

# When and Where Biota Matter

## *Linking Disturbance Regimes, Species Characteristics, and Dynamics of Communities and Ecosystems*

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### Key Points

- Individual biota or taxa sometimes have a disproportionate effect on food web or ecosystem dynamics.
- The differences in the architecture of tree species (e.g., *Dacryodes excelsa*) alter wind disturbance magnitude and effects through the dissipation of wind energy.
- Ferns and earthworms can enhance the recolonization rate on bare soils following disturbances through modification of the physical microenvironment and nutrient availability.
- Freshwater shrimp and earthworms alter nutrient availability in the streams and soils, altering processing rates through effects on detrital processing.
- Small vertebrate species such as anolis lizards and tree frogs (*Coquis*) significantly alter food web dynamics through direct consumption of herbivorous insects and their cycling of important, limiting nutrients.

### Introduction

Organismal ecologists traditionally have been interested in the distribution and abundance of organisms, whereas ecosystem ecologists have been interested in the biological and chemical controls of the pools and fluxes of nutrients and materials.

Over the past 2 decades, however, the importance of species, species traits, and populations affecting ecosystem processes has emerged. As critical components of biodiversity are lost, so too might be a number of critical ecosystem services (Loreau et al. 2001, 2002; Raffaelli 2004; Solan et al. 2004; Zavaleta and Hulvey 2004), although uncertainty and dissent characterize the generality of the association. Thus, understanding the way in which variation in biodiversity is connected to variation in ecosystem processes is a grand, but elusive, challenge in ecology (Naeem et al. 1995; Chapin et al. 1997; Naeem 1998) that has generated controversy in recent years (Hodgson et al. 1998; Lawton et al. 1998; Emmerson and Raffaelli 2000). From the beginning of the Rain Forest Project (Odum and Pigeon 1970; see chapter 1) and continuing into the Luquillo Long-Term Ecological Research (LTER), research in the Luquillo Mountains has addressed the entire ecological continuum from individual ecophysiology and behavior to populations, communities, and ecosystems. In this chapter, we explore how particular species or groups of similar species affect the disturbance sequence and ultimately affect community and ecosystem function in our highly disturbed forest ecosystem.

### *Species Diversity and Ecosystem Function*

Several reviewers have examined the links among levels of the biological hierarchy (Schultze and Mooney 1994; Jones and Lawton 1995; Johnson et al. 1996; Chapin et al. 1997, 1998; Grime 1997; Loreau 2000; Kinzig et al. 2002; Duffy et al. 2007). Three major hypotheses regarding the role of species diversity in ecosystem function have emerged. The suggestion that every species matters (the rivet hypothesis) was the first hypothesis (Ehrlich and Ehrlich 1981). Other hypotheses were posed that suggested a more holistic view. The second and third hypotheses both come under the rubric of the "redundancy hypothesis" (Walker 1992; Lawton and Brown 1993; Frost et al. 1995). These hypotheses are similar in suggesting that, rather than individual species dictating ecosystem function, it is the presence of functional groups within communities that is critical (Covich et al. 2004; Boulton et al. 2008). For example, as long as all trophic levels of a food web exist, the overall ecosystem properties will be maintained. Similarly, with regard to plant communities, ecosystem function is thought to depend on functional plant groups defined by phenology, physiology, and morphology (Vitousek and Hooper 1993; Hooper et al. 2005).

These ideas have coalesced into suggested relationships between species diversity and the maintenance of ecosystem function (Ricklefs and Schluter 1993; Schultze and Mooney 1994; Jones and Lawton 1995; Rosenzweig 1995; Walker and Steffan 1996; Kinzig et al. 2002). A number of investigators have found that high species diversity yields high and stable levels of primary productivity (Tilman and Downing 1994; Naeem et al. 1995; Naeem 1998), although debate continues regarding patterns and mechanisms (Waide et al. 1999; Mittelbach et al. 2001). Studies in aquatic ecosystems have focused on species richness and are just beginning to consider other components of diversity such as the relative abundances of species, functional dominance relationships, and trophic structure (Covich et al. 2004; Boyero et al. 2006; Boulton et al. 2008; Duffy et al. 2007).

To date, several studies have identified linkages between species composition and ecosystem properties. Perhaps the most common pattern is the relationship between biogeochemical cycles and species composition (Carpenter et al. 1987; Pastor et al. 1987; Vitousek and Walker 1989; Zak et al. 1990). For example, carbon storage and fluctuations have been tied to species properties. Ewel et al. (1991) found that soil organic matter increased with increasing species richness to an intermediate level but did not respond to further species additions. In most cases, the nutrient availability and exchange rates are higher and more available when the primary consumer biomass and species diversity are high (Tilman 1982; McNaughton 1985; Carpenter 1988; Power 1990), although some biomes such as mangroves or pine forests show high productivity and nutrient use efficiency with relatively few species (Lugo et al. 1990).

### *Ecosystem Engineers*

Another hypothesis relating species to ecosystem function holds that particular species or groups of species have such disproportionate effects on energy flux (keystone species *sensu* Paine [1966]) that they drive or control ecosystems. It has also been stated that the ability of an organism to regulate a system might not be related to its abundance, biomass, or rate of energy use, but rather to the ability of the organism to affect the organisms with which it interacts (Chew 1974; Paine 1980; Moore and Walter 1988). Therefore, the resolution of food web interactions requires the consideration of both taxa and trophic levels, in which functional groups then serve as a link between species interactions and energy flow (Moore and Walter 1988). The disproportionate effects of a particular species on ecosystem functions or processes could occur through biotic interactions (Paine 1966) or through alterations to the physicochemical environment. Species affecting the localized physical environment have been termed "ecosystem engineers" (Lawton and Jones 1993; Willig and McGinley 1999).

The activities of animal species, especially primary consumers, are linked to the rate and quantity of resource availability (Huntley 1991). Animals affect the movement of energy through the ecosystem by feeding directly on living tissue (herbivory), which affects the rate of primary production and alters plant community composition (MacLean 1974). Animals can also affect decay processes and nutrient cycling; thus if key taxa are excluded from or added to litter, the decomposition of plant material might be altered (Butcher et al. 1971; Seastedt 1984; Moore and Walter 1988; Wall and Moore 1999; González and Seastedt 2001). This is the evidence for most arguments regarding species effects on ecosystem function, in which the predicted response depends on changes to the system following species loss (regarding species gained, see Lugo and Helmer 2003; Helmer 2004; Lugo and Brandeis 2005). Most of the empirical data summarized to date have generally documented changes in a critical ecosystem process such as productivity or decomposition rates as a function of the number of species present (Cuevas et al. 1991; Pimm 1991; Lugo 1992; Tilman and Downing 1994; Cuevas and Lugo 1998; Doak et al. 1998; Kinzig et al. 2002). Fewer reviews look at how the existing

species affect and modify local environmental conditions in the face of both external (exogenous) and internal (endogenous) factors.

### *Studying Species Effects on Ecosystems in the Luquillo Mountains*

This focus on understanding the relationships among species, communities, and ecosystem functions and dynamics is now at the forefront of ecology. It is a subject that is effectively addressed by multidisciplinary, long-term ecological research teams such as those in LTER. The LTER programs are designed to collect and synthesize information linking species and population dynamics with key ecosystem properties (e.g., Hobbie et al. 2003), and the Luquillo LTER, in particular, is well suited to address the question of the importance of species to ecosystems for several reasons. First, as a tropical wet forest biome, Luquillo has the highest diversity of plant species of any LTER site (see chapter 3). Second, it has a long history of population monitoring and experimentation. Indeed, the site has had a large number of organismal ecologists involved with it since its conception. These strengths, as well as the legacy provided by the efforts of H. T. Odum to understand material and energy flux at this site, solidify the Luquillo LTER's background and approach to tying all levels of ecological organization together.

In the Luquillo Mountains, disturbance followed by species and ecosystem response provides an opportunity to look at the relationships discussed above. Thus far in this book, the authors have argued that disturbances, both natural and anthropogenic, are critical organizing and determining events in the Luquillo Mountains. They have shown that, through localized changes in environmental conditions, disturbances dictate the potential ecological space and the potential niches available to the species pool. Moreover, they have suggested that in order to understand the spatial and temporal dynamics of a community and its ecosystem processes, one must understand the immediate local effects of single disturbance events, as well as the cumulative effects of the disturbance regime (chapter 2). In this chapter, we show how this conceptual approach can be applied to relations between various species or functional groups and ecosystem responses to disturbance in the Luquillo Mountains. First, we review the events during and after a disturbance that form the context of these relationships. Then we look at examples, including detailed case studies, of the interface between biota and the disturbance sequence that illustrate the effect of particular species and functional groups on ecosystem function in the Luquillo Mountains. Finally, we summarize our findings and suggest further work on these questions.

### **The Disturbance Sequence**

A single disturbance in a localized area can be represented as a sequence of related events (figure 6-1). First, the agent of the disturbance (the physical force) impinges on some set of the existing community (the interface between the force and the biota). That physical force then affects some subset of the biota through direct mortality, changes in reproductive success, altered metabolism, the redistribution of

nutrients, or changes in environmental gradients. The amount of change in biomass redistribution and environmental parameters determines the physical severity of the disturbance, sets the stage for the remaining community response, and provides an opportunity for species invasions. Finally, the remaining species and any invaders in the affected area respond to the physical effects through changes in resource acquisition, food web linkages, and colonization dynamics.

Organisms both interact with and respond to the sequence of events associated with a disturbance (Walker 1999). First, some species might dampen or ameliorate the immediate effects of a disturbance through structural attributes (for example, tall height or deep roots of trees) or other life-form or life history adaptations that allow organisms to physically buffer the direct effects of the disturbance agent. If a tree species has a tall, strong stem with deep roots, its presence might deflect or absorb much of the energy associated with high winds (Zimmerman et al. 1994). The presence of that species will then decrease the overall force, decreasing the severity for the rest of the community. This can result in lowered biomass redistribution and mortality, as well as decreased changes in primary environmental drivers such as light and soil moisture.

Following disturbances, the residual and newly arriving species (chapter 2) might affect the response of the local community through physical modification (e.g., soil aeration, habitat structure, or nutrient cycling), environmental gradient change (shading, increased moisture, energy availability), or biotic interactions (seed banks, dispersal, decomposition, competition). If the remaining species do

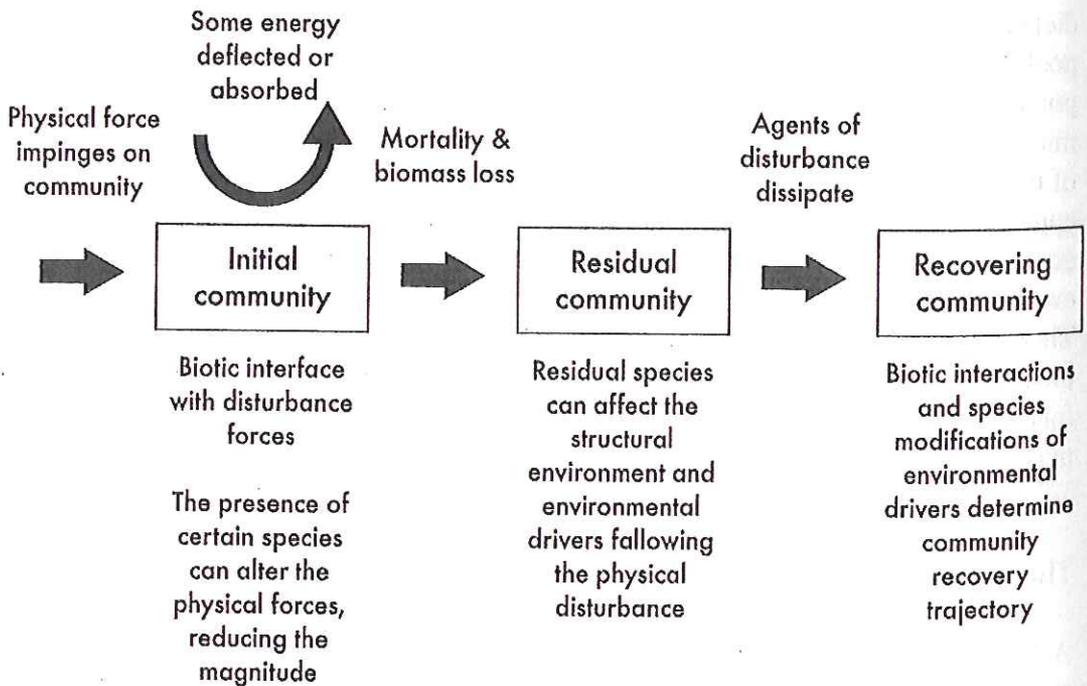


Figure 6.1 The disturbance sequence. The first event is some physical event impinging on an existing community. Certain key species might be able to diminish the physical force (and effects) due to a structural adaptation. The physical force then manifests itself through direct mortality effects, as well as the loss and redistribution of biomass.

not significantly alter the physical environment, then response to disturbance will simply follow the trajectory determined by the resultant change in the physical attributes (figure 6-1). However, if some of the new species combinations do alter the localized environment, the rate of response might be faster, with the previous species composition being reconstituted rapidly or replaced by a new combination.

## The Biotic Interface with the Disturbance Sequence

The common natural disturbance events in the Luquillo Mountains are treefalls, landslides, and hurricanes, all of which are related to high wind and rainfall (chapters 3, and 4). Hurricanes and treefalls open the canopy, increase light availability, change soil moisture and humidity, and redistribute carbon and nutrients from living biomass in standing vegetation to dead biomass on or near the ground or into streams (Lodge and McDowell 1991; Walker et al. 1991; Fernández and Myster 1995; Lugo and Lowe 1995; Fetcher et al. 1996; see chapter 4). Landslides include similar changes, as well as the mass movement of soils and the nutrients therein (Walker et al. 1996). The examples that follow suggest that the rate of succession and the resultant community depend heavily on biotic feedbacks during and after disturbances (see figure 2-7, chapter 2).

### *Biotic Interface with Disturbance Forces*

The amount of alteration to the forest canopy following hurricanes is highly variable (Walker et al. 1992). This variation is explained in part by the topographic location, especially the aspect and proximity to ridgetops (Boose et al. 1994), but also by the tree species composition (Walker 1991). For example, the abundant sierra palm (*Prestoea montana*) resists wind effects (Frangi and Lugo 1991; Reed 1998; Zimmerman and Covich 2007). These trees often lose their leaves, but the stems are left unaffected and quickly produce new leaves (Brokaw and Walker 1991). The groups of deeply rooted and root-grafted tabonuco trees (*Dacryodes excelsa*) might contribute to this species' evident resistance to wind, as it is common on ridge tops (Basnet et al. 1992, 1993). Presumably, it might also shelter other trees from wind (Lugo et al. 2000). The two architectural characteristics of having flexible stems and being short relative to the surrounding canopy are the best predictors of which tree species will maintain their importance values following disturbances (Frangi and Lugo 1991; Brokaw and Walker 1991). At a larger scale, smooth canopies (no emergent trees) reduce wind impacts and effects (Lugo et al. 2000).

### *Biotic Effects on the Postdisturbance Environment*

After a disturbance event, the remaining species (residuals) affect the environmental drivers (e.g., light, moisture, nutrients) of the local environment. Some modifications are instantaneous, owing to structural attributes such as residual tree canopies

or leaf resprouting from surviving trees. The rate and amount of these ameliorating factors depend on the presence of species that are resistant to the physical disturbance forces or which have adaptations for quick recovery. Above, we discuss the effects of resistant trees. Here we discuss the resilience of colonizing trees and the formation of debris dams, with biotic and abiotic components, that affect the post-disturbance environment.

### Biotic Feedbacks on Environmental Drivers after Disturbance

Many tree species in the Luquillo Mountains have adapted to quickly releaf following disturbances or to germinate from a predisturbance seed bank (seeds dormant in the soil). *Casearia arborea*, *Tabebuia heterophylla*, *Myrica deflexa*, *Cecropia schreberiana*, and *Prestoea montana* (sierra palm) all began releafing within 1 to 2 weeks following Hurricane Hugo (Fernández and Fetcher 1991; Walker 1991). As a result, within 10 months of Hurricane Hugo, most light hitting the forest floor was diffuse light with photosynthetic photon flux densities (PPFD) below  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Fernández and Fetcher 1991). For the 10 months after Hurricane Hugo, levels of understory PPFD were highly variable at a scale of 1 m, but the median was 7.7 to  $10.8 \text{ mol m}^{-2} \text{d}^{-1}$ , which is comparable to PPFD levels in a  $400 \text{ m}^2$  treefall gap (Fernández and Fetcher 1991; Turton 1992; Bellingham et al. 1996; Fetcher et al. 1996). Values had fallen to  $0.8 \text{ mol m}^{-2} \text{d}^{-1}$  by 14 months, when the rapid growth of *Cecropia schreberiana* and other species overtopped the light sensors in this study. This is a clear example of how ecological space shifts rapidly over points in geographic space, owing to disturbance and resilient biotic response (chapter 2).

Species make a difference in the cycling of nutrients in the Luquillo Mountains, and these differences are important for succession after a natural disturbance or forest restoration after land abandonment following agricultural use (Lugo et al. 2004). Table 6-1 contains 12 parameters that influence nutrient cycling and which are themselves affected by the tree species. Each of these parameters differs with species, giving us an understanding of how ecosystem function is influenced as species change through succession, and providing us with an opportunity to manage stand characteristics by manipulating the species composition of the stand. Scatena et al. (1996) found that following Hurricane Hugo, early successional species such as *Cecropia schreberiana* exhibited rapid rates of biomass accumulation and nutrient immobilization while returning nutrient-rich leaves to the forest floor (box 6-1). Nutrient use efficiency was low during this period of early secondary succession after a hurricane. Brown and Lugo (1990) reported that, in general, successional species and young forests are characterized by high rates of nutrient uptake and high rates of nutrient circulation through litterfall. Retranslocation rates for these species are usually low. In contrast, mature forest species, such as *Dacryodes excelsa*, have low rates of nutrient uptake and high rates of nutrient retranslocation (Lugo 1992). Their litterfall is low in nutrients, and their nutrient use efficiency is high. These species tend to conserve and reuse nutrients.

Table 6.1 Examples of how tree species influence nutrient cycling attributes of stands (from Lugo et al. 2004)

Nutrient cycling attribute	Implications for restoration
Uptake rate	Capacity to grow in the site
Retranslocation rate	Regulates the quality of litterfall, reduces the uptake requirement
Return to the forest floor	Opportunity for recycling and improvement of site fertility
Accumulation in biomass	Sink function and retention of nutrients on site
Distribution between above- and belowground compartments	Determines opportunity for building soil fertility belowground vs. circulating nutrients aboveground
Quality of tissue	Influence on decomposition and consumption rates by fungi, bacteria, and soil organisms
Efficiency of recycling	High efficiency favors living plants (reuse); low efficiency makes more nutrients available for the rest of the system
Efficiency of storage	High efficiency favors the sink function
Episodic return	Introduces pulses of nutrient availability
Episodic retranslocation	Causes periodic changes in the quality of litterfall
Episodic mast production	Can dominate the nutrient return pathway and favor particular nutrient cycling pathways
Episodic change in use efficiency	Causes periodic changes in the quality of plant tissue

### Box 6.1. Case Study 1—*Cecropia schreberiana* recruitment affects forest structure and nutrient dynamics.

The biology of *Cecropia schreberiana* both reflects the hurricane-driven dynamics of forest in the Luquillo Mountains and helps drive those dynamics (Brokaw 1998). *Cecropia schreberiana* is a light-demanding, fast-growing pioneer tree, and its population responds dramatically to hurricanes (chapter 5). After Hurricane Hugo, *C. schreberiana* was recruited abundantly from a soil seed bank; for example, there were about 11,200 *C. schreberiana* stems  $\geq 1$  cm in diameter at breast height (dbh) in the 16 ha Luquillo Forest Dynamics Plot after Hurricane Hugo, whereas there had been no more than 200 before (J. Thompson, unpublished data). This abundant colonization helped reestablish the forest canopy and modified the microclimate of the understory (see above). In many places in the Luquillo Mountains, *C. schreberiana* was the only tree forming a canopy after the hurricane.

As a rapidly and abundantly colonizing species, *C. schreberiana* plays key roles in ecosystem function and in the development of forest structure and composition after disturbance. Silander (1979) hypothesized that colonizing stands of *C. schreberiana* conserve nutrients in the recovering

forest ecosystem by efficiently acquiring nutrients. Colonizing *C. schreberiana* did quickly concentrate nutrients after Hurricane Hugo. In heavily damaged tabonuco stands in the Bisley watersheds, the highest above-ground net primary productivity in the 5 years after the hurricane occurred in the second year as a result of massive recruitment of *C. schreberiana* saplings to the  $\geq 1.3$  m tall size class (Scatena et al. 1996). This productivity was achieved as large amounts of nutrient-poor necromass in the watersheds were replaced by nutrient-rich tissue in fast-growing colonizers. *Cecropia schreberiana* was prominent among these pioneers and had particularly high concentrations of potassium (K) and magnesium (Mg) in its foliage. In addition, leaf litter from *C. schreberiana* decays relatively slowly due to high lignin concentrations (La Caro and Rudd 1985; González and Seastedt 2001), releasing nutrients gradually. *Cecropia schreberiana* might similarly store nutrients in landslides (Walker et al. 1996) and treefall gaps (Walker 2000). Thus it appears that *C. schreberiana* performs a "key function" at the plant - soil interface (Silver et al. 1996; cf. Silander 1979) by having a disproportionately large role in capturing and storing nutrients from decomposing plants after disturbances.

The posthurricane dynamics of *C. schreberiana* are also directly important to some animals. The coquí frog (*Eleutherodactylus coqui*) uses the large fallen leaves of *C. schreberiana* as nest sites, and in the 5 years after Hurricane Hugo this frog was especially abundant where *C. schreberiana* was abundant (Woolbright 1996). Similarly, the lizard *Anolis gundlachi* was more abundant where it could use *C. schreberiana* saplings as understory perches (Reagan 1991).

### Debris Dams and Root Mats after Disturbance

In steep forested ecosystems such as the Luquillo Mountains, terrestrial debris dams, created by boulders and tree roots, are important for the retention of leaf litter and the nutrients therein on slopes. Dams also promote the creation of litter mats by linked fungi that protect the soil surface and reduce losses of soil nutrients through erosion while at the same time reducing siltation in streams and reservoirs. The effects of debris dams in reducing erosional losses are quite evident in the Luquillo Mountains. Evidence of erosion on bare, steep slopes has been observed as "erosion columns," small columns of soil protected from the impact of raindrops by pebbles. Furthermore, approximately one-quarter to one-third of the forest floor at El Verde shows evidence of overland flow during extreme rainfall events.

Terrestrial debris dams created by boulders are relatively permanent. Long-lived debris dams include large surface structural roots of certain tree species (*Dacryodes excelsa*, *Pterocarpus officinalis*, and *Pisonia subcordata*). Moderately long-lived debris mats are bound together by rootlike structures (rhizomorphs) consisting of

cords and the hyphae of white rot basidiomycete fungi. Some individual mycelia of *Collybia johnstonii* persist in more or less the same place for at least 20 years (D. J. Lodge, personal observation).

*Collybia johnstonii* is one of the dominant litter-binding basidiomycete species on the forest floor of the tabonuco forest during long interhurricane periods (Lodge and Asbury 1988). The rootlike structures of *C. johnstonii* and various species of *Marasmius* and *Marasmiellus* significantly reduced the rate of leaf litter export on slopes exceeding 30 percent (Lodge and Asbury 1988). Unlike most of the other litter-mat forming basidiomycetes, however, *C. johnstonii* produces a superficial mycelium on leaf surfaces and is very sensitive to drying of the litter layer (Miller and Lodge 1997). Of the 20 mycelial mats of *C. johnstonii* that had been monitored at El Verde beginning before Hurricane Hugo, 8 individuals died, and 9 others were so reduced that they went undetected and were nonfunctional for 5 years after the hurricane opened the canopy (Lodge and Cantrell 1995). Following Hurricane Hugo, more stress-tolerant species of *Marasmiellus* and *Marasmius* partially replaced the diminished function of *C. johnstonii* in binding litter together into mats, and fallen branches and trunks took on a greater role in creating terrestrial debris dams.

Debris dams in streams also form via the accumulation of leaf litter by roots and boulders. Erosional processes along stream channels expose roots, which entrap palm fronds and other leaves. Woody lianas are also associated with these accumulations whenever they hang into the stream channel. These living roots and lianas can remain in place for many years. Following Hurricane Hugo, large amounts of palm fronds and branches were held in place for months by debris dams. The dams retained fine sediments and organic matter. Dam formation in numerous pools slowed down the high stream flow during the intense rainfall associated with the hurricane and reduced the washout of benthic invertebrates. Large accumulations of leaf litter in debris dams provided detrital food resources and protective cover from predators for numerous decapod crustaceans following the hurricane (Covich et al. 1991). Stream flows slowly undercut the organic debris, and within 12 months the sediments and leaf litter had been washed downstream. By then, additional riparian leaf production had resulted in a relatively continuous supply of leaf litter to the stream detritivores, and debris dams were much smaller and transitory.

### *Biotic Feedbacks and Successional Community Dynamics*

There has been much debate about the mechanisms and trajectories of succession and the predictability of ecosystem states following disturbances (see Walker and del Moral [2003] for a review). One paradigm emerging from this debate is that biotic factors (e.g., the effect of species on biogeochemical cycling, shifts in trophic interactions, the loss of native seed sources) are crucial elements that influence the rate and trajectory of succession (Suding et al. 2004). Individual species that either remain or colonize following disturbances often have distinctive traits that can change ecosystem characteristics such as rates of resource turnover, nutrient distribution, and competitive balances (D'Antonio and Meyerson 2002). These observations have resulted in a number of autogenic models of succession in which species' interactions with each other and the local environment drive the rates and trajectories of succession

(Connell and Slatyer 1977; Grime 1979; Noble and Slatyer 1980). Below, we describe species interactions and feedbacks that have strong influences on how communities respond to various disturbances in the Luquillo Mountains.

### Animal - Soil - Ecosystem Interactions after Disturbance

Soil fauna modify the soil environment by mixing organic and mineral particles and by changing the water infiltration and aeration regimes (figure 6-2). Tillering by soil fauna directly alters the soil's physical, chemical, and biological properties, and the effects of substrate modification by soil fauna on decomposition are diverse. The breakdown of litter by soil fauna increases the leaching of nutrients and expands the surface area for microbial use. Soil fauna can also augment the nutrient pool in soil solution by adding nitrogenous compounds present in their excreta and dead tissue (González and Zou 1999a, 1999b; Hendrix et al. 1999; González 2002).

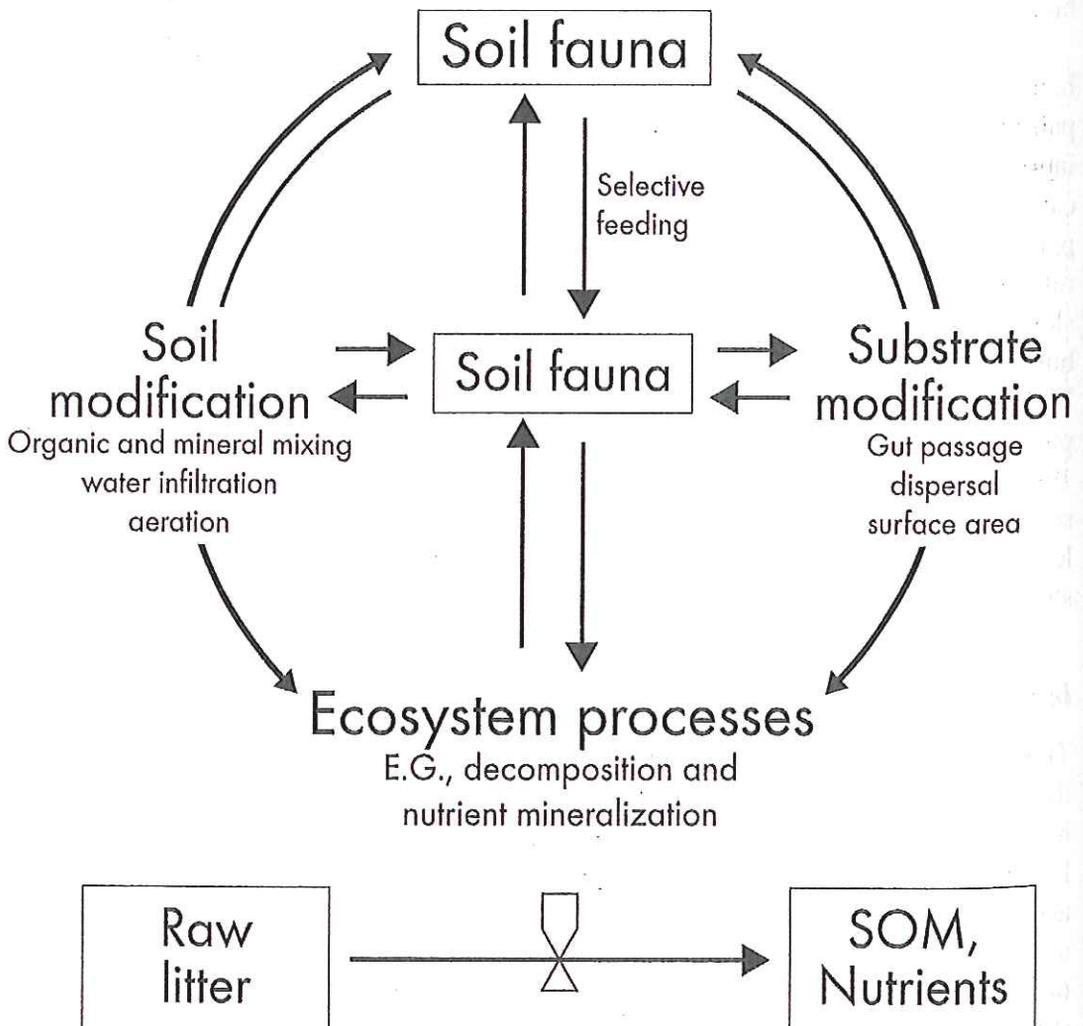


Figure 6.2 Conceptual model indicating direct and indirect paths by which soil fauna affect ecosystem processes (e.g., decomposition and mineralization) and the interaction with microorganisms. SOM = soil organic matter. (Modified from González et al. 2001.)

The majority of the energy and nutrients obtained by plants eventually becomes incorporated in dead organic matter or detritus (Wiegert and Evans 1967; Seastedt 1984). The fragmentation of the detritus, the transfer of organic matter and nutrients into the soils, and the release of carbon dioxide to the atmosphere are essential for sustaining the productivity of ecosystems (Vitousek 1982). In the Luquillo Mountains, soil fauna greatly influence these processes (González 2002); faunal effects on litter decomposition can account for up to 66 percent of the decay rate (González and Seastedt 2001) (figure 6-3). The Luquillo Mountains are a site of high abundance of soil micro- and macrofauna and diversity of functional groups (González and Seastedt 2000, 2001).

Earthworms make up the highest biomass among the soil fauna in the tabonuco forest (Odum and Pigeon 1970), and their abundance and community composition can be greatly altered by disturbance (González et al. 1996; Zou and González 1997) (box 6-2). Earthworms appear to be a significant factor in postdisturbance soil nutrient dynamics (Liu and Zou 2002). Following Hurricane Hugo, Liu and Zou (2002) experimentally removed earthworms via electro-shocking. In areas that had earthworms removed, litter decay rates decreased by 20 to 50 percent. In addition, the soil respiration decreased from 4.7 to 9.4  $\text{g m}^{-2} \text{d}^{-1}$  in control plots to 3.8 to 6.6  $\text{g m}^{-2} \text{d}^{-1}$  in earthworm removal plots, for a 20 to 36 percent increase in carbon dioxide ( $\text{CO}_2$ ) evolution with earthworms. Liu and Zou (2002) concluded that the change in soil respiration was due to a decrease in microbial activity when earthworms were absent. This conclusion was based on the lack of response of any other physical changes to the soils, such as pH or moisture or oxygen content.

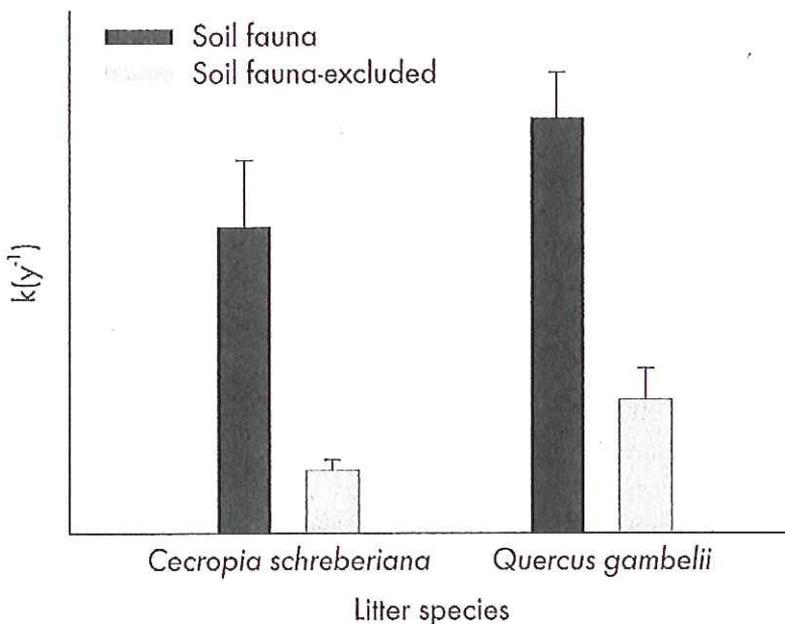


Figure 6.3 Mean decay rates ( $k$ ) for *Cecropia schreberiana* and *Quercus gambelii* litter in soil fauna and soil fauna-excluded treatments in the tabonuco forest. (Redrawn from González and Seastedt 2001.)

Box 6.2. Case Study 2—Earthworms affect soil processes and nutrient cycling.

About 29 earthworm species have been described in Puerto Rico. Twelve of these have been recorded in the tabonuco forest of the Luquillo Mountains (González et al. 1996; Zou and González 1997; González et al. 1999a, 1999b). Among those 12 earthworm species, *Pontoscolex corethrurus*, *Amyntas rodericensis*, and *Ocnerodrilus occidentalis* are not native to Puerto Rico. *Pontoscolex corethrurus* and *A. rodericensis* are found in anthropogenically disturbed sites. The other species are native to Puerto Rico and include *P. spiralis*, *Estherella gatesi*, *E. montana*, *Borgia sedecimsetae*, *B. montana*, *Onychochaeta borincana*, *Neotrigaster rufa*, *Trigaster longissimus*, and *T. yukiyu*. Earthworms are classified into endogeic, anecic, and epigeic species, representing soil, soil and litter, and litter feeders, respectively. Endogeic earthworms in the tabonuco forest include *P. corethrurus*, *P. spiralis*, *B. sedecimsetae*, and *O. borincana*. *Trigaster longissimus* and *N. rufa* are considered anecic and epigeic species, respectively. *Amyntas rodericensis*, *E. gatesi*, and *E. montana* are epianecic species.

Earthworm abundance and community structure differ between upland areas and riparian areas in the mature tabonuco forest. Earthworm density and fresh weight in the upland area average 118 individuals  $m^{-2}$  and 43.4  $g m^{-2}$ , respectively (González et al. 1999a). These values are 68 individuals  $m^{-2}$  and 23.5  $g m^{-2}$  in the riparian area. The distribution pattern of earthworms in both upland and riparian areas is clumped, but it is more aggregated in the riparian areas (González et al. 1999a, 1999b).

Disturbances play an important role in altering earthworm abundance and community structure. Although the overall earthworm abundance might recover quickly, anecic earthworms often disappear in newly exposed soils or where root mats were lifted during a treefall (Camilo and Zou 2001). Human activities can drastically change both earthworm abundance and community structure in the Luquillo Mountains. The conversion of tabonuco forest to tropical pastures increased the earthworm density from less than 100 to over 1,000 earthworms  $m^{-2}$  (Zou and González 1997; Sánchez et al. 2003). This was largely due to an increase in the nonnative endogeic *P. corethrurus*; native earthworms and earthworm diversity decreased. However, the natural regeneration of secondary forests on abandoned pastures promotes the recovery of both anecic earthworms and native species (González et al. 1996; Sánchez et al. 2003). Earthworm density and fresh weight in secondary forests are twice those in pine (*Pinus caribaea*) and mahogany (*Swietenia macrophylla*) plantations and do not differ between plantations (González et al. 1996).

*Pontoscolex corethrurus* dominated both secondary forests and plantations, but native earthworms occurred only in secondary forests, suggesting that naturally regenerated secondary forests are preferable to plantations for maintaining high levels of earthworm density, biomass, and native species (González et al. 1996).

Earthworms are closely associated with ecosystem processes in the tabonuco forest. An exclusion experiment demonstrated that a reduction in earthworm density could reduce the decomposition rate of plant leaf litter and soil respiration by 20 to 30 percent (Liu and Zou 2002). Earthworm exclusion also increased surface runoff of water, soil erosion, and down-slope exports of organic materials. Furthermore, the presence of earthworms increased soil nitrogen (N) availability and the growth of *Cecropia* seedlings (González and Zou 1999a, 1999b).

### *Animal – Plant – Ecosystem Interactions after Disturbance*

Walking sticks (Phasmidae) preferentially frequent treefall gaps, and lepidoptera populations increased after Hurricane Hugo in response to the flush of new leaves (chapter 5). These herbivores can have a significant effect on hydrology and nutrient turnover after a hurricane. Loss of foliage can increase throughfall and canopy turnover of N, K, and calcium (Ca.). As mentioned in chapter 5, hurricanes appear to generally promote sap-suckers and inhibit defoliators in the forest canopy (Schowalter 1994; Schowalter and Ganio 1999). Sap-sucking insects excrete honeydew, thereby creating a flow of water and sugars from plants to soil that can affect soil processes. Contributions of labile carbon to soils by sap-suckers during recovery might contribute to nutrient retention in microbial biomass. Canopy opening and the increased flux of water and nutrients by defoliators during later successional stages might contribute to greater nutrient cycling via their excretions and to reduced moisture stress owing to leaf consumption during dry periods. Schowalter (1995) reported that although the overall densities of herbivorous insects (primarily heteropterans) did not change following Hurricane Hugo, their spatial distribution was altered, resulting in high-density patches. In these areas, herbivory increased significantly, especially on early-successional plant species. Schowalter (1995) speculated that concentrating herbivores in localized areas could alter the production and survivorship of some species.

Some of the most dramatic examples of animals affecting primary producer biomass, plant decomposition, and nutrient cycling come from the streams draining the Luquillo Mountains (box 6-3). Numerous studies on the role of freshwater shrimp have found significant linkages between shrimp, the algal community, leaf decomposition, and fine particulate organic matter (FPOM) dynamics (Covich 1988a, 1988b; Covich et al. 1991, 1996, 1999; Pringle et al. 1993; Pringle and Blake 1994; Pringle et al. 1999; Crowl et al. 2000, 2001, 2002, 2006; see also chapter 8).

Box 6.3. Case Study 3—Freshwater shrimp and crabs affect primary producers, detrital processing, and nutrient cycling.

The streams of the Luquillo Mountains are dominated both numerically and in terms of biomass by two species of freshwater shrimp (Crowl and Covich 1994; Covich and McDowell 1996; Covich et al. 1996, 2009; Cross et al. 2008; Kikkert et al. 2009). *Atya lanipes* is primarily a filter feeder/collector/scrapper (Fryer 1977; Hobbs and Hart 1982; Covich 1988a), and *Xiphocaris elongata* is a shredder/predator/particle feeder (Fryer 1977; Covich 1988a). Over the past 10 years, field and laboratory experiments, as well as large-scale monitoring, have shown how each of the two major decapod guilds (shredders and collectors) affect the composition, rate, and transport of the detrital pool derived from baseline litter inputs (e.g., Pringle and Blake 1994; Pringle et al. 1999; March et al. 2001) and from pulses associated with disturbances such as hurricanes and droughts (Covich et al. 2000; Crowl et al. 2001). Shrimp species composition has a significant effect on the retention of organic carbon and nitrogen within the small tributary streams draining the Luquillo Mountains. Moreover, species-specific (or functional group) processing significantly alters the size fraction and nutrient concentrations available to the remaining community. Microbial or physical processing of detrital material is also important, but these shrimp species are important in fundamentally different ways, in terms of both transport and retention of detritus and nutrient cycling. Furthermore, unique effects of these shrimp species operate during typical flow conditions (pulsed flows often interrupting base flows), during periods of low stream flow (droughts), and following large litter inputs (e.g., hurricanes).

*Xiphocaris elongata* and *A. lanipes* have dramatic effects on organic matter accumulation, decomposition, and nutrient composition during base flows in the headwaters of the Luquillo Mountains (Pringle et al. 1993; Crowl et al. 2001; Cross et al. 2008). In electric exclusion experiments within pools, scraping and brushing by *A. lanipes* maintained low standing stocks of epilithic biofilms and fine particulate organic matter (FPOM), carbon, and nitrogen in control treatments. In contrast, exclusion treatments had high and variable levels of FPOM and nutrients occurring on rocks (Pringle and Blake 1994; Pringle et al. 1999; March et al. 2002). Although *A. lanipes* feeding decreases the quantity of epilithic FPOM, the remaining FPOM is of a higher food quality (i.e., lower carbon-to-nitrogen ratio) (Pringle et al. 1999). Similarly, shredding by *X. elongata* causes higher leaf decomposition rates in controls than in electric exclusion treatments (March et al. 2001). These base-flow effects of shrimp species act to obscure the effects of high flows, which scour and redistribute organic

materials throughout the stream channel. Pulsed flows caused high variability in FPOM and nutrient levels in exclusion treatments, but not in controls. *Atya lanipes* rapidly removes deposited FPOM, restoring low levels of epilithic organic matter within 1 to 2 days following storm-flow events (Pringle and Blake 1994; Pringle et al. 1999).

The patch-scale experiments discussed above have shown that *X. elongata* and *A. lanipes* play an important role in detrital processing during base flows and following the frequent pulsed flows characteristic of Luquillo Mountain streams. Experimental simulation of hurricane-level leaf fall shows that these decapods are particularly critical to detrital processing following hurricane disturbance. The presence of *X. elongata* results in high rates of direct leaf breakdown and downstream export of suspended fragments within 7 days, and these rates continued until the end of the experiment (figure 6-4). For coarse particulate organic matter (CPOM) and medium particulate organic matter (MPOM), pools with *X. elongata* continued to have the highest amounts of export throughout the experiment, with up to 90 percent of the original leaf material being broken down and exported as smaller size fractions.

*Atya lanipes* did not appear to significantly alter concentrations of medium or coarse particulates until the end of the experiment (figure 6-4). More CPOM was exported from pools containing *A. lanipes* than from the pools without shrimp. This difference suggests that *A. lanipes* enhanced the amount of leaf breakdown once microbial conditioning occurred. The FPOM export was significantly decreased in pools with *A. lanipes* relative to pools with *X. elongata* or without shrimp. These results are expected, given that *A. lanipes* is known to be an effective filter feeder (Covich 1988b). The transport of all size fractions of leaf material was greatly increased during the first 17 days of the experiment. These results suggest that both species of shrimp are extremely important in both the breakdown and the retention of leaf-litter-derived organic particles, especially of disturbance-level inputs.

The results show increased concentrations of dissolved organic matter (DOC) as high as  $6.5 \text{ mg L}^{-1}$  resulting from shrimp-mediated leaf decomposition; pools without shrimp never exceeded  $3.8 \text{ mg L}^{-1}$  (Crowl et al. 2001). The increase in stream DOC concentrations that we observed in the presence of *X. elongata* is large relative to typical conditions. Before Hurricane Hugo, low-flow DOC concentrations for streams in the Luquillo Mountains were 1 to  $1.5 \text{ mg L}^{-1}$ , with peak concentrations of 4 to  $5 \text{ mg L}^{-1}$  found during storms (McDowell and Asbury 1994). *Xiphocaris elongata* produced considerably more DOC ( $328 \text{ } \mu\text{g mg}^{-1}$ ) (DOC production was estimated as the difference in concentrations between pools with and without shrimp). This difference suggests that the mechanism of DOC

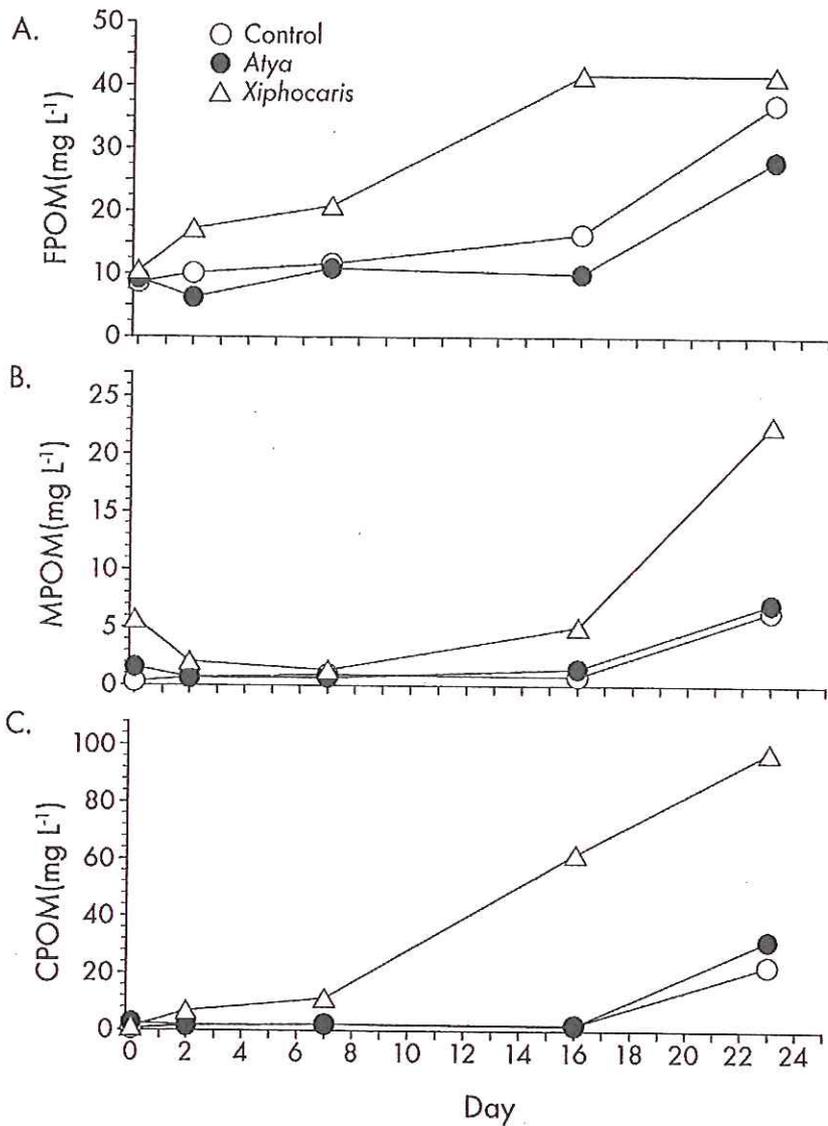


Figure 6.4 Particulate organic matter production as a function of shrimp species. *Xiphocaris* increase all three size fractions ([A]–[C]) of coarse particulate matter. The presence of the filter-feeding *Atya* results in a decrease in the smallest particles (A), presumably due to consumption. (Modified from Crowl et al 2001.)

production differs between the genera, perhaps because of differences in feeding techniques.

Although the effects of shrimp on detrital processing have been examined under a variety of disturbance conditions (i.e., base flows, flash floods, droughts, and hurricane detrital pulses), the effects of shrimp on in-stream primary producers have been studied only in the context of typical Luquillo Mountain stream flow conditions (base flows periodically interrupted by flash floods).

The conversion of leaf litter and primary production into shrimp biomass and the breakdown of CPOM into smaller particles that are more readily available to insect larvae provide a mechanism for retaining carbon and other nutrients following disturbance events in these steeply sloped headwater streams. In the absence of these consumers, nutrients would be flushed downstream and out of the drainage basin. Juvenile crabs and shrimps are confined to the stream, and their grazing and detritivore functions enhance the release of nutrients available to primary producers and bacteria. These detritivorous and algivorous shrimp and juvenile crabs in turn are prey for larger shrimp, crabs, fish, and birds that might further serve to keep the nutrients from being washed downstream. Some of these consumers (e.g., amphibious crabs such as *Epilobocera sinuatifrons*) move the nutrients from the stream back to the surrounding forest and enhance nutrient cycling (Covich and McDowell 1996; Zimmerman and Covich 2003; Fraiola 2006) and act to conserve nutrients locally. These connections potentially have significant effects on the food web structure and overall productivity of these streams.

At a larger scale, organic matter transport and storage appear to be highly dependent on the species composition and abundance of the shrimp assemblages among streams. In a one-time sampling survey of six streams varying in decapod abundance, Pringle et al. (1999) found that standing stocks of FPOM were highly correlated with shrimp abundance. When we combined all information on discharge, physical characteristics, and decapod assemblage and densities across four streams over 8 years, we were able to explain between 32 and 62 percent of the variation in organic matter storage and transport (table 6-2). In almost all cases, the density and species composition of the shrimp explained the highest amount of variation, with physical variables rarely being important. This suggests that biotic processing by decapods is the most important driving variable for organic matter processing, at least in these small headwater streams.

Previous work reported important biotic effects of decapods on the overall community dynamics (e.g., Crowl and Covich 1994; Pringle et al. 1999; Crowl et al. 2001; March et al. 2001) and organic matter transport (Crowl et al. 2002) in small pool experiments. These analyses suggest that biotic interactions occur at a larger scale and over a wider range of hydrologic conditions than previously noted. The species-specific roles of benthic macroinvertebrates that shred leaf litter in tropical streams are being studied over a wide biogeographical range (Meyer and O'Hop 1983; Dobson et al. 2002; Covich et al. 2004; Boyero et al. 2006; Boulton et al. 2008). Our results indicate a major role for macroinvertebrates such as decapod crustaceans, while also demonstrating that microbial processing is especially important for some types of leaf litter, with distinct effects of secondary chemicals in leaves (Wright and Covich 2005a, 2005b).

Table 6.2 Stepwise regression results for the relationship between particulate organic matter storage and transport and decapod and hydrologic parameters

Response variable	Predictor	R-square	F	p
CPOM (drift)	<i>Xiphocaris</i> density	61.4	24.2	<0.0001
FPOM (drift)	<i>Atya</i> density	20.2	5.3	0.0313
	<i>Xiphocaris</i> density	10.1	3.9	0.0587
CPOM (benthic)	<i>Xiphocaris</i> density	22.5	8.0	0.0181
	Discharge	9.3	3.3	0.0951
FPOM (benthic)	<i>Atya</i> density	22.8	8.7	0.0098
	Pool depth	6.1	2.8	0.1013

### Secondary Consumers and Ecosystems following Disturbance

Although most experiments involving food web dynamics and succession have just recently begun, a number of studies provide anecdotal evidence that animals (largely frogs and lizards) might be important in terms of altering herbivorous insect populations, herbivory rates, and nutrient cycling in regrowing forest patches. Dial and Roughgarden (1995) reported that reductions in the numbers of anolis lizards resulted in a twofold increase in herbivory on plants. This occurred via two distinct pathways. First, lizards directly consume herbivorous insects (especially orthopterans), thereby decreasing herbivore pressure. Lizards also consume spiders that consume predacious insects. When lizard densities were decreased, spider densities were increased. This resulted in a decrease in insect predators and an ensuing increase in insect herbivores.

Perhaps the most conspicuous species in the Luquillo Mountains are the endemic terrestrial frogs (box 6-4). Although 16 *Eleutherodactylus* species are recognized in Puerto Rico, of the species found in the Luquillo Mountains, *Eleutherodactylus coqui* is the most widespread and abundant (Rivero 1978). *Eleutherodactylus coqui* attains extremely high densities (20,570 individuals ha<sup>-1</sup> on average) and has the greatest biomass of any vertebrate in the tabonuco forests (Reagan and Waide 1996; Stewart and Woolbright 1996). At these densities, frog predation on insects and frog excretion have important effects on food web dynamics and nutrient cycling (Beard et al. 2002), and these should be even more important after hurricane disturbances, when debris on the forest floor increases frog reproduction and abundance (chapter 5).

### Biodiversity: Structure and Function

Most of the research on the relationship between biodiversity and ecosystem processes has focused on patterns with respect to species richness and productivity (Kinzig et al. 2002; Loreau et al. 2002; Wilsey et al. 2005), frequently in ecosystems dominated by low-stature vascular plants (e.g., Gross et al. 2000; Chalcraft et al. 2004). Theory concerning richness and productivity predicts positive monotonic,

Box 6.4. Case Study 4—*Eleutherodactylus coqui* influence invertebrate communities, nutrient cycling, and plant growth rates.

*Eleutherodactylus coqui* are generalist predators, consuming an estimated 114,000 prey items (mostly invertebrates)  $\text{ha}^{-1} \text{night}^{-1}$  (Stewart and Woolbright 1996). In order to study *E. coqui* effects on invertebrate communities, experiments were conducted in the Bisley Experimental Forest at both large (20 m  $\times$  20 m plots) and small scales (1 m  $\times$  1 m) using exclosures and enclosures, respectively (Beard et al. 2003a). The effects of *E. coqui* on herbivorous invertebrates was reflected in reduced herbivory rates on two potted plant species, *Piper glabrescens* and *Manilkara bidentata*, at both spatial scales (Beard et al. 2003a) (figure 6-5). *Eleutherodactylus coqui* were also found to reduce flying invertebrates (mostly Dipterans) at both scales (figure 6-6), although there was a positive relationship between *E. coqui* and flying invertebrate abundances in control plots at the larger scale (Beard et al. 2003a) (figure 6-7). Despite the fact that stomach content

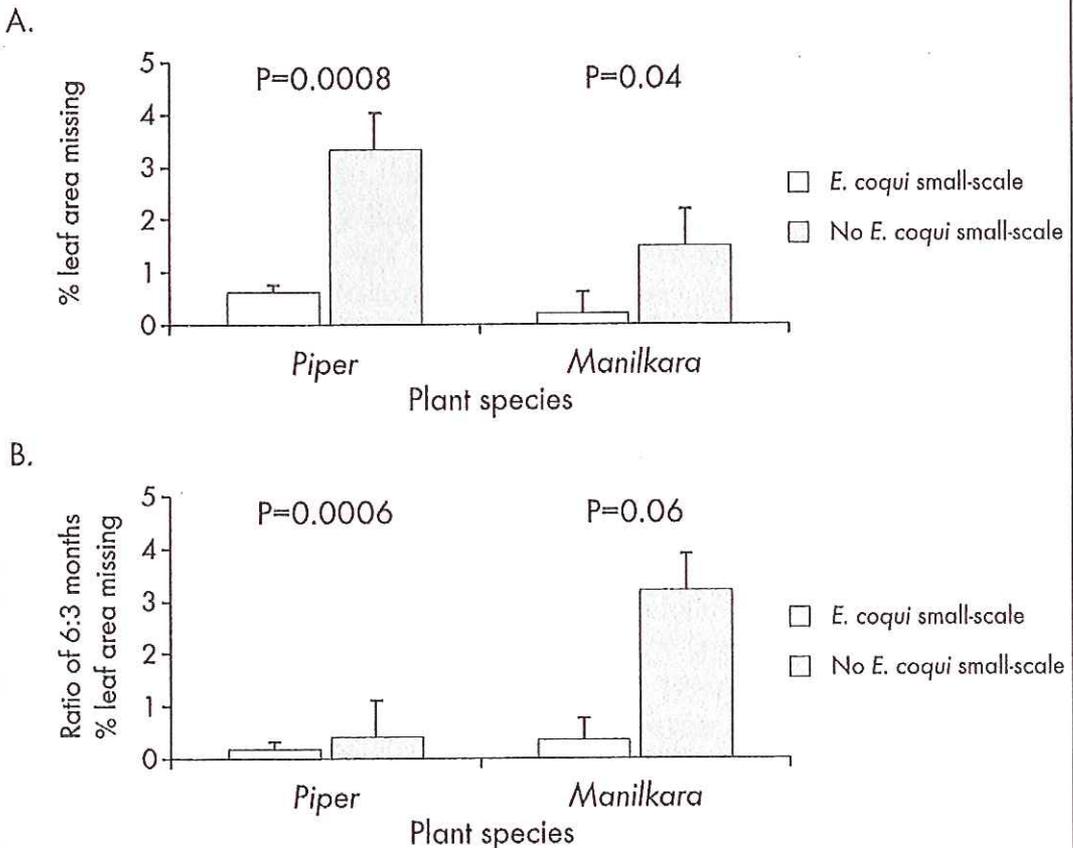


Figure 6.5 Herbivory measurements for plants (+ SE) grown in enclosures and plots with and without *Eleutherodactylus coqui* in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. (A) Mean percent leaf area missing after 4 months for both *Piper* and *Manilkara* in the small-scale experiment. (B) Mean ratio of percent leaf area missing from new leaves at 6 months compared to that missing at 3 months for both *Piper* and *Manilkara* in the large-scale experiment.

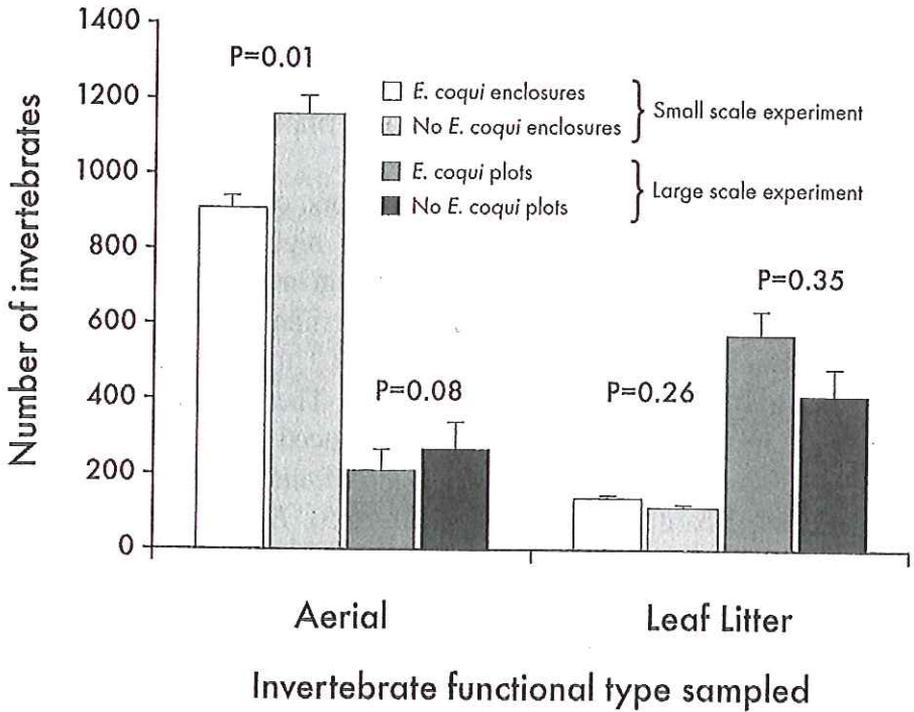


Figure 6.6 Mean total number of aerial and leaf litter invertebrates (+ SE) in enclosures and plots with and without *Eleutherodactylus coqui* in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico.  $N = 10$  for the small-scale experiment, and  $N = 3$  for the large-scale experiment.

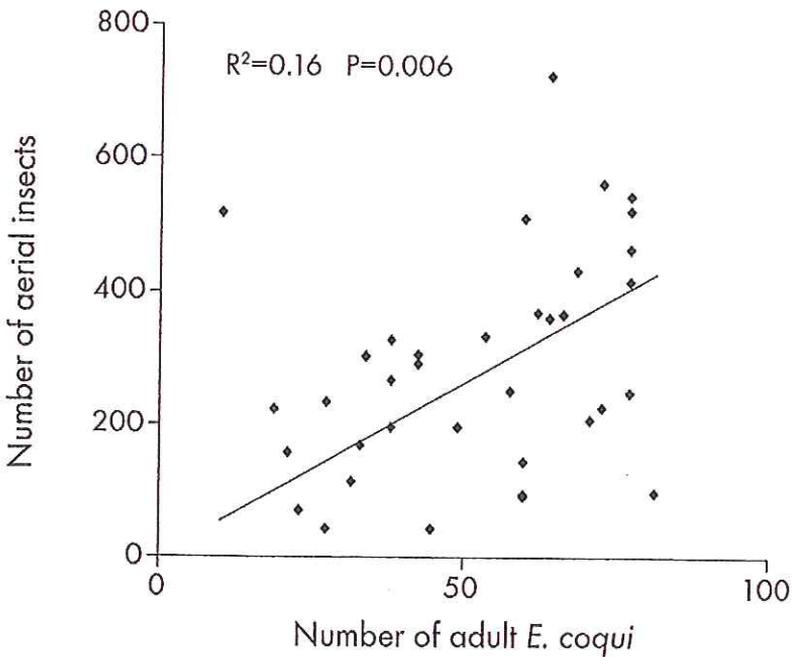


Figure 6.7 Number of aerial insects as a function of adult *Eleutherodactylus* densities.

analyses revealed that *E. coqui* consumes leaf litter invertebrates (Stewart and Woolbright 1996), populations of litter invertebrates did not change significantly with treatment in either experiment (Beard et al. 2003a) (figure 6-6). As would be expected of a predator consuming large numbers of prey items, *E. coqui* increased nutrient availability in the small-scale experiment (the increase was measurable as changes in the throughfall chemistry). More specifically, *E. coqui* increased concentrations of DOC, ammonia ( $\text{NH}_4^+$ ), nitrate ( $\text{NO}_3^-$ ), dissolved organic nitrogen, Ca, iron (Fe), Mg, Mn, phosphorus (P), K, and zinc (Zn) in leachate coming off foliage by 60 to 100 percent (Beard et al. 2002). *Eleutherodactylus coqui* also increased leaf litter decomposition rates and nutrient concentrations of K and P in decomposed litter by 14 percent and 16 percent, respectively (Beard et al. 2002). The leaf area of the two potted plant species, *P. glabrescens* and *M. bidentata*, also increased with *E. coqui* (figure 6-8). For *P. glabrescens*, other plant growth variables increased, including stem height growth and the number of new leaves and stems produced (Beard et al. 2003a). Both the higher rate of leaf litter decomposition and the increase in leaf production suggest that *E. coqui* might significantly contribute to the rates at which limiting nutrients cycle in this forest, especially at a microsite scale.

The increases in leaf litter decomposition rates and plant growth rates with *E. coqui* present occur through a nutrient cycling effect, as opposed to a trophic cascade (Sin et al. 2008). Although top-down effects on ecosystem productivity through nutrient cycling by a vertebrate predator have been demonstrated in aquatic ecosystems, this is one of the first examples demonstrating the importance of this mechanism for a vertebrate predator in a terrestrial ecosystem. Nutrient cycling effects might be important in this system because frog nitrogenous waste products are in the form of urea, whereas invertebrate waste products are often the least soluble form of nitrogenous waste, uric acid (Beard et al. 2002). Similarly, frog carcasses are more likely to decompose faster and thus release nutrients faster into the substrate than invertebrate remains would. In contrast, invertebrate remains could act as a nutrient sink owing to the slow decomposition of chitinous exoskeletons (Seastedt and Tate 1981).

The effects of *E. coqui* are likely to be greatest following disturbance events because increases in population abundance occur when breeding habitat increases near the forest floor (Woolbright 1996). The type, frequency, and severity of the disturbance (i.e., the amount of habitat structure added to the forest floor) will determine the extent of the increase in abundance (Woolbright 1991). For example, Hurricane Georges was not as severe as Hurricane Hugo, and whereas adult numbers roughly doubled after Hurricane Georges, adult numbers increased sixfold following Hurricane Hugo (Woolbright 1996).

In order for the ecosystem to recover after a hurricane, and for net primary production to return to the predisturbance level, plants must regain the foliage area lost (Scatena et al. 1993). Heavy grazing of postdisturbance invertebrates could slow this recovery (Torres 1992), but postdisturbance

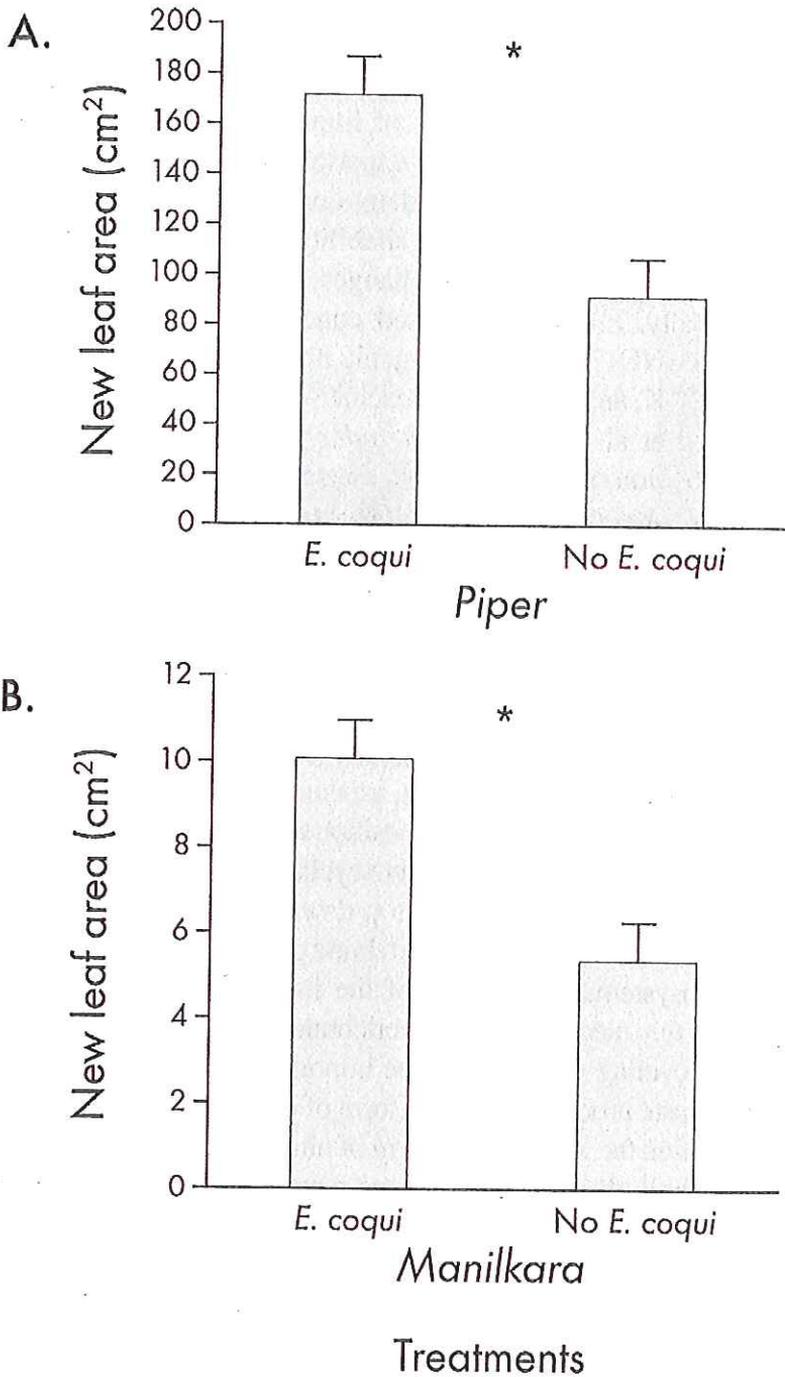


Figure 6.8 Leaf production (+ SE) with and without coqui for *Piper* (A) and *Manilkara* (B).

increases of *E. coqui* could reduce this effect. *Eleutherodactylus coqui* abundance might also increase the rate of recovery by increasing the supply of limiting nutrients to microbes that decompose increased necromass. In addition, greater *E. coqui* densities might aid recovery by increasing nutrient availability to plants because of higher nutrient content in throughput and soils (Vogt et al. 1996). These effects might be especially manifested at the scale of individual plant species and especially relevant for early-successional plant species (Beard et al. 2003b).

negative monotonic, or modal relationships (Rosenzweig 1995), with empirical support for all three (Waide et al. 1999; Mittelbach et al. 2001). Moreover, a growing consensus is that the form and parameterization of such relationships are scale dependent (Moore and Keddy 1989; Pastor et al. 1996; Weiher 1999; Chase and Leibold 2002; Scheiner et al. 2008).

Despite the spectacular diversity of species in tropical forests, little is known about their relationship or that of species traits with productivity in tropical forests, much less the extent to which other aspects of community structure (e.g., species evenness, dominance, rarity, or diversity) alter ecosystem function (Wilsey et al. 2005). Equally true, it is unclear how biota and their linkage with ecosystem processes will depend on the manner in which the importance of species is weighted in measures of evenness, dominance, or diversity (i.e., weighting by proportional abundance or proportional mass). Although to date we have not designed studies to specifically test the role of biodiversity (species richness and abundances) in the disturbance sequence in the Luquillo Mountains, we have initiated analyses across our existing long-term plots and along our various gradients toward this end. We have also provided a number of examples of cases in which individual species and their traits are important in affecting the disturbance sequence through physical and biological pathways.

## Summary

We have documented a number of species or species groups that have considerable impacts on the disturbance regime and the ensuing dynamics following disturbances. Measurable effects include the dissipation of energy during wind events (*Dacryodes excelsa*), the enhanced recolonization of bare soils (ferns), and alterations of nutrient availability through food web dynamics (frogs and lizards) and detrital processing (earthworms and freshwater shrimp). Although we have not directly addressed the importance of biodiversity itself, it is clear that the loss of species from the aforementioned taxa would certainly result in a significant alteration of pattern and process in this forest ecosystem.

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# A Caribbean Forest Tapestry

*The Multidimensional Nature of  
Disturbance and Response*

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*Edited by*

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