1991).

(Used with permission from the Association for Tropical Biology and Conservation.)

### Fruit Production, Seed Dispersal, and Seedling and Sapling Dynamics

After Hurricane Hugo, forest-wide fruit production declined (figure 5-6) (You and Petty 1991; Wunderle 1999), as trees presumably put energy into refoliation and sprouting. However, many seeds germinated and seedlings became established in response to altered microclimates at ground level (Guzmán-Grajales and Walker 1991; Everham et al. 1996; Scatena et al. 1996). At Bisley, seedling numbers peaked at 12 months after Hurricane Hugo, remained high until 36 months, and then declined (Scatena et al. 1996).

**Figure 5.6**

Monthly leaf litterfall (continuous line) and fruitfall (columns) in tabonuco forest in 1988–2006 at the Bisley Experimental Watersheds, Puerto Rico (F. Scatena). Named hurricanes are shown near the peaks of litterfall caused by the storms. Mean and standard deviation are shown.

Posthurricane germination and establishment differed greatly among tree species in the tabonuco forest, depending on levels of light, nutrients, and litter (Guzmán-Grajales and Walker 1991; Everham et al. 1996; Walker et al. 2003). An experiment showed that the overall density of seedlings and number of seedling species were highest where litter was removed (Guzmán-Grajales and Walker 1991). However, it was mainly seedlings of early-successional species, such as *Cecropia schreberiana* and *Chionanthus domingensis*, that were denser at litter removal sites. The density of late-successional species did not increase or was reduced after litter removal. For example, *Dacryodes excelsa* seedlings declined where litter was removed, whereas *Sloanea berteriana* was not affected by litter removal. Among all species together, seedling mortality was higher and growth less where litter was removed. Given that hurricane litter is deposited unevenly on the forest floor, these different establishment patterns would lead to a patchy and diverse distribution of tree species.

Seedling recruitment after Hurricane Georges was modeled for nine tree species in the LFDP using maximum likelihood methods (Uriarte et al. 2005). Field data on seedlings and light were fitted to different models that included spatially explicit seedling recruitment functions. The majority of the nine species tested supported models that included at least one of several recruitment functions, as follows: (1) the estimated minimum reproductive size of parents, ranging from 9 to 48 cm dbh, influenced seedling spatial distributions; (2) bath recruitment (the presence of a uniform number of seedlings over space, regardless of the local distribution of conspecific adults) accounted for 6 to 81 percent of observed seedling recruitment; (3) light availability appeared to divide species into two groups: one that requires low light levels (<5 percent of full sunlight) for recruitment and one that performs best at high light levels (>30 percent of full sunlight); and (4) density-dependent mortality during the period between seed germination and seedling establishment shifted the mode of seedling distribution away from potential parent trees for most species. This last effect is thought to result from species-specific seed or seedling predators or pathogens. It should promote the species richness of trees by favoring the survival of rare species (Volkov et al. 2005; Wills et al. 2006), and it is noteworthy that it operates in this forest, where frequent hurricane disturbance might be expected to reduce the precision of species-specific interactions with pests.

p. 214 In larger size classes (saplings through mature trees), a study of the survival and growth of 12 dominant tree species in the LFDP after Hurricane Georges (1998) revealed complex relationships among life history type, density, effects of Hurricane Hugo (1989), and size class (Uriarte et al. 2004a). However, some rough generalizations can be made. Competitive thinning of densely packed saplings that grew after the storm accounted for the majority of posthurricane mortality, particularly for secondary species. The species identity of competitors was important mainly for secondary species, whereas functional equivalence of competitors was more common among shade-tolerant species. Effects of the earlier Hurricane Hugo influenced the growth and survival of large stems of some shade tolerant species, and previously affected trees had less of a competitive effect on their neighbors (cf. Ostertag et al. 2005). Thus, the regeneration and regrowth of trees after a severe hurricane reflects a variety of influences, legacies, and species-specific patterns, all contributing to heterogeneity among stands.

### Hurricane Disturbance and Tree Life Histories

Two general tree life-history types appear well adapted to hurricane disturbance (Zimmerman et al. 1994). The first type is pioneers, including *Cecropia schreberiana*, *Schefflera morototoni*, and *Miconia tetrandra*. These species show little resistance to hurricanes; that is, they suffer high effects and mortality and have relatively little ability to sprout (Zimmerman et al. 1994). However, they exhibit much resilience, as they recruit abundantly from seed and grow quickly in response to conditions resulting from canopy opening (Brokaw 1998). The second type, nonpioneers, includes *Dacryodes excelsa*, *Sloanea berteriana*, *Prestoea montana*, and *Guarea guidonia*. These species lose leaves and limbs but resist fatal hurricane effects and exhibit resilience by refooliating and sprouting new branches. Other species exhibit a mix of the characteristics of these two types (Walker 1991; McCormick 1995; Lugo and Zimmerman 2002; Uriarte et al. 2004a).

*Cecropia schreberiana* is an example of a pioneer. It is light- and nutrient-demanding, fast growing, fecund, and short-lived (Silander and Lugo 1990; Walker et al. 1996b). Its population dynamics respond dramatically to hurricanes (Brokaw 1998). At the time of Hurricane Hugo, there were 136 *C. schreberiana* trees  $\geq 10$  cm dbh in the LFDP and fewer small stems (Brokaw 1998). More than half (52.9 percent) of these stems were killed by the hurricane (the mean mortality for other common species was 8.4 percent) (Zimmerman et al. 1994). After the hurricane, *C. schreberiana* was recruited abundantly from a soil seed bank (especially in treefall pits and mounds) (Walker 2000). Within 40 months after the hurricane, there were 10,635 *C. schreberiana* stems 1 to 10 cm dbh and 565 stems  $\geq 10$  cm dbh in the 16 ha LFDP, amounting to a 400 percent increase of trees  $\geq 10$  cm dbh (Brokaw 1998). There was much thinning of these recruits, but some survivors grew fast; at Bisley a *C. schreberiana* grew to 27 cm dbh in the 5 years after Hurricane Hugo (Scatena et al. 1996). Posthurricane, *C. schreberiana* colonizers mature, senesce, and decline in large numbers (Crow 1980; Weaver 1989, 2002), but the species remains abundant as seeds in the soil, lying dormant and ready to form cohorts after the next hurricane disturbance (see the section "Interactions among Disturbances"). The abundance of this species seems to depend on hurricane disturbance; the regeneration of *C. schreberiana* in background treefall gaps is not sufficient to maintain the species' observed numbers in Luquillo forests (see above and Brokaw 1998).

*Dacryodes excelsa* is an example of a nonpioneer. During Hurricane Hugo, individuals of *D. excelsa* lost leaves and branches, but few trunks were snapped, and few stems died (Zimmerman et al. 1994). Mature *D. excelsa*

are interconnected by lateral roots that form tree unions and also appear to be strongly anchored in the soil, often on rocky ridges, and thus resist uprooting (Basnet et al. 1992). The species' resilience is shown by vigorous sprouting on standing trunks (Zimmerman et al. 1994), which might be helped by its habit of root grafting to conspecifics, which could direct resources from unaffected to affected stems (Basnet et al. 1992, 1993). *Dacryodes excelsa* recruits moderately from seed. Another nonpioneer, the sierra palm *Prestoea montana*, demonstrates both high resistance and resilience. It is often defoliated by hurricanes but is infrequently snapped or uprooted. It usually retains at least its youngest leaf and refoiliates vigorously (Frangi and Lugo 1991; Weaver 1999). *Prestoea montana* also tolerates burial by storm debris and regrows after the debris decays (Beard et al. 2005). As with *C. schreberiana*, in places the age structure of *P. montana* exhibits clear cohorts corresponding to disturbance events (Lugo and Rivera Batlle 1987).

Not surprisingly, the tree species that seem especially resistant and/or resilient to hurricanes are among the most abundant species in this hurricane-affected forest. Other studies in the Luquillo Mountains and elsewhere also show that tree species in the tropics are resistant to hurricanes in that they generally suffer little mortality relative to effects, and they are resilient after hurricanes through sprouting, recruitment from seed, and release from suppression (Whigham et al. 1991; Bellingham et al. 1992, 1994, 1995; Boucher et al. 1994; Franklin et al. 2004). Chronic hurricanes could possibly have selected for these characteristics of trees in the Luquillo Mountains (Lugo and Zimmerman 2002); however, it is not clear that trees in the Luquillo Mountains have in fact evolved unique adaptations in response to hurricanes (but see Francis and Alemañy 2003). The responses one sees in Luquillo forests after hurricane effects (sprouting, recruitment, release) are the same responses one sees in large treefall gaps in tropical forests that lack hurricanes (e.g., Brokaw 1985; Putz and Brokaw 1989; Fraver et al. 1998) and in hurricane-affected forests where these storms are infrequent (Boucher et al. 1994). Nevertheless, though we cannot yet demonstrate any adaptation specifically to hurricanes, we can assume that hurricanes in the Luquillo Mountains have filtered out any tree species that cannot cope with these storms (Willig and Walker 1999).

### Stand-Level Tree Response

Early papers on large-scale, chronic storm effects emphasized how disturbance history could explain stand characteristics and tree species composition (Browne 1949; Webb 1958; Whitmore 1974; Crow 1980) and concluded that storm-prone areas might never attain equilibrium (Lugo et al. 1983). In the Luquillo Mountains, the response by trees at the stand level after major hurricane effects is first rapid and then slower but long-lasting, as in most successional sequences. The initial mortality reduces stem numbers. Stem numbers then rise with recruitment but later decline with thinning, whereas diameter class distributions shift to larger trees (Weaver 1986, 1989, 1998; Dallmeier et al. 1998; Frangi and Lugo 1998). The 16 ha LFDP was established at El Verde in 1990, the year after Hurricane Hugo, and was inventoried three times through 2002, overlapping Hurricane Georges in 1998. From a peak of recruitment after Hurricane Hugo, the overall stem numbers declined from 1993 to 2002 (table 5-2). The number of species also declined, with species losses exceeding additions at each census. Losses included some originally rare species and some uncommon and short-lived posthurricane colonizers (e.g., *Trema micrantha*).

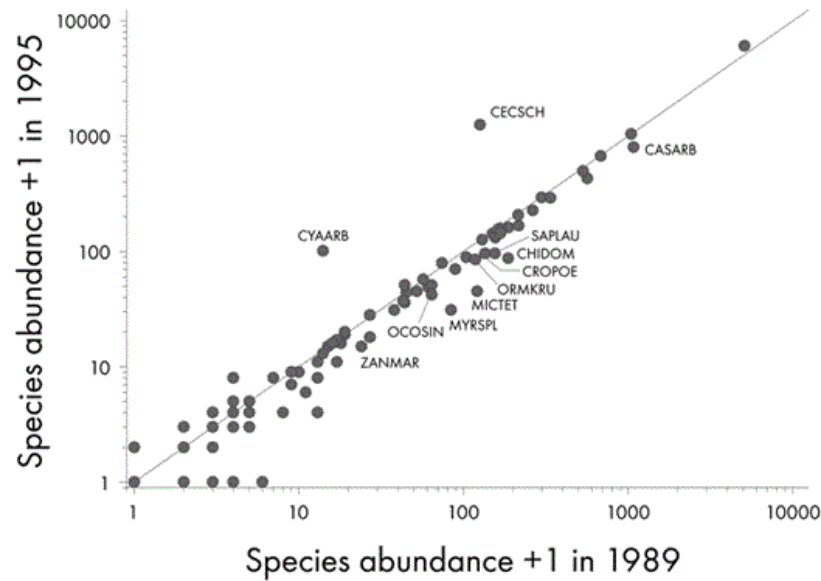
**Table 5.2** Changes in numbers of individuals, stems, and species of self-supporting woody plants  $\geq 1.0$  cm dbh in the 16 ha Luquillo Forest Dynamics Plot, El Verde, Puerto Rico (J. Thompson, unpublished data). Negative numbers in parentheses are the numbers of species recorded in a previous census but not in the indicated census; positive numbers are the numbers of species recorded in the indicated census but not in the previous census. (Stems  $\geq 10$  cm dbh were censused soon after Hurricane Hugo, whereas stems  $\geq 1$  and  $< 10$  cm dbh were censused in 1991–1993, after their numbers had risen due to recruitment.)

Total $\geq 1.0$ cm dbh	1990	1995	2000
Individuals	90,166	71,828	68,099
Stems	108,891	89,014	85,883
Species	150	143 (–8, +1)	135 (–11, +2)

Overall, although the numbers of a few pioneer species increased greatly (figure 5-7), the relative abundances of tree species in the LFDP changed little after Hurricane Hugo, as observed elsewhere in Puerto Rico (Fu et al. 1996; Dallmeier et al. 1998; Frangi and Lugo 1998; Pascarella et al. 2004) and in some other hurricane-affected forests worldwide (Burslem et al. 2000; Tanner and Bellingham 2006; but see Dittus

1985; Imbert et al. 1998). In fact, recurrent disturbances might tend to stabilize species composition through repeated selection for resistant and resilient species (Willig and Walker 1999). Due to this process, individual hurricanes would have a minor effect on the tree species composition (Burslem et al. 2000).

**Figure 5.7**



Log number of stems  $\geq 10$  cm dbh of tree species in 1989 (estimated) and in 2000 in the Luquillo Forest Dynamics Plot, El Verde, Puerto Rico. Equal numbers at both censuses lie on the diagonal line. Numbers below the line indicate population declines in the interval; numbers above indicate population increases (Zimmerman et al. 2010).

(Used with permission from the British Ecological Society.)

p. 217 The longest records of change in tabonuco forest come from a 0.72 ha plot established in 1943 (Crow 1980; Lugo 2008) and a 0.4 ha plot established in 1946 (Weaver 2002), 11 and 14 years, respectively, after the passage of Hurricane San Ciprián in 1932. Several tree inventories (stems  $\geq 4.0$  cm dbh) in these plots through 2005 show that the numbers of stems (Weaver 2002) and species peaked in the first 10 to 15 years after the hurricane and then decreased, as natural thinning reduced numbers and more species went locally extinct than entered the plot (Crow 1980; cf. Tanner and Bellingham 2006). In particular, secondary species (pioneers) died out after an initial pulse of recruitment (Weaver 2002). Similar patterns are evident in the colorado forest (see chapter 3), where the long-term posthurricane response includes shifts to larger tree diameters, shifts from pioneer to mature forest species, and an eventual decline in species richness over the period measured (Weaver 1986, 1989). A generalized scenario of posthurricane forest dynamics includes (1) a phase in years 0 to 10 of increasing stem density; (2) a phase in years 10 to 45 of slow but steady ingrowth, strong competition, and high and then lower mortality, especially of secondary species; and (3) a phase after about 50 years of slow ingrowth and low mortality, in which secondary species would be maintained by background treefall gap dynamics (Weaver 1998). Another suggested scenario includes a 10-year aggrading phase, a 10-year reorganization phase, a 25-year transition period, and then a 15-year period of maturity (Lugo et al. 1999). Beyond 50 to 60 years of stand development—that is, without further hurricane effects—we do not know what forests in the Luquillo Mountains would be like. Hints might come from looking at the compositionally similar *Dacryodes-Sloanea* forest on the Lesser Antillean island of Dominica. This forest experiences fewer hurricanes and is much taller than the tabonuco forest in the Luquillo Mountains (Perez 1970).

Some climate models predict an increased intensity of hurricanes (Emanuel 1987; Overpeck et al. 1990). With increased intensity, or frequency, the forest model ZELIG predicts reduced tree height and diversity in tabonuco forest (O'Brien et al. 1992), due to a reduction in the number of large, climax species. Another model, FORICO, agrees with ZELIG that the tree species richness would decline if the hurricane frequency were significantly higher, but FORICO also predicts a decline in species richness when the hurricane frequency is much less, because pioneer species would drop out (Doyle 1981; cf. Tanner and Bellingham 2006). FORICO, however, does not take into account long-term processes that might enrich forests in the absence of hurricanes. It does not take into account the possibility that absent hurricanes, the forest would grow taller and background treefall gaps would be larger, creating a more heterogeneous vertical and horizontal forest habitat that could sustain more tree species, including pioneers (as well as other plant life



forms and animals) (Brokaw and Lent 1999; Brokaw et al. 2004; also see above). Also, FORICO includes only the present complement of tree species. It assumes no in situ evolution of species, which might occur more frequently in a more structurally varied forest, and it assumes no immigration of species, which might occur more frequently without the harsh filter of chronic hurricane disturbance. This filter might explain the high dominance of some tree species in the LFDP (Thompson et al. 2004) and in Puerto Rican forests generally (Lugo et al. 2002) relative to forests elsewhere.

## p. 218 Understory Plants and Lianas

Shrubs in the LFDP were affected by falling debris during Hurricane Hugo but then flowered abundantly (N. Brokaw, personal observation; Wunderle 1995), sprouted vigorously (Hammond 1996), and reached high densities (J. Thompson, unpublished data). An experimental study showed that the germination and establishment of a common shrub in tabonuco forest, *Palicourea riparia*, is enhanced by conditions created by disturbance (Lebrón 1979). Shrubs thus show little resistance but much resilience to hurricanes.

Ferns respond markedly to hurricane disturbance to the canopy and then to canopy closing. Depending on the species, these responses can include increased plant and leaf mortality, increased or decreased spore production and leaf production, and changes in the size of leaves produced (Sharpe 1997; Halleck et al. 2004). For example, after Hurricane Hugo, leaf production in *Nephrolepis rivularis* increased via runners sent out under the litter from existing plants, but almost all these new leaves disappeared within 5 years. Following Hurricane Georges, small plants of *Thelypteris reticulata* increased in leaf size, leaf production, and fertility, but within 5 years the same plants were again producing small, sterile leaves. In elfin forests, ferns and grasses proliferate after hurricane disturbance and can delay tree recruitment (Weaver 1986; Walker et al. 1996b). After Hurricane Hugo, herbaceous climbers and vines proliferated in some areas, but stem numbers declined rapidly with time (Walker et al. 1996b; China 1999). Lianas (large, woody vines) are less abundant in the tabonuco forests studied at El Verde and Bisley than in most other tropical forests, perhaps because hurricanes strip lianas, as well as potential supporting branches, from trees (Rice et al. 2004). The common, large herb *Heliconia caribaea* was recruited where the canopy was opened by Hurricane Georges (Meléndez-Ackerman et al. 2003) but has greatly declined since (J. Thompson, unpublished data). Thus, many shrubs, herbaceous vines, herbs, and ferns capitalize on the changed ecological space in the understory after a hurricane, but some effects are short-lived.

## Hurricanes and Terrestrial Consumers

Hurricanes have mixed effects on terrestrial consumers, depending on their ecologies and preferences for different ecological spaces. The increased debris promotes populations of decomposer species, but the altered three-dimensional structure and microclimate of the forest have negative effects on many other species.

### Arthropods

p. 219 After Hurricane Hugo, the numbers of Diptera, bark beetles, pin-hole borers, scale insects, and orb-weaving spiders all increased (Torres 1992; Schowalter 1994; Pfeiffer 1996). Herbivores increased in response to the flush of new plant growth. For example, 15 species of Lepidoptera flourished; the most common of these was *Spodoptera eridania*, which fed on 56 plant species in 31 families (Torres 1992). All these plants were early-successional species, and *S. eridania* fed exclusively on herbs and on young leaves of saplings or on sprouts of older trees; it was not found on mature leaves in tree canopies. The herbivore outbreak might have been stimulated by the abundance of palatable, young leaves in the posthurricane regeneration. Drought (which followed Hurricane Hugo) also tends to concentrate leaf nutrients and carbohydrates and reduce secondary chemicals, further increasing the leaves' palatability (Lawrence 1996). The outbreak of *S. eridania* ended when host plants were consumed and ichneumonid wasps increasingly parasitized *S. eridania* (Torres 1992). It was the first time these natural enemies of *S. eridania* had been observed.

Insect herbivores respond differently to particular tree host species after hurricanes, perhaps because tree species typically suffer different degrees of effects (Schowalter 1994; Zimmerman et al. 1994; Schowalter and Ganio 1999). The sap-sucker functional group was generally more abundant on saplings and sprouts in gaps than on trees in intact stands. This probably reflects the rapid production of shoots and foliage on

which this group feeds. Not all plant species were eaten; in one study, eight tree species flushed new leaves without an increase in herbivory (Angulo-Sandoval et al. 2004). Generally, hurricanes appear to promote sap-suckers and inhibit defoliators in the forest canopy. Leaf concentrations of nitrogen, phosphorus, potassium, and calcium did not affect herbivore abundances or leaf area missing (a proxy of leaf area eaten) (Schowalter and Ganio 1999).

As mentioned, walking sticks are herbivores that can reach high densities in background treefall gaps (Willig et al. 1986), but they seem to be negatively affected by larger scale and more intense disturbances. Hurricane Hugo drastically reduced densities of the walking sticks *Lamponius portoricensis* and *Agamemnon iphimedia* for at least 5 years (Willig and Camilo 1991; M. Willig, personal observation). *Lamponius portoricensis*, previously common, was still quite uncommon 15 years later in most areas of the Luquillo Mountains (M. Willig, unpublished data). This 15-year reduction in numbers suggests that *L. portoricensis*, and walking sticks generally, are among the least resistant and resilient of species in the tabonuco forest of Puerto Rico.

Orb-weaving spiders benefited when hurricane debris created more places for webs, as well as more sites for larval flies, adding to the spiders' food supply (Pfeiffer 1996). Debris also created diurnal refuges from predators, increasing spider survival. The big beneficiary of these changes was the orb-weaver *Leucauge regnyi*. But some species declined—for example, *Modisimus signatus*, which attaches to undersides of live leaves in the understory; many of these sites were eliminated during the hurricane.

## Snails

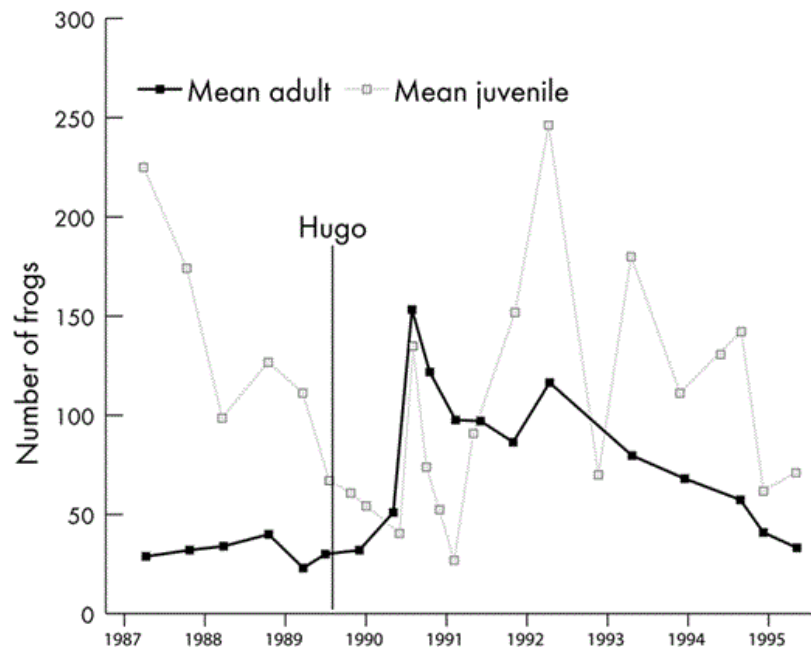
Studies of snail response to hurricanes illustrate the complex effects of hurricanes on populations. The densities of four common snail species declined greatly after Hurricane Hugo. Six months after the hurricane, the densities of *Caracolus caracola*, *Polydontes acutangula*, *Nenia tridens*, and *Gaeotis nigrolineata* were 22, 25, <1, and <1 percent, respectively, of their prehurricane values (Willig and Camilo 1991; Secrest et al. 1996; Willig et al. 1998). But, remarkably, 5 years after the hurricane, the densities of *C. caracola* and *N. tridens* had increased to three and six times their prehurricane densities, respectively. In general, the four snail populations responded in the same fashion because the hurricane-caused changes did not disrupt patterns of correlation among environmental characteristics of the vegetation structure and plant species composition that affect snails (Secrest et al. 1996).

The steep declines followed by increases in snail populations might have been caused by strongly contrasting negative and positive effects of hurricane on snails. Hurricane effects on the forest canopy produce hot and dry microclimates (Denslow 1980; Fernández and Fetcher 1991) inhospitable to snails. Desiccation kills snails (Solem 1984), especially eggs and snails in early growth stages (Heatwole and Heatwole 1978; Riddle 1983). Thus the microclimate of canopy gaps caused by hurricanes probably restricts activity, increases mortality, and limits reproduction. However, hurricanes also produce dead plant material covered with fungi and algae, which snails eat (Alvarez and Willig 1993). After the snails had suffered the effects of a changed microclimate, canopy closure might have allowed them to take advantage of increased food and rebound strongly.

Snail response, however, is not uniform among species after every hurricane (Bloch and Willig 2006). *Oleacina glabra*, *Polydontes portoricensis*, and *Subulina octona* were more abundant after Hurricane Georges (the less intense storm) than after Hurricane Hugo, whereas *P. acutangula* exhibited the opposite pattern. This might be due to the smaller effect of Hurricane Georges in terms of gap size and debris deposition, coupled with the variable sensitivities of the snail species.

## Frogs and Lizards

Hurricanes greatly affect frog and lizard populations. Numbers of adult *Eleutherodactylus coqui* frogs were not immediately affected by Hurricane Hugo but increased sharply a year later (figure 5-8), although adults were smaller than before (Woolbright 1991, 1996). In contrast, numbers of juvenile *E. coqui* at first declined but also peaked a year after the storm, and then declined and continued to vary greatly (figure 5-8). Five years after the storm, both adult and juvenile numbers had decreased to prehurricane levels. Among congeners, *E. hedricki* increased by 14 percent and *E. richmondi* decreased by 83 percent in the first 2 years after the hurricane.

**Figure 5.8**

Mean population estimates for juvenile and adult *Eleutherodactylus coqui* frogs in four long-term study plots (each 400 m<sup>2</sup>) from 1987 to 1995. Population estimates for adults for each plot were the total number of individuals marked during four nocturnal surveys. Population estimates for juveniles were the maximum count during one of three nights. Standard error for adults ranged from 1.2 to 16.1, and for juveniles from 2.5 to 51.5 (Woolbright 1996).

(Used with permission from the Association for Tropical Biology and Conservation.)

Disturbance affects *E. coqui* by changing the forest floor habitat structure and microclimate. Treefalls and hurricanes add structure to the forest floor and understory by depositing debris and promoting the growth of herbs, seedlings, and saplings. All this creates moist microhabitats and refuges from predators (Reagan 1991). For example, hurricane-caused patches of *Cecropia schreberiana* and *Heliconia caribaea* (Meléndez-Ackerman et al. 2003) provide high-quality nest and retreat sites for frogs (Woolbright 1996). These favorable microsites created by hurricanes are transient; eventually, decomposition and forest maturation reduce the understory structure. Relative to background treefalls, which affect only small areas of the forest, Hurricane Hugo added understory structure at a larger scale, temporarily increasing frog survival and reproduction throughout the forest.

After Hurricane Hugo, populations of anoline lizards declined (Reagan 1991) along with the reduction in overall forest structure (figure 5-2). *Anolis* species also moved nearer to the ground, where structure increased. As the forest structure and microclimate returned to prestorm characteristics (figure 5-2), anoles responded by reoccupying higher levels in the forest; this is a good example of organisms tracking changes in ecological space.

## Bats

As with snails, hurricane effects on bat species illustrate the complex interaction between species and disturbance (Gannon and Willig 1994, 1998). Three species dominate the bat fauna of the tabonuco forest in the Luquillo Mountains. *Artibeus jamaicensis* (Jamaican fruit bat) and *Stenoderma rufum* (red fig-eating bat) are principally frugivorous, whereas *Monophyllus redmani* (Greater Antillean long-tongued bat) is nectarivorous. The effects of disturbance on bats can occur at two levels: direct effects of the hurricane (high winds, heavy rain) on the animals themselves, and indirect effects, in which changes in habitat structure or resources stimulate emigration or cause differential survivorship and reproduction (Willig and McGinley 1999).

The abundance of *Artibeus jamaicensis* quickly declined after Hurricane Hugo and remained low for about 18 months, but it was the first bat species to return to and exceed its pre-Hurricane Hugo population level. Rather than reflecting direct hurricane-caused mortality, these shifts might have reflected migration—first fleeing the Luquillo Mountains to areas of the island that were less affected by the hurricane, and then returning to the mountains when fruiting recovered (figure 5-6). Thus, the typical demographics of *A. jamaicensis* might integrate effects over a large area, which would confer resilience after disturbance. In

response to Hurricane Georges, *A. jamaicensis* declined more gradually and its numbers remained low for a longer period than after Hurricane Hugo. Because effects were more widespread from Hurricane Georges than from Hurricane Hugo throughout Puerto Rico, feeding opportunities for this frugivore might have been affected more widely by Hurricane Georges.

*Stenoderma rufum* was affected negatively by both hurricanes. Its numbers decreased steadily after Hurricane Hugo and were lowest at 18 months postdisturbance. An inability to disperse out of the tabonuco forest, as suggested by its normally limited foraging and home ranges (Gannon and Willig 1994), combined with increased exposure to high temperature, precipitation, and wind at roost sites (tree canopy), as well as the decreased availability of fruit, might account for its decline after Hurricane Hugo. Changes in the age structure and the scarcity of reproductive females also suggested a decline in *S. rufum* reproduction after the storm. The decline of *S. rufum* after Hurricane Georges was much faster, and even 6 years after Hurricane Georges, recovery was not obvious. Other known populations of this species are few in number and occur as isolated pockets, separated by miles of urban and deforested areas (Gannon et al. 2005). This, along with the fact that *S. rufum* is not a strong flier, suggests that immigration that restores declining populations is unlikely in this species.

Whether these changes in bat populations reflect mortality or the temporary emigration of individuals from the affected sites is not proven. For canopy-roosting species, such as *S. rufum*, mortality due to direct effects of disturbance is likely. For frugivorous species, such as *A. jamaicensis*, that roost in caves or other solid structures, direct mortality from hurricane disturbance might play a small role; instead, indirect effects (e.g., fruit crop loss) of a hurricane on these species might stimulate their dispersal to less affected areas. Consistent with these possibilities, a Puerto Rican cave population of the frugivorous bat *Erophylla sezekorni* showed no direct responses to disturbance immediately after Hurricane Georges but declined rapidly in the following weeks, possibly owing to a scarcity of food (Jones et al. 2001). In contrast, the abundance of nectarivorous *Monophyllus redmani* increased slightly after both hurricanes. The small increase might be due to a local increase of posthurricane flowering in gaps that predated the hurricanes (Gannon and Willig 1994; Wunderle 1995).

Reduced bat populations also have been reported after severe storms at other island sites (Willig and McGinley 1999). For example, declines after cyclones in the Pacific and Indian Oceans have been reported for populations on Guam (Wiles 1987), Samoa (Craig et al. 1984; Pierson et al. 1996), Mauritius (Cheke and Dahl 1981), and Rodrigues (Carroll 1984), and in the Caribbean on Montserrat declines have been noted after hurricanes (Pedersen et al. 1996).

## Birds

Bird species were either little affected by Hurricane Hugo or resilient afterward, depending on their diet (Waide 1991a; Wunderle 1995). Insectivores (e.g., Puerto Rican Tody, *Todus mexicanus*) and omnivores (e.g., Pearly-Eyed Thrasher, *Margarops fuscatus*; Puerto Rican Tanager, *Nesospingus speculiferus*; and Puerto Rican Woodpecker, *Melanerpes portoricensis*) were little affected. For insectivores, this might be because insect prey survived in sheltered sites as pupae. As with lizards, insectivorous birds adjusted their foraging height to the posthurricane vegetation structure, occupying a reduced vertical range in their search for food (Waide 1991a). In contrast, nectarivores (e.g., Bananaquit, *Coereba flaveola*; Puerto Rican Emerald, *Chlorostilbon maugaeus*), a frugivore (Scaly-Naped Pigeon, *Columba squamosa*), and possibly one granivore (Ruddy Quail-Dove, *Geotrygon montana*) declined, either as a direct result of changes in forest structure or, in most cases, because flowers, fruit, and seeds were stripped from trees and new fruiting declined overall. The quail-dove forages while walking on the ground, looking for seeds and fruits in the litter. This movement would have been difficult in the debris- and regeneration-choked ground layer after Hurricane Hugo, and fruit and seed supplies declined in any case.

When fruiting returned to prehurricane levels, all frugivore populations (except the quail-dove) also returned to prehurricane levels, before the next breeding season, suggesting that migration rather than mortality caused the declines (Waide 1991a). Two nonforest bird species moved into the affected areas before fruiting and forest structure had recovered: the Black-Faced Grassquit (*Tiaris bicolor*), probably to eat seeds of grasses that colonized open areas, and the Red-Legged Thrush (*Turdus plumbeus*), which prefers open habitat (Waide 1991a).

Birds in the Luquillo Mountains and other hurricane-prone areas seem to have evolved plasticity in their habitat and food requirements (Waide 1991b; Wunderle et al. 1992; Whigham and Lynch 1998). In the Dominican Republic, the use of different foraging substrates and maneuvers separates bird species ecologically; they are not separated by foraging height relative to forest structure, as are some bird species in mainland forests (Latta and Wunderle 1998). This might be because hurricanes affect the forest and make it difficult for species to specialize on structure. Therefore, birds are flexible in terms of their foraging mode. Overall, the responses of the bird community are consistent with an adaptation to frequent and large-scale disturbance, which should select for flexible diet and behavior (Reagan et al. 1996; Willig and Walker 1999).

An interesting legacy of background treefall gaps is that the relatively small plants already present in these gaps at the time of Hurricane Hugo suffered relatively few effects and were oases of fruit production after the storm (Wunderle 1995; cf. Levey 1990). Both fruit production and bird abundance in these gaps peaked 93 to 156 days after the hurricane.

## Hurricanes, Decomposition, and Nutrient Cycling

A hurricane transforms large quantities of live biomass to dead biomass. Massive amounts of aboveground biomass and nutrients from the live tree compartment are transferred to the forest floor in the form of leaves and coarse and small woody debris. Falling debris kills smaller plants (see above), adding to the litterfall. Dying roots add belowground detritus. These large, rapid transfers and the subsequent detrital dynamics regulate carbon and nutrient fluxes and have a profound effect on the response to hurricane disturbance (Sanford et al. 1991; Lodge et al. 1994; Scatena et al. 1996; Vogt et al. 1996; Ostertag et al. 2003).

### p. 224 Hurricane Debris

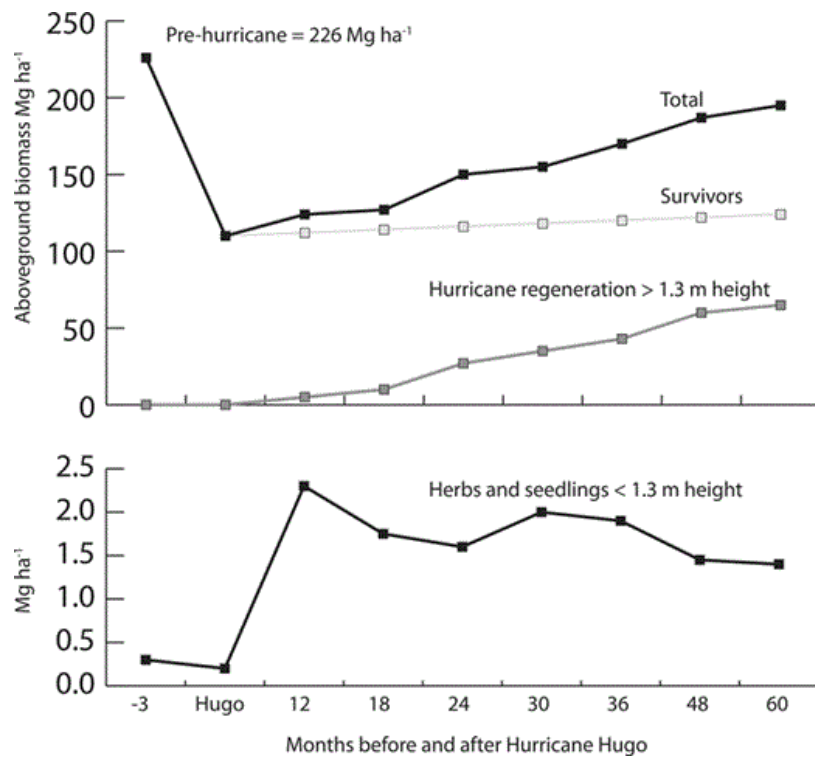
Normally, litterfall is fairly even through time in the forests of the Luquillo Mountains, but in just a few hours Hurricane Hugo deposited a mass of fine litter (leaves, wood < 1.0 cm in diameter) on the tabonuco forest floor at El Verde that was about 400 times (1,006 to 1,083 g m<sup>-2</sup>) the average daily amount (Lodge et al. 1991; Scatena et al. 1996). Another 928 g m<sup>-2</sup> fell but was suspended in the vegetation above ground. In the tabonuco forest at Bisley, the total fine litterfall during the hurricane was 1.2 times the mean annual litterfall. Altogether, the storm moved 50 percent of the prehurricane aboveground biomass to the forest floor at Bisley (figure 5-9) (Scatena et al. 1996). It moved 10 percent in a palm forest, where the fine litterfall was 2.3 g m<sup>-2</sup> d<sup>-1</sup> before Hurricane Hugo but 1,029 g m<sup>-2</sup> during the hurricane (Frangi and Lugo 1991), or 123 percent of the prehurricane annual fine litterfall. At an elfin forest site, the storm deposited 682 times the average daily amount of fine litterfall, and another 45 g m<sup>-2</sup> was suspended above ground (Lodge et al. 1991).

p. 225

↳ Much root biomass also was killed by the death or swaying of trees, by the drought after Hurricane Hugo, and perhaps by the depletion of nonstructural carbohydrate reserves (Parrotta and Lodge 1991; Beard et al. 2005). These strong pulses of litter and dead roots were patchy in space (Lodge et al. 1991).



**Figure 5.9**



Aboveground biomass in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (Scatena et al. 1996). “Survivors” indicates the biomass of individuals that survived the hurricane.

(Used with permission from the Association for Tropical Biology and Conservation.)

### Hurricane Nutrient Input, Decomposition, and Decomposers

As with the patchy litterfall during a hurricane, nutrient fluxes and pools after a hurricane are patchy in time and space due to abiotic effects such as locally variable soil, topography, and debris. Posthurricane nutrient fluxes and pools are also patchy due to biotic effects, such as variable nutrient content and decomposition time of debris, as well as variable local uptake among different plant species. The leaf litter deposited by a hurricane is green and relatively nutrient rich, unlike normal brown, senescent litter from which some nutrients have been translocated back into plants before leaf shedding (table 5-3). For example, the phosphorus content, often a limiting factor in tropical forests (Vitousek and Sanford 1986), in hurricane litter was 4.7 times (per unit volume) that in normal litter in a palm forest (Frangi and Lugo 1991). Thus, hurricanes produce an immediate pulse of nutrients from leaf litter on the forest floor, and later hurricane inputs come from the litter suspended above ground. Likewise, decomposing woody debris makes a sustained contribution to nutrient contents for years after a storm (Lodge et al. 1991; Vogt et al. 1996).

**Table 5.3** Ratios of hurricane-caused nutrient input to total mean annual nutrient input in fine litterfall at Pico del Este (lower montane rainforest) and El Verde and Bisley (subtropical wet forest; data from Lodge et al. 1991). The site at El Verde was an especially heavily affected site

	N	P	K	Ca	Mg
Pico del Este	2.21	2.5	4.47	1.21	1.05
Bisley	1.29	1.53	2.99 <sup>a</sup>	1.25	1.27
El Verde	1.25	2.42 <sup>b</sup>	1.26	0.93	0.91

a Probably an overestimate due to leaching losses in prehurricane samples.

b Possibly an overestimate due to differences in classifying fine wood (see Lodge et al. 1991).

In a study imitating the decomposition of nutrient-rich, green litter (defined as having a higher nitrogen concentration and a lower lignin:nitrogen ratio), the green leaves of four common tabonuco forest tree species (*Manilkara bidentata*, *Dacryodes excelsa*, *Guarea guidonia*, *Cecropia schreberiana*) decomposed faster than brown leaves of those species (Fonte and Schowalter 2004). This faster decomposition can fuel

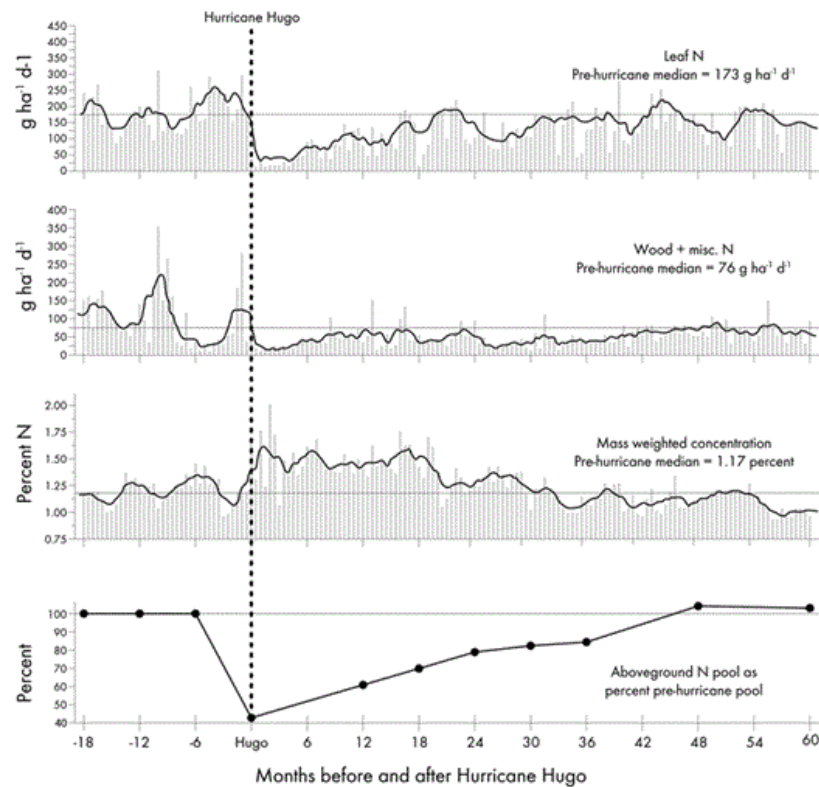
nutrient cycling and primary productivity, which might be affected by the timing and spatial variation of decomposition. However, after Hurricane Hugo, the decomposition rates of leaf litter and fine roots of the dominant tree species tabonuco (*D. excelsa*) and sierra palm (*Prestoea montana*) did not differ between the period immediately after Hurricane Hugo and a period several years later (Bloomfield 1993; Bloomfield et al. 1993; Vogt et al. 1996). Decay constants (the time required for 99 percent material loss) of tabonuco leaf and root litter were the same in both Bisley and El Verde, as well as across different topographic positions (Vogt et al. 1996), but the decay rate of fine and medium-diameter woody debris (<10 cm diameter) did vary according to the topography, possibly reflecting the effects of the hurricane on the local soil moisture (Vogt et al. 1996; Beard et al. 2005). For example, *D. excelsa* wood (3 to 6 cm in diameter) at El Verde decayed faster in riparian areas (9.9 y for 99 percent weight loss) than in upslope areas (16.1 y), where the effect of Hurricane Hugo was less. This is in contrast with Bisley, where the decay rates of wood of the same diameter were significantly faster in the drier, upslope areas (6.7 y for 99 percent weight loss) than in the riparian areas (8.4 y). Greater changes in the soil water content at Bisley than at El Verde due to Hurricane Hugo appeared to increase the decay rate of woody material, especially in the upslope areas (Vogt et al. 1996). The decomposition rates of coarse woody debris (>10 cm diameter) also differed across the Luquillo landscape and by location within each habitat (Vogt et al. 1996). For roots, the belowground decomposition of fine material took 1.5 years, but the decomposition of large roots was slower (Silver et al. 1996).

The large quantities of high-quality organic debris deposited by hurricanes stimulate the growth of microbial decomposers (Miller and Lodge 1997). For example, cord-forming fungi, such as the stinkhorns (Phallales) and *Phanerochaete flava*, were abundant after Hurricane Hugo, presumably in response to the abundant debris. On the other hand, hurricane effects allow sunlight to penetrate to the forest floor and dry the litter in some locations, which inhibits fungi (Lodge 1993).

### Nutrient Export and Cycling

The massive effects of Hurricane Hugo on trees and other plants caused large losses of aboveground nutrients in vegetation (52 to 55 percent loss; see figure 5-10) and some small initial losses of nutrients in soils (Scatena et al. 1993, 1996), but these small losses were temporary, as regrowth over about 2 years restored control of the nutrient cycling. Aboveground, the largest nutrient losses were of K and N. Belowground, soils lost K and nitrate-N initially, but most exchangeable soil nutrient pools were either the same or greater than before the hurricane. Thus, most nutrients were not lost. After the hurricane, there was a temporary increase in the concentration of macronutrients in litterfall, herb, and woody seedling biomass that could be explained in part by the rise and fall in the abundance of pioneer plant species with high nutrient contents (Scatena et al. 1996). For example, aboveground N, K, and magnesium (Mg) in plants declined after Hugo due to the loss of tree stems but then accumulated rapidly in colonizing pioneers. In soils, there was increased ammonium availability and net N-mineralization and nitrification rates 4 months after Hugo, followed by a gradual decline (Stuedler et al. 1991). The return of inorganic N levels in soils to prestorm values can be explained by the regrowth of roots (Parrotta and Lodge 1991), as well as by N immobilization by microbes (Zimmerman et al. 1995b). The soil organic matter content did not change after Hurricane Hugo (Silver et al. 1996).

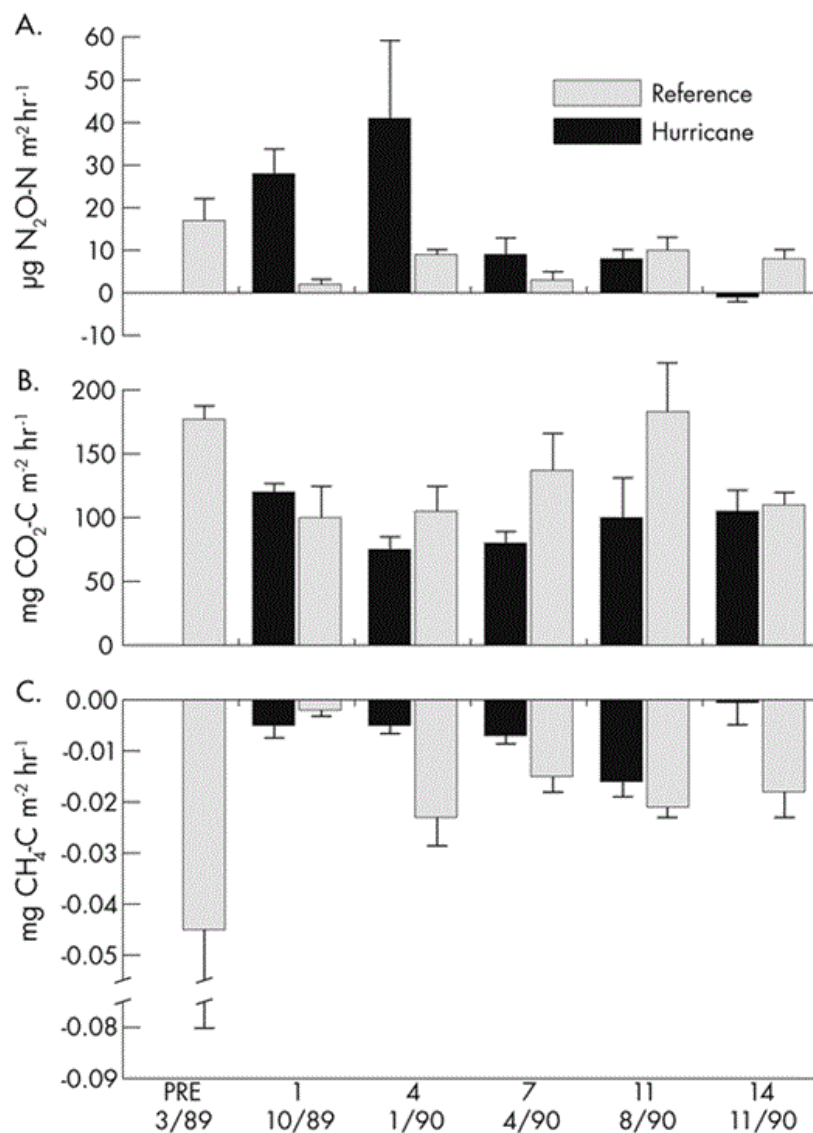
Figure 5.10



Nitrogen flux in leaf litter and wood and miscellaneous litter, the mass-weighted concentration of total litter, and the aboveground N pool as a percentage of the prehurricane pool, Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (Scatena et al. 1996). The horizontal line is the median of prehurricane values; the curve is the 2-month running average.

(Used with permission from the Association for Tropical Biology and Conservation.)

After Hurricane Hugo, nitrous oxide ( $N_2O$ ) emissions increased more than 15-fold in the first month and remained high for 7 months, at a rate three times the predisturbance value (figure 5-11) (Stuedler et al. 1991). The maximum rates of this  $N_2O$  flux coincided with peaks in N mineralization, nitrification, and soil nitrate pools. Carbon dioxide ( $CO_2$ ) emissions were initially 64 percent those of undisturbed areas and returned to normal after 14 months. Soils were generally sinks for methane ( $CH_4$ ), and its consumption decreased by half, perhaps owing to disturbance-induced changes in the nitrogen cycle. Emissions of  $N_2O$  for up to 7 months after Hurricane Georges were five times the fluxes at the same sites measured for 16 months before the storm (Erickson and Ayala 2004). During the 27 posthurricane months of this study,  $N_2O$  emissions remained at levels more than twice those of the prestorm fluxes. Soil ammonium pools decreased after Hurricane Georges and remained low during the study. Nitrate pools increased during the first year after Hurricane Georges, but not significantly (Erickson and Ayala 2004).



Fluxes of  $\text{N}_2\text{O}$  (A),  $\text{CO}_2$  (B), and  $\text{CH}_4$  (C) from reference (El Verde, Puerto Rico) and hurricane-affected (Bisley Experimental Watersheds) sites over time following disturbance (mo) and by sampling date (mo/y). Positive flux values indicate emission from the soil to the atmosphere. Negative values indicate uptake by the soil. Flux rates are the means of four chamber measurements; bars show standard errors (Stuedler et al. 1991).

(Used with permission from the Association for Tropical Biology and Conservation.)

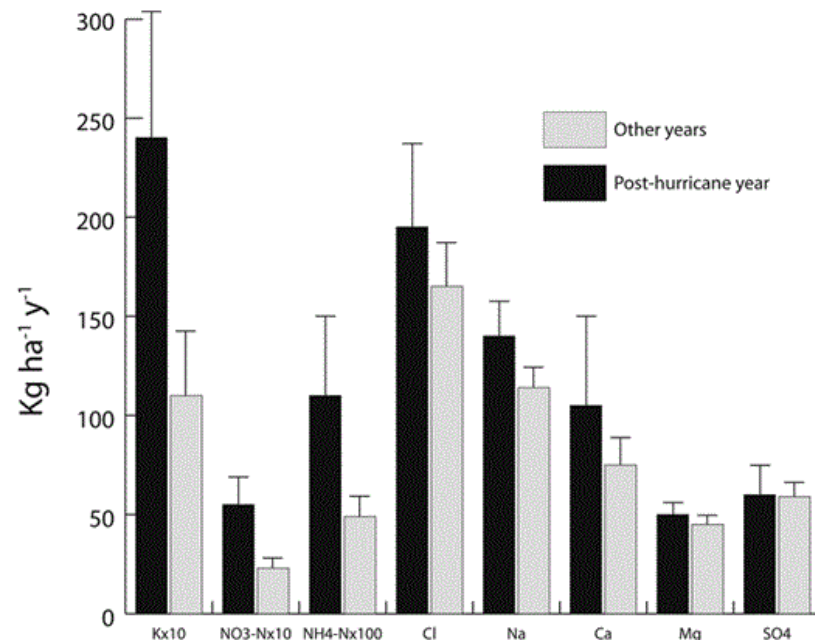
## p. 229 Riparian Groundwater and Stream Water

Reflecting the temporary decreases of living biomass during the first 5 months after Hurricane Hugo, concentrations of all forms of nitrogen increased in riparian groundwater in a Bisley catchment, including nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ), and dissolved organic N (McDowell et al. 1996). Base cations, chloride ( $\text{Cl}^-$ ), and silicon dioxide ( $\text{SiO}_2$ ) also increased in groundwater over this period. The largest relative change in concentration occurred for  $\text{K}^+$ , which had increased from  $0.7 \text{ mg L}^{-1}$  to as high as  $13 \text{ mg L}^{-1}$  5.5 years after the hurricane. At another study site, the Icacos catchment,  $\text{NO}_3^-$  concentrations peaked at  $1.1 \text{ mg L}^{-1}$  a year after the hurricane and had decreased to nearly  $0.0 \text{ mg L}^{-1}$  5.5 years after the hurricane. At both sites,  $\text{NO}_3^-$  concentrations were higher in upslope sampling wells than in those closer to the stream. Most solutes had returned to background levels within 1 to 2 after the hurricane, except for  $\text{K}^+$ . Overall, riparian processes appear to reduce but not eliminate hydrologic losses of N following hurricane disturbance (McDowell et al. 1996; McDowell 2001). In the absence of riparian N retention, the total dissolved N export would be 50 percent greater at the scale of the whole Río Icacos basin (Chestnut and McDowell 2000; Madden 2004). Rapid dissimilatory nitrate reduction to  $\text{NH}_4^+$  by microbes probably has a significant role in this process (Silver et al. 2001, 2005).

The massive defoliation caused by Hurricane Hugo produced large but short-lived increases in nutrient export in streams (figure 5-12) (Schaefer et al. 2000). Average concentrations of nitrate, potassium, and ammonium in stream water increased by 13.1, 3.6, and  $0.54 \text{ kg ha}^{-1} \text{ y}^{-1}$ , respectively, for up to 2 years, representing increases of 119, 182, and 102 percent. (Nitrate, however, was not detected in streams for

several weeks immediately after the hurricane, perhaps due to an increase in dead fine roots that stimulated microbial immobilization [Parrotta and Lodge 1991]). The later increase in stream water nitrate concentrations might have been caused by reduced plant uptake of nutrients or the loss of nutrients released by microbial mineralization of hurricane-derived litter. Sulphate ( $\text{SO}_4$ ), chlorine (Cl), Na, Mg, and Ca showed smaller increases, and the N and K were equivalent to only 1 and 3 percent, respectively, of the N and K in the hurricane-derived plant litter (Scatena et al. 1996). After 2 years, export in streams returned to prehurricane rates, in synchrony with revegetation. Despite extensive effects on the forest, the high survival of plants, rapid revegetation, microbial immobilization of nutrients (see below), and riparian retention led to a rapid return of the stream chemistry to prestorm conditions.

**Figure 5.12**



Comparison of stream chemical fluxes in the first year after Hurricane Hugo in several watersheds in the Luquillo Experimental Forest, Puerto Rico, to fluxes averaged over all other years of record (1983 to 1991–1994) (Schaefer et al. 2000). Bars show mean values across watersheds and the 95 percent confidence intervals.

(Used with permission from Cambridge University Press.)

## Posthurricane Productivity and Biomass

### Measurements of Productivity and Biomass

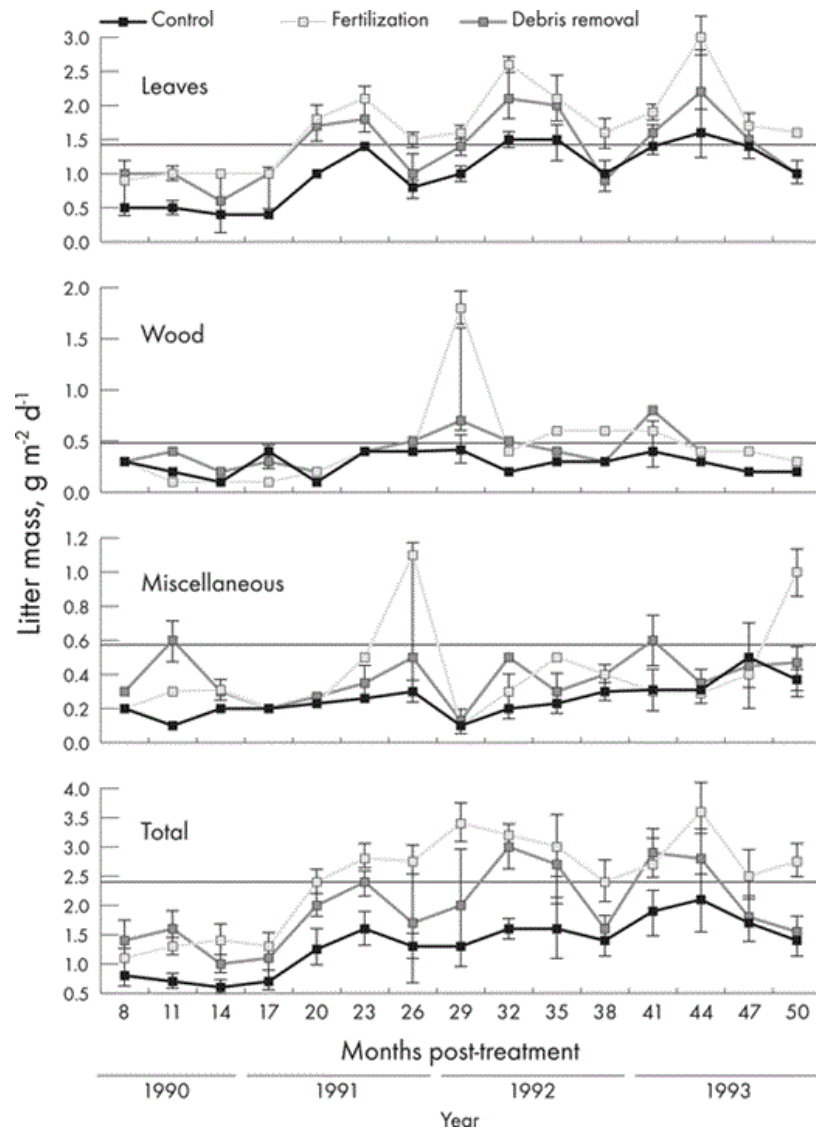
Hurricane Hugo reduced the aboveground forest biomass by as much as 50 percent. However, the posthurricane productivity was higher than that before the storm, and the biomass recovered quickly (Scatena et al. 1996; Weaver 2000). At Bisley, the net primary productivity (NPP) peaked within 12 to 18 months after Hurricane Hugo, and the accumulation of aboveground biomass was nearly 7 to 10 times the annual average, mainly due to regeneration of the pioneer *Cecropia schreberiana* (Scatena et al. 1996). Five years after Hurricane Hugo, the aboveground NPP had reached  $21.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ , triple the prehurricane rate, and the aboveground biomass had reached 86 percent of the prehurricane level (Scatena et al. 1996). Of this, 35 percent was from the postdisturbance regeneration of pioneer trees, still mainly *C. schreberiana*. Nonpioneer species also responded to canopy opening, and possibly to reduced root competition, with increased growth, as in a posthurricane Jamaican forest (Tanner and Bellingham 2006). Seedlings of the dominant, nonpioneer tree *Manilkara bidentata* grew 17 times as fast after Hurricane Hugo than before, as mentioned previously (You and Petty 1991). At Bisley 1 year after Hurricane Hugo, the biomass of seedlings 0.2 to 0.5 m in height had increased to five times what it had been before the storm, and after 5 years it was three times greater than before the storm. In other parts of the forest, the aboveground net productivity of the palm *Prestoea montana* was 20 percent greater after Hurricane Hugo (Weaver 1999). This species and others respond with faster growth when coarse woody debris, the decomposition of which might supply nutrients for growth, is added to experimental plots (Beard et al. 2005; also see Zalamea-Bustillo 2005). Over the long term, in a plot established in 1943 after the 1932 hurricane, the basal area and biomass increased until the 1970s, when they appeared to reach a steady state (Crow 1980; Weaver 1986).



In the short term, Hurricane Hugo substantially reduced root biomass and aboveground biomass (Vogt et al. 1995; Beard et al. 2005). Four weeks after the storm, standing stocks of live fine roots (<3 mm diameter, to a depth of 10 cm) were 0 to 2 g m<sup>-2</sup> and fluctuated greatly, probably in response to rainfall (Parrotta and Lodge 1991). In one study, it took more than a year for fine-root standing stock to return to prehurricane levels (Parrotta and Lodge 1991). In another study after Hurricane Hugo, fine roots recovered in 7 months and increased greatly at 8 months, when rainfall increased after a posthurricane drought (Beard et al. 2005). The coarse woody debris added to experimental plots increased the fine root biomass (Beard et al. 2005). This regrowth of fine roots is fast compared to regrowth in areas of tabonuco forest where all roots were experimentally removed (Kangas 1992).

One measure of productivity, litterfall, took 5 years to return to pre-Hurricane Hugo values in tabonuco forest (figure 5-6) but only 1 month to recover after minor hurricane effects (Beard et al. 2005). Elsewhere in the tabonuco forest after Hurricane Hugo, fine litterfall was at 55 to 77 percent of prestorm values at El Verde immediately after the hurricane, and at 39 to 82 percent after 5 years (Vogt et al. 1996). Variation was associated with topography; inputs of litterfall into a stream returned to prehurricane levels at a slower rate than did those into riparian and upslope areas (Vogt et al. 1996). As with fine roots and basal area increment, litter production increased with the addition of coarse woody debris (Beard et al. 2005). After Hurricane Hugo, leaf litter production was slower to recover in the high-elevation elfin forest than in tabonuco forest (Walker et al. 1996b), where tree growth is 10 times faster (figure 5-13) (Walker et al. 1996b; Waide et al. 1998).

**Figure 5.13**



Comparison of leaf, wood, miscellaneous, and total components of litter trapped in control, fertilized, and debris removal plots in tabonuco forest following Hurricane Hugo at El Verde, Puerto Rico (Walker et al. 1996b). Horizontal lines show prehurricane annual mean litter mass (Zou et al. 1995). Mean and standard error are shown.  $n = 4$  plots per 3-month period.

(Used with permission from the British Ecological Society.)

As mentioned, coarse woody debris is potentially a long-lasting supply of nutrients, and its presence increased the basal area increment, fine root biomass, and litterfall of established trees, including the abundant palm *Prestoea montana* (Beard et al. 2005). Although coarse woody debris can boost long-term productivity, it can also depress it during the short-term pulse of nutrients after a hurricane. After Hurricane Hugo, the abundant carbon source in woody debris is thought to have stimulated the growth of microbial decomposers, which then outcompeted trees for soil N and possibly other nutrients, thereby slowing response (Lodge et al. 1994; Zimmerman et al. 1995b). Thus the removal of woody debris from experimental plots at El Verde increased the short-term rate of canopy closure and forest productivity, and fertilization without debris removal appeared to reduce competition for nutrients (Zimmerman et al. 1995b).

p. 232 Tree species seem to differ in their ability to compete with decomposers for nutrients. The diameter growth of the canopy trees *Dacryodes excelsa* and *Manilkara bidentata* increased when coarse woody debris was added in their vicinity, and growth decreased when the debris was removed (Beard et al. 2005), suggesting that *Dacryodes* and perhaps *Manilkara* were able to compete effectively with decomposer microbes for nutrients. In contrast, *Cecropia schreberiana* growth declined with the addition of wood, suggesting that *Cecropia* is less well adapted for acquiring nutrients from decomposing wood and competing with microbes. Other studies have

p. 233 shown *Cecropia* to be especially nutrient demanding (Walker et al. 1996b). Species effects might also depend on the relative availability of nutrients; at a nutrient-rich site, neither wood addition nor removal affected the growth of *Dacryodes* (Beard et al. 2005). Moreover, the inherent growth rates of trees, including palms, were generally maintained despite the vagaries of disturbance (Beard et al. 2005). Thus local posthurricane productivity reflects inherent site and species differences as much as, or more than, it reflects local variation in storm effects (Walker et al. 1996b; Beard et al. 2005).

The thorough study of response to Hurricane Hugo at Bisley suggested a sequence of phases in ecosystem reorganization in the first 5 years following this hurricane (Scatena et al. 1996). The first phase was a period of foliage production as hurricane survivors releafed and herbaceous vegetation and woody regeneration became established. During this phase, 75 to 92 percent of the nutrient uptake remained in aboveground vegetation. There was a relatively low rate of aboveground carbon accumulation per mole of nutrient cycled, and thus a low level of “nutrient use efficiency,” measured as organic matter produced per unit of nutrient uptake (Vitousek 1982). In the second phase, there was a peak in aboveground productivity when early successional species entered the sapling and pole stages. In the third phase, the litterfall nutrient cycle was reestablished, and there was an increase in the net productivity per mole of nutrient cycled, and thus a higher nutrient use efficiency. During the 5 years following Hurricane Hugo, the Bisley forest had some of the lowest within-stand nutrient use efficiencies and some of the highest levels of aboveground productivity ever observed in the Luquillo Mountains. Thus, high productivity and rapid aboveground ecosystem reorganization can be achieved with rapid within-system cycling and inefficient within-stand nutrient use.

## Modeling of Production, Biomass, and Nutrient Dynamics

The Century Soil Organic Matter Model (CENTURY) was used to synthesize knowledge of nutrient cycling and productivity and to project trends over centuries of repeated hurricanes (Sanford et al. 1991). A spatial version of CENTURY, the model TOPOECO, was used to simulate these factors over the Luquillo Mountains landscape, taking into account elevation, exposure, and effects from Hurricane Hugo (Wang et al. 2002a, 2002b, 2003; Wang and Hall 2004).

The typical biomass of the tabonuco forest is about 300 Mg ha<sup>-1</sup> (Sanford et al. 1991). This is low compared to the values in many tropical lowland forests, but that is expected given that chronic hurricanes seem to limit tree size (see above). According to CENTURY simulations, biomass in the tabonuco forest would increase for up to 400 years of forest development without major disturbance, a developmental stage hurricanes never permit the forest to attain (figures 5-14 and 5-15) (Sanford et al. 1991). Although the forest biomass is low, productivity is high due to the repeated establishment of young, fast-growing trees and the repeated pulses of available nutrients. With high productivity but a low biomass because of disturbance, organic carbon ends up in the soil, and this in turn fuels productivity. Model simulations show that high soil

organic carbon results in comparatively high rates of P and N mineralization. The model results are

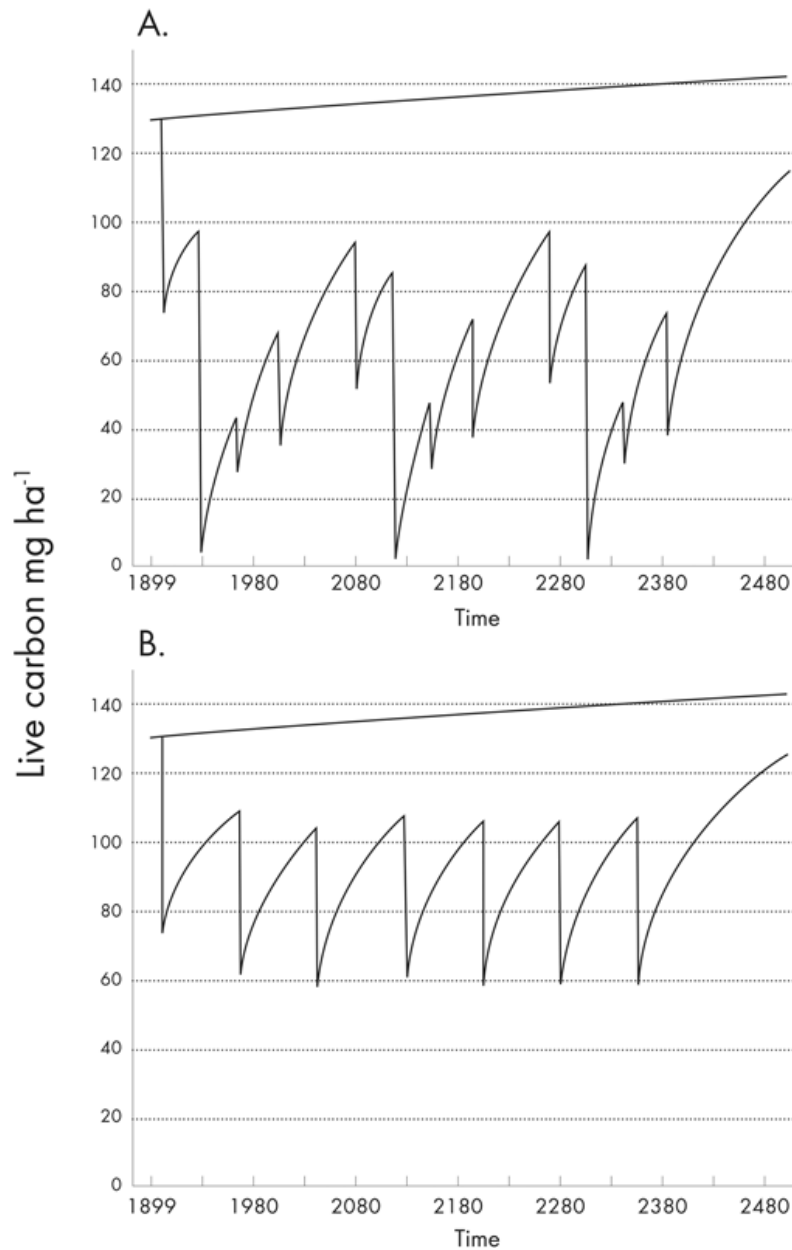
p. 234 supported by observed increases in ammonium ↴

p. 235 ↴

p. 236 ↴

availability and net N-mineralization and nitrification rates (after an initial short-term decline owing to microbial immobilization), followed by a gradual decline 4 months after Hurricane Hugo (also matching the stream water chemistry results; see above).

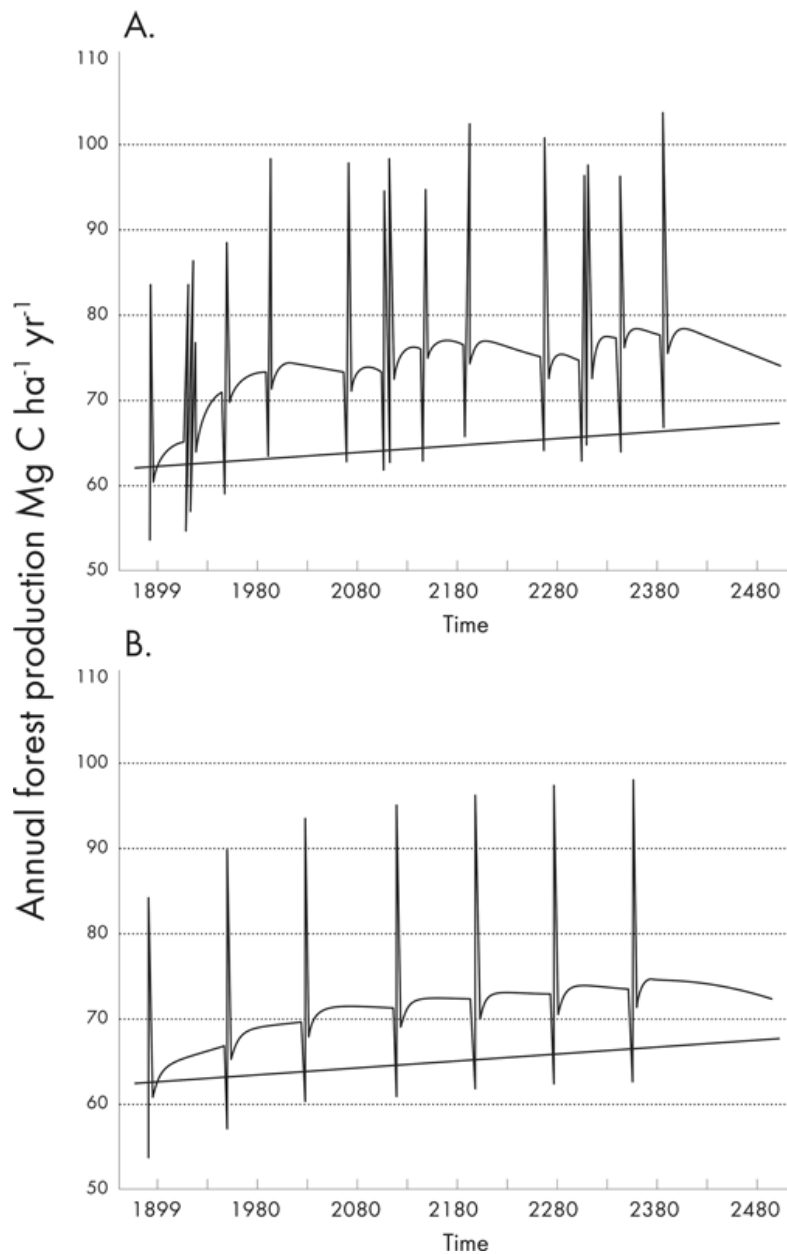
**Figure 5.14**



Above- and belowground carbon simulations as a function of hurricane frequency (Sanford et al. 1991). Straight line is a control (no storms). Irregular lines indicate periodic hurricane disturbance. (A) Historical hurricane disturbance projected into the future using the sequence of six hurricanes that occurred in 1899–1989. (B) Hurricane sequence of repeated Hurricane Hugo strength storms at c. 60-year intervals.

(Used with permission from the Association for Tropical Biology and Conservation.)

Figure 5.15



Forest production simulations in tabonuco forest as a function of hurricane frequency (Sanford et al. 1991). Straight line is a control (no storms). Irregular lines indicate periodic hurricane disturbance. (A) Historical hurricane disturbance projected into the future using the sequence of six hurricanes that occurred in 1899–1989. (B) Hurricane sequence of repeated Hurricane Hugo–strength storms at c. 60-year intervals.

(Used with permission from the Association for Tropical Biology and Conservation.)

The landscape model TOPECO posits that the leaf area index (LAI) recovers within 2 years in the tabonuco forest, 3 years in colorado forest, and more slowly in palm and elfin forests (Wang and Hall 2004). The elfin forest lacks pioneer species that quickly restore LAI at lower elevations (Walker et al. 1996b). The model further suggests that the recovery of tabonuco forest LAI and increases in soil organic carbon (SOC) and mineralized P would spur increases in the gross primary productivity (GPP) by an average of 30 percent 5 years after Hurricane Hugo. In palm and elfin forest, slow recovery of LAI keeps the GPP 20 percent lower than before the storm for 5 years after Hurricane Hugo. In all four vegetation types, storages of SOC, CO<sub>2</sub> emissions from the decomposition of SOC, and the total soil N increase slightly. However, N mineralization rates increase significantly due to the massive input of plant materials from Hurricane Hugo at low elevations and the slow decomposition at higher elevations. There is much variation in these measures because of topography as well (see above). Both CENTURY and TOPECO suggest that these responses last only a few (about 5) years.

Within only 5 years after Hurricane Hugo severely affected forests in the Luquillo Mountains, many populations and ecosystem functions had returned to prehurricane states (Zimmerman et al. 1996; Lugo et al. 1999), but some populations and the physical structure of the forest had not. After 10 years of observation and experiment, through both hurricane and drought events, it was still evident that ecosystem processes, such as plant growth and decomposition rates, had recovered faster than elements of ecosystem structure, such as foliage and fine root biomass (Beard et al. 2005). At Harvard Forest (Massachusetts, USA), an experiment that pulled down trees in order to simulate hurricane effects revealed a similar disconnection between forest structure and function: the rapid regrowth of trees and understory vegetation quickly restored patterns of nutrient cycling, despite the slow recovery of structure (Foster et al. 1997; Cooper-Ellis et al. 1999).

A system attains steady state when its recovery time is less than the interval between disturbances (White et al. 1999). The resistance and posthurricane resilience of many populations in the Luquillo Mountains help them return to prehurricane states within the average 60-year storm interval. Examples among dominant tree species are *Dacryodes* and *Prestoea*, which resisted winds and suffered low mortality; *Manilkara*, which displayed advance regeneration that was released from suppression and helped maintain the species' abundance; and *Cecropia*, the population structure of which changed drastically but was rapidly returning to its prestorm state. Among animals, the abundances of many dominant snail, frog, lizard, bat, and bird species 5 years after Hurricane Hugo were within the range of prehurricane variation.

p. 237 Overall, nutrient cycling is likewise resilient after the passage of a hurricane, for several reasons (McDowell et al. 1996; Scatena et al. 1996; Schaefer et al. 2000; Beard et al. 2005). First, the removal of aboveground biomass does not necessarily lead to a loss of soil nutrients (Silver et al. 1996). Second, many poststorm processes (microbial uptake of nutrients, root recovery, the establishment of fast-growing pioneers, high survival of dominant trees and their rapid refoliation and branch sprouting) quickly take up and store nutrients from decomposing debris. Third, coarse woody debris provides a long-term source of nutrients for continued productivity in soils that are relatively rich in any case. The result is that turnover rates of nutrients and biomass are faster than the hurricane return time, which allows ecosystem functions to achieve steady state in those intervals (Scatena 1995).

In contrast to some populations and ecosystem functions, the three-dimensional structure and biomass of the forest are slow to recover and would probably continue to change over centuries in the absence of subsequent disturbance (Sanford et al. 1991). Structure in forests of the Luquillo Mountains might always be in a state of development (cf. Lugo et al. 1983) if the time to steady state exceeds the hurricane return time. As an extreme model, it is estimated that 500 years must pass after land clearing before a recovering dipterocarp forest in Asia reaches steady state in structure and composition (Riswan et al. 1985). In the Luquillo Mountains, the time from a hurricane-affected state to a steady state of structure and composition might be faster, but it is surely longer than the average 60-year recurrence interval measured for severe hurricanes. Many tree species would continue growing large boles and spreading crowns well after 60 years, thus changing the structure and biomass of the forest, with consequences for other organisms. Two hundred years are thought to be necessary for the recovery of elfin forest in the Luquillo Mountains after effects caused by a plane wreck (Weaver 2000), and modeling suggests that, in the absence of hurricane disturbance, 400 years are required in order for biomass to level off in tabonuco forest (Sanford et al. 1991).

### Some Unmet Expectations

One might expect to see certain hurricane effects that are not observed in the Luquillo Mountains. As reported above, after a short interval of response, Luquillo forests do not have highly irregular canopies (Brokaw et al. 2004) as described for the "cyclone scrub" in Australia (Webb 1958) and the "hurricane forest" in St. Vincent, which consists of low thickets with occasional vine-covered emergent trees (Beard 1945). Also, the number of true pioneer tree species, such as *Cecropia*, is not high in Luquillo forests (cf. Brokaw 1985), possibly because there are few treefall gaps to sustain pioneers between hurricanes. For the same reason, the understory of Luquillo forests is minimally cluttered with the background treefall debris and regeneration frequently encountered in some forests not struck by hurricanes (N. Brokaw, personal observation). Lastly, lianas are not as common in tabonuco forests that have been studied (Rice et al. 2004) as they are in disturbed forests elsewhere (Schnitzer and Bongers 2002).

Hurricanes usually bring heavy rain, high river discharge, and fast currents, and they dump much debris into streams. They also alter the stream microclimate through effects on neighboring forest. All of this has strong effects on stream organisms and processes. Heavy rain not associated with hurricanes also produces high discharges (see chapter 4), but these are not necessarily accompanied by large inputs of debris and changed microclimates.

During Hurricane Hugo, high discharge and fast currents redistributed inorganic and detrital material, as well as stream organisms, throughout the benthic environment along the stream continuum (Vannote et al. 1980) of the Luquillo Mountains (Covich et al. 1996). Litterfall added nutrients and detritus. Debris dams formed, catching detrital food and reducing the washout of invertebrate consumers. Large debris dams persisted for months, continuously releasing microbially conditioned leaves that were carried downstream and eaten by shrimp, a key animal group in stream ecosystems (chapter 3; Crowl et al. 2001). Also after the storm, sunlight poured through the open canopy, promoting the growth of periphytic algae and increasing food for shrimp. In some areas silt covered detrital and algal food sources and refuges from predators, but it washed out within 3 months (Covich et al. 1996). Thus hurricane floods created strong residuals in Luquillo Mountain streams.

Shrimp, especially those in the family Atyidae, are abundant herbivores and detritivores in the headwater streams in the tabonuco forest and make up most of the stream biomass (Covich and McDowell 1996). Their populations were greatly affected by the immediate effects of Hurricane Hugo and by changes in the stream environment and food resources. One month after Hurricane Hugo, atyid shrimp densities were reduced on average by 50 percent in upstream pools, the shrimp apparently having been washed out, and they increased by 80 percent in downstream pools (340 to 460 masl) (Covich et al. 1991). In the next 6 months, shrimp densities increased rapidly to the highest abundances ever recorded in all sites. These high densities most likely resulted from shrimp migrating upstream from riverine pools and from the increased availability of algae and decomposing leaves as food. Shrimp populations in the middle-elevation pools then declined (Covich et al. 1996). A long-term effect appears to be that, in response to floods, shrimp favor pools where they and their food are seldom washed out (Covich et al. 1991).

*Atya* spp. and *Xiphocaris* shrimps respond directly to the redistribution of sedimentary material by rapidly consuming it and clearing it away via bioturbation (Pringle et al. 1993, 1999). This relationship between storms and shrimp was studied by manipulating the presence and absence of shrimp with electric fences in streams (Pringle and Blake 1994; Pringle et al. 1999). Where shrimp were excluded, there was a greater mass of fine and particulate organic material and algal biovolume than in controls with natural densities of shrimp, and there was a larger increase in the mass of sedimentary material following storms. In controls, there was no measurable accumulation of sediment under base flow conditions, and shrimp rapidly removed sediments that accumulated during storms, reducing them to near-prestorm levels within 30 hours. Thus shrimp have a significant effect on the posthurricane, postflood distribution of inorganic sediments and on fine and coarse particulate organic materials.

p. 239 Benthic communities are resilient after intermediate levels of storm disturbance because debris dams catch food and reduce the washout of invertebrate consumers. Storms producing less wind and/or greater streamflow than Hurricane Hugo could cause extensive, longer-lasting decreases in populations of benthic-dwelling shrimp because there might be less input of debris and greater washout of the shrimp and their food.

## Response to Droughts

Droughts affect the Luquillo Mountains, and research is beginning to reveal their effect on forests and streams. Understanding current droughts might help us foresee the consequences of predicted change toward reduced and more variable rainfall in the Luquillo Mountains.

Following Hurricane Hugo, and again in 1994–1995, there were exceptionally dry periods in the tabonuco forest (chapter 4), with measurable effects on microbes, plants, and animals. Fungal decomposers that produce mycelia on leaf surfaces appear to be especially susceptible to this drought. One such species, *Collybia johnstonii*, was a common litter decomposer in tabonuco forest before Hurricane Hugo, but during



the 5 years after canopy destruction by the storm, some mycelia of *C. johnstonii* were smaller or extirpated and were replaced by more drought-tolerant species (Lodge and Cantrell 1995; Lodge 1996; see chapter 6). Fungal biovolumes in soil are closely correlated with soil moisture and decreased slowly in response to drought (Lodge 1993). For trees, hurricane effects reduced fine-root biomass, which recovered in 7 months, but the frequent droughts that followed reduced fine-root biomass such that it did not recover to prestorm levels for 10 years (Parrotta and Lodge 1991; Silver et al. 1996; Beard et al. 2005). Thus droughts can have a greater effect than hurricanes on fine roots and, consequently, on nutrient acquisition and productivity. Litterfall rates also reflected the effect of the drought. After Hurricane Hugo, aboveground litterfall inputs did not recover to prehurricane rates even after 5 years, apparently because of the posthurricane droughts (Vogt et al. 1996). For the riparian fern *Thelypteris angustifolia*, the overall leaf production did not change during the drought year of 1994; however, leaf life spans did decrease relative to earlier years (Sharpe 1997; J. Sharpe, personal observation). The possibility that drought enhanced posthurricane herbivory is discussed above.

Juvenile coquí frogs (*Eleutherodactylus coqui*) cannot survive drought (Stewart 1995), but no effects of drought on adults have been recorded that are distinguishable from background variation (L. Woolbright, personal observation). Females that retain their egg clutches during dry weather typically lay them when it starts to rain again. However, some frog species might be less hardy than *E. coqui*. Both *E. portoricensis* and *E. richmondi* disappeared from mid-elevation forests at a time roughly corresponding to the drought following Hurricane Hugo (L. Woolbright, personal observation). Posthurricane drought appears to have depressed *Anolis* lizard numbers, and a drought coincided with the lowest recorded density of spiders in one study (Pfeiffer 1996; Reagan 1996).

p. 240 Droughts have many effects on stream communities and processes (Covich et al. 1998, 2000, 2003, 2006; Covich and Cowl 2002). Droughts alter the local food-web structure, detrital processing dynamics, and predator-prey dynamics. During droughts there are no or fewer flushing events, and first- and second-order streams might accumulate organic detritus and inorganic sediments that can decrease pool depth and volume. The reduced pools expose prey to predators at the top and bottom of the water column. When the pool size contracted during a drought in 1994, the density of the dominant shrimp *Atya lanipes* rose from 22 to 75 shrimp m<sup>-2</sup> of pool area, and the density of another species, *Xiphocaris elongata*, increased from 5 to 14 shrimp m<sup>-2</sup> of pool area. Gravid adults of both species were fewer during the drought, and the reproductive activity of *X. elongata* remained low during the year. The lowest mean abundance of the predatory shrimp *Macrobrachium* spp. occurred during the 1994 drought, the driest year of 28 years on record in the Río Espíritu Santo drainage. After that drought *Macrobrachium* increased in abundance for 6 years. Droughts increase crowding, reduce both predator and prey populations of detritivores in the short term, increase predator populations over the longer term, and depress reproduction among key detritivores. In addition, the lack of flushing during droughts reduces mortality due to physical scour and results in detrital storage that appears to provide shelter for prey in some pools.

## Response to Landslides

Landslides are frequent disturbances in tropical mountains, including the Luquillo Mountains (Garwood et al. 1979; Guariguata 1990; Larsen and Torres-Sánchez 1992). Landslides provide good opportunities for research on disturbance and response because they include strong temporal and spatial gradients in light, moisture, and soil fertility and stability. These gradients permit examination of the roles of dispersal, competition, and facilitation in order to explain vegetative responses. The primary succession that occurs on landslides follows clear trajectories of response and a sequence of processes that clearly alters the ecological space (Myster and Fernández 1995; Walker et al. 1996a; Myster and Walker 1997).

Landslides consist of two or three relatively discrete zones in which soil and vegetation removal, subsequent stability, and regeneration vary. These zones include (1) an upper zone nearly devoid of vegetation that is unstable and which is colonized slowly, because it has few residuals of the previous system; (2) a lower zone in which soil and vegetation from the upper zone are deposited and which is more stable and able to support faster revegetation, as residuals of the previous vegetation are still present; and sometimes (3) a middle zone that is a “transport chute” between the upper and lower zones (Walker et al. 1996a). Soil organic matter and nutrient concentrations are generally higher in the lower zone, but light levels are typically higher in the upper zone (Fernández and Myster 1995). Temperature and soil moisture are generally higher

in landslides than in adjacent forest. Low-fertility patches in landslides contrast with hurricane-affected or cleared sites where soils remain intact (Myster et al. 1997).

p. 241 **Succession on Landslides**

The rates of change and the particular sequences of plant community composition during succession in landslides are affected by elevation, landslide size, compass orientation, surrounding vegetation, soil development, colonization dynamics, and biotic interactions (Myster and Walker 1997). Plant replacements during succession are especially evident in landslides, where there is little advance regeneration to obscure the sequence of colonization. Succession is slow, having a long plant-to-plant replacement phase, and early plant colonists have a strong influence on later dynamics (Walker et al. 1996a; see chapter 6 for details). Development is faster at lower than at higher elevations and on volcaniclastic than on other substrates. Hurricane effects can retard landslide succession. The severe disturbance of a landslide can erase land use history as an influence, but the past land use of areas of neighboring vegetation that contribute propagules is important (Myster and Walker 1997). On landslide areas in the Luquillo Mountains, the levels of soil nutrients, basal area, and plant composition start to resemble mature forest levels after about 55 years (Guariguata 1990; Zarin and Johnson 1995a, 1995b).

Landslide colonization in the Luquillo Mountains is primarily limited by the availability of dispersed seed (Walker and Neris 1993); the availability of germination microsites within the landslide itself (Myster 1997); and competition for light, water, and soil nutrients (Fetcher et al. 1996). Seed dispersal into a site is particularly important in landslide succession when the seed bank and seed producing plants were removed when soil slid downslope (Walker and Neris 1993; Myster and Fernández 1995). Seed-dispersing birds avoid barren landslide areas where there are no perches (Shiels and Walker 2003). Seed loss to predators and pathogens in landslides is small (Myster 1997). Germination varies among sites within slides, and fertilization has increased the germination of two common plant species on landslides (Shiels et al. 2006). Shrubs have the highest levels of germination among life forms (Walker and Neris 1993). Once they have germinated, the mortality of *Cecropia schreberiana* and *Inga vera* is due more to presumed competition for nutrients and less to pathogens and herbivores (Myster and Fernández 1995). However, in another study, fertilization did not increase the seedling growth of two common plant species on landslides (Shiels et al. 2006).

Succession on landslides might be slowed by the low nutrient availability in areas of soil loss. Both the base saturation and major nutrient cation concentrations are low on new landslide scars (Zarin and Johnson 1995a), but these increased in surface mineral soil (0 to 10 cm) over a 1-to-55+-year chronosequence. During this period, the recovery of N, P, K, and Mg to levels present in mature forests near landslides occurred, suggesting that, ultimately, forest recovery is not limited by a lack of those nutrients (Zarin and Johnson 1995b).

p. 242

Potential sources of nutrients on landslides include atmospheric deposition, substrate weathering, and litterfall, the importance of which can change with succession. For example, there is a net increase in labile P supplied from the atmosphere and litter input, and probably from the pool of inorganic occluded P. The added P is used by the biota and returned to the soil in organic combinations. Eventually, the main source of plant-available P seems to become the labile P pool, as plants increasingly rely on the processing of readily mineralizable organic P (Frizano et al. 2002). The nutrient flux from allochthonous litterfall would differ depending on the identities of colonizing species (Shiels 2006). For example, leaves of the common colonizers *Cecropia schreberiana* and *Cyathea arborea* differ in chemical composition and decomposition rate. Similarly, nutrient flux would change as the species composition shifts during succession.

## Ferns in Landslides

Ferns have a large role in succession on landslides. They stabilize soil, build organic matter, and increase soil nutrients and soil moisture, but they also inhibit the establishment of woody species (Walker 1994). Ferns are commonly found throughout the tropics on disturbed soils (Kochummen 1977; Maheswaran and Gunatilleke 1988). In fact, bare soil, such as that on landslides, is required for the germination and establishment of ferns, which can colonize abundantly in suitable conditions (Moran 2004). In the Luquillo Mountains, *Gleichenia bifida* and *Dicranopteris pectinata* can form dense thickets up to 2 m tall, in adjacent monocultures of each species or in mixed stands. Ferns spread via extensive rhizomes that grow along the soil surface. This might allow fern rhizomes to colonize nutrient-poor soils from parent plants rooted in more fertile soils on the landslide edge. The rhizomes both stabilize the soil on landslides (resistance to erosion) and are sources of invasive propagules following disturbance (resilience). Ferns have an indeterminate growth form that maximizes their use of available space, and old fronds generally remain attached while new growth rises above them. This growth habit forms a dense layer of suspended leaf litter that, together with the newer fronds, greatly reduces the light penetration below (Walker 1994). Long-term observations suggest that these fern thickets in landslides might persist at least several decades before they are eventually shaded out and replaced by trees (cf. Kochummen 1977).

## Response to Human Disturbance

---

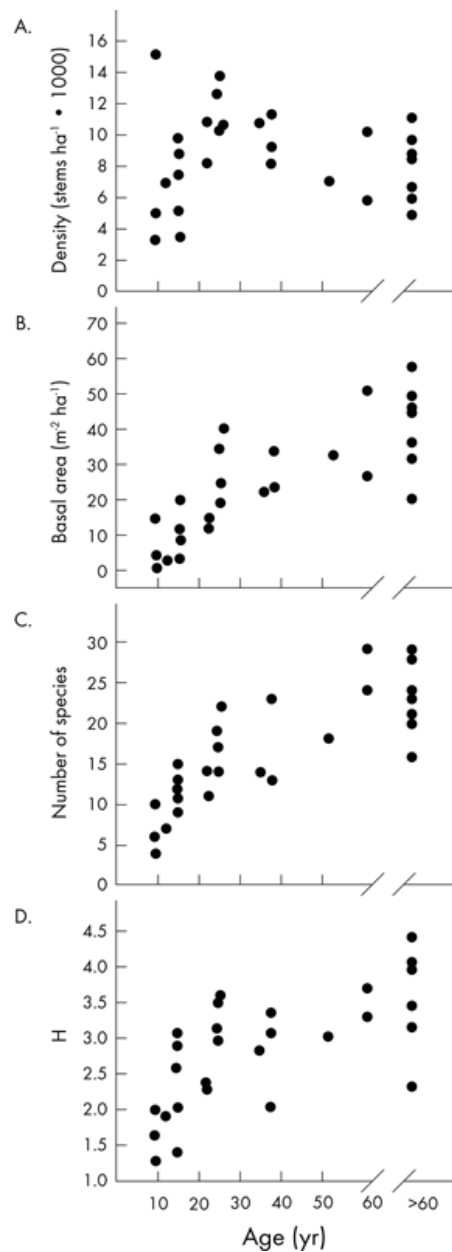
Human effects on tropical ecosystems are widespread in the present and pervasive in the past (Keay 1957; Barrera et al. 1977; Hartshorn 1980; Sanford et al. 1985; Gómez-Pompa and Kaus 1992; Clark 1996; chapter 7). Human disturbance can be more severe than natural disturbance, because human disturbance typically eliminates more of the previous ecosystem more uniformly and more often while leaving fewer residuals to assist in recovery (Franklin et al. 2000). In the past 500 years alone, the extensive forest cover of pre-Columbian Puerto Rico has been reduced by humans to only 6 percent of the island (Birdsey and Weaver 1987). Currently, contemporary reforestation, suburbanization, water extraction, and perhaps climate change are accelerating ecosystem change. In this section we discuss the response to past human disturbances in the Luquillo Mountains, including agriculture, forest clearcutting, road building, and radiation disturbances. (See chapters 3 and 7 for discussions of water extraction and dams and chapters 3 and 8 for discussions of introduced species.)

p. 243 In 1936, about 40 percent of the area of the Luquillo Mountains was unforested or covered with secondary forest, and less than half of the overall area was continuous-canopy forest (>80 percent canopy cover) (Foster et al. 1999). Most of the unforested and secondary forest areas were below 600 masl. In fact, the tabonuco forest zone (below about 600 m) included only 8 percent “mature” forest (Wadsworth 1950; Foster et al. 1999). Many stands were never completely deforested but were heavily affected by charcoal manufacture, coffee growing, or selective tree cutting (García-Montiel and Scatena 1994; Thompson et al. 2002). Much of this area was purchased by the U.S. Forest service in the 1930s and allowed to revert to forest. By 1989, 96 percent of the Luquillo Mountains was continuous forest, and the forest area had also increased elsewhere in Puerto Rico (Birdsey and Weaver 1987; Thomlinson et al. 1996; Grau et al. 2003). Thus, in order to interpret the present structure, species composition, and ecosystem function of many Luquillo Mountains forests, we must study responses to land uses.

### Secondary Forest Structure and Composition: Animals

Studies of a chronosequence of abandoned pastures in the vicinity of the Luquillo Mountains show that after about 40 years of regrowth, forests recover most structural and functional characteristics found in older-growth forests affected only by natural disturbance (Crow and Grigal 1979; Aide et al. 1995; Pascarella et al. 2000). At 40 years of age, these secondary forests cannot be distinguished from old-growth forest in terms of their tree density, basal area, species number, or diversity. However, the tree species composition differs greatly (Zimmerman et al. 2000). Many species composing old growth are absent, and introduced species can dominate secondary stands at low elevations and in alluvial areas (Abelleira Martínez and Lugo 2008), especially the trees *Spathodea campanulata* and *Syzygium jambos*. This pattern obtains across Puerto Rico in lower elevation secondary forests, in which the structure and tree species richness are similar to those in less disturbed forests, but species differ from those in less disturbed forests, and endemics and very large trees are fewer (Lugo and Helmer 2004). With succession, species dominance decreases and more rare species are represented, yet the predisturbance tree species composition will take centuries to recover (Aide et al. 1996). At higher elevations, in contrast, the native species *Miconia prasina* and *Tabebuia heterophylla* dominate abandoned pastures. Dominant species in recently abandoned pastures are those good at coppicing.

Age is the key correlate of forest development in these abandoned pastures (figure 5-16) (Aide et al. 1996). The distance to old-growth forest patches had no effect on any measure of forest recovery; however, the original pastures were not so large as the old pastures studied elsewhere—for example, in the Amazon, where pasture size is important because seed input is clearly limited (Uhl 1987). The lack of *Cecropia* until late in development in these secondary forests on old pastures suggests how different human disturbance is from natural disturbances in the Luquillo Mountains, such as hurricane effects and landslides, after which *Cecropia* colonizes early in development.



Relationship between age since pasture abandonment and (A) tree density, (B) basal area, (C) number of species, and (D) species diversity ( $H'$ ) in 23 abandoned cattle pastures (ages 9.5 to 690 y) and 7 sites that had been forested for  $\geq 60$  y (Aide et al. 1996). Only data from abandoned pastures were used to calculate the regression lines.

(Used with permission from the Association for Tropical Biology and Conservation.)

p. 244

↳

p. 245 Old pastures, abandoned coffee plantations, and relatively mature forest are dominated by different tree species. *Guarea guidonia* tends to dominate old coffee plantations, possibly in response to elevated N (Pascarella et al. 2000). In the Cayey Mountains, in central Puerto Rico, abandoned coffee plantations have a higher basal area than abandoned pastures with forest regrowth, because the coffee areas had more residual woody plants at the time of abandonment (Pascarella et al. 2000). As a result, coffee plantations do not rapidly accumulate plant species richness after abandonment. Age and elevation were also related to tree species composition in this study.

Naturally, the animal community also changes with succession in abandoned agricultural areas. The dominant frog and lizard species change as the vegetation becomes more structurally complex and the microenvironment becomes less variable during succession in abandoned pastures (Herrera Montes 2008). Earthworms, which play a key role in decomposition, shift from dominance by nonnative species to natives during succession on old agricultural lands (González et al. 2008).

## Land Use and Species Composition on the Luquillo Forest Dynamics Plot

The present tree, fungal, slime mold, and bacterial species compositions of the 16 ha LFDP (see above) in tabonuco forest at El Verde all differ according to past land use on the plot (Willig et al. 1996; Huhndorf and Lodge 1997; Lodge 1997; Thompson et al. 2002). Historical records show that land use in the LFDP ranged along a gradient of severity from clearing for agriculture and clearcutting for plywood to coffee planting (probably under residual trees), timber stand improvement (thinning to improve growth), and selective logging (Thompson et al. 2002). All of these uses, except stand improvement, ended by about 1930. Aerial photographs from 1936 indicate four areas of different-percentage canopy cover in the LFDP that match historical information about previous land uses in those areas.

These historical land uses are the main determinant of present-day tree species composition among subplots in the LFDP (Thompson et al. 2002). A detailed comparison of the effects of historical land use intensity, soils, topography, elevation, and other environmental variables showed the overriding effect of historical land use intensity. In the most intensely used area, *Prestoea montana* dominated. In areas severely harvested for plywood, *Casearia arborea* was especially common. Areas of past coffee farming had few *Dacryodes excelsa* and *Manilkara bidentata*; both of these species would have been cut for timber and to decrease shade too heavy for coffee growth. Instead, a common species was *Guarea guidonia* (see above). *Dacryodes excelsa* and *M. bidentata* were relatively abundant in the area that had been selectively cut and improved for timber. The most intensely used area in the LFDP had a markedly lower stem number, richness, and diversity of tree species on both an area and a per-stem basis (Thompson et al. 2002) and fewer rare and endemic species, whereas the least affected area had the highest values for all these measures (table 5-4). Basal area was higher in the least disturbed area (Zou et al. 1995; cf. Aide et al. 1996). In the LFDP, past land use had a greater effect on forest composition and community characteristics than did either strong environmental gradients or the effects of several hurricanes after intensive land use had ceased.



**Table 5.4** Forest structure, species totals, and diversity of trees with stems  $\geq 10$  cm  $D_{130}$  in the 16 ha Luquillo Forest Dynamics Plot at El Verde, Puerto Rico, in 1989 at the time of Hurricane Hugo. Data are presented for the whole plot and as a function of canopy cover class as determined from aerial photographs taken in 1936. Cover Classes 1, 2, and 3 had been clearcut or heavily logged and farmed or locally planted with tree crops before 1936; Class 4 was selectively logged before 1936 and from 1944 to 1953

Forest in 1989	LFDP total	Cover class (% canopy cover) in 1936			
		1 (0–20%)	2 (20–50%)	3 (50–80%)	4 (80–100%)
Area (ha)	16.00	1.16	3.96	5.64	5.24
Number of stems	13,167	866	3,401	4,572	4,328
Stem density ( $\text{ha}^{-1}$ ) <sup>a</sup>	822.9	746.6	858.8	810.6	826.0
BA ( $\text{m}^2 \text{ha}^{-1}$ ) <sup>a</sup>	36.7	36.5	35.7	35.4	40.8
Total number of species (w/o exotics)	89 (83)	32 (30)	66 (63)	62 (60)	76 (75)
Species $\text{ha}^{-1}$ : mean	44.3 (5.7)	32	44.5 (3.5)	42.7 (2.5)	48.0 (2.9)
(s.d.) and range <sup>b</sup>	33–52		42–47	40–45	45–51
Shannon-Wiener $H'$ (w/o exotics) <sup>c</sup>	2.90 (2.86)	2.18 (2.06)	2.69 (2.68)	2.65 (2.63)	2.93 (2.92)
Rare species (w/o exotics) <sup>d</sup>	44 (41)	3 (2)	21 (19)	17 (17)	32 (30)
Unique species (w/o exotics) <sup>e</sup>	19 (16)	1 (0)	1 (0)	5 (5)	12 (11)
Endemic to Luquillo Mountains <sup>f</sup>	4	0	2	1	4
Endemic to Puerto Rico <sup>f,g</sup>	14	2	10	8	13

- a Calculated by dividing total stems or basal area by total area for the LFDP or Cover classes.
- b Calculated by using species totals in nonoverlapping hectares delimited within the LFDP or the cover classes (see text); includes exotics.
- c Totals in parentheses exclude exotics.
- d  $<1$  stem  $\text{ha}^{-1}$  in LFDP. Totals in parentheses exclude exotics.
- e Number found in only one cover class in LFDP; under heading “LFDP,” the total of such species in the plot is given. Totals in parentheses exclude exotics.
- f Little and Woodbury (1976).
- g Including Luquillo Mountain endemics.

p. 246 At Bisley, human land use varied with landscape position (García-Montiel and Scatena 1994). Ridges were left uncut in tabonuco forest at Bisley, slopes were planted with a coffee understory, and valleys were planted with bananas. Charcoal manufacture was controlled by the U.S. Forest Service and limited to selected nontimber trees. As in the LFDP, the local tree species composition at Bisley also reflects past local land use.

The present diversity and species composition of wood-inhabiting ascomycete and pyrenomycete fungi were compared among the areas in the LFDP with different land use histories (Lodge 1997). Only 25 to 31 percent overlap in fungal species composition occurred between areas differing in past land use. Although these areas within the LFDP also differ in tree species composition, host differences alone cannot account for the differences in the fungal communities, because only 3 to 8 of the 253 fungal species found were clearly host-specific (Lodge 1997). Both mycomycete and dictyostelid slime molds were more diverse and abundant in the more intensively used areas of the LFDP (Stephenson and Landolt 1998).

Bacteria are another group in the LFDP having a composition that differs according to land use history (Willig et al. 1996). The functional diversity of bacteria in surface soils can be assessed as the diversity of abilities to degrade different substrates (Willig et al. 1996). Bacterial functional diversity and total catabolic activity were highest in the parts of the LFDP that had the greatest human disturbance more than 60 years previously. For these bacterial communities, the higher concentrations of labile carbon in the leaf litter of

secondary tree species might provide more energy with which to produce enzymes to degrade complex substrates than do the lower concentrations in the litter of primary forest trees (Willig et al. 1996).

## Secondary Forest Nutrient Dynamics

During secondary forest succession, most of the important carbon fluxes associated with litter production and decomposition reestablish within a decade or two (Ostertag et al. 2008). Decomposition is affected by the tree species composition resulting from agriculture. Areas of El Verde that were farmed or clearcut during the early 1900s were colonized by secondary tree species (Thompson et al. 2002). The leaves of secondary species generally have relatively less lignin and other secondary plant compounds (Coley 1987) and should decompose relatively fast. In a comparison between a forest stand that had been a farmed area 50 years previously and a mature tabonuco forest disturbed only naturally and dominated by primary tree species, the litterfall rates were similar, but litter accumulation on the ground was less in the secondary forest (Zou et al. 1995). This suggests that decomposition was faster in the secondary forest, consistent with expectations. An experiment showed that litter from the secondary forest initially decomposed faster than litter from the less disturbed forest, a process that could be stimulated by the higher content of N and K in the secondary forest litter, as well as by the presumably lower levels of secondary compounds. However, long-term decomposition rates were the same in both forests (Zou et al. 1995). Another study of ecosystem processes along a successional sequence confirmed that litterfall rates remain similar through time (even though the basal area and tree density increase) (Marín-Spiotta et al. 2007), but litter standing stocks are lower in secondary forests (Ostertag et al. 2008).

The accumulation of soil C during secondary succession varies among sites. There was a net accumulation of soil C (at depths of 0 to 60 cm) in a 61-year-old secondary forest of  $102 \pm 10 \text{ Mg ha}^{-1}$  (mean  $\pm 1$  standard error), compared to values in a nearby pasture of  $69 \pm 16 \text{ Mg ha}^{-1}$  (Silver et al. 2004). This gain in soil C was due to a fast rate of soil C gain in forest soils ( $0.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ) and a slow rate of C loss from surface soils in the pastures ( $0.4 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ). However, a separate study revealed no net change in total soil C (0 to 1.0 m) across 80 years of reforestation (Marín-Spiotta 2006).

p. 248 Soils in tabonuco forest were highly resilient to nutrient loss following a clearcutting experiment in which two  $1,024 \text{ m}^2$  plots were stripped of all aboveground vegetation (Silver et al. 1994, 1996). Most belowground nutrient changes in the plots lasted no more than a year. Nearly all pools increased or did not change over the first 1 to 2 years following the clearcutting. During the first 5 to 6 years of succession, soil nutrient cations increased above predisturbance levels, whereas amounts of soil P and aluminum (Al) (not a nutrient) were not statistically different from predisturbance values (Silver et al. 1996). Potassium was an exception; it increased in soils shortly after disturbance, presumably due to leaching from litter, and then decreased shortly thereafter. The potassium nutrient pool was the only one to drop below the predisturbance size. Nutrient immobilization and the slow release of nutrients from the decay of dead root biomass were important means of conservation (Silver and Vogt 1993). Live root replacement was slow; it took about 10 years for fine, live root biomass to reach predisturbance levels in the clearcut plots.

The presence of certain tree species planted in order to provide shade in coffee plantations, such as *Guarea guidonia* and *Inga* spp. (Zimmerman et al. 1995a), can influence nutrient dynamics after abandonment. The experimental addition of coarse woody debris did not increase growth in old coffee plantations where there were N-fixing trees, such as *Inga* spp., but it did in areas where there had been no coffee (Beard et al. 2005) and N was perhaps limiting.

Three other types of disturbances—road building, small clearings in elfin forest, and a single radiation experiment—reveal response patterns in the Luquillo Mountains. Vegetation, environmental, and soil characteristics were compared between “roadfills” (road shoulders created by road building, 6 months and 35 y old) and the mature colorado and elfin forest nearby (Olander et al. 1998). The 6-month-old roadfills had higher light and soil temperatures, higher soil bulk densities, larger pools of exchangeable soil nutrients, and higher soil oxygen (O) than the forest sites. The roadfills also had lower soil moisture, soil organic matter, and total soil N than the forest. In the 35-year-old roadfill, the bulk density, soil pH, and P pools were statistically similar to those in mature forest, but the soil moisture, total N, and base cations were different. The biomass and plant density were much less on the 35-year-old roadfill. If roadfill areas were abandoned to revegetation, it is estimated that it would take 200 to 300 years for them to attain the biomass of mature forest. Roads also induce landslides; half the landslides in the Luquillo Mountains are associated with roads (Walker et al. 1996a).

Small clearcuts and a plane crash in the elfin forest (c. 900 masl) on Pico del Este provided information about secondary succession at this elevation (Byer and Weaver 1977; Weaver 2000). As observed after the natural disturbance of Hurricane Hugo (Walker et al. 1996b), vegetation regrowth in the elfin forest is slow compared to that in lower elevation forests. In the first 18 years of regrowth at the crash site (0.078 ha), woody sprouts, ferns, and graminoids dominated, unlike with secondary succession in the tabonuco forest, where woody plants dominate. The ferns might be favored by the very moist soil, and the graminoids by the lack of shading from taller plants. The scarcity of seedlings might be caused by rain washout on the soil surface or the lack of colonizing adaptations in a habitat that historically has had few disturbances as intensive as clearcutting or a plane crash. After 18 years in the crash site, plant heights and diameters were about half, and the biomass one-quarter, of those in surrounding undisturbed vegetation. Species compositions were similar. The radiation experiment took place in tabonuco forest, where a small area was exposed for 3 months to 10,000 curies of cesium (Odum and Drewry 1970). The radiation killed most plants and seeds within 40 m of the source and produced a forest gap with higher temperature and light and lower humidity than in surrounding forest (McCormick 1970). Because seeds and nearly all advance regeneration of primary species were killed, regenerating plants consisted almost entirely of secondary species, all of which were native. The extensive mortality also made regeneration through the first 23 years slow compared to regrowth in natural gaps and in an experimentally cleared area of similar size that was cleared at the same time as the radiation-exposure treatment (Taylor et al. 1995).

p. 249

## Discussion

---

Disturbance and response are central to the patterns and processes woven into the tapestry of the Luquillo Mountains; disturbance legacies underlie the tapestry and form the ecological palimpsest. In this section, we discuss responses to disturbance in the Luquillo Mountains in order to illustrate the concepts of ecological space, resistance and resilience, and residuals and legacies (chapter 2). We also discuss interactions among disturbances.

## Ecological Space

In order to understand the biotic response to disturbance in terms of ecological space (chapter 2), we need detailed knowledge of the changes in abiotic conditions caused by disturbance (that is, the relationship of abiotic variables to geographical space), the characteristics of the multidimensional niche occupied by each species (the relationship between species abundance and abiotic variables), and the feedback of the biota on the abiotic variables. Applying the concept of ecological space emphasizes the degree to which disturbance decouples the linkage between a species' abundance and its location in geographical space, producing through time a varying ecological tapestry. In this section, we demonstrate this by contrasting the response of vegetation to hurricane versus landslide disturbance, and by looking at the response of two groups of animals (lizards and frogs) to hurricanes in the Luquillo Mountains.

Hurricanes remove forest canopy and have relatively little effect on soil (tree tip-ups by Hurricane Hugo exposed 5 percent of the soil surface area in the LFDP) (Zimmerman et al. 1994; and see Walker 2000). Removal of the forest canopy produces increased light (Fernández and Fetcher 1991), higher temperatures,

and drier soil surfaces. These effects can be exacerbated by posthurricane drought (Waide 1991a). Changes to the canopy structure and the resulting debris deposition (Brokaw and Grear 1991; Lodge et al. 1991) are both patchy, so that in addition to having changed mean values, the abiotic conditions are more variable than they were before the hurricane. Following a hurricane, the hues and contrasts of the forest tapestry are more extreme.

p. 250 In response to canopy opening by a severe hurricane, shrubs, herbs, seedlings, and saplings thrive in the understory (Walker et al. 1991; Scatena et al. 1996), as increased light levels reach much of the forest floor and suitable ecological conditions for these plants expand from previously isolated treefall gaps and stream edges. However, hurricanes do not set in motion changes in the vegetation that are like those of a typical secondary succession (Yih et al. 1991; Zimmerman et al. 1994). In all but the most severe cases of hurricane disturbance (Basnet et al. 1992), hurricanes do not kill many of the canopy trees, and the survivors resprout vigorously, quickly shading the understory and limiting the time for shade intolerant species in the understory to grow and reproduce (Fernández and Fetcher 1991; Walker 1991; Yih et al. 1991; Bellingham et al. 1992, 1994; Angulo-Sandoval et al. 2004). A largely undisturbed soil layer, the nutrient levels of which remain largely the same through the disturbance and beyond, supports this rapid recovery (Silver et al. 1996).

In contrast to hurricanes, landslides remove both vegetation and surface soil and expose the nutrient-poor subsoil in the zone at the top of the slide while depositing a jumbled pile of vegetation and surface soil at the bottom zone (Walker et al. 1996a). The tapestry is torn. The responses of the vegetation to these two zones contrast sharply, with the difference controlled by levels of soil organic matter and associated nutrients (Walker et al. 1996a). In the exposed mineral soil, community changes proceed slowly and include a period in which climbing ferns, grasses, and other herbaceous species dominate. In the residual forest soil in the slide, where nutrient and propagule levels are high, succession proceeds rapidly. Here, rapidly growing pioneer species are able to take advantage of high levels of light and quickly establish a canopy. Subsequent community changes follow a sequence of replacement driven by changes in ecological space (defined by nutrient and light availability) that is commonly associated with secondary succession (Walker et al. 1996a).

For animals in the forest, changes in the forest structure and in temperature and moisture regimes are the critical factors that define ecological space. We consider the hurricane responses of lizards and frogs as examples. Different *Anolis* lizard species occupy different height strata in the forest (Reagan 1996). Hurricanes disrupt forest strata (Brokaw and Grear 1991) and compress *Anolis* habitats and species within a range near the forest floor (Reagan 1991). Thus their ecological requirements leave all *Anolis* spp. in close geographical proximity after this disturbance. The understory species *Anolis gundlachi* was observed to restrict itself to the interior of debris piles after the hurricane, presumably in order to avoid high heat and desiccation (Reagan 1996), but it might have suffered increased competition from the other two canopy lizard species. In contrast, coquí frogs, whose reproduction is limited by available nesting sites on the forest floor (Stewart and Woolbright 1996), increased in abundance following Hurricane Hugo, as the animals took advantage of the increased structure at ground level (Woolbright 1996). Yet this numerical increase of coquí was delayed, possibly by negative effects of posthurricane drought on juveniles (Woolbright 1996). These examples show the degree to which disturbance decouples geographical space and the abiotic variables that constitute ecological space, which governs animal distribution and abundance.

As discussed above, two important components of ecosystem stability are resistance and resilience (chapter 2). Resistance is the degree to which a system is not affected by disturbance. Resilience is the time required for a system to return to a state that is indistinguishable from that before the disturbance. An ecosystem is considered resilient if the recovery time is less than the recurrence interval of disturbance. When discussing the response of forested ecosystems to disturbance, it is important to distinguish between structural (state) and functional (flux) variables (Herbert et al. 1999; Beard et al. 2005), because structural components tend to show less resilience than functional ones. For example, after Hurricane Hugo, forest biomass recovered slower (to two-thirds of the prehurricane values by 5 y posthurricane) (Scatena et al. 1996) than leaf litterfall and net primary productivity (fully recovered 3 to 5 y posthurricane) (Scatena et al. 1996; Beard et al. 2005). Some state variables recover remarkably quickly. Forest floor biomass and soil and stream nutrient pools that exhibit posthurricane change return to prehurricane levels in less than 2 years (Zimmerman et al. 1996). Population densities of many organisms that have responded positively or negatively to hurricane disturbance also return to prehurricane levels in relatively few years. Some state variables do not appear resilient to hurricane disturbance. Fine root biomass (Silver et al. 1996; Beard et al. 2005) and densities of walking sticks (insect herbivores in the Phasmodidae; M. Willig, unpublished data) have been slow to return to prehurricane levels. The community composition of canopy trees might be in eternal flux (Crow 1980; Lugo et al. 1999; Weaver 2002), changing constantly through the average interhurricane interval. Overall, however, in comparison to an average return interval of about 60 years, the Luquillo forest ecosystem seems highly resilient to hurricane disturbance, which is a surprise to those who saw the immense tangle of downwood and open canopies caused by Hurricane Hugo. Similar conclusions regarding the overall ecosystem resilience apply to drought; for example, the return intervals for many variables appeared short relative to the recurrence intervals of severe droughts (chapter 4; Beard et al. 2005). To a certain degree, the same can be said of the resilience after landslides (Walker et al. 1996a). Recovery times in the mineral soil exposed by landslides appear to be about equal to the recurrence interval (chapter 4), whereas recovery in residual forest soil is much faster than the recurrence interval of landslides.

Ecosystem resistance and resilience can be inversely related, as seen in Hawaii (Herbert et al. 1999). After being struck by a hurricane, Hawaiian forest plots that lost much leaf area (low resistance) recovered leaf area rapidly (high resilience). Plots losing less leaf area (high resistance) recovered it more slowly (low resilience). Similarly, more severe disturbance can be associated with faster recovery in the Luquillo Mountains. The Bisley area suffered more effects on and mortality of trees from Hurricane Hugo than El Verde did, but Bisley also had a faster recovery of basal area (Beard et al. 2005). A corollary to the putative trade-off in ecosystem resistance and resilience is that more resistant/less resilient ecosystems should be less responsive to supplemental nutrients in terms of growth and turnover in comparison to ecosystems that are less resistant/more resilient (Chapin et al. 1986). Indeed, changes in leaf litterfall and other community and ecosystem components of elfin forest were much less responsive to supplemental nutrients than were the same components in tabonuco forest (Walker et al. 1996b); supplemental nutrients caused leaf litterfall in tabonuco forest to return to prehurricane values only 20 months after Hurricane Hugo.

p. 252

## **Residuals, Legacies, and Human Disturbance**

The response to disturbances in the Luquillo Mountains can be interpreted in terms of residuals and legacies (chapter 2). Residuals are the immediate manifestations of disturbance, including biotic residuals, such as fallen trees, and abiotic residuals, such as the resulting increased light at the forest floor. Legacies are the subsequent behavior of the ecosystem as influenced by those residuals of the prior community. Residuals and legacies can persist for short to long terms, influencing subsequent disturbance and response and building the layers of the palimpsest covered by the current landscape tapestry. The longest-term legacies persist beyond the normal recovery time of the ecosystem and can be relatively permanent (Franklin et al. 2000). Residuals such as fallen trees, debris suspended in trees (Lodge et al. 1991), and slowly dying trees that continue to fall after a hurricane, leave legacies in the form of available nutrients and soil organic matter. Similarly, landslides leave residuals such as debris and forest soil, including buried seeds, at the base of the slide, all of which are key determinants of the ensuing legacy of successional dynamics (Walker et al. 1996a).

Human disturbance has left strong legacies in the Luquillo Mountains (García-Montiel and Scatena 1994; Zimmerman et al. 1995a; Aide et al. 1996; Erickson et al. 2001; Thompson et al. 2002; Beard et al. 2005). The residuals of charcoal production, clearcutting, coffee plantations, and pastures all leave different legacies in the ecosystem in the composition of the vegetation, the soil characteristics, or both. Some human-induced effects can be permanent, because the scale of human disturbance is large relative to the ability of species to disperse into and recolonize abandoned agricultural areas, because of permanent changes in soil characteristics, or because of both causes, evident in the characteristics of early plant regeneration and soil in abandoned pastures (Zimmerman et al. 1995a). The close correspondence of current floristic differences with past land use boundaries in the LFDP suggests that the vegetation differences are not being quickly “blurred” by seed dispersal and colonization from adjacent forest types (Thompson et al. 2002). Coffee cultivation, which required the shade of nitrogen-fixing trees (a residual of disturbance), appears to have a long-term legacy evident in the forest composition and nutrient dynamics (Erickson et al. 2001; Beard et al. 2005). Similarly, the legacy of charcoal pits is evident in local hydrology and the local persistence of palms (García-Montiel and Scatena 1994). Thus, human disturbance produces soil residuals that in turn produce long-term legacies in the vegetation composition.

## Interactions among Disturbances

p. 253 Having described the disturbance regime of the Luquillo Mountains (chapter 4) and begun to understand the response to disturbance events, we can begin to investigate interactions among disturbances and how they shape ecosystem dynamics in the long term. Putting the interactions between disturbances in a matrix (table 5-5) shows how the ecosystem is affected by a sequence of disturbances of either the same or a different type. At present, the interactions among hurricanes, landslides, and human disturbance are well characterized, but interactions among these disturbances and treefalls and drought are less well known (table 5-5). In the case of drought, the interaction strength is probably weak (Beard et al. 2005), except where soil drying could reduce the effects of a subsequent storm (table 5-5). Thus, these cells in the matrix might never be filled, even as we continue to study the effects of drought. It seems that the components of the ecosystem affected by interacting disturbances are largely structural or population-based, rather than functional. As noted above, many of the functional attributes of the ecosystem exhibit high resilience and might therefore be expected to be affected less by interactions among disturbances.



**Table 5.5** Summary of some interactions among disturbances noted in the Luquillo Mountains

<b>Initial disturbance</b>					
<b>Subsequent disturbance</b>	<b>Treefall</b>	<b>Hurricane</b>	<b>Landslide</b>	<b>Drought</b>	<b>Human</b>
Treefall		Rate of isolated treefalls following hurricane disturbance determined by the death of affected trees (Walker 1995; Uriarte et al. 2004a; Ogle et al. 2006)		Might reduce susceptibility of some trees to uprooting in a rainstorm	Effects on species composition might have indirect effects on treefall rate and recovery dynamics; see below
Hurricane	Low stature of recovering vegetation reduces disturbance; fruiting shrubs become important for frugivorous birds (Wunderle 1995)	Depends on interhurricane interval and time for which forest canopy has recovered, particularly woody biomass; shorter intervals reduce disturbance effects (Lugo et al. 1999; Canham et al. 2010). Many populations (e.g., trees [Canham et al. 2010], snails [Bloch and Willig 2006]) exhibit individualistic responses based on life histories, habitat affinities, and other factors.	Existing landslides might suffer additional slides (Walker et al. 1996a). Elsewhere, there is little effect because of the low stature of vegetation; important exceptions have been described in which a hurricane has altered the successional trajectory of a landslide (Myster and Walker 1997).		Important in secondary forests because the low stature of recovering vegetation reduces disturbance (Pascarella et al. 2004; Uriarte et al. 2004b) while secondary species dominating older forest lead to increased damage (Everham and Brokaw 1996; Ogle et al. 2006)
Landslide		High rainfall associated with hurricanes causes many slides in susceptible areas (e.g., Scatena and Larsen 1991)	Additional sliding is common in many landslides; this instability is important in vegetation dynamics (Walker et al. 1996a)	Will increase rainfall amounts necessary in order to cause landslides	Human modification of topography might promote landslides, e.g., roads (Guariguata 1990; Walker et al. 1996a)

Drought	Drying of soil surface might be increased, but reduced root biomass might leave higher levels of moisture at depth (Becker et al. 1988).	Drought following Hurricane Hugo in Luquillo had manifest effects on the ecosystem (Walker et al. 1991), but drought does not always follow hurricanes. Debris from hurricanes reduces drying at the forest floor and regulates stream habitat changes at low flows.	Additional sliding is suppressed due to drying; promotes drought-resistant vegetation in exposed mineral soil (Walker et al. 1996a)	At large scale, deforestation might promote drought frequency; this is untested below the scale of the island of Puerto Rico (van der Molen et al. 2010). Higher productivity secondary forests might be resistant to drought effects (Beard et al. 2005).
Human		Lower elevations of Luquillo mountains were abandoned in the 1930s due to hurricane effects (Scatena 1989).	Along roads, a landslide will result in stabilization efforts associated with road rebuilding or, alternatively, road abandonment (e.g., southern portion of Rt. 191).	

A matrix depiction of the interactions among disturbance types (table 5-5) suggests a way in which to conceptualize and model ecosystem dynamics in the Luquillo Mountains using Markovian or similar processes. Each position in the landscape is defined by a disturbance regime, and each disturbance causes a change in the ecosystem state and sets in motion subsequent ecosystem changes as determined by the biota (whose position in geographic space is determined by their ecological requirements or ecological space). The effects—immediate and long-term—of a particular disturbance are modified by the history of disturbance, and some (e.g., human effects) have more persistent effects than others (e.g., drought). More important, one can begin to see a way out of Margalef's (1968) difficulty whereby it is impossible to define the ecosystem state of a particular geographic space because each location has its own unique history. He wrote, "An ecosystem is a historical construction, so complex that any actual state has a negligible *a priori* probability" (Margalef 1968:30). This problem is less severe if we understand the effects of disturbances on the ecosystem, even if the interactions among disturbances are common. The situation is further resolved by the fact that ecosystem resilience erases many effects of previous disturbances. Finally, this approach emphasizes the value of long-term observations of particular ecosystems. It is only through long-term measurements of disturbance and response that we can begin to fully understand how disturbances interact and determine ecosystem dynamics.

The organisms of the Luquillo Mountains respond to background treefalls, hurricanes, landslides, floods, droughts, and human disturbances. Background treefalls (not caused by hurricanes) are filled with plant regrowth as in other tropical forests. There is limited response by animals to treefall gaps, probably because background treefall gaps are relatively less important in these forests dominated by chronic, widespread hurricane effects. Hurricanes in the Luquillo Mountains appear to create a low, smooth-canopied forest (after regrowth), which is in contrast to the growth in some other forests that are not disturbed by these storms. Regrowth occurs via sprouting, the growth of advance regeneration, and recruitment from seed, and tree species exhibit both resistance to and resilience after hurricanes. Despite ↵

p. 255 ↵

the effects on trees, the tree species composition changed little in the tabonuco forest after two recent hurricanes. Density-dependent mortality partly controls the species composition of regrowth. Understory plants grow and flower vigorously after hurricanes, but lianas apparently do not proliferate. Animal species show various responses to the changes in forest architecture and food resources caused by hurricanes. The populations of most herbivorous arthropods increase in response to vigorous plant regrowth. Snails capitalize on hurricane detritus while suffering from exposure to hot and dry conditions where canopy is removed. Lizards change their foraging locations, and the population of the abundant frog *Eleutherodactylus coqui* increases because hurricane litter provides juveniles with refuges from predators. Bat populations decline or emigrate after hurricanes, as fruiting declines, but they return as fruiting recovers, with variations among bat species. Bird species ↵ tend to be plastic in habitat and dietary requirements, probably due to the large changes in forest structure caused by hurricanes and regrowth, which make it necessary for birds to change their foraging locations and diets. Although hurricane-produced debris is substantial (litterfall up to 400 times the average daily amount), decomposition, nutrient export, and trace gas emissions after hurricanes change only briefly, as rapid regrowth reasserts control over most ecosystem processes. For example, concentrations of nitrogen increased in riparian groundwater after a hurricane, but within 2 years the export in streams returned to prehurricane rates. Hurricanes reduce aboveground forest biomass by as much as 50 percent, but productivity is stimulated, and biomass accumulates rapidly. Woody debris boosts productivity, but it also stimulates microbial decomposers, which can outcompete trees for soil N and possibly other nutrients, thereby slowing tree response. In general, terrestrial ecosystem functions recover faster than structure. Hurricanes dump debris in streams, and floods redistribute inorganic and detrital material, as well as stream organisms, throughout the benthic environment along the stream continuum. Hurricanes create debris dams that catch detrital food and reduce the washout of invertebrate consumers. A hurricane flood apparently washed shrimp downstream, but in the next 6 months shrimp densities increased rapidly to the highest abundances ever recorded in all sites, probably owing to migration upstream and the increased availability of algae and decomposing leaves as food. Droughts concentrate inorganic and detrital material and make stream organisms more susceptible to predation. In terrestrial habitats, droughts limit juvenile frog survival and fungi and limit fine root and litterfall recovery after hurricanes. Landslides consist of relatively discrete zones in which soil and vegetation removal, subsequent stability, and regeneration vary. Succession in landslides is slow, with a long plant-to-plant replacement phase, and early plant colonists, especially ferns, have a strong influence on later dynamics. Landslide colonization is primarily limited by the availability of dispersed seed and by low nutrient availability. The natural reforestation of pastures in the Luquillo Mountains area has produced forests that resemble older growth in most measures of structure and function; for example, most of the important C fluxes associated with litter production and decomposition reestablish within a decade or two. However, these secondary forests are dominated by introduced tree species, and some old growth species are missing. Past land use is the most important determinant of species composition in secondary tabonuco forest, despite repeated hurricane effects and underlying environmental variation, such as in soil and topography. The organisms of the Luquillo Mountains are more resilient after natural than human disturbances.

# Literature Cited

---

Abelleira Martínez, O., and A. E. Lugo. 2008. Post sugar cane succession in moist alluvial sites in Puerto Rico. Pages 73–92 in R. W. Myster, editor, *Post-agricultural succession in the Neotropics*. New York: Springer.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Aide, T. M. 1987. Limbfalls: A major cause of sapling mortality for tropical forest plants. *Biotropica* 19:284–285.

[Google Scholar](#) [WorldCat](#)

Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management* 77:77–86.

[Google Scholar](#) [WorldCat](#)

p. 257 Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28:537–548.

[Google Scholar](#) [WorldCat](#)

Alvarez, J., and M. R. Willig. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 25:100–110.

[Google Scholar](#) [WorldCat](#)

Angulo-Sandoval, P., H. Fernández-Marín, J. K. Zimmerman, and T. M. Aide. 2004. Changes in patterns of understory leaf phenology and herbivory following hurricane damage. *Biotropica* 36:60–67.

[Google Scholar](#) [WorldCat](#)

Barrera, A., A. Gómez-Pompa, and C. Vásquez-Yanes. 1977. El manejo de las selvas por los Mayas: Sus implicaciones silvícolas y agrícolas [The management of forests by the Mayans: Implications for forestry and agriculture]. *Biotica* 2:47–61.

[Google Scholar](#) [WorldCat](#)

Basnet, K., F. N. Scatena, G. E. Likens, and A. E. Lugo. 1992. Hurricane Hugo: Damage to a tropical rain forest in Puerto Rico. *Journal of Tropical Ecology* 8:47–55.

[Google Scholar](#) [WorldCat](#)

Basnet, K., F. N. Scatena, G. E. Likens, and A. E. Lugo. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 25:28–35.

Beard, J. S. 1945. The progress of plant succession on the Soufriere of St Vincent. *Journal of Ecology* 33:1–9.

[Google Scholar](#) [WorldCat](#)

Beard, K. H., K. A. Vogt, D. J. Vogt, F. N. Scatena, A. P. Covich, R. Sigurdardottir, T. C. Siccama, and T. A. Cowl. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs* 75:345–361.

[Google Scholar](#) [WorldCat](#)

Becker, P., P. E. Rabenold, J. R. Idol, and A. P. Smith. 1988. Water potential gradient for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* 4:173–184.

[Google Scholar](#) [WorldCat](#)

Bellingham, P. J., V. Kapos, N. Varty, J. R. Healey, E. V. J. Tanner, D. L. Kelly, J. W. Dalling, L. S. Burns, D. Lee, and G. Sidrak. 1992. Hurricanes need not cause high mortality: The effects of Hurricane Gilbert on forests in Jamaica. *Journal of Tropical Ecology* 8:217–223.

[Google Scholar](#) [WorldCat](#)

Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1994. Sprouting of Jamaican montane forests, after a hurricane. *Journal of Ecology* 82:747–758.

[Google Scholar](#) [WorldCat](#)

Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* 76:2562–2580.

[Google Scholar](#) [WorldCat](#)

Birdsey, R. A., and P. L. Weaver. 1987. Forest area trends in Puerto Rico. Research note SO-331. New Orleans, LA: USDA Forest Service, Southern Experiment Station.

Bloch, C. P., and M. R. Willig. 2006. Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. *Journal of Tropical Ecology* 22:111–122.

[Google Scholar](#) [WorldCat](#)

Bloomfield, J. 1993. Nutrient dynamics and the influence of substrate quality on the decomposition of leaves and fine roots of selected tree species in a lower montane tropical rain forest in Puerto Rico. Ph.D. dissertation. Yale University, New Haven, CT.

Bloomfield, J., K. A. Vogt, and D. J. Vogt. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil* 150:233–245.

[Google Scholar](#) [WorldCat](#)

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* 64:369–400.

[Google Scholar](#) [WorldCat](#)

Boucher, D. H., J. H. Vandermeer, M. A. Mallona, N. Zamora, and I. Perfecto. 1994. Resistance and resilience in a directly regenerating rainforest: Nicaraguan trees of the Vochysiaceae after Hurricane Joan. *Forest Ecology and Management* 68:127–136.

[Google Scholar](#) [WorldCat](#)

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.

[Google Scholar](#) [WorldCat](#)

Brokaw, N. V. L. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *The Botanical Review* 64:91–120.

p. 258 Brokaw, N., and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183–188.

[Google Scholar](#) [WorldCat](#)

Brokaw, N., S. Fraver, J. S. Gear, J. Thompson, J. K. Zimmerman, R. B. Waide, E. M. Everham III, S. P. Hubbell, and R. B. Foster. 2004. Disturbance and canopy structure in two tropical forests. Pages 177–194 in E. Losos and E. G. Leigh, Jr., editors, *Tropical forest diversity and dynamism: Results from a long-term tropical forest network*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Brokaw, N. V. L., and J. S. Gear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* 23:386–392.

[Google Scholar](#) [WorldCat](#)

Brokaw, N. V. L., and R. A. Lent. 1999. Vertical structure. Pages 373–399 in M. L. Hunter, Jr., editor, *Maintaining biodiversity in forest ecosystems*. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* 23:442–447.

[Google Scholar](#) [WorldCat](#)

Browne, F. G. 1949. Storm forest in Kelantan. *Malayan Forester* 12:28–33.

[Google Scholar](#) [WorldCat](#)

Burslem, D. F. R. P., T. C. Whitmore, and G. C. Brown. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* 88:1063–1078.

[Google Scholar](#) [WorldCat](#)

Byer, M. D., and P. L. Weaver. 1977. Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. *Biotropica* 9:35–47.

[Google Scholar](#) [WorldCat](#)

Canham, C. D., J. Thompson, J. K. Zimmerman, and M. Uriarte. 2010. Variation in susceptibility to hurricane damage as a function of storm severity in Puerto Rican tree species. *Biotropica* 42:87–94.

[Google Scholar](#) [WorldCat](#)

Carroll, J. B. 1984. The conservation and wild status of the Rodrigues fruit bat, *Pteropus rodricensis*. *Myotis* 21–22:148–154.

[Google Scholar](#) [WorldCat](#)

Chapin, F. S. III, P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American*

Cheke, A. S., and J. F. Dahl. 1981. The status of bats on western Indian Ocean islands with special reference to *Pteropus*. *Mammalia* 45:205–238.

Chestnut, T. J., and W. H. McDowell. 2000. Nitrogen and carbon dynamics in the riparian and hyporheic zones of a tropical stream: Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society* 19:199–214.

China, J. D. 1999. Changes in the herbaceous and vine communities at the Bisley experimental watersheds, Puerto Rico, following Hurricane Hugo. *Canadian Journal of Forest Research* 29:1433–1437.

Clark, D. B. 1996. Abolishing virginity. *Journal of Tropical Ecology* 12:735–739.

Clark, D. B., and D. A. Clark. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79:447–457.

Coley, P. D. 1987. Interspecific variation in plant anti-herbivore properties: The role of habitat quality and rate of disturbance. *New Phytologist* 106:251–263.

Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: Results from an experimental hurricane. *Ecology* 80:2683–2696.

Covich, A. P., and T. A. Crowl. 2002. Reorganization of benthic stream food webs in response to drought-altered population densities: Effects on rainforest streams. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 28:1172–1175.

Covich, A. P., T. A. Crowl, and T. Heartsill-Scalley. 2006. Effects of drought on palaemonid river shrimp (*Macrobrachium* spp.) in headwaters of the Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society* 25:99–107.

p. 259 Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: Response to disturbance. *Biotropica* 28:484–492.

Covich, A. P., T. A. Crowl, S. L. Johnson, and F. N. Scatena. 1998. Drought effects on pool morphology and benthic macroinvertebrates in headwater streams of the Luquillo Experimental Forest, Puerto Rico. *American Water Resources Association TPS* 98:91–96.

Covich, A. P., T. A. Crowl, S. L. Johnson, D. Varza, and D. L. Certain. 1991. Post-Hurricane Hugo increases in Atyid shrimp abundances in a Puerto Rican montane stream. *Biotropica* 23:448–454.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2000. Linking habitat stability to floods and droughts: Effects on shrimp in montane streams, Puerto Rico. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 27:2430–434.

Covich, A., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* 48:1199–1206.

Covich, A. P., and W. H. McDowell. 1996. The stream community. Pages 433–459 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.



Craig, P., P. Trail, and T. E. Morrell. 1984. The decline of fruit bats in American Samoa due to hurricanes and overhunting. *Biological Conservation* 69:261–266.

[Google Scholar](#) [WorldCat](#)

Crow, T. R. 1980. A rainforest chronicle: A 30 year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica* 12:42–55.

[Google Scholar](#) [WorldCat](#)

Crow, T. R., and D. F. Grigal. 1979. Numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. *Vegetatio* 40:135–146.

[Google Scholar](#) [WorldCat](#)

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology* 82:775–783.

[Google Scholar](#) [WorldCat](#)

Dallmeier, F., J. A. Comiskey, and F. N. Scatena. 1998. Five years of forest dynamics following Hurricane Hugo in Puerto Rico's Luquillo Experimental Forest. Pages 231–248 in F. Dallmeier and J. A. Comiskey, editors, *Forest biodiversity in North, Central and South America, and the Caribbean*. UNESCO Man and the Biosphere Series, Vol. 21. Pearl River, NY: Parthenon Publishing Group.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Debski, I., D. F. R. P. Burslem, and D. Lamb. 2000. Ecological processes maintaining differential tree species distributions in an Australian subtropical rain forest: Implications for models of species coexistence. *Journal of Tropical Ecology* 16:387–415.

[Google Scholar](#) [WorldCat](#)

de Gouvenain, R. C., and J. A. Silander, Jr. 2003. Do tropical storm regimes influence the structure of tropical lowland rainforests? *Biotropica* 35:166–180.

[Google Scholar](#) [WorldCat](#)

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18–21.

[Google Scholar](#) [WorldCat](#)

Denslow, J. S. 1995. Disturbance and diversity in tropical rain forests: The density effect. *Ecological Applications* 5:962–968.

[Google Scholar](#) [WorldCat](#)

Denslow, J. S., and G. S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. Pages 120–127 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors, *La Selva: Ecology and natural history of a Neotropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Dittus, W. P. J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica* 17:1–14.

[Google Scholar](#) [WorldCat](#)

Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. Pages 56–73 in D. C. West, H. H. Shugart, and D. B. Botkin, editors, *Forest succession: Concepts and application*. New York: Springer-Verlag.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

p. 260 Elmqvist, T., W. E. Rainey, E. D. Pierson, and P. A. Cox. 1994. Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain forest. *Biotropica* 26:384–391.

[Google Scholar](#) [WorldCat](#)

Emanuel, K. A. 1987. The dependence of hurricane intensity on climate. *Nature* 362:483–485.

[Google Scholar](#) [WorldCat](#)

Erickson, H. E., and G. Ayala. 2004. Hurricane-induced nitrous oxide fluxes from a wet tropical forest. *Global Change Biology* 10:1155–1162.

[Google Scholar](#) [WorldCat](#)

Erickson, H. E., M. Keller, and E. Davidson. 2001. Nitrogen oxide fluxes and nitrogen cycling during secondary succession and forest fertilization in the humid tropics. *Ecosystems* 4:67–84.

[Google Scholar](#) [WorldCat](#)

Everham, E. M. III, and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *The Botanical Review* 62:113–185.

[Google Scholar](#) [WorldCat](#)

Everham, E. M. III, R. W. Myster, and E. VanDeGenachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* 83:1063–1068.

[Google Scholar](#) [WorldCat](#)

Fernández, D. S., and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* 23:393–399.

[Google Scholar](#) [WorldCat](#)

Fernández, D. S., and R. W. Myster. 1995. Temporal variation and frequency distribution of photosynthetic photon flux densities on landslides in Puerto Rico. *Tropical Ecology* 36:73–87.

[Google Scholar](#) [WorldCat](#)

Fetcher, N., R. A. Cordero, and J. Voltzow. 2000. Lack of ecotypic differentiation: Plant response to elevation, population origin, and wind in the Luquillo Mountains, Puerto Rico. *Biotropica* 32:225–234.

[Google Scholar](#) [WorldCat](#)

Fetcher, N., B. L. Haines, R. A. Cordero, D. J. Lodge, L. Walker, D. S. Fernández, and W. T. Lawrence. 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology* 84:331–341.

[Google Scholar](#) [WorldCat](#)

Fonte, S. J., and T. D. Schowalter. 2004. Decomposition of greenfall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* 36:474–482.

[Google Scholar](#) [WorldCat](#)

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. *BioScience* 47:437–445.

[Google Scholar](#) [WorldCat](#)

Foster, D. R., M. Fluet, and E. R. Boose. 1999. Human or natural disturbance: Landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications* 9:555–572.

[Google Scholar](#) [WorldCat](#)

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53:77–88.

[Google Scholar](#) [WorldCat](#)

Foster, R. B. 1980. Heterogeneity and disturbance in tropical vegetation. Pages 75–92 in M. E. Soulé and B. A. Wilcox, editors, *Conservation Biology: An Evolutionary–Ecological Perspective*. Sunderland, MA: Sinauer, Inc.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Francis, J. K., and S. E. Alemañy. 2003. Hurricane damage to mahogany crowns associated with seed source. Pages 94–102 in A. E. Lugo, J. C. Figueroa Colón, and M. Alayón, editors, *Big-leaf mahogany: Genetics, ecology, and management*. New York: Springer.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Frangi, J., and A. E. Lugo. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* 23:324–335.

[Google Scholar](#) [WorldCat](#)

Frangi, J., and A. E. Lugo. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. *Biotropica* 30:339–348.

[Google Scholar](#) [WorldCat](#)

Franklin, J., D. R. Drake, K. R. McConkey, F. Tonga, and L. B. Smith. 2004. The effects of Cyclone Waka on the structure of lowland tropical rain forest in Vava'u, Tonga. *Journal of Tropical Ecology* 20:409–420.

[Google Scholar](#) [WorldCat](#)

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: Ecosystem disturbance, recovery, and the theory of biological legacies. *Conservation Biology in Practice* 1:9–16.

[Google Scholar](#) [WorldCat](#)

Fraver, S., N. V. L. Brokaw, and A. P. Smith. 1998. Delimiting the gap phase in the growth cycle of a Panamanian forest. *Journal of Tropical Ecology* 14:673–681.

[Google Scholar](#) [WorldCat](#)

- p. 261 Frizano, J., A. H. Johnson, D. R. Vann, and F. N. Scatena. 2002. Soil phosphorus fractionation during forest development on landslide scars in the Luquillo Mountains, Puerto Rico. *Biotropica* 34:17–26.

[Google Scholar](#) [WorldCat](#)

Fu, S., C. Rodríguez Pedraza, and A. E. Lugo. 1996. A twelve year comparison of stand changes in a mahogany plantation and a paired natural forest of similar age. *Biotropica* 26:515–524.

[Google Scholar](#) [WorldCat](#)

Gannon, M. R., M. R. Duran, A. Kurta, and M. R. Willig. 2005. *Bats of Puerto Rico: An island focus and Caribbean perspective*. Lubbock, TX: Texas Tech University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Gannon, M. R., and M. R. Willig. 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 26:320–321.

[Google Scholar](#) [WorldCat](#)

Gannon, M. R., and M. R. Willig. 1998. Long-term monitoring protocol for bats: Lessons from the Luquillo Experimental Forest of Puerto Rico. Pages 271–291 in F. Dallmeier and J. Comiskey, editors, *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*. Man and the Biosphere Series, Vol. 21. Pearl River, NY: Parthenon Publishing Group.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

García-Montiel, D. C., and F. N. Scatena. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *Forest Ecology and Management* 63:57–78.

[Google Scholar](#) [WorldCat](#)

Garrison, R. W., and M. R. Willig. 1996. Arboreal invertebrates. Pages 183–245 in R. B. Waide and D. P. Reagan, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Garwood, N. C., D. P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: A major disturbance to tropical forests. *Science* 140:997–999.

[Google Scholar](#) [WorldCat](#)

Gómez-Pompa, A., and A. Kaus. 1992. Taming the wilderness myth. *BioScience* 42:271–279.

[Google Scholar](#) [WorldCat](#)

González, G., C.-Y. Huang, and S.-S. Chuang. 2008. Earthworms and post-agricultural succession. Pages 115–138 in R. W. Myster, editor, *Post-agricultural succession in the Neotropics*. New York: Springer.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Grau, H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer, and X. Zou. 2003. The ecological consequences of socioeconomic and land-use changes in postagricultural Puerto Rico. *BioScience* 53:1159–1168.

[Google Scholar](#) [WorldCat](#)

Grove, S. J., S. M. Turton, and D. T. Siegenthaler. 2000. Mosaics of canopy openness induced by tropical cyclones in lowland rain forests with contrasting management histories in northeastern Australia. *Journal of Tropical Ecology* 16:883–894.

[Google Scholar](#) [WorldCat](#)

Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *Journal of Ecology* 78:814–832.

[Google Scholar](#) [WorldCat](#)

Guzmán-Grajales, S. M., and L. R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:407–413.

[Google Scholar](#) [WorldCat](#)

Halleck, L. F., J. M. Sharpe, and X. Zou. 2004. Understory fern responses to post-hurricane fertilization and debris removal. *Journal of Tropical Ecology* 20:173–183.

[Google Scholar](#) [WorldCat](#)

Hammond, E. P. 1996. Regeneration of understory shrubs in the Luquillo Experimental Forest, Puerto Rico. M.S. thesis. University of Georgia, Athens, GA.

Hartshorn, G. S. 1978. Treefalls and tropical forest dynamics. Pages 617–638 in P. B. Tomlinson and M. H. Zimmerman, editors, *Tropical trees as living systems*. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Hartshorn, G. S. 1980. Neotropical forest dynamics. *Biotropica* 12:23–30.

[Google Scholar](#) [WorldCat](#)

Heatwole, H., and A. Heatwole. 1978. Ecology of the Puerto Rican camaenid tree-snails. *Malacologia* 17:241–315.

[Google Scholar](#) [WorldCat](#)

Henderson, A., G. Galeano, and B. Bernal. 1995. *Field guide to the palms of the Americas*. Princeton, NJ: Princeton University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

p. 262 Herbert, D. A., J. H. Fownes, and P. M. Vitousek. 1999. Hurricane damage to Hawaiian forest: Nutrient supply rate affects resistance and resilience. *Ecology* 80:908–920.

[Google Scholar](#) [WorldCat](#)

Herrera Montes, A. 2008. The relation between forest structure and herpetofaunal community structure during forest succession. M.S. thesis. University of Puerto Rico-Río Piedras, Río Piedras, Puerto Rico.

Huhndorf, S. M., and D. J. Lodge. 1997. Host specificity among wood inhabiting pyrenomycetes (Fungi, Ascomycetes) in a wet tropical forest in Puerto Rico. *Tropical Ecology* 38:307–315.

[Google Scholar](#) [WorldCat](#)

Imbert, D., A. Rousteau, and P. Labbé. 1998. Ouragans et diversité biologique dans les forêts tropicales. L'exemple de la Guadeloupe [Hurricanes and biological diversity in tropical forests. The example of Guadeloupe]. *Acta Oecologica* 19:251–262.

[Google Scholar](#) [WorldCat](#)

Jones, K. E., K. E. Barlow, N. Vaughan, A. Rodríguez-Durán, and M. R. Gannon. 2001. Short-term impact of extreme environmental disturbance on the bats of Puerto Rico. *Animal Conservation* 4:59–66.

[Google Scholar](#) [WorldCat](#)

Kangas, P. 1992. Root regrowth in a subtropical wet forest in Puerto Rico. *Biotropica* 24:463–465.

[Google Scholar](#) [WorldCat](#)

Keay, R. W. J. 1957. Wind-dispersed species in a Nigerian forest. *Journal of Ecology* 45:471–478.

[Google Scholar](#) [WorldCat](#)

Kochummen, K. M. 1977. Natural plant succession after farming in Kepong. *Malaysian Forester* 40:61–78.

[Google Scholar](#) [WorldCat](#)

Larsen, M. C., and A. J. Torres-Sánchez. 1992. Landslides triggered by Hurricane Hugo in eastern Puerto Rico, September 1989. *Caribbean Journal of Science* 28:13–120.

[Google Scholar](#) [WorldCat](#)

Latta, S. C., and J. M. Wunderle, Jr. 1998. The assemblage of birds foraging in native West Indian pine (*Pinus occidentalis*) forests of the Dominican Republic during the nonbreeding season. *Biotropica* 30:645–656.

Lawrence, W. T. 1996. Plants: The food base. Pages 17–51 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lawton, R. O. 1982. Wind stress and elfin stature in a montane rain forest tree: An adaptive explanation. *American Journal of Botany* 69:1224–1230.

[Google Scholar](#) [WorldCat](#)

Lebrón, M. L. 1979. An autecological study of *Palicourea riparia* Benthham as related to rain forest disturbance in Puerto Rico. *Oecologia* 42:31–46.

Levey, D. J. 1990. Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6:409–420.

Little, E. L., Jr., and R. O. Woodbury. 1976. *Trees of the Caribbean National Forest, Puerto Rico*. Forest Service Research Paper ITF-20. Río Piedras, PR: International Institute of Tropical Forestry.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lodge, D. J. 1993. Nutrient cycling by fungi in wet tropical forests. Pages 37–57 in S. Isaac, J. C. Frankland, R. Watling, and A. J. S. Whalley, editors, *Aspects of tropical mycology*. British Mycological Society Symposium Series 19. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lodge, D. J. 1996. Microorganisms. Pages 53–108 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lodge, D. J. 1997. Factors related to diversity of decomposer fungi in tropical forests. *Biodiversity and Conservation* 6:681–688.

[Google Scholar](#) [WorldCat](#)

Lodge, D. J., and S. Cantrell. 1995. Fungal communities in wet tropical forests: Variation in time and space. *Canadian Journal of Botany* 73(Suppl. 1):S1391–1398.

[Google Scholar](#) [WorldCat](#)

Lodge, D. J., W. H. McDowell, and C. P. McSwiney. 1994. The importance of nutrient pulses in tropical forests. *Trends in Ecology and Evolution* 9:384–387.

[Google Scholar](#) [WorldCat](#)

Lodge, D. J., F. N. Scatena, C. E. Asbury, and M. J. Sánchez. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* 23:336–342.

[Google Scholar](#) [WorldCat](#)

p. 263 Lomascolo, T., and T. M. Aide. 2001. Seed and seedling bank dynamics in secondary forests following Hurricane Georges in Puerto Rico. *Caribbean Journal of Science* 37:259–270.

[Google Scholar](#) [WorldCat](#)

Lorimer, C. G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* 70:565–567.

[Google Scholar](#) [WorldCat](#)

Lugo, A. 1970. Photosynthetic studies on four species of rain forest seedlings. Pages 181–1102 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lugo, A. E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral Ecology* 33:368–398.

[Google Scholar](#) [WorldCat](#)

Lugo, A. E., M. Applefield, D. J. Pool, and R. B. McDonald. 1983. The impact of Hurricane David on the forests of Dominica. *Canadian Journal of Forest Research* 13:201–211.

[Google Scholar](#) [WorldCat](#)

Lugo, A. E., J. Figueroa Colón, and F. N. Scatena. 1999. The Caribbean. Pages 593–622 in M. G. Barbour and W. D. Billings, editors, *North American terrestrial vegetation*. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lugo, A. E., and J. L. Frangi. 2003. Changes in necromass and nutrients on the forest floor of a palm floodplain forest in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 39:265–272.

[Google Scholar](#) [WorldCat](#)

Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190:145–161.

[Google Scholar](#) [WorldCat](#)

Lugo, A. E., and C. T. Rivera Batlle. 1987. Leaf production, growth rate, and age of the palm *Prestoea montana* in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 3:151–161.

Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28:585–599.

[Google Scholar](#) [WorldCat](#)

Lugo, A. E., F. N. Scatena, W. Silver, S. Molina Colón, and P. G. Murphy. 2002. Resilience of tropical wet and dry forests in Puerto Rico. Pages 195–225 in L. H. Gunderson and L. Pritchard, Jr., editors, *Resilience and the behavior of large-scale systems*. Washington, DC: Island Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Lugo, A. E., and J. K. Zimmerman. 2002. Ecological life histories. Pages 191–213 in J. A. Vozzo, editor, *Tropical tree seed manual*. Agriculture Handbook 721. Washington, DC: U.S. Department of Agriculture Forest Service.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Madden, N. T. 2004. Scaling up: Nitrogen flux at the stream-soil interface in the Río Icacos, PR. M.S. thesis. University of New Hampshire.

Maheswaran, J., and I. A. U. N. Gunatilleke. 1988. Litter decomposition in a lowland rain forest and a deforested area in Sri Lanka. *Biotropica* 20:90–99.

[Google Scholar](#) [WorldCat](#)

Margalef, R. 1968. *Perspectives in ecological theory*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Marín-Spiotta, E. 2006. Controls on above and belowground carbon storage during tropical reforestation. Ph.D. dissertation. Berkeley, CA: University of California.

Marín-Spiotta, E., R. Ostertag, and W. L. Silver. 2007. Long term patterns in reforestation of tropical pastures: Plant community composition and aboveground biomass accumulation. *Ecological Applications* 17:828–839.

[Google Scholar](#) [WorldCat](#)

McCormick, J. F. 1970. Direct and indirect effects of gamma radiation on seedling diversity and abundance in a tropical forest. Pages D201–D211 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

McCormick, J. F. 1995. A review of the population dynamics of selected tree species in the Luquillo Experimental Forest, Puerto Rico. Pages 224–257 in A. E. Lugo and C. Lowe, editors, *Tropical forests: Management and ecology*. New York: Springer-Verlag.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

McDowell, W. H. 2001. Hurricanes, people, and riparian zones: Controls on nutrient losses from forested Caribbean watersheds. *Forest Ecology and Management* 154:443–451.

[Google Scholar](#) [WorldCat](#)

p. 264 McDowell, W. H., C. P. McSwiney, and W. B. Bowden. 1996. Effects of hurricane disturbance on groundwater chemistry and riparian function in a tropical forest. *Biotropica* 28:577–584.

[Google Scholar](#) [WorldCat](#)

Meléndez-Ackerman, E., C. Calisto-Pérez, M. Morales-Vargas, and J. Fumero-Cabán. 2003. Post-hurricane recovery of a herbaceous understorey plant in tropical rain forest in Puerto Rico. *Journal of Tropical Ecology* 19:677–684.

[Google Scholar](#) [WorldCat](#)

Miller, R. M., and D. J. Lodge. 1997. Fungal responses to disturbance-agriculture and forestry. Pages 65–84 in K. Esser, P. A. Lemke, and D. T. Wicklow, editors, *Environmental and microbial relationships*. Vol. V. New York: Springer-Verlag.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Moran, R. C. 2004. *A natural history of ferns*. Portland, OR: Timber Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Myster, R. W. 1997. Seed predation, disease and germination on landslides in Neotropical lower montane wet forest. *Journal of Vegetation Science* 8:55–64.



Myster, R. W., and D. S. Fernández. 1995. Spatial gradients and patch structure on two Puerto Rican landslides. *Biotropica* 27:149–159.

[Google Scholar](#)   [WorldCat](#)

Myster, R. W., and N. Fetcher. 2005. Ecotypic differentiation and plant growth in the Luquillo Mountains of Puerto Rico. *Journal of Tropical Forest Science* 16:413–419.

[Google Scholar](#)   [WorldCat](#)

Myster, R. W., J. R. Thomlinson, and M. C. Larsen. 1997. Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. *Landscape Ecology* 12:299–307.

[Google Scholar](#)   [WorldCat](#)

Myster, R. W., and L. R. Walker. 1997. Plant successional pathways on landslides in Puerto Rican landslides. *Journal of Tropical Ecology* 13:165–173.

[Google Scholar](#)   [WorldCat](#)

O'Brien, S. T., B. P. Hayden, and H. H. Shugart. 1992. Global climatic change, hurricanes, and a tropical forest. *Climatic Change* 22:175–190.

[Google Scholar](#)   [WorldCat](#)

Odum, H. T. 1970. Rain forest structure and mineral cycling homeostasis. Pages H3–H52 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#)   [Google Preview](#)   [WorldCat](#)   [COPAC](#)

Odum, H. T., and G. Drewry. 1970. The cesium source at El Verde. Pages C23–C36 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#)   [Google Preview](#)   [WorldCat](#)   [COPAC](#)

Ogle, K., M. Uriarte, J. Thompson, J. Johnstone, A. Jones, Y. Lin, E. McIntire, and J. Zimmerman. 2006. Implications of vulnerability to hurricane damage for long-term survival of tropical tree species: A Bayesian hierarchical analysis. Pages 98–123 in J. S. Clark and A. E. Gelfand, editors, *Applications of computational statistics in the environmental sciences: Hierarchical bayes and MCMC Methods*. Oxford, England: Oxford University Press.

[Google Scholar](#)   [Google Preview](#)   [WorldCat](#)   [COPAC](#)

Olander, L. P., F. N. Scatena, and W. L. Silver. 1998. Impacts of disturbance initiated by road construction in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* 109:33–49.

[Google Scholar](#)   [WorldCat](#)

Ostertag, R., E. Marin-Spiotta, W. L. Silver, and J. Shulten. 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems* 11:701–714.

[Google Scholar](#)   [WorldCat](#)

Ostertag, R., F. N. Scatena, and W. L. Silver. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. *Ecosystems* 6:261–273.

[Google Scholar](#)   [WorldCat](#)

Ostertag, R., W. L. Silver, and A. E. Lugo. 2005. Factors affecting mortality and resistance to damage following hurricanes in a subtropical moist forest. *Biotropica* 37:16–24.

[Google Scholar](#)   [WorldCat](#)

Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343:51–53.

[Google Scholar](#)   [WorldCat](#)

Parrotta, J., and D. J. Lodge. 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. *Biotropica* 23:343–347.

[Google Scholar](#)   [WorldCat](#)

Pascarella, J. B., T. M. Aide, M. I. Serrano, and J. K. Zimmerman. 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems* 3:217–228.

[Google Scholar](#)   [WorldCat](#)



Puerto Rico, USA. *Forest Ecology and Management* 199:379–393.  
[Google Scholar](#) [WorldCat](#)

Pedersen, S. C., H. H. Genoways, and P. W. Freeman. 1996. Notes on bats from Montserrat (Lesser Antilles) with comments concerning the effects of Hurricane Hugo. *Caribbean Journal of Science* 32:206–213.

[Google Scholar](#) [WorldCat](#)

Perez, J. W. 1970. Relation of crown diameter to stem diameter in forests of Puerto Rico, Dominica, and Thailand. Pages B105–B122 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Pérez Viera, I. E. 1986. Tree regeneration in two tropical rain forests. M.S. thesis. University of Puerto Rico–Río Piedras, Río Piedras, Puerto Rico.

Pfeiffer, W. J. 1996. Arboreal arachnids. Pages 247–271 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Pierson, E. D., T. Elmquist, W. E. Rainey, and P. A. Cox. 1996. Effects of tropical cyclonic storms on flying fox populations on the South Pacific Islands of Samoa. *Conservation Biology* 10:438–451.

[Google Scholar](#) [WorldCat](#)

Pringle, C. M., and G. A. Blake. 1994. Quantitative effects of atyid shrimps (Decapoda: Atyidae) on the depositional environment in a tropical stream: Use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1443–1450.

[Google Scholar](#) [WorldCat](#)

Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of omnivorous shrimp in a montane tropical stream: Sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia* 93:1–11.

[Google Scholar](#) [WorldCat](#)

Pringle, C. M., N. H. Hemphill, W. McDowell, A. Bednarek, and J. March. 1999. Linking species and ecosystems: Effects of different macrobiotic assemblages on interstream differences in organic matter. *Ecology* 80:1860–1872.

[Google Scholar](#) [WorldCat](#)

Putz, F. E., and N. V. L. Brokaw. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* 70:508–512.

[Google Scholar](#) [WorldCat](#)

Reagan, D. P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. *Biotropica* 23:468–474.

Reagan, D. P. 1996. Anoline lizards. Pages 321–345 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Reagan, D. P., G. R. Camilo, and R. B. Waide. 1996. The community food web: Major properties and patterns of organization. Pages 462–510 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Rice, K., N. Brokaw, and J. Thompson. 2004. Liana abundance in a Puerto Rican forest. *Forest Ecology and Management* 190:33–41.

[Google Scholar](#) [WorldCat](#)

Riddle, W. A. 1983. Physiological ecology of land snails and slugs. Pages 431–461 in W. D. Russell-Hunter, editor, *The Mollusca*. Vol. 6. Orlando, FL: Academic Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Riswan, S., J. B. Kenworthy, and K. Kartawinata. 1985. The estimation of temporal processes in tropical rain forest: A study of primary mixed dipterocarp forest in Indonesia. *Journal of Tropical Ecology* 1:171–182.

[Google Scholar](#) [WorldCat](#)

Sandlin, E. A., and M. R. Willig. 1993. The effects of age, sex, prior experience, and intraspecific food variation on diet composition of a tropical folivore (Phasmatodea: Phasmatidae). *Environmental Entomology* 22:625–633.

[Google Scholar](#) [WorldCat](#)

Sanford, R. L., W. J. Parton, D. S. Ojima, and D. J. Lodge. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: Results of simulation modeling. *Biotropica* 23:364–372.

[Google Scholar](#) [WorldCat](#)

Sanford, R. L., J. Saldarriaga, K. E. Clark, C. Uhl, and R. Herrera. 1985. Amazon rainforest fires. *Science* 227:53–55.

[Google Scholar](#) [WorldCat](#)

p. 266 Scatena, F. N. 1989. *An introduction to the physiography and history of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico*. U.S. Forest Service General Technical Report SO-72. Washington, DC: USDA Forest Service.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Scatena, F. N. 1990. Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto Rico. *Journal of Hydrology* 113:89–102.

[Google Scholar](#) [WorldCat](#)

Scatena, F. N. 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. Pages 103–111 in *Natural and anthropogenic influences in fluvial geomorphology*. Geophysical Monograph 89. Washington, DC: American Geophysical Union.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Scatena, F. N., and M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23:317–323.

[Google Scholar](#) [WorldCat](#)

Scatena, F. N., and A. E. Lugo. 1995. *Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steep-land watersheds of Puerto Rico*. *Geomorphology* 13:199–213.

Scatena, F. N., S. Moya, C. Estrada, and J. D. Chinea. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:424–440.

[Google Scholar](#) [WorldCat](#)

Scatena, F. N., W. Silver, T. Siccama, A. Johnson, and M. J. Sánchez. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo. *Biotropica* 25:15–27.

[Google Scholar](#) [WorldCat](#)

Schaefer, D. A., W. H. McDowell, F. N. Scatena, and C. E. Asbury. 2000. Effects of hurricane disturbance on stream water concentrations and fluxes in eight tropical forest watersheds of the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 16:189–207.

[Google Scholar](#) [WorldCat](#)

Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62:938–945.

[Google Scholar](#) [WorldCat](#)

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17:223–230.

[Google Scholar](#) [WorldCat](#)

Schwalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Biotropica* 26:312–319.

[Google Scholar](#) [WorldCat](#)

Schwalter, T. D., and L. M. Ganio. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* 24:191–201.

[Google Scholar](#) [WorldCat](#)

Secrest, M. F., M. R. Willig, and L. L. Peppers. 1996. The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:502–514.

[Google Scholar](#) [WorldCat](#)

Sharpe, J. M. 1997. Leaf growth and demography of the rheophytic fern *Thelypteris angustifolia* (Willdenow) Proctor in a Puerto

Shiels, A. B. 2006. Leaf litter decomposition and substrate chemistry of early successional species on landslides in Puerto Rico. *Biotropica* 38:348–353.

[Google Scholar](#) [WorldCat](#)

Shiels, A. B., and L. R. Walker. 2003. Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology* 11:457–465.

[Google Scholar](#) [WorldCat](#)

Shiels, A. B., L. R. Walker, and D. B. Thompson. 2006. Organic matter inputs create variable resource patches on Puerto Rican landslides. *Plant Ecology* 184:223–236.

[Google Scholar](#) [WorldCat](#)

Silander, S. R., and A. E. Lugo. 1990. *Cecropia peltata* L.: Yagrumo hembra, trumpet tree. Pages 244–249 in *Silvics of North America: Hardwoods*. Vol. 2. Agricultural Handbook 654. Washington, DC: U.S. Department of Agriculture.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Silver, W. L., D. J. Herman, and M. K. Firestone. 2001. Dissimilatory nitrate reduction to ammonium in tropical forest soils. *Ecology* 82:2410–2416.

[Google Scholar](#) [WorldCat](#)

p. 267 Silver, W. L., L. M. Kueppers, A. E. Lugo, R. Ostertag, and V. Matzek. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. *Ecological Applications* 14:1115–1127.

[Google Scholar](#) [WorldCat](#)

Silver, W. L., F. N. Scatena, A. H. Johnson, T. G. Siccama, and M. J. Sánchez. 1994. Nutrient availability in a montane wet tropical forest in Puerto Rico: Spatial patterns and methodological considerations. *Plant and Soil* 164:129–145.

[Google Scholar](#) [WorldCat](#)

Silver, W. L., F. N. Scatena, A. H. Johnson, T. G. Siccama, and F. Watt. 1996. At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica* 28:441–457.

[Google Scholar](#) [WorldCat](#)

Silver, W. L., A. W. Thompson, A. Reich, J. J. Ewel, and M. K. Firestone. 2005. Nitrogen cycling in tropical plantation forests: Potential controls on nitrogen retention. *Ecological Applications* 15:1604–1614.

[Google Scholar](#) [WorldCat](#)

Silver, W. L., and K. A. Vogt. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology* 81:729–738.

[Google Scholar](#) [WorldCat](#)

Smith, R. F. 1970. The vegetation structure of a Puerto Rican rain forest before and after short-term gamma radiation. Pages D103–D140 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Solem, A. 1984. A world model of land snail diversity and abundance. Pages 6–22 in A. Solem and A. C. van Bruggen, editors, *World-wide snails: Biogeographical studies on non-marine Mollusca*. Leiden, The Netherlands: E. J. Brill.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Stephenson, S. L., and J. C. Landolt. 1998. Dictyostelid cellular slime molds in canopy soils of tropical forests. *Biotropica* 30:657–661.

[Google Scholar](#) [WorldCat](#)

Stuedler, P. A., J. M. Melillo, R. D. Bowden, M. S. Castro, and A. E. Lugo. 1991. The effects of natural and human disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. *Biotropica* 23:356–363.

[Google Scholar](#) [WorldCat](#)

Stewart, M. M. 1995. Climate driven population fluctuations in rain forest frogs. *Journal of Herpetology* 29:437–446.

[Google Scholar](#) [WorldCat](#)

Stewart, M. M., and L. L. Woolbright. 1996. Amphibians. Pages 273–320 in D. P. Reagan and R. B. Waide, editors, *The food web of a*

tropical rain forest. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Tanner, E. V. J., and P. J. Bellingham. 2006. Less diverse forest is more resistant to hurricane disturbance: Evidence from montane forests in Jamaica. *Journal of Ecology* 94:1003–1010.

[Google Scholar](#) [WorldCat](#)

Taylor, C. M., S. Silander, R. B. Waide, and W. J. Pfeiffer. 1995. Recovery of a tropical forest after gamma irradiation: A 23-year chronicle. Pages 258–285 in A. E. Lugo and C. Lowe, editors, *Tropical forests: Management and ecology*. Berlin: Springer-Verlag.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Thomlinson, J. R., M. I. Serrano, T. del M. López, T. M. Aide, and J. K. Zimmerman. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). *Biotropica* 28:525–536.

[Google Scholar](#) [WorldCat](#)

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.

[Google Scholar](#) [WorldCat](#)

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, and D. A. Schaefer. 2004. Luquillo Forest Dynamics Plot. Pages 540–550 in E. Losos and E. G. Leigh, Jr., editors, *Tropical forest diversity and dynamism: Results from a long-term tropical forest network*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Torres, J. A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. *Journal of Tropical Ecology* 8:285–298.

[Google Scholar](#) [WorldCat](#)

Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology* 75:377–407.

[Google Scholar](#) [WorldCat](#)

p. 268 Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004a. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs* 74:591–614.

[Google Scholar](#) [WorldCat](#)

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005. Seedling recruitment in a hurricane-driven forest: Light limitation, density-dependence, and the spatial distribution of parent trees. *Journal of Ecology* 93:291–304.

[Google Scholar](#) [WorldCat](#)

Uriarte, M., L. W. Rivera, J. K. Zimmerman, T. M. Aide, A. G. Power, and A. S. Flecker. 2004b. Effects of land use history on hurricane damage and recovery in a neotropical forest. *Plant Ecology* 174:49–58.

[Google Scholar](#) [WorldCat](#)

van der Molen, M. K., H. F. Vugts, L. A. Bruijnzeel, F. N. Scatena, R. A. Pielke, Sr., and L. J. M. Kroon. 2010. Meso-scale climate change due to lowland deforestation in the maritime tropics. Pages 527–537 in L. A. Bruijnzeel, F. N. Scatena, and L. S. Hamilton, editors, *Tropical montane cloud forests: Science for conservation and management*. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal Fisheries and Aquatic Sciences* 37:130–137.

[Google Scholar](#) [WorldCat](#)

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119:553–572.

[Google Scholar](#) [WorldCat](#)

Vitousek, P. M., and R. L. Sanford, Jr. 1986. Nutrient cycling in tropical forest. *Annual Review of Ecology and Systematics* 17:137–167.

[Google Scholar](#) [WorldCat](#)

Vogt, K. A., D. J. Vogt, H. Asbjornsen, and R. A. Dahlgren. 1995. Roots, nutrients and their relationship to spatial patterns. *Plant and Soil* 168–169:113–123.

[Google Scholar](#) [WorldCat](#)

Vogt, K. A., D. J. Vogt, P. Boon, A. Covich, F. N. Scatena, H. Asbjornsen, J. L. O'Hara, J. Pérez, T. G. Siccama, J. Bloomfield, and J. F. Ranciato. 1996. Litter dynamics along stream, riparian and upslope areas following Hurricane Hugo, Luquillo Experimental forest, Puerto Rico. *Biotropica* 28:458–470.

[Google Scholar](#) [WorldCat](#)

Volkov, I., J. R. Banavar, F. He, S. P. Hubbell, and A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438:658–661.

[Google Scholar](#) [WorldCat](#)

Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester* 11:38–47.

[Google Scholar](#) [WorldCat](#)

Waide, R. B. 1991a. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:475–480.

[Google Scholar](#) [WorldCat](#)

Waide, R. B. 1991b. Summary of the response of animal populations to hurricanes in the Caribbean. *Biotropica* 23:508–512.

[Google Scholar](#) [WorldCat](#)

Waide, R. B., and D. P. Reagan. 1996. The rain forest setting. Pages 1–16 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Waide, R. B., J. K. Zimmerman, and F. N. Scatena. 1998. Controls of primary productivity: Lessons from the Luquillo Mountains in Puerto Rico. *Ecology* 79:31–37.

[Google Scholar](#) [WorldCat](#)

Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:379–385.

[Google Scholar](#) [WorldCat](#)

Walker, L. R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science* 5:525–532.

[Google Scholar](#) [WorldCat](#)

Walker, L. R. 1995. Timing of post-hurricane tree mortality in Puerto Rico. *Journal of Tropical Ecology* 11:315–320.

[Google Scholar](#) [WorldCat](#)

Walker, L. R. 2000. Seedling and sapling dynamics of treefall pits in Puerto Rico. *Biotropica* 32:262–275.

[Google Scholar](#) [WorldCat](#)

Walker, L. R., N. V. L. Brokaw, D. J. Lodge, and R. B. Waide, editors. 1991. Special issue: Ecosystem, plant, and animal responses to hurricanes in the Caribbean. *Biotropica* 23:313–521.

[Google Scholar](#) [WorldCat](#)

p. 269 Walker, L. R., D. J. Lodge, S. M. Guzmán-Grajales, and N. Fetcher. 2003. Species-specific seedling responses to hurricane disturbance in a Puerto Rican forest. *Biotropica* 35:472–485.

[Google Scholar](#) [WorldCat](#)

Walker, L. R., and L. E. Neris. 1993. Posthurricane seed rain dynamics in Puerto Rico. *Biotropica* 25:408–418.

[Google Scholar](#) [WorldCat](#)

Walker, L. R., J. Voltzow, J. Ackerman, D. S. Fernández, and N. Fetcher. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology* 73:691–694.

[Google Scholar](#) [WorldCat](#)

Walker, L. R., D. J. Zarin, N. Fetcher, R. W. Myster, and A. H. Johnson. 1996a. Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica* 28:566–576.

[Google Scholar](#) [WorldCat](#)

Walker, L. R., J. K. Zimmerman, D. J. Lodge, and S. Guzmán-Grajales. 1996b. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal of Ecology* 84:877–889.

[Google Scholar](#) [WorldCat](#)

Wang, H., J. D. Cornell, C. A. S. Hall, and D. P. Marley. 2002a. Spatial and seasonal dynamics of surface soil carbon in the Luquillo Experimental Forest, Puerto Rico. *Ecological Modelling* 147:105–122.

[Google Scholar](#) [WorldCat](#)

Wang, H., and C. A. S. Hall. 2004. Modeling the effects of Hurricane Hugo on spatial and temporal variation in primary productivity and soil carbon and nitrogen in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil* 262:69–84.

[Google Scholar](#) [WorldCat](#)

Wang, H., C. A. S. Hall, J. D. Cornell, and M. H. P. Hall. 2002b. Spatial dependence and the relationship of soil organic carbon and soil moisture in the Luquillo Experimental Forest, Puerto Rico. *Landscape Ecology* 17:671–684.

[Google Scholar](#) [WorldCat](#)

Wang, H., C. A. S. Hall, F. N. Scatena, N. Fetcher, and W. Wu. 2003. Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. *Forest Ecology and Management* 179:69–94.

[Google Scholar](#) [WorldCat](#)

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 22:53–70.

[Google Scholar](#) [WorldCat](#)

Weaver, P. L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia* 14:181–192.

[Google Scholar](#) [WorldCat](#)

Weaver, P. L. 1998. Hurricane effects and long-term recovery in a subtropical rain forest. Pages 249–270 in F. Dallmeier and J. A. Comiskey, editors, *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*. UNESCO Man and the Biosphere Series, Vol. 21. Pearl River, NY: Parthenon Publishing Group.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Weaver, P. L. 1999. Impacts of Hurricane Hugo on the dwarf cloud forest of Puerto Rico's Luquillo Mountains. *Caribbean Journal of Science* 35:101–111.

[Google Scholar](#) [WorldCat](#)

Weaver, P. L. 2000. Elfin woodland recovery 30 years after a plane wreck in Puerto Rico's Luquillo Mountains. *Caribbean Journal of Science* 36:1–9.

[Google Scholar](#) [WorldCat](#)

Weaver, P. L. 2002. A chronology of hurricane-induced changes in Puerto Rico's lower montane forest. *Interciencia* 27:252–258.

[Google Scholar](#) [WorldCat](#)

Webb, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, north Queensland. *Australian Journal of Botany* 6:220–228.

[Google Scholar](#) [WorldCat](#)

Whigham, D. F., M. B. Dickinson, and N. V. L. Brokaw. 1999. Background canopy gap and catastrophic wind disturbances in tropical forests. Pages 223–252 in L. R. Walker, editor, *Ecosystems of the world: 16 Ecosystems of disturbed ground*. Amsterdam: Elsevier.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Whigham, D. F., and J. F. Lynch. 1998. Responses of plants and birds to hurricane disturbances in a dry tropical forest of Quintana Roo, Mexico. Pages 165–186 in F. Dallmeier and J. A. Comiskey, editors, *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*. UNESCO Man and the Biosphere Series, Vol. 21. Pearl River, NY: Parthenon Publishing Group.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Whigham, D. F., I. Olmsted, E. C. Cano, and M. E. Harmon. 1991. Impacts of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23:434–441.

[Google Scholar](#) [WorldCat](#)

p. 270 White, P. S., J. Harrod, W. H. Romme, and J. Betancourt. 1999. Disturbance and temporal dynamics. Pages 281–312 in W. T. Sexton, R. C. Szaro, N. C. Johnson, and A. J. Malk, editors, *Ecological stewardship: A common reference for ecosystem management*. New York: Elsevier.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Whitmore, T. C. 1974. *Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands*.



Whitmore, T. C. 1978. Gaps in the forest canopy. Pages 639–655 in P. B. Tomlinson and M. H. Zimmerman, editors, *Tropical trees as living systems*. Cambridge, England: Cambridge University Press.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Wiles, G. J. 1987. Current research and future management of Marianas fruit bats (Chiroptera: Pteropodidae) on Guam. *Australian Mammalogy* 10:93–95.

[Google Scholar](#) [WorldCat](#)

Willig, M. R., and G. R. Camilo. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23:455–461.

[Google Scholar](#) [WorldCat](#)

Willig, M. R., R. W. Garrison, and A. Bauman. 1986. Population dynamics and natural history of a neotropical walking stick, *Lamponius portoricensis* Rehn (Phasmatodea, Phasmatidae). *Texas Journal of Science* 38:121–137.

Willig, M. R., and M. A. McGinley. 1999. Animal responses to natural disturbance and roles as patch generating phenomena. Pages 633–657 in L. R. Walker, editor, *Ecosystems of the world: 16 Ecosystems of disturbed ground*. Amsterdam: Elsevier.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Willig, M. R., D. L. Moorhead, S. B. Cox, and J. C. Zak. 1996. Functional diversity of soil bacterial communities in the tabonuco forest: Interaction of anthropogenic and natural disturbance. *Biotropica* 28:471–483.

[Google Scholar](#) [WorldCat](#)

Willig, M. R., E. A. Sandlin, and M. R. Gannon. 1993. Structural and taxonomic components of habitat selection in the Neotropical folivore, *Lamponius portoricensis* (Phasmatodea: Phasmatidae). *Environmental Entomology* 22:634–641.

Willig, M. R., M. F. Secretst, S. B. Cox, G. R. Camilo, J. F. Cary, J. Alvarez, and M. R. Gannon. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: Heterogeneity, scale, disturbance, and recovery. Pages 293–322 in F. Dallmeier and J. Comiskey, editors, *Forest biodiversity in North, Central and South American, and the Caribbean: Research and monitoring*. Pearl River, NY: Parthenon Publishing Group.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Willig, M. R., and L. R. Walker. 1999. Disturbance in terrestrial ecosystems: Salient themes, synthesis, and future directions. Pages 747–767 in , and L. R. Walker, editor, *Ecosystems of the world: 16 Ecosystems of disturbed ground*. Amsterdam: Elsevier.

[Google Scholar](#) [Google Preview](#) [WorldCat](#) [COPAC](#)

Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, R. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. Loo de Lao, M. Massa, C. Nath, M. N. S. Noor, A. R. Kassim, R. Sukumar, H. S. Suresh, I.-F. Sun, S. Tan, T. Yamakura, and J. Zimmerman. 2006. Non-random processes contribute to the maintenance of diversity in tropical forests. *Science* 311:527–531.

[Google Scholar](#) [WorldCat](#)

Woolbright, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica* 23:462–467.

[Google Scholar](#) [WorldCat](#)

Woolbright, L. L. 1996. Disturbance influences long-term population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). *Biotropica* 28:493–501.

Wunderle, J. M., Jr. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: The first 18 months. *The Condor* 97:879–896.

[Google Scholar](#) [WorldCat](#)

Wunderle, J. M., Jr. 1999. Pre- and post-hurricane fruit availability: Implications for Puerto Rican Parrots in the Luquillo Mountains. *Caribbean Journal of Science* 35:249–264.

[Google Scholar](#) [WorldCat](#)



Jamaica. *Auk* 109:148–166.

[Google Scholar](#) [WorldCat](#)

Wunderle, J. M., Jr., M. R. Willig, and L. M. P. Henriques. 2005. Avian distribution in treefall gaps and understorey of *terra firme* forest in the lowland Amazon. *Ibis* 147:109–129.

Yih, K., D. H. Boucher, J. H. Vandermeer, and N. Zamora. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica* 23:106–113.

[Google Scholar](#) [WorldCat](#)

You, C., and W. H. Petty. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23:400–406.

Zalamea-Bustillo, M. 2005. Soil biota, nutrients, and organic matter dynamics under decomposing wood. M.S. thesis. University of Puerto Rico-Río Piedras, Río Piedras, Puerto Rico.

Zarin, D. J., and A. H. Johnson. 1995a. Base saturation, nutrient cation, and organic matter increases during early pedogenesis on landslide scars in the Luquillo Experimental Forest, Puerto Rico. *Geoderma* 65:317–330.

[Google Scholar](#) [WorldCat](#)

Zarin, D. J., and A. H. Johnson. 1995b. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal* 59:1444–1452.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995a. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* 77:65–76.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., L. S. Comita, J. Thompson, M. Uriarte, and N. Brokaw. 2010. Patch dynamics and community metastability of a subtropical forest: Compound effects of natural disturbance and human land use. *Landscape Ecology* 25:1099–1111.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., E. M. Everham III, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. *Journal of Ecology* 82:911–922.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in abandoned pastures in Puerto Rico. *Restoration Ecology* 8:350–360.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., W. M. Pulliam, D. J. Lodge, V. Quiñones, N. Fetcher, S. Guzmán-Grajales, J. A. Parrotta, C. E. Asbury, L. R. Walker, and R. B. Waide. 1995b. Nitrogen immobilization by decomposing woody debris and the recovery from tropical wet forest from hurricane damage. *Oikos* 73:23–45.

[Google Scholar](#) [WorldCat](#)

Zimmerman, J. K., M. R. Willig, L. R. Walker, and W. L. Silver. 1996. Introduction: Disturbance and Caribbean ecosystems. *Biotropica* 28:414–423.

[Google Scholar](#) [WorldCat](#)

Zou, X., C. P. Zucca, R. B. Waide, and W. H. McDowell. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. *Forest Ecology and Management* 78:147–157.

[Google Scholar](#) [WorldCat](#)