

Long-Term Research in the Luquillo Mountains

Synthesis and Foundations for the Future

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Key Points

- The biota responds to disturbance and, equally important, influences the frequency, magnitude, and intensity of disturbances.
- Environmental gradients provide a context for contrasting the roles of particular species with respect to resilience and resistance during the interplay between disturbance and succession.
- Disturbance increases the complexity of interactions (i.e., macro- and microclimatic, biogeochemical, biotic) that control the flow of energy and cycling of materials through ecosystems.
- Soil microorganisms, as well as the timing, quantity, and quality of litter deposition, play a critical role in affecting the dynamics of carbon and nutrient cycling over short and long temporal scales.
- Disturbance affects the life history and demographic parameters of species at fine spatial scales and creates a mosaic of patches at large spatial scales, which together influence the dispersal of individuals among patches (i.e., the degree of connectedness) in a species-specific fashion. Such a cross-scale perspective provides a spatially explicit metacommunity framework for understanding the assembly of species in disturbance-mediated environments.
- Differences in biodiversity affect ecosystem processes through species complementarity, organismal traits, and trophic interactions. These effects are mediated by scale and ultimately determine the resistance and resilience of ecosystems to disturbance.

- The effects of multiple disturbances on riparian and stream communities have complex spatial and temporal linkages. Life histories of species that connect freshwater and marine communities with those in headwater tributaries and riparian forests provide pathways for pulsed flows of energy and materials.
- Anthropogenic disturbance facilitates invasions by introduced tree species, sometimes culminating in the emergence of new forest communities dominated by introduced taxa. The development of these new emerging forests does not necessarily result in the loss of native species or a reduction in species richness.
- In mature forests not subject to intense anthropogenic degradation, introduced species can occur sporadically as rare species in hurricane-induced gaps, but these populations rapidly decrease in numbers after canopy closure.
- The recognition and study of emerging new forests is important for developing an ecological understanding of how organisms respond to anthropogenic disturbances, including global climate change.
- Forecasting environmental change requires the integration of biophysical and social science perspectives. We outline an approach for developing an integrated social-ecological system for the Luquillo Experimental Forest of Puerto Rico.

Introduction

A leitmotif of research in the Luquillo Mountains is that a deep understanding of the spatial and temporal dynamics of a tropical system is predicated on consideration of the effects of disturbance and associated succession at the levels of populations, communities, and biogeochemical processes. This focus is useful because patterns of biotic change represent integrators of a disturbance regime. In addition, successional theory provides a framework within which to interpret the temporal dynamics of ecosystems in disturbance-mediated environments. Moreover, biotic responses and disturbances of the physical environment have reciprocal influences with both positive and negative feedback. Consequently, the rate and pattern of biotic change will influence and to some degree control future disturbances. Studying disturbance without understanding biotic feedbacks is useful only when the disturbance is independent of biotic influences (e.g., some earthquakes or volcanic events).

The effects of hurricanes, landslides, agricultural clearings, river flooding, and most other disturbances in the Luquillo Mountains, as well as in most other biotic systems, are influenced by human activities, the landscape configuration of biotic and abiotic characteristics, and the stage of successional development. For example, the effects from any hurricane are related to the stage of forest recovery from previous hurricanes, as well as to the hurricane's wind speed, directionality, and rate of movement across the terrain. Landslides are most frequent on slopes destabilized by roads and in early or late stages of recovery from previous landslides. Intermediate

stages of vegetative succession on landslides have not developed tall trees and presumably unstable aboveground biomass, and instead they stabilize slopes through root growth and the interception of rain. Forest regrowth on abandoned pastures is a function of interactions between agricultural weeds and native woody species, as well as between nonnative and native seed dispersers. The natural flooding of streams and rivers can be exacerbated by landslides or other erosional processes or reduced by stable, well-vegetated banks. Thus, disturbance initiates succession, which in turn mediates changes associated with future disturbances. Similar feedback and complexity characterize drought effects on riparian forests. These trees decrease water loss by dropping leaves that provide energy subsidies to stream detritivores. Such leaf loss results in pulses of increased sunlight and nutrients (leaching from leaves) that stimulate the growth of periphyton and populations of aquatic grazers.

Despite considerable effort over more than a century, we cannot predict how particular communities will change over time (Walker and del Moral 2003). This inability is not surprising, considering the diverse responses of many interacting organisms to the frequency, intensity, and extent of multiple interacting disturbance types. However, both intellectual and societal motivations compel us to forecast rates and trajectories of successional change.

Paradigm Shifts

Until the 1950s, the dominant view of succession was that species change was largely predictable, with convergence to a stable climax condition after any of a number of initial disturbances (Odum 1969). An opposing view that gained credence in the following decades espoused an unpredictable outcome based on individualistic interactions of species subjected to a constantly changing disturbance regime (Drury and Nisbet 1973). An uneasy combination of these two approaches currently dominates successional theory (Glenn-Lewin et al. 1992). Although functional attributes of some successional sequences are predictable, forecasts of complete successional trajectories remain elusive (Walker and del Moral 2003), in part because of conditions generated by global change.

Ecological research in the Luquillo Mountains is poised to develop a comprehensive understanding of the spatial and temporal dynamics of populations, communities, and nutrients via an integration of succession and disturbance from both theoretical and empirical perspectives, including applications to critical issues in management. Diverse personnel with multiple perspectives using complementary approaches, a long history of collaboration, and a varied physical setting with a well-documented history of land uses are particular strengths of the Long-Term Ecological Research Program in the Luquillo Mountains of Puerto Rico. For example, the responses of soil nutrients, decomposers, autotrophs, herbivores, and carnivores all have been documented at 1- and 5-year intervals following Hurricane Hugo (Walker et al. 1991; Walker et al. 1996a). The unique, decades-long research history in the Luquillo Mountains provides long-term data sets, chronosequences for successional studies, and a legacy of comprehensive experiments in ecology.

The remarkable physical setting of the Luquillo Mountains provides excellent opportunities for research on the spatial and temporal dynamics that are affected by disturbance and succession. First, the presence of many ecological gradients (e.g., urban to rural, high to low elevation, wet to dry forests, high to low disturbance intensity, terrestrial to aquatic) encourages experiments across distinctly different environments and facilitates robust generalizations. Second, the Luquillo Mountains mark the high-precipitation and high-temperature endpoints for the 26 sites included in the U.S. Long-Term Ecological Research (LTER) Network, thereby providing opportunities for cross-site comparisons with respect to even more expansive ecological gradients. Third, the numerous mountains within Puerto Rico and the location of Puerto Rico within the island-rich Caribbean present the potential to replicate mountains or even islands, thereby providing strong and expansive inference for ecological conclusions. Fourth, multiple disturbance types frequently interact and have a significant effect on ecological patterns and processes in the Luquillo Mountains. Fifth, the wide range of disturbance severities that initiate both primary and secondary succession represents a point of departure for testing different successional hypotheses and paradigms.

Succession—Looking to the Future

Research in the Luquillo Mountains is well suited to address several unresolved issues about succession within a broader context of disturbance. Some of these involve large spatial (landscape or larger) or temporal (decadal data sets) scales. Measurements across climatic, elevational, disturbance, or fertility gradients provide strong tests of ecological theory. Interactions between disturbance and succession, especially the effects of multiple disturbances, provide opportunities for understanding the mechanistic bases of complex biotic systems. The role of particular taxa during succession and the influence of taxa on ecosystem processes are species-based issues that continue to be explored in the Luquillo Mountains, particularly the roles of microbes, plants, and animals. Comparing effects on nutrients, as well as responses of populations and communities, offers a powerful way to address the relative importance of each with respect to resistance and resilience, providing a science-based understanding of restoration that can link science to management and policy.

Extensive Environmental Gradients

Many ecologists generally focus research at a small spatial scale (i.e., plots), with environmental measurements recorded over the course of a typical grant period (3 to 6 years). However, the LTER Program in the Luquillo Mountains was designed to address larger spatial scales and longer temporal dynamics. Nonetheless, more emphasis in the future on even larger spatial scales and the incorporation of additional types of long-term measurements that are synoptic in nature will enhance our understanding of landscape-level interactions between disturbance and succession.

Gradient analysis is an underused tool that can clarify the mechanistic bases of the distribution and abundance of species, their activities, and their succession. Climatic gradients of the Luquillo Mountains (e.g., temperature and precipitation change from low to high elevation) have been used recently in terms of static community descriptions and some soil processes. Extending manipulative experiments along such gradients (and incorporating fertility and disturbance) will clarify the successional responses to disturbance at landscape levels. For example, much is known about landslide succession in the Luquillo Mountains, but the overall importance of landslides compared to that of background treefall gaps along an elevational gradient with respect to carbon cycling or forest succession is unknown. Manipulations of fertility along steep fertility and elevational gradients might illustrate the successional responses of vegetation to variations in climate, disturbance, and soil fertility (Walker et al. 1996b). Response variables could include the performance of existing plant species and transplanted individuals of the same or different species. The one relevant experiment in the Luquillo Mountains (Fetcher et al. 1999) assessed the effects of wind on seedlings at multiple elevations. Eventually, comparisons of replicated gradients will offer even more comprehensive insights (e.g., how species responses to a hurricane vary across elevation among several watersheds or mountain ranges).

Successional Trajectories and Multiple Disturbances

The complex disturbance regime of the Luquillo Experimental Forest (LEF) provides opportunities for transformative research. Specifically, successional trajectories after a disturbance are modified by subsequent episodic disturbances. The effects of these repeated disturbances on succession, soil stability, canopy birds, soil microbiota, and many other forest and associated aquatic components are unknown. For example, are effects of multiple disturbances additive, and if not, are the synergisms positive or negative? Do population-level or community-level responses cascade in a particular order that represents successional replacements? In this regard, landslide succession is altered by selective damage to recovering vegetation by hurricanes. During Hurricane Hugo, many large fallen trees and branches accumulated in stream channels. This woody material formed debris dams that retained leaf litter and sediment washed into the streams during the storm. These debris dams formed because many older trees had grown along the riparian zone during the more than 50 years since the previous hurricane. At the time of Hurricane Georges, the same stream channels were not filled with fallen trees and sediments, and leaf litter was not retained in headwater channels, because few trees had regrown in the riparian zone during the 9-year interval between Hurricanes Hugo and Georges. Consequently, wood was not present to slow stream discharge, and floods had greater effects in removing bottom-dwelling-organisms (A. P. Covich, personal observation). Furthermore, unlike the situation after Hurricane Georges, streams that flooded during Hurricane Hugo experienced a drought in subsequent months. Comparisons of various interactions between disturbances of the same (e.g., hurricane to hurricane) or different (e.g., road construction to landslide) types will deepen the understanding of forest dynamics and the interplay of disturbance history and succession (see Willig and Walker 1999).

The Role of Species

The roles of particular species or functional groups of species provide potential avenues for developing useful insights. Experimental manipulations of keystone species might reveal mechanisms whereby the biota influences successional trajectories. Palms, *Cecropia*, tree ferns, ground ferns, snails, walking sticks, crabs, and rats are candidates for more extensive research regarding their responses to disturbance and roles during succession. Do these species inhibit or facilitate species change, and is it done directly or through their interactions with other species? How do the effects of these species on nutrient turnover and biomass accumulation affect the mode, tempo, or direction of succession? Additions or removals of key species might provide experimental corroboration of their importance to succession. Alternatively, key functions might not be associated uniquely with any one species. Rather, ecosystem attributes such as soil stability, soil aeration, or rates of nutrient turnover might be the direct drivers of regeneration. For example, differences in soil oxygen levels might be the most critical constraint on responses to disturbance and successional dynamics. If assembly rules exist in the Luquillo Mountains, they likely revolve around the establishment of processes that are critical to succession. The LTER Program in the Luquillo Mountains is well prepared to provide comprehensive answers to such questions. For example, Zimmerman et al. (1996) identified six types of response to hurricanes exhibited by nutrients, plants, and animals (see figure 2-3). This exciting discovery—that a limited set of curves summarizes responses to a disturbance—provides a fruitful avenue for further investigation, particularly when placed in a successional context. Do organisms with similar functional roles respond in similar ways to similar disturbances, thereby constituting response groups during succession? How do the various characteristics of disturbance (e.g., intensity, extent) modify responses, particularly aspects of resistance and resilience? Finally, what are the evolutionary forces that select for adaptive traits of these “response groups” in rain forest ecosystems?

Disturbance, Succession, and Society

Research in the Luquillo Mountains must continue to address societal needs. Predictive modeling of the responses of populations, communities, and biogeochemical fluxes and pools to increased water extraction, increased roadway construction, the erosion of riparian zones, and changes in the distribution of precipitation or increased hurricane frequency depend on knowledge of the successional responses to disturbance. Forest restoration and management directly benefit from realistic goals cast in a successional context. For example, can any successional stages be skipped and time saved in restoring forests derived from abandoned agricultural land? Are the processes the same for roadside or riparian restoration at low and high elevations? Are endpoint goals realistic, given the constraints of soils or vegetation?

Ecological Vignettes

We present here a number of ecological vignettes to characterize the depth and breadth of integrated or emerging ecological research in the Luquillo Mountains.

These vignettes were selected to represent a range of products from recent syntheses of the LTER Program in Puerto Rico. In all cases, they arise from the study of disturbance and succession, and they promise to advance ecological theory from basic and applied perspectives. Although speculative in places, these vignettes point to promising areas of future research that will advance the site-specific understanding of ecological patterns and processes and catalyze the development of theory associated with them.

First, we describe insights from a long-term experiment to decouple the influence of the immediate effects of a hurricane (increased temperature and decreased litter moisture versus the simultaneous addition of biomass from branch and leaf fall) on the subsequent structure and functioning of tabonuco forest. Second, we consider the advantages of employing a metacommunity perspective for understanding responses of the biota to disturbance and to environmental gradients in general. Third, we explore ways in which research in the Luquillo Mountains can provide a deeper understanding of the linkage between biotic structure and ecosystem functioning. Fourth, we reveal how food webs connect terrestrial and aquatic compartments of tropical forest ecosystems in dynamic ways following hurricane disturbances, with implications for integrated ecosystem management. Fifth, we discuss the consequences of invasions of introduced species in the structure and functioning of Puerto Rican ecosystems. Sixth, we advance the view that distinctively new forests with uncompromised functionality can arise in tropical landscapes after extensive historical deforestation. Seventh, we explore the benefits of integrating social and natural science perspectives in environmental models that forecast spatial and temporal dynamics of tropical ecosystems.

Disentangling Mechanisms of Ecosystem Response to Disturbance

Tropical forests are exposed to a wide range of disturbances that differ in spatial extent, severity, intensity, and frequency (Boose et al. 1994; Foster and Boose 1995). Considerable research in the Luquillo Mountains has documented the effects of different disturbances on plants, animals, and ecosystem processes over short (Frangi and Lugo 1991; Walker et al. 1991; Scatena et al. 1993; Silver and Vogt 1993; Wunderle 1995; Zimmerman et al. 1995a; Everham and Brokaw 1996; Ostertag et al. 2005) and intermediate (Crow 1980; Weaver 1986, 2002; Gregory and Sabat 1996; Walker et al. 1996a, 1996b) time scales. The documentation of changes in organismal, population, community, and ecosystem characteristics following disturbance has provided a rich context in which to explore fundamental mechanisms controlling the dynamics during the recovery of strongly interconnected biotic systems. Nonetheless, the many simultaneous and interacting attributes of disturbance make it difficult to distinguish proximate and ultimate causes.

The mechanisms responsible for ecosystem responses to disturbance are complex because they differ according to the spatial and temporal scales of the analysis. Large-scale disturbances (e.g., hurricanes) create a spatial mosaic of effects across a landscape, with the initial effect and subsequent response to disturbance being affected by the topography, aspect, and initial vegetation structure (Wunderle et al. 1992; Boose et al. 1994; Bellingham et al. 1995, 1996; Everham

and Brokaw 1996; Lundquist et al. 2011). This complexity is particularly evident in highly dissected environments with steep slopes, such as the Luquillo Mountains. Secondary succession is characterized by changes in resource availability, which in turn are linked to population and community dynamics, creating a complexity of interacting causes and effects.

In order to disentangle the complex and interacting factors associated with responses to disturbance, we present a conceptual model that links direct and indirect effects of disturbance with key physical, biological, and chemical characteristics of the environment. We emphasize the rapid mechanistic response to disturbance by the microbial community because it is responsible for most of the processing of organic matter in ecosystems—primarily through decomposition—and for controlling the supply of key resources (nutrients) to primary producers (Lodge 1996). Microbes also play important long-term roles in nutrient retention and loss from ecosystems (Lodge and McDowell 1991; Lodge 1993; Lodge et al. 1994; Zimmerman et al. 1995b; Miller and Lodge 1997; Silver et al. 2001). They contribute to the composition of the soil atmosphere shared with roots and other organisms and are dominantly responsible for the production of three globally important greenhouse gases (carbon dioxide [CO₂], nitrous oxide [N₂O], and methane [CH₄]) that are produced in great quantity in tropical forests (Keller et al. 1986; Silver et al. 1999, 2005a, 2005b; Teh et al. 2005). Although we chose microbes as a concise and illustrative example, other organisms or processes could be substituted within this framework because many other types of organismal processes are interconnected in strong and complex ways.

The framework starts with three key effects of disturbance: the reduction of structural complexity, increased plant mortality, and transfers of organic material to the forest floor. Although these are not the only changes associated with large-scale disturbances in a tropical forest, they are arguably the most important in terms of rapid and sustained environmental changes to the ecosystem. These three attributes of disturbance alter physical (e.g., moisture and temperature) and chemical (e.g., availability of carbon, nutrients, and toxic elements and compounds) conditions, as well as biological processes (e.g., nutrient uptake, photosynthesis, and herbivory) that eventually feed back to the microbial community composition and metabolic activity.

Reduction of Structural Complexity

One of the primary effects of large-scale disturbances such as hurricanes is the reduction of structural complexity. Severe hurricanes relocate the canopy to the soil surface, or at least to within a few meters of the soil surface (Brokaw and Grear 1991; Lodge et al. 1991; Wunderle et al. 1992; Wunderle 1995). Several associated physical changes occur as a consequence of this canopy disturbance. Decreased canopy cover results in increased light levels at or near the soil surface (Fernández and Fetcher 1991; Bellingham et al. 1996) and a corresponding increase in temperature. In terrestrial habitats, greater temperatures and increased air circulation at the ground surface lead to increased evaporation from litter and soils, and this can decrease litter and soil moisture (Lodge 1996; Richardson et al. 2010), although

reduced transpiration can offset soil moisture losses (Silver and Vogt 1993; Richardson et al. 2010) (figure 8-1). Several of these physical changes can affect microbial activity, such as decomposition (figure 8-1). All else being equal, higher temperatures generally stimulate biochemical and physiological activity of microbes, resulting in higher rates of decomposition and nutrient mineralization (Lloyd and Taylor 1994; Wang et al. 2002). Decreased moisture could provide either a positive or negative feedback to microbial processes (Lodge et al. 1994).

In dry microsites, a decrease in litter and soil moisture is likely to result in plant and microbial moisture stress, slowing the rate of decomposition and associated nutrient mineralization (Miller and Lodge 1997). Basidiomycete fungi, the microbes

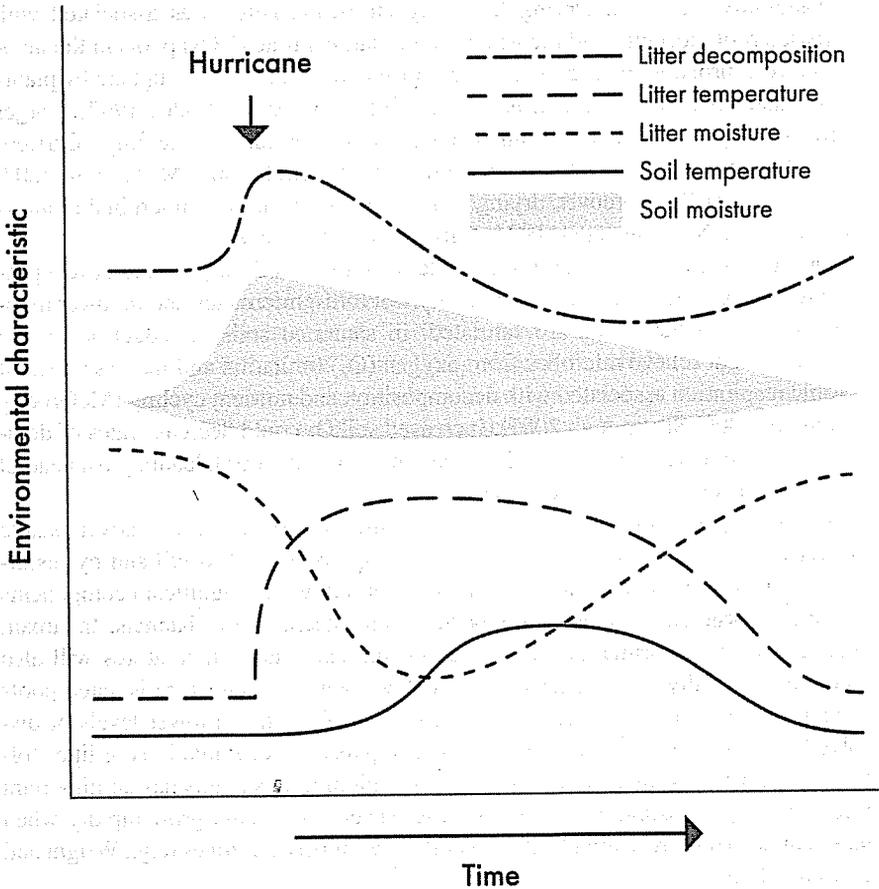


Figure 8.1 Predicted effects of hurricane disturbance on forest floor and soil environments and on rates of litter decomposition. Soil moisture is represented as a probability cloud, as it could either increase initially because of decreased transpiration losses or decrease because of increased temperature and evaporation interacting with drought. In contrast, litter moisture should decrease because of higher temperature and evaporation, especially as the depth of storm debris decreases over time because of higher initial rates of decomposition and reduced litterfall inputs.

primarily responsible for delignification through white-rot, are especially susceptible to drying in the litter layer following disturbance (Lodge and Cantrell 1995; Lodge 1996; Miller and Lodge 1997). Basidiomycete litter decomposer fungi use rootlike structures (rhizomorphs, cords, and strands) to translocate nutrients among resource bases (Lodge 1996). The abilities of basidiomycetes to translocate nutrients and degrade lignin increase the overall rate of litter decomposition (Lodge et al. 2008). Furthermore, the products of degradation by basidiomycetes differ from those of other microbial groups, which affects soil fertility (Hintikka 1970). Thus, although increased temperature can stimulate decomposition, if higher temperatures are coupled with lower moisture in the litter layer, decomposition rates might decline and decomposition products might be altered via the differential inhibition of basidiomycete fungi. Drying following Hurricane Hugo was associated with increased root mortality and the generation of large nitrate (NO_3) pools in the tabonuco forest, probably owing to increased nitrification and reduced uptake by plants (Silver and Vogt 1993; Zimmerman et al. 1995b; Miller and Lodge 1997). Larger nitrogen (N) pools could also diminish the activity of basidiomycete fungi (Carriero et al. 2000; Berg et al. 2001; Lodge 2001; Schröter et al. 2003; Mack et al. 2004; Lodge et al. 2008). Moreover, drying can reduce the capacity of microbial biomass to immobilize N (Lodge et al. 1994; Miller and Lodge 1997).

Drying associated with increased soil temperatures or drought could have a positive feedback on microbial activity in very wet forest microsites and in lower topographic zones where soils are saturated. In saturated soils, a reduction in soil moisture might relieve microbes from oxygen (O_2) limitation and increase rates of aerobic respiration associated with decomposition and nutrient cycling (McGroddy and Silver 2000; Silver et al. 2001). Increased soil O_2 could decrease rates of denitrification and increase rates of CH_4 oxidation (Teh et al. 2005), leading to a general decline in the emissions of greenhouse gases.

Water temperatures and concentrations of dissolved oxygen are relatively stable in headwater streams even after the forest canopy is opened to full sun by disturbances (hurricane and landslides) if groundwater inflows are significant components of the discharge and turbulent flow occurs along steep, rocky channels. In stream channels receiving primarily surface runoff, diurnal water temperatures will also increase, especially during periods of low flow such as droughts. In isolated pools during low-flow periods of drought, microbial respiration can lower levels of dissolved oxygen following pulses of leaf-litter inputs and accumulations of litter following windstorms. In general, microbial conditioning in streams has an important role in litter processing, especially because bacteria and fungi grow rapidly when pulses of nutrients are available after disturbances of riparian zones (e.g., Wright and Covich 2005b).

Increased Plant Mortality

Hurricanes generally increase plant mortality through both direct and indirect effects (Walker et al. 1991; Bellingham et al. 1995; Zimmerman et al. 1995a; Everham and Brokaw 1996). In addition to causing substantial structural changes, plant mortality affects soil moisture and nutrient dynamics. The reduction of live plant

biomass in turn decreases the rate of water loss via transpiration and, if high rainfall continues (which was not the case after Hurricane Hugo), increases soil moisture (Silver and Vogt 1993; Richardson et al. 2010) and runoff to streams. Decreased plant activity also reduces nutrient uptake from soils, thereby increasing the standing stocks of nutrients adsorbed on soil surfaces or dissolved in soil solution (Steudler et al. 1991). As with drying, increased soil moisture could either favor or inhibit aerobic respiration, depending on the redox potential of the soil. Increased soil moisture could lead to the soil O_2 limitation of plant and microbial processes, slowing decomposition and increasing rates of N_2O and CH_4 emissions (Silver et al. 1999, 2001; Teh et al. 2005). Greater nutrient availability is likely to enhance microbial activity, and it can augment the growth rates of surviving plants (Scatena et al. 1996) or increase nutrient losses via denitrification or leaching (Steudler et al. 1991; McDowell et al. 1996).

Transfers of Organic Matter to the Forest Floor

Hurricane winds defoliate trees, break fine branches, sever roots, and snap or topple stems, resulting in large inputs of fresh organic material to the forest floor (Lodge et al. 1991; Silver et al. 1996; Ostertag et al. 2003) and to stream channels (Crowl et al. 2001). These inputs of organic matter initially insulate soils from evaporative water loss, thereby increasing litter and soil moisture and decreasing soil temperature (figure 8-1; Richardson et al. 2010). However, litter mass decreases during subsequent decomposition, and its insulating effect is thus reduced. In combination with the higher temperatures that result from an open canopy, the remaining litter (and sometimes soil) layer can become dry in these gaps (figure 8-1). We conducted a factorial experiment in order to disentangle the confounded effects of canopy opening and debris deposition on litter and soil processes (figure 8-2). Litter moisture decreased in plots that were trimmed to simulate hurricane damage, unlike in control plots that were neither cut nor subject to debris addition (figure 8-3), resulting in slower rates of decomposition in the upper, green leaf layer (Lodge, unpublished data). Increased soil temperature and moisture affected microbial communities and, together with additions of carbon [C] and nutrients in organic matter, increased soil microbial activity significantly (Silver, unpublished data).

Control of Carbon and Nitrogen Fluxes following Disturbances

Canopy disturbance results in a large pulse of carbon and nitrogen to the forest floor and soil and, with time, to streams. The pulse of carbon and nitrogen from fine debris associated with Hurricane Hugo in tabonuco forest (Lodge et al. 1991) was more than the cumulative total for a year without hurricane disturbance, but the pulse was slightly less than yearly litterfall totals in various forest types after Hurricane Georges (Ostertag et al. 2003). Although the decomposition of this litter pulse was rapid, with the forest floor returning to prehurricane standing stocks of litter within 2 to 10 months after Hurricane Georges, the rate of mass loss might not have been elevated above normal background levels (Ostertag et al. 2003). The addition of green leaves having higher nutrient concentrations than

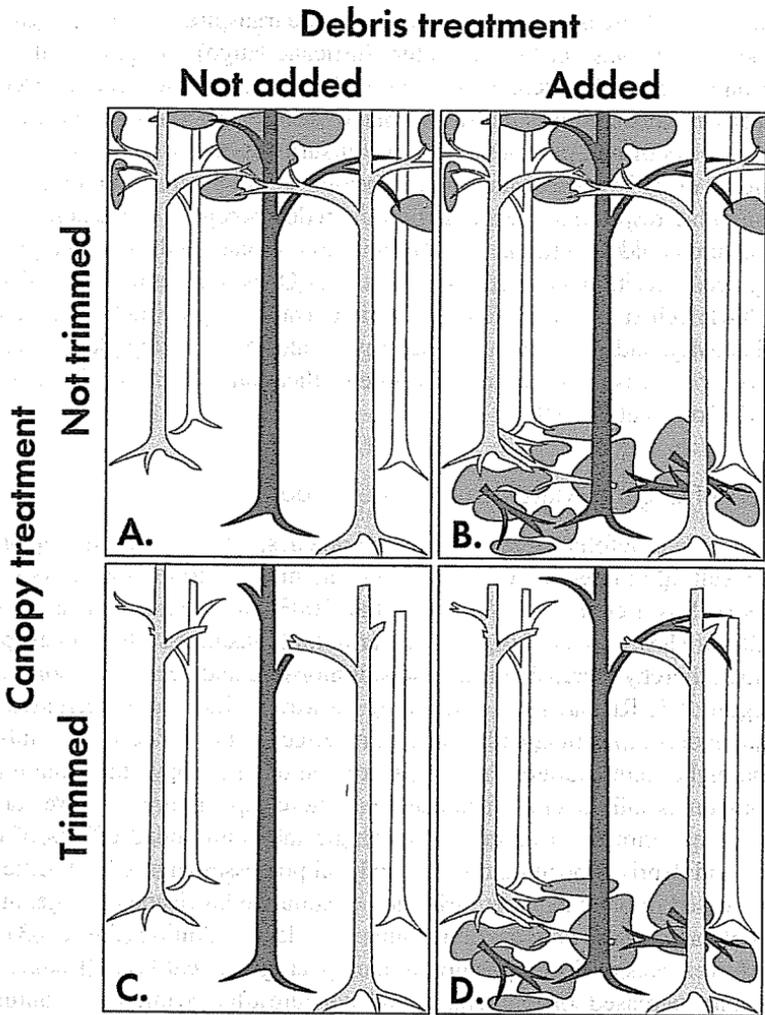


Figure 8.2 The canopy-trimming experiment employed a factorial design (canopy vs. debris treatments) to disentangle the interacting effects of increased inputs of organic matter associated with hurricane windfall (i.e., debris addition) and the effects of solar insolation and warming associated with canopy removal (canopy trimming). (A) Control (i.e., not trimmed and no debris addition). (B) Debris addition without canopy trimming. (C) Canopy trimming without debris addition, (D) Canopy trimming with debris addition.

normally senesced leaves (Lodge et al. 1991), together with the large mass of fallen litter, which helped retain moisture on the forest floor, counteracted greater evaporative losses resulting from canopy opening, thus maintaining high rates of decomposition. Consequently, rates of decomposition were high following both Hurricanes Hugo and Georges, despite the possible negative effects of high concentrations of secondary compounds (e.g., tannins, phenolics, or alkaloids) in fresh leaves of some species in certain forest types that are toxic to microbes and

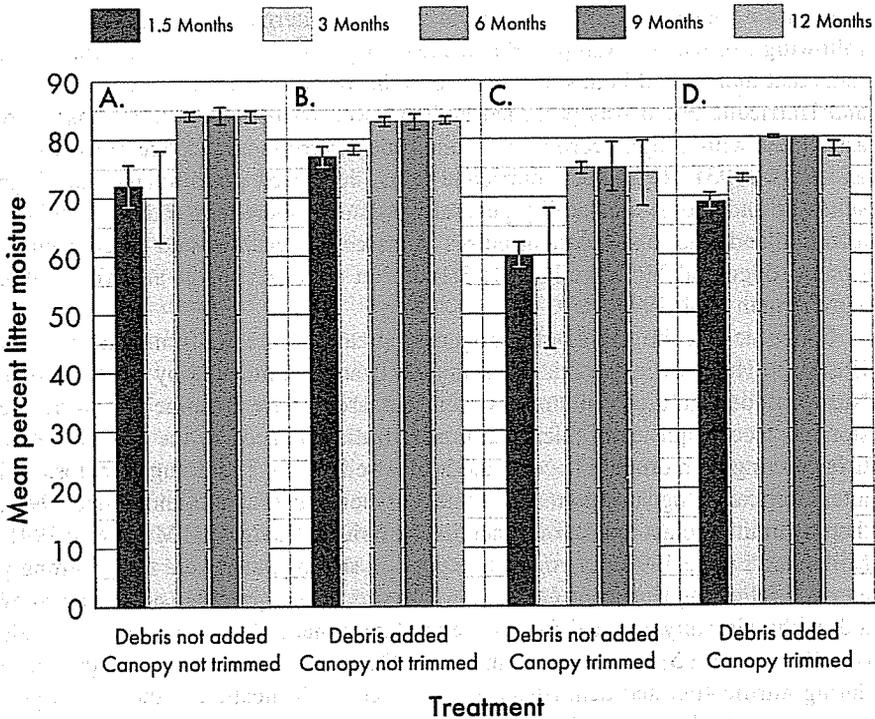


Figure 8.3 Changes in the percentage of litter moisture over 1 year in a cohort of senesced leaves from the canopy-trimming experiment (see figure 8-2) for each of four combinations of levels of treatment: (A) control (i.e., not trimmed and no debris addition), (B) debris addition without canopy trimming, (C) canopy trimming without debris addition, and (D) canopy trimming with debris addition. Data are from a weighed layer of freshly fallen leaves sandwiched between 1-mm-mesh screens in litter baskets and placed directly on the forest floor. Treatments with debris addition were capped with fresh green leaves (mass equivalent to the mean input of fine litter during Hurricane Hugo). Debris addition increased the litter moisture of the cohort below and buffered the drying effect of canopy trimming.

can inhibit decomposition (Silver, unpublished data). This maintenance of high posthurricane decomposition rates held true despite different characteristics of the storms and poststorm environments, and it prevented any substantial accumulation of soil organic carbon when averaged over the landscape (Silver et al. 1996; Ostertag et al. 2005). Although those results conflict with model predictions by Sanford et al. (1991) that coarse woody debris would increase tree productivity in tabonuco forest by increasing phosphorus availability associated with increased soil carbon, Lodge (unpublished data) and Zalamea et al. (2007) found higher total and extractable soil carbon, respectively, under decaying logs than in carefully paired samples taken near logs. Zalamea et al. (2007) found that sodium hydroxide (NaOH)-extractable C and water-extractable organic matter were higher in the soil influenced by 15-year-old logs. Such pulses can create hot spots that are readily exploited by plants (Lodge et al. 1994). The fate of nitrogen was

less certain, but it might be coupled to weather patterns preceding, during, and following storms. For example, Hurricane Georges was preceded and followed by rains that maintained high soil moisture in the warm, open canopy environment, and Hurricane Hugo was preceded and followed by drier conditions that were associated with a high necromass of fine roots (Parrotta and Lodge 1991; Silver and Vogt 1993). Regardless, hurricane rains, decreased plant uptake, and high substrate and energy availability generally stimulate short-term rates of N mineralization and lead to subsequent pulses in losses via leaching and gaseous emissions (Lodge and McDowell 1991; Steudler et al. 1991; Silver and Vogt 1993; Zimmerman et al. 1995b).

Consequently, the export of nitrogen in streams decreased immediately after Hurricane Hugo owing to microbial immobilization stimulated by labile carbon. Nitrogen concentrations in streams then increased above baseline following the storm as a consequence of microbial mineralization induced by the pulse of labile C interacting with drought (Lodge and McDowell 1991). The droughts before and after Hurricane Hugo caused massive fine root mortality (Parrotta and Lodge 1991), thereby limiting plant uptake of mineralized nutrients (Lodge and McDowell 1991; Miller and Lodge 1997). In contrast, exports in stream water were not as strongly elevated following Hurricane Georges, which was neither preceded nor followed by a drought. Globally, tropical forests are the largest natural source of nitrous oxide (Prather et al. 1995), a radiatively important N trace gas. Nitrous oxide is produced during nitrification and denitrification, although denitrification is thought to predominate under humid conditions in which soils experience periodic anaerobiosis and have sufficient labile C to fuel the process (Groffman and Tiedje 1989). Following Hurricane Hugo, nitrate accumulated in soils owing to high nitrification and low assimilation rates (Silver and Vogt 1993). The high nitrification probably resulted in nitrous oxide emissions; short-term anaerobic events stimulated by high biological activity during infrequent storms also could have resulted in considerable denitrification to nitrous oxide (Steudler et al. 1991). Research in the LEF and other tropical forests (Silver et al. 2001, 2005b) suggests that nitrogen also can be retained following disturbances via dissimilatory nitrate reduction to ammonium (DNRA). An anaerobic microbial process, DNRA rapidly reduces nitrate to ammonium, which can be assimilated easily by roots and soil microbes. DNRA can be limited, primarily by nitrate, in humid tropical forest soils, effectively competing with denitrification and contributing to nitrogen retention following disturbance events. The fate of nitrogen derived from pulsed hurricane inputs thus depends greatly on the soil moisture and soil oxygen regime following the disturbance.

In addition to controlling DNRA, soil microbes can play an important role in retaining nitrogen in the ecosystem via assimilatory processes. Nitrogen immobilization by soil microbial biomass increased 3 months after Hurricane Hugo and continued for about 5 years in tabonuco forest (Zimmerman et al. 1995b). Nutrient immobilization from the decay of woody debris from Hurricane Hugo might have contributed to slow canopy recovery, as plots in which hurricane debris was removed within a month of the disturbance recovered canopies more quickly than did those without such treatment (Zimmerman et al. 1995b). However, bole diameters increased more rapidly in the control than with the debris-removal treatment

after 4 years (Walker et al. 1996b). This is consistent with predictions by Sanford et al. (1991) based on expected increases in the availability of nutrients from the decomposed debris. Less structural modification of the forest characterized Hurricane Georges, partly because it had slower windspeeds, but also probably because trees had previously been pruned by Hurricane Hugo (chapter 5). As such, it is unclear whether the amount of N immobilized by soil microbes depends on the ratio of fine to woody debris, resulting from differences in hurricane windspeeds, or is a consequence of the conditions that characterized the response of the forest to earlier disturbance.

The rate of decay of surface litter and nutrient mineralization in fine litter is controlled largely by fungi and litter arthropods. Nonetheless, the manner in which a large pulse of storm debris affects fungal processes on the forest floor is unclear. The quality of storm-produced litter is different from that of litterfall that comprises senescent leaves, and storm-produced litter has greater concentrations of nutrients that normally would be translocated from the leaves before abscission (Lodge et al. 1991). In some cases, the mixing of green and senescent litter can inhibit litter decomposition, perhaps through the effects of phenolic compounds contained in the green leaves (but see Xu et al. 2004). Basidiomycete fungi that form rootlike structures (rhizomorphs, cords and hyphal strands) that allow them to translocate N, phosphorus (P), and other nutrients between old and new substrata are favored by greater litter depths but are often diminished by the dry conditions associated with litter in canopy openings (Lodge 1993; Miller and Lodge 1997; Lodge et al. 2008) (figure 8-3) and by higher nitrogen availability in such disturbed areas (Carriero et al. 2000; Berg et al. 2001; Lodge 2001; Schröter et al. 2003; Mack et al. 2004; Sjöbe et al. 2004).

Rates of tree growth were higher in tabonuco forest in the decade after a major hurricane than in subsequent decades (Briscoe and Wadsworth 1970; Weaver 2001; Uriarte et al. 2004), consistent with ecosystem model predictions (Sanford et al. 1991; Wang and Hall 2004). The extent to which this stimulatory effect is the result of decreased competition (thinning effect), increased nitrogen mineralization (Wang and Hall 2004), or increased P availability associated with organic and inorganic inputs (Sanford et al. 1991) and lower redox potential (Chacón et al. 2005) is unclear. Rapid recruitment of fast-growing, N-demanding species such as *Cecropia schreberiana* occurred after Hurricane Hugo (Guzmán-Grajales and Walker 1991; Scatena et al. 1996; Brokaw 1998) and might have played an important role in stemming the loss of N (Silver 1992; Walker 2000). However, recruitment of *C. schreberiana* was low following Hurricane Georges. If repeated disturbance depletes the soil seed bank of common secondary successional species, the role of these species in N retention will decline.

Mechanisms of Response: Directions for the Future

A long history of monitoring and observational studies in the Luquillo Mountains has provided a wealth of data detailing the severity of disturbance and documenting biotic and abiotic responses in a comprehensive manner. Nonetheless, the mechanistic basis of these responses is difficult to uncover because the major effects of

large-scale disturbances (reduced structural complexity, increased plant mortality, translocation of organic matter, and consequent changes in abiotic conditions) are confounded as "treatment effects" in an uncontrolled experiment or observational study. Thus, understanding the mechanistic basis of the observed severity of a hurricane and subsequent population, community, and ecosystem responses requires approaches capable of isolating or decoupling these effects.

Two such approaches that facilitate mechanistic understanding are experimental manipulations and mathematical modeling. Modeling has a long history in the Luquillo Mountains, whereas long-term experiments have been implemented only recently. In an attempt to disentangle the confounded effects of hurricanes, we initiated a long-term manipulative experiment that will guide further modeling of successional dynamics. The experiment involves two factors: trimming of the canopy and the transfer of litter and branches to the forest floor in quantities similar to those associated with Hurricane Hugo. These treatments were applied using a factorial design (figure 8-2), resulting in four types of experimental plots: (1) unmanipulated control (i.e., intact canopy with no litter added), (2) intact canopy with litter deposition, (3) trimmed canopy with no litter addition, and (4) trimmed canopy with litter deposition. A suite of microenvironmental, biotic, and edaphic factors and processes were measured prior to the treatment application and will be continued throughout the experimental period. In order to simulate the increased frequency of intense hurricanes that is predicted for the Caribbean region (Webster et al. 2005; Hopkinson et al. 2008), the treatments will be reapplied every 6 years. Changes in litter moisture in response to the four treatment combinations (figure 8-3) suggest that the addition of debris to the forest floor shields it from the drying effects of canopy opening. In relation to the processes discussed here, factorial and repeated-measures analyses of data from the canopy-trimming experiment will help to disentangle the confounded effects of disturbance on the fungal processes on the forest floor. They will allow us to carefully track rates of decomposition and nutrient immobilization in different litter cohorts and quantify the connectedness between litter cohorts via fungal organs for nutrient translocation with and without the associated canopy opening. We will also be able to determine whether increased rates of nutrient translocation are associated with increased rates of fine litter decomposition. The repetition of canopy trimming at regular intervals should help elucidate the latter point. By repeatedly disturbing the system at relatively close intervals, the canopy-trimming experiment will also illuminate seedling dynamics and the capacity of seedling recruitment to absorb excess nitrogen released as a consequence of disturbances.

Synopsis

Our framework of responses to disturbance highlights the role of a few key physical changes associated with hurricane disturbances as potential controls on microbial activity. Changes in temperature clearly play an important role, even in a tropical forest that experiences little day-to-day variation in temperature. Temperature likely is responsible, either directly or indirectly, for the large decrease in litterfall production from low to high elevations in the LEF (Weaver and Murphy 1990), although

the mechanisms are unclear (Silver 1998). Temperature changes with elevation also might contribute to patterns in soil respiration along the elevational gradient (McGroddy and Silver 2000). Patterns of soil moisture likely have strong influences on microbial processes in tropical forests. Soil water stress (e.g., rapid wetting and drying cycles) leads to the lysing of microbial cells and the release of nutrients and organic compounds to the soil (Lodge et al. 1994). High soil moisture leads to conditions in which O_2 consumption exceeds diffusive transport (Silver et al. 1999). The direct effects of soil moisture and the indirect effects of soil temperature on soil moisture are difficult to predict at an ecosystem scale because of the many disturbance-related changes that feed back on microclimatic conditions. The canopy-trimming experiment is designed to explore how single and repeated disturbances affect these microenvironmental, biotic, and edaphic dynamics. The data on moisture and temperature, combined with detailed studies of litter quantity and quality, decomposition, and microbial identity and activity, will allow us to disentangle the wide range of factors that affect detrital processing and C and N dynamics following hurricanes.

Metacommunity Perspectives on Environmental Gradients and Disturbance

Spatial variation and heterogeneity in the Luquillo Mountains, with attendant variation in ecological characteristics (chapter 3), provides a rich template by which to address contemporary questions concerning the organization of biotic communities. In particular, hurricane-induced heterogeneity in environmental characteristics at the local scale, along with elevation-induced variation in environmental characteristics at the landscape scale, can determine key aspects of biodiversity and species composition. A consideration of metacommunity theory in this context promises significant insights regarding answers to the recurrent question of what determines the nature of ecological communities.

A community comprises a suite of species at a particular site, whereas the set of all communities that occur in a particular area represents a metacommunity within the landscape (Leibold and Mikkelsen 2002). Effectively, the distinction between community and metacommunity reflects a change in focal scale and extent (Scheiner et al. 2000). Within a metacommunity, constituent species populations variously link the site-specific communities to each other through different degrees of dispersal. An incidence matrix that details the presence or absence of species, or their abundances, for all communities that collectively occur in an area is a convenient visualization of a metacommunity. Importantly, the distinction between community and metacommunity frequently is guided by operational expedience, methodological constraints, or insights based on considerations of natural history. Nonetheless, the concept has considerable heuristic value. It facilitates an assessment of the manner in which underlying variation in species composition within a landscape changes over time or in response to disturbance. From a landscape perspective, the metacommunity concept is useful in understanding why different species inhabit different sites and why different sites contain different suites of species. Via two examples—one at a relatively large extent, defined by the elevational gradient in the

Luquillo Mountains (tabonuco, palo colorado, and elfin forests), and one at a relatively small extent, defined by the Luquillo Forest Dynamics Plot (tabonuco forest)—we begin to explore the utility of the metacommunity approach in clarifying spatial and temporal dynamics.

Elevational Gradients of Biodiversity

In the Luquillo Mountains, foresters and ecologists have long recognized geographic patterns of species composition, but the degree to which they are related to environmental gradients and the extent to which these patterns change as a result of disturbance are less understood (see Weaver 1991; Lugo 2005). At higher elevations in the Luquillo Mountains, the climate becomes cloudier, wetter (2,500 to 4,500 mm rainfall per year), and cooler (25°C to 18.5°C), and forests become shorter, denser, and less productive (Waide et al. 1998). Four forest types have been historically recognized within this elevational gradient: tabonuco forest, palo colorado forest, elfin woodland, and sierra palm forest (Wadsworth 1951; Weaver 1994). Tabonuco forest, palo colorado forest, and elfin woodland forest are thought to form a geographic sequence from low to high elevations, with sierra palm forest occurring throughout all elevations, particularly on poorly drained slopes. Recently, these forests were quantitatively described and classified and related to environmental controls such as climate, substrate, and topographic position (Gould et al. 2006), providing a useful classification of vegetation and the mechanisms underlying its spatial distribution. However, sampling sites were selected based on a priori conceptions of compositional differences among forest types, and locations considered to occupy ecotones and forest edges were avoided (contrast with Barone et al. 2008). Consequently, the data and subsequent analyses do not provide incontrovertible evidence that each of these four forest types is a distinct entity that reflects geographic discontinuities in species composition.

A metacommunity perspective (Holyoak et al. 2005) can shed light on this topic, as it inherently considers the ways in which variation among sites in species composition can result in particular geographic patterns. Metacommunities can be characterized by three metrics: coherence, species turnover, and boundary clumping. *Coherence* is the degree to which variation among sites (i.e., communities) can be represented by a single axis of variation, and potentially by a single underlying environmental gradient to which the biota responds. *Species turnover* reflects the extent of species replacement along this continuum, and *boundary clumping* reflects the degree to which the edges of species ranges are distributed in a nonrandom fashion, thereby suggesting the possibility of zonation. Quantifying all three measures (figure 8-4) allows the organization of the biota within a landscape to be classified as a (1) random, (2) checkerboard, (3) nested, (4) Clementsian, (5) Gleasonian, or (6) evenly spaced metacommunity (Leibold and Mikkelsen 2002; Presley et al. 2010). Such analyses should provide useful insights into changes along geographic gradients and complement recent expositions of the structure and composition of forests in Puerto Rico (Gould et al. 2006).

A recent study addressed the metacommunity structure of trees along two transects in the Luquillo Mountains (paralleling the Río Mameyes and Quebrada

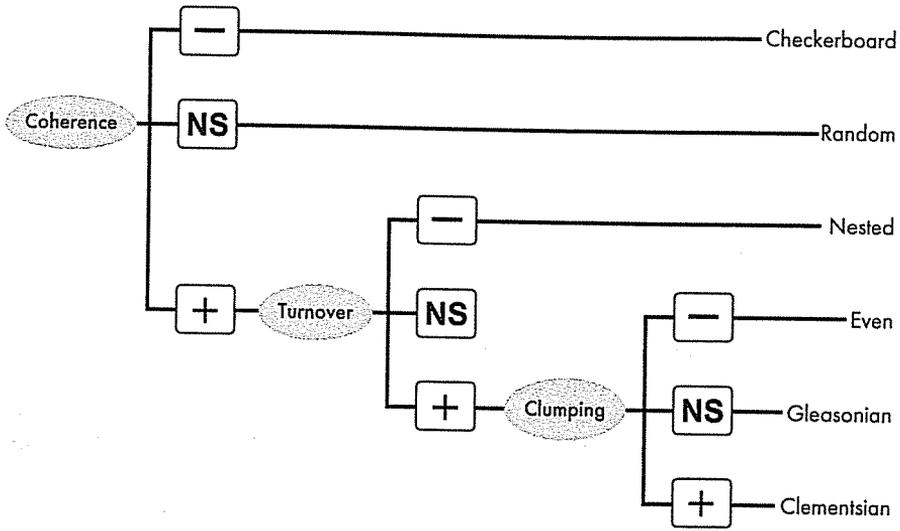


Figure 8.4 Hierarchical assessment of patterns in the distribution of species (i.e., random, checkerboards, nested, Clementsian, Gleasonian, or even gradients) based on an ordinated (reciprocal averaging) incidence matrix of sites and a statistical consideration of coherence, turnover, and boundaries. A significant positive test is indicated by a plus (+), a significant negative test is indicated by a minus (-), and a nonsignificant test is indicated by NS. For metacommunities with a nonrandom distribution of range boundaries, Morisita's index > 1 indicates clumped boundaries and Clementsian structure, whereas Morisita's index < 1 indicates hyperdispersed range boundaries and evenly spaced structure. Details of this approach for understanding the spatial organization of metacommunities appear in Leibold and Mikkelsen (2002).

Sonadora; see chapter 3). This study, based on the approaches of Hoagland and Collins (1997) and Leibold and Mikkelsen (2002), quantified complex patterns of nestedness and clumping of species boundaries (Barone et al. 2008) that differed between transects. Although the upper boundaries of species distributions were clumped on both transects, only one cluster of upper boundaries was detected on the Mameyes transect (850 m), whereas three clusters were visible on the Sonadora transect (500 m, 700 m, and 900 m). Neither lower boundaries of species distributions nor modal abundances of species were clumped on either transect. Finally, one test suggested that species distributions were nested, whereas another suggested that they were antinested. Taken together, these analyses do not support the contention that distinctive Clementsian community types exist in the Luquillo Mountains corresponding to tabonuco, palo colorado, or elfin forest. Indeed, Barone et al. (2008) never refer to tabonuco, palo colorado, or elfin forest.

Using a comprehensive framework (Leibold and Mikkelsen 2002; Presley et al. 2011), the metacommunity structure of terrestrial gastropods has been explored extensively in the Luquillo Mountains (Presley et al. 2010, Willing et al. 2011) along extensive elevational transects. One transect passed through traditionally recognized tabonuco, palo colorado, and elfin forest (mixed-forest transect), reflecting variation

in abiotic characteristics and in forested habitat types, whereas another parallel transect included only palm forest patches (palm-forest transect), reflecting variation in abiotic characteristics alone. The mixed-forest transect exhibited a Clementsian structure (species distributions forming recognizable compartments), whereas the palm-forest transect exhibited a quasi-Gleasonian structure (idiosyncratic species distributions that are independent of each other). The variation in species composition among elevational strata within each transect was highly correlated with the elevation along each transect, even though patterns of composition were not correlated between transects. This suggests that the identity of environmental characteristics, or the form of response by the fauna to those characteristics, differed between mixed- and palm-forest transects. Despite the proximity of the transects to each other, the patchy configuration of palm forest in the Luquillo Mountains, and the pervasive distribution of the dominant palm species (*Prestoea acuminata*), the relative importance of abiotic variables and habitat in structuring gastropod metacommunities differed between transects.

Future research in the Luquillo Mountains should take advantage of elevational transects established within each of three replicate watersheds: Sonadora, Icosos, and Mameyes Rivers. This infrastructural network provides a critical resource for measuring in tandem suites of environmental measurements concerning mesometeorological characteristics (e.g., precipitation, temperature), population and community characteristics (e.g., species abundances, species richness), and biogeochemical characteristics (i.e., fluxes and pools of nutrients). As such, it enables the application of hierarchical models of metacommunity organization to a variety of taxa, and it provides an opportunity to understand the way in which environmental correlates of elevation mold the spatial organization of the biota and attendant ecosystem processes.

Cross-Scale Interactions and Disturbance

Linking patterns of metacommunity structure to underlying ecological mechanisms is challenging. The spatial and temporal dynamics of biotic systems might arise as a consequence of cross-scale interactions—processes at one spatial or temporal scale that interact with processes at another scale to create nonlinear dynamics or thresholds (Peters and Havstad 2006). These interactions alter the association between pattern and process across scales because broad-scale drivers, especially those associated with disturbance, change local conditions and alter the configuration of patches in landscapes, thereby molding system dynamics (Peters et al. 2007a, 2007b). In general, disturbances affect the life-history and demographic parameters of species at fine spatial scales by altering the local abiotic, biotic, or structural environment. Environmental differences among local patches, as well as their spatial configuration, affect the interpatch dispersal of individuals (i.e., a transfer process). This alters the effective degree of connectedness among patches in a species-specific manner, coincident with the niche characteristics of species.

In the course of secondary succession, the biotic, abiotic, and structural characteristics of local sites change because of interactions between fine-scale processes and transfer processes among sites. Importantly, alterations of environmental

characteristics at a local scale alter the nature and configuration of patches at the landscape scale. Such cross-scale interactions (figure 8-5) can significantly influence spatial patterns of biodiversity in complex ways, especially during posthurricane secondary succession. This view parallels conceptions that a strictly hierarchical view of systems might be insufficient to capture dynamic aspects of complex and evolving systems (Gunderson and Holling 2002).

A landscape perspective that explicitly considers cross-scale interactions (Peters and Havstad 2006; Peters et al. 2007a, 2007b) as well as metacommunity dynamics (Holyoak et al. 2005) represents an emerging view of biotic responses to disturbance (Willig et al. 2007). The metacommunity dynamics of gastropods, a taxonomic subset of the community best referred to as an assemblage (Fauth et al. 1996), in the Luquillo Forest Dynamics Plot (chapter 5) illustrate the potential of this quantitative approach to have broad applicability for furthering the understanding of community succession in the Luquillo Mountains and elsewhere. This example focuses on nestedness (Patterson and Atmar 1986; Atmar and Patterson 1993), the propensity of species-poor sites to be proper subsets of more species-rich sites. It is one of the most frequently studied patterns of assemblage structure. It has been incorporated into studies involving both large and small extents of time and

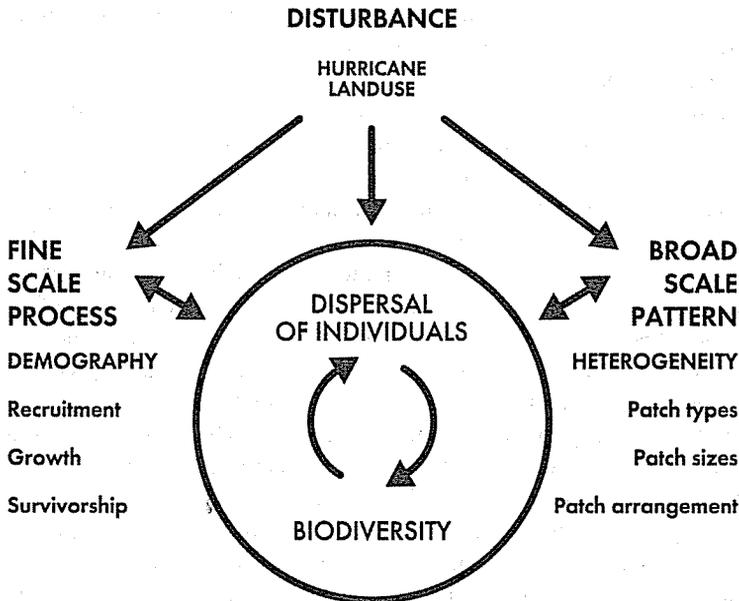


Figure 8.5 Disturbances such as hurricanes affect broad-scale patterns of habitat heterogeneity (i.e., characteristics of patchiness) in addition to fine-scale demographic processes of species associated with environmental characteristics of particular patches. The dispersal of individuals of different species and patterns of biodiversity are critically dependent on cross-scale linkages between growth, recruitment, and survivorship at the scale of particular patches, and on landscape heterogeneity regarding the types, sizes, and arrangement of patches in a landscape comprising multiple patches. (Modified from Willig et al. 2007.)

space (Kaufman et al. 2000; Leibold and Mikkelsen 2002; Norton et al. 2004; Azeria et al. 2006), and it responds to disturbance (Bloch et al. 2007).

In the Luquillo Mountains, the immediate consequence of disturbance associated with hurricanes was a decrease in the nestedness of terrestrial gastropods (Bloch et al. 2007; Willig et al. 2007). Thereafter, the nestedness of gastropods increased over time; this was the case after both Hurricane Hugo and Hurricane Georges (figure 8-6). However, the rate of increase in nestedness was greater after Hurricane Hugo than after Hurricane Georges. The magnitude of nestedness differed among areas that differed in historical land use (Thompson et al. 2002). These differences in nestedness, on average, persisted after both hurricanes. Moreover, the rates of increase in nestedness did not differ as a consequence of differences in historical land use. In concert, these observations suggest that the reassembly of metacommunities (for a discussion of assembly rules, see Diamond 1975; Weiher and Keddy 2001) adheres to general patterns during posthurricane succession. Moreover, the application of neutral theory (Hubbell 2001) to metacommunity dynamics holds great promise for research in the Luquillo Mountains. This is especially true if the spatial distribution of intensities or severities of disturbance can be used to predict the patch-to-patch (or site-to-site) dispersal of individuals of different species under assumptions of equivalence (dispersal-based assembly) or nonequivalence (niche-based assembly). Indeed, the balance between these two mechanisms in terms of affecting metacommunity dynamics might itself differ during secondary succession in disturbance-prone landscapes.

Prior to hurricane disturbance, when canopy cover is extensive and environmental conditions at the level of the understory are more homogeneous, the gastropod assemblage in tabonuco forest might represent a metacommunity with a high degree of nestedness and connectivity among sites. If high connectivity enhances the likelihood that individuals will be randomly distributed among sites, a nested pattern of species occurrence manifests, regardless of the species abundance distribution in the landscape (Higgins et al. 2006). Such interconnectedness among sites probably was extensive before Hurricane Hugo, as no major hurricanes had affected the forest in decades. Each hurricane altered abundances of species at some sites more than others and caused local extirpations, thereby decreasing the degree of nestedness. Hurricanes also modify habitat by causing treefalls and moving branches and leaves from the canopy to the forest floor (chapter 5). The resultant environmental conditions (i.e., increased light and temperature, decreased humidity) generally are more stressful for terrestrial gastropods, especially in severely disturbed sites. Such abiotic changes differentially affected local populations via fine-scale processes throughout secondary succession. The reconfigured landscape of patches created by hurricanes modifies transfer processes among sites (i.e., the dispersal of particular species). Gastropod activity is reduced by unfavorable microclimatic conditions (see Cook 2001) because movement is costly in terms of water balance. Consequently, the dispersal of gastropods across severely disturbed patches is likely limited, and species that are driven to local extinction might not be rescued via immigration from subpopulations in other patches.

As forest cover and vegetation structure regenerated during succession, microclimatological conditions improved from the perspective of gastropods. These

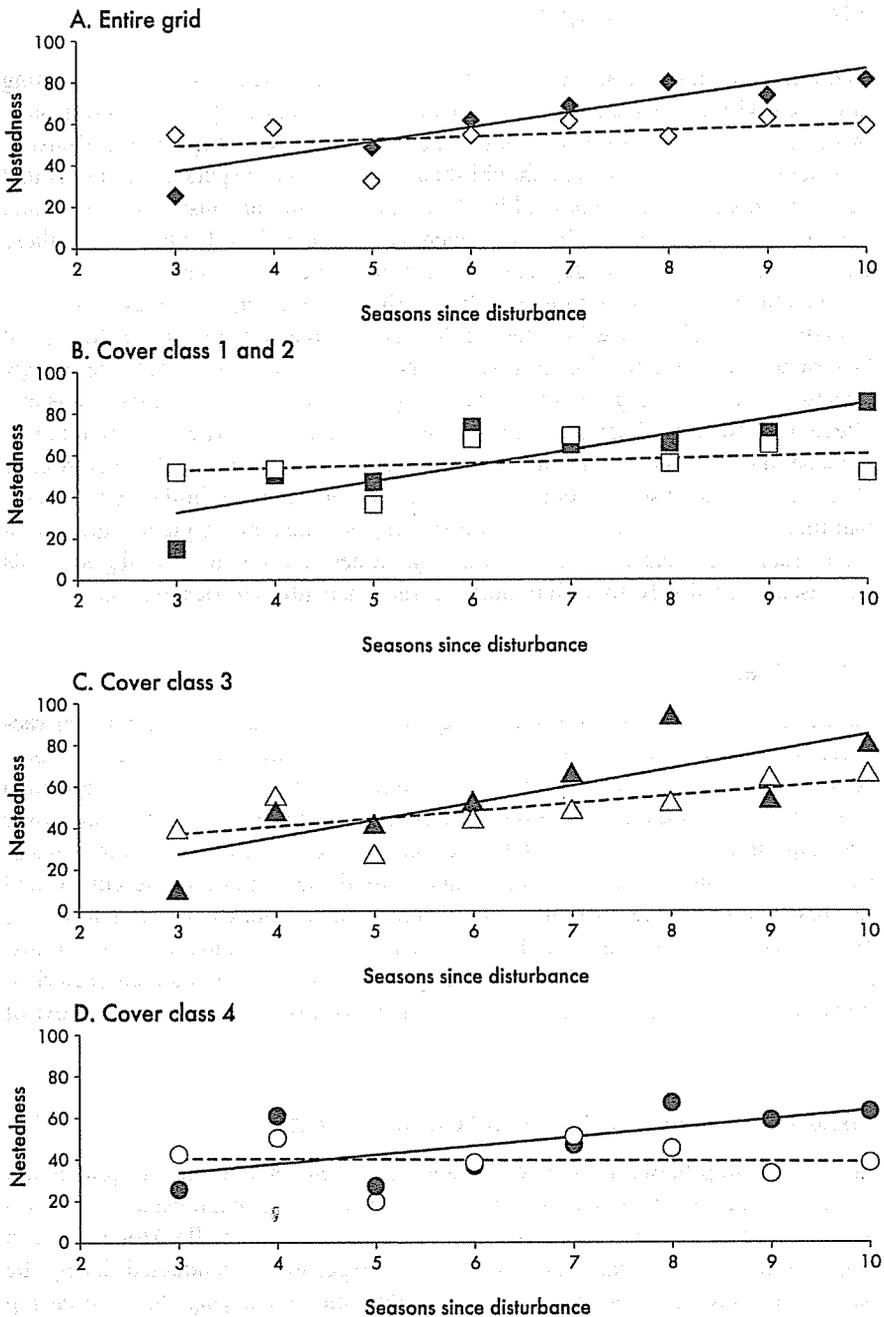


Figure 8.6 Long-term variation in the nestedness of terrestrial gastropods during wet (even numbers on abscissa) and dry (odd numbers on abscissa) seasons on the Luquillo Forest Dynamics Plot, with a focus on trajectories of change after Hurricane Hugo (solid symbols and solid lines) and after Hurricane Georges (open symbols and dashed lines). Spatial extents for analyses include (a) the entire Luquillo Forest Dynamics Plot, (b) cover classes 1 and 2, (c) cover class 3, and (d) cover class 4 (see chapter 3). Nestedness is presented using the N_c metric of Wright and Reeves (1992), standardized to eliminate the effects of matrix size (Wright et al. 1998). (Modified from Willig et al. 2007.)

ameliorated conditions at local sites likely altered fine-scale processes, resulting in decreased mortality and increased fecundity. Consequently, gastropod density increased over time following hurricanes (Bloch and Willig 2006). Density-dependent selective pressures should then have favored dispersal into areas that had been more severely modified by disturbance. Simultaneously, environmental homogeneity and connectivity likely increased among sites. Cumulatively, these effects would enhance the degree of nestedness in the assemblage.

The effect of disturbance on nestedness differed between hurricanes. The initial nestedness after Hurricane Georges was higher than that after Hurricane Hugo in all historical land use areas. Because Hurricane Georges did not disrupt the canopy structure to the same degree as Hurricane Hugo did (chapter 5), nestedness was less affected as an immediate consequence of the disturbance. The smaller input of branches and leaves to the forest floor from Hurricane Georges than from Hurricane Hugo also provided smaller quantities of organic carbon for assimilation by microbial food sources and induced only minor changes in understory plants during subsequent secondary succession. Consequently, the nestedness of terrestrial gastropods increased more slowly after Hurricane Georges than after Hurricane Hugo.

Future Directions

Future research from the metacommunity perspective should focus on the characterization of fine-scale, spatially explicit population- and assemblage-level processes, especially local emigration and immigration among sites in tabonuco forest. Concomitant quantification of broad-scale patterns of heterogeneity over the Luquillo Forest Dynamics Plot is needed in order to determine patch connectivity. To this end, it is vital to implement a synoptic network of measurements and sensors that simultaneously and syntopically assess features of the abiotic and biotic environment to which snails respond, so that the mechanistic bases of transfer processes at a small scale can be integrated with broader scale characterizations of heterogeneity to understand the effects of disturbance in the context of succession.

Disturbance, Biotic Structure, and Ecosystem Function

The relationship between biodiversity and ecosystem function has engendered a contentious debate on the importance of biodiversity to the maintenance of ecosystem services of interest to humans, and research in the Luquillo Mountains can help illuminate this debate. Observations and experiments conducted during the past decade provide new insights into mechanisms underlying the relationship between biodiversity (particularly species richness) and ecosystem processes (particularly productivity). However, there is substantial and often acrimonious disagreement about the relative importance of different mechanisms by which species richness influences productivity, with the complementarity of species and the traits of particular species proposed as the key factors (Mooney 2002). Synthesis of the ideas emerging from this debate has helped scientists to develop a more focused research agenda (Loreau et al. 2002). Recommendations arising from this synthesis

correspond with research opportunities available in Puerto Rico and the research focus of the Luquillo LTER program (Hooper et al. 2005).

Specifically, the state of knowledge of ecosystems in the Luquillo Mountains provides a solid base for the advancement of four key areas of investigation: (1) the mechanism (taxonomic and functional diversity, community structure) by which changes in biodiversity affect ecosystem processes (understanding diversity–function relationships), (2) the importance of the trophic level at which changes in biodiversity take place, (3) the assessment of the temporal stability of ecosystem properties and its relationship to disturbance, and (4) the scale at which changes in biodiversity operate to affect ecosystem processes. Uncertainty about the mechanism by which biodiversity affects ecosystem function arises in part because of the relationships among taxonomic diversity, functional diversity, and community structure (Stevens et al. 2003; Willig 2003; Hooper et al. 2005; Stevens et al. 2006; chapter 6). These relationships can be addressed in the Luquillo Mountains through studies of the variation in these characteristics in time and space, which might be caused by either abiotic gradients or disturbance. The historical focus on trophic structure and dynamics in the Luquillo Mountains (Reagan and Waide 1996) establishes the foundation for comparative studies in which biodiversity manipulations take place at different trophic levels. Natural and experimental disturbances in the Luquillo Mountains provide the opportunity to evaluate the long-term stability of many elements of biotic structure and ecosystem processes. Multiple gradients in the biotic structure at different scales (e.g., local, landscape, within Puerto Rico, within the tropics, tropic-temperate) provide additional opportunities to compare the effects of biotic structure on functionality at different scales. Because of these research opportunities, the Luquillo LTER program is in a position to advance a mechanistic understanding of the relationship between biodiversity and a number of critical ecosystem functions.

Taxonomic Diversity, Functional Diversity, and Community Structure

A mechanistic understanding of how biodiversity relates to ecosystem processes depends on knowledge of the functional traits of species (Hooper et al. 2005). Species traits provide a critical link between biodiversity and ecosystem processes by affecting energy and nutrient fluxes or by modifying abiotic conditions that indirectly affect these factors (Chapin et al. 2000; Covich et al. 2004a). Moreover, the expression of these traits depends on spatial and temporal variation in elements of biodiversity such as species richness, evenness, composition, and interactions (Chapin et al. 2000). In the Luquillo Mountains, studies of the traits of stream organisms have contributed to a clear understanding of the relationship between diversity and ecosystem processes in relatively simple communities (see below). However, a similar understanding of the traits of terrestrial organisms and the factors affecting the expression of these traits is lacking, and this is an impediment to the advancement of a comprehensive understanding of the relationship between biodiversity and functionality in the Luquillo Mountains.

The Luquillo Mountains have 830 plant species, including at least 250 tree species (chapter 3), thereby providing ample opportunities for biodiversity research.

The taxonomy of most organisms in the Luquillo Mountains is well understood, and this critically informs the comparative study of species traits. Disturbances themselves, as well as the environmental variability produced by disturbance and succession, encourage frequent, significant shifts in the local components of biodiversity (e.g., species composition, diversity, evenness), providing an observational framework for the study of diversity–function relationships. The trophic structure of one of the major Luquillo ecosystem types, tabonuco forest, has been articulated in a comprehensive fashion (Reagan and Waide 1996), detailing important ecological information concerning predator–prey and competitive relationships. Long-term measurements of flows and storages are available for many biogeochemical processes. Lacking are coordinated efforts to determine the biological characteristics of organisms and to understand how these properties interact to mold ecosystem function. Studies of such interactions are critical for an understanding of the relationship between biodiversity and ecosystem function.

A key gap in knowledge concerning biodiversity–function relationships relates to the scarcity of research on species-rich natural communities (Chapin et al. 2000). Moreover, much of the research on the relationship between diversity and function has emphasized small, artificial communities in which functional responses (e.g., biomass, cover, net primary productivity [NPP]) approach an asymptote at a low number of species (Tilman et al. 1996; Hector et al. 1999). The diversity and variability of forest communities in the Luquillo Mountains, coupled with frequent disturbance, provide an opportunity to evaluate the contribution of high species richness to ecosystem function. Moreover, life-history studies of numerous tree species (McCormick 1994; Zimmerman et al. 1995a; Lugo and Zimmerman 2002), as well as comprehensive investigations concerning the productivity of forest trees under a variety of conditions (Wadsworth 1947; Crow and Weaver 1977; Weaver 1979, 1983; Wadsworth et al. 1989), provide rich data from which to assess the importance of species traits to ecosystem productivity. For example, long-term studies of the response of tree assemblages to disturbance in the Luquillo Forest Dynamics Plot can be coupled to ecosystem-level responses (e.g., successional change, NPP, decomposition) through knowledge of species traits such as the response to light levels, growth and mortality rates, and leaf chemistry (see chapter 6 for examples).

Biodiversity has been identified as an important factor in determining rates of decomposition, an essential process in all ecosystems (Salonius 1981). In the Luquillo Mountains, research has established a detailed understanding of the factors that contribute to rates of decomposition (see above). Microbes and their attendant invertebrate associates are keystone taxa that control decomposition, and many of the microbial organisms important in decomposition in the Luquillo Mountains have been studied in detail.

Willig et al. (1996) examined the effect of disturbance on the functional diversity of microbes in the Luquillo Mountains. They found that the functional diversity of microbes was related positively to the degree of damage from a hurricane, but they were not able to detect an effect of historical land use. However, the particular species having catabolic profiles that make them critical to the process of decomposition (e.g., the ability to metabolize lignin versus starch) require identification and study, focusing on the possible existence of mutualisms among different microorganisms (Paerl and

Pinckney 1996). Specifically, the degree to which decomposing organisms form highly integrated functional communities (consortia), with different microorganisms contributing unique enzymatic functions (Chapin et al. 2000), is unknown, especially in tropical systems. Moreover, the effect of disturbance on these functional consortia and the means by which they are reestablished require further study if the successional dynamics of decomposition are to be understood from a mechanistic perspective.

Specialization by decomposer microfungi for particular leaf types within naturally occurring mixtures of litter on the rainforest floor strongly contributes to the high diversity of these fungi and results in more efficient processing of debris (i.e., faster rates of decomposition) than if such specialization were absent. Indeed, Polishook et al. (1996) found that two-thirds of the microfungal taxa were present in only one of two contrasting litter types from natural mixtures on the forest floor in tabonuco forest. Moreover, Santana et al. (2005) found that dominant microfungi from a particular leaf species caused greater mass loss of leaves than did microfungi that were dominant decomposers in other leaf species. Matching the microfungi to leaf substrates based on physical or chemical characteristics of the source and substrate plants or the source-substrate phylogenetic relatedness of the plants significantly increased rates of mass loss relative to plant mass loss when leaves were inoculated with microfungi from mismatched source-substrates. Thus, the high diversity of microfungi associated with decomposing leaves, and the strong association of these microfungi with particular leaf types, likely influences rates of decomposition. Although basidiomycete fungi that degrade lignin but are not host-specific had a stronger effect on mass loss than did microfungi, Santana et al. (2005) found that microfungi and basidiomycetes acted synergistically during decomposition.

Similarly, the traits of terrestrial invertebrates that determine their contribution to decomposition have been established only in general terms (Pfeiffer 1996; González 2002). For example, the fragmentation of litter by invertebrates increases the surface-to-volume ratio of fragments and therefore increases the rates of leaching and microbial decomposition. However, pellets of unassimilated material that pass through the guts of some millipedes decompose at a rate similar to that of the parent leaf material (Nicholson et al. 1966; Webb 1977). A better understanding of the relationship between biodiversity and the rate of ecosystem processes such as decomposition and nutrient cycling requires more detailed knowledge of the collective functional traits of decomposer assemblages (Balsler et al. 2002; Mikola et al. 2002). The correspondence between taxonomic and functional diversity in macroinvertebrates has yet to be examined, but the moderate diversity of these groups in the Luquillo Mountains (Garrison and Willig 1996) makes the goal of understanding this correspondence attainable. Comprehensive research on terrestrial decomposer communities would advance understanding of the trait-based linkages between biodiversity and ecosystem function during recurrent cycles of distribution and succession.

Multitrophic Manipulations to Understand Diversity–Function Relationships

An improved understanding of the relationship between biodiversity and ecosystem function requires more sophisticated theoretical and experimental treatments than have been attempted to date (Hooper et al. 2005). The relative paucity of theoretical

studies involving multitrophic interactions limits understanding of the relationship between diversity and function. Theoretical studies that do manipulate species richness in multitrophic systems suggest variable responses that depend on elements of trophic structure such as connectivity. Hooper et al. (2005) suggested that a theory that includes multitrophic interactions will lead to more complex responses than will models based on a single trophic level.

Experimental work on the relationship between biodiversity and ecosystem function has also focused principally on manipulations of a single trophic level, generally primary producers. Observations and experiments that manipulate consumers are less common but critical for determining how effects that cascade across multiple trophic levels affect ecosystem functionality (Hooper et al. 2005). Studies that manipulate heterotrophs generally have more variable and idiosyncratic results than those that manipulate primary producers. Additional experiments aimed at elucidating the effects of changes in diversity at multiple trophic levels are necessary in order to address the subtleties of the diversity–function relationship (Hooper et al. 2005).

In the Luquillo Mountains, the relative simplicity of the food web and the dominance of small vertebrates and large invertebrates as top predators (Reagan et al. 1996) facilitate manipulative studies of terrestrial consumers. The few experiments that have been conducted demonstrate significant effects of consumers on terrestrial ecosystem processes (e.g., earthworms on nutrient cycling [González and Zou 1999; Liu and Zou 2002], litter invertebrates on decomposition rates [González and Seastedt 2001], canopy invertebrates on leaf consumption [Schowalter 1995], and understory vertebrates on herbivory [Beard et al. 2003] and nutrient cycling [Beard et al. 2002; chapter 6]). In one experiment, Dial and Roughgarden (1995) manipulated anolis lizards in the forest canopy, which caused cascading effects on populations of invertebrate herbivores and leaf consumption. Experiments that manipulate the diversity or composition of consumers instead of primary producers are likely to yield new insights into the relationship between biodiversity and ecosystem function (Hooper et al. 2005). Moreover, experiments that manipulate diversity or composition at multiple trophic levels often yield complex and revealing results because of interactions within and across trophic levels (Hulot et al. 2000; Bradford et al. 2002; Holt and Loreau 2002).

Observational approaches to the examination of the effects of trophic structure on ecosystem function rely on comparisons of community composition (and, thus, trophic structure) across time or space. Disturbance and succession provide natural experiments in which community composition changes along a temporal trajectory, with concomitant effects on trophic structure and ecosystem processes. Although much is known about community changes after disturbance in the Luquillo Mountains (chapter 5), this information has not been integrated into models of food web structure that predict functional changes (e.g., decomposition rates) over time. The development and implementation of models linking trophic structure and ecosystem function are critical challenges for the future, especially as a means of developing a mechanistic understanding of the effects of an altered trophic structure on ecosystem processes.

Elevational variation in community composition and trophic structure provides a spatial approach for linking biodiversity and ecosystem function. Because species richness in the Luquillo Mountains declines with elevation across a broad range of taxa (Waide et al. 1998), leading to a simpler trophic structure, elevational comparisons can shed light on the diversity–function relationship, provided that other environmental characteristics (e.g., slope, aspect, soil type, forest structure) can be controlled in analyses to disentangle the effects of correlated factors. Ongoing surveys of variation in community compositions with elevation (e.g., trees, gastropods, insects) provide information with which to examine elevational changes in trophic structure. For example, Richardson et al. (2005) compared invertebrate communities in the litter of palm (*Prestoea montana*) and matched dicot forest stands that changed in plant species composition along a gradient of elevation. They found that the composition of the invertebrate community was affected more by forest type than by changes in temperature or rainfall.

A productive new research approach for the Luquillo Mountains would link new theoretical approaches to the diversity–function relationship with multitrophic experimental manipulations informed by observational studies of trophic webs along the elevational gradient. Previous, detailed work on the food web of tabonuco forest (Reagan and Waide 1996) provides a point of departure for this new research focus. In addition, such a focus is compatible with the research objectives of the LTER Decadal Plan (U.S. Long Term Ecological Research Network 2007), which provides a mechanism for expanding research on trophic webs to other sites in the LTER Network.

Stability, Disturbance, and the Relationship between Structure and Function

The relationship between stability (the extent to which the parameters that characterize an ecosystem remain unchanged in response to perturbation; chapter 2) and diversity has long been a popular theme in ecology (MacArthur 1955; May 1974; Pimm 1984). Theoretical examinations of this relationship are plentiful and provide a wealth of hypotheses for examination. However, Ives and Carpenter (2007) suggested that the focus of research properly belongs on stability and the multiple factors that influence it, including biodiversity. Because stability is measured in many ways and is influenced by a complex of interacting factors, a critical need exists to understand the mechanisms responsible for stability. An enhanced mechanistic understanding of stability requires long-term measurements to assess temporal stability, as well as experimental manipulations to examine the factors affecting recovery from disturbance (Hooper et al. 2005). Long-term studies of natural (Waide and Lugo 1992; Lugo and Waide 1993) and experimental disturbances are central elements of research in the Luquillo Mountains and provide opportunities to examine the mechanisms underlying the long-term stability of biotic structure (e.g., vertebrates, invertebrates, microbes) and ecosystem processes (e.g., decomposition, nutrient cycling) affected by repeated experimental perturbations.

Since its inception, the Luquillo LTER program has used disturbance as a unifying theme for integrating studies of population, community, ecosystem, and landscape

ecology (figure 8-7). Periodic disturbances decouple structural and functional characteristics of ecosystems (Willig and Walker 1999) and provide an opportunity to observe how such relationships change during secondary succession. Within the Luquillo Mountains, the rate of change after disturbance can be rapid or slow depending on the particular structural (e.g., biomass) or functional (e.g., nutrient retention) element under consideration (Zimmerman et al. 1996; chapter 2). For example, forest structure might change for decades after a hurricane, whereas nutrient retention might rapidly return to predisturbance levels. Mechanistic models of stability must provide explanations for the full range of responses to disturbance in order to link theory and empirical results successfully (Ives and Carpenter 2007). Tests of theory about the effects of species and functional diversity on stability require an understanding of the mechanistic basis of the diversity–stability relationship. One approach to developing such a mechanistic understanding involves long-term measurements of systems in which differences in diversity are not confounded by other characteristics (such as climate or disturbance) (Hooper et al. 2005).

The Greater Caribbean Basin provides the necessary conditions for examining ecosystem stability across a gradient of biodiversity. In the Caribbean, biogeographic factors create an east-west gradient of biodiversity from Puerto Rico to the Yucatan Peninsula. Across this biodiversity gradient, the major drivers of climate and disturbance are similar, and thus the gradient provides an opportunity to examine the relationship between diversity and stability for several forested ecosystems, including subtropical wet, dry, and mangrove forests. One ongoing effort to make such comparisons involves the Luquillo LTER program (wet Caribbean forest), the Florida Coastal Everglades LTER site (mangroves), the Atlantic Neotropical Domain of the National Ecological Observatory Network (dry Caribbean forest at Guánica), and three sites from the Mexican LTER Network: Celestún (mangrove

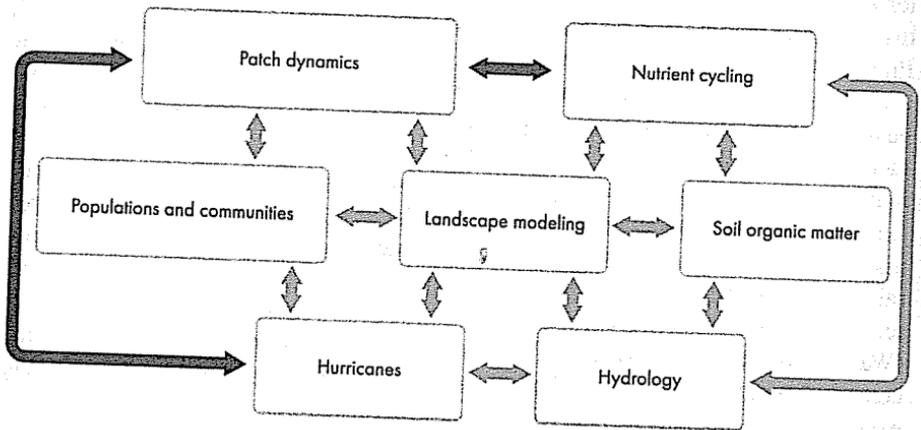


Figure 8.7 Relationships (gray arrows) among research components (boxes) of the Luquillo Mountains LTER proposal that were originally funded by the National Science Foundation. Since that time, additional foci on the connections between hurricanes and patch dynamics, and between patch dynamics and nutrient cycling (black arrows), have been undertaken as well.

forest sites in the Yucatan peninsula), Los Tuxtlas (wet forest), and Chamela (dry forest).

The Effects of Scale on the Relationship between Biotic Structure and Function

Biodiversity in general and biotic structure in particular, as well as the distribution of biomass among species and ecosystem compartments, are determined by biogeographic, biogeochemical, and climatic factors, which often are distributed along spatial gradients of latitude or elevation. On the broadest scale, the Luquillo Mountains anchor gradients of climate and biotic structure within the LTER Network. The warm and wet climate, relatively high species richness and landscape heterogeneity, and complex forest structure in the Luquillo Mountains provide important opportunities for comparisons with temperate mainland sites. For example, the Long-Term Intersite Decomposition Experiment showed that the diverse, warm Luquillo site had higher decomposition rates than less diverse, cooler sites, but it had similar rates of nitrogen mineralization (Parton et al. 2007). The Lotic Intersite Nitrogen Experiment demonstrated that ammonium turnover in streams is more rapid in the N-rich Luquillo site than in most temperate sites, owing largely to high nitrification rates (e.g., Peterson et al. 2001). The second phase of this multisite experiment showed that the total biotic uptake and the denitrification of nitrate increase with stream nitrate concentrations across 72 streams in eight biomes, but the efficiency of these processes declines with concentration (Mulholland et al. 2008). The Luquillo LTER program operates one of 15 sites in the Center for Tropical Forest Science (Smithsonian Institution) network of large, long-term forest plots. Cross-site comparisons among these plots have produced much new understanding of tropical forests and biodiversity maintenance (Brokaw et al. 2004; Losos et al. 2004; Condit et al. 2005).

At a less extensive scale, comparisons with other tropical island and mainland sites at latitudes similar to that of Puerto Rico allow examination of the relationship between structure and function over a biodiversity gradient. For example, sites along the Gulf coast of Mexico are similar to those of Puerto Rico in terms of climate and disturbance regime, but they generally have a higher taxonomic richness (chapter 3). These factors provide the necessary conditions for comparing the effects of variation in biodiversity on ecosystem processes (e.g., nutrient cycling) and properties (e.g., stability).⁵

Within the Luquillo Mountains, the interaction of landform- and landscape-scale gradients affects the rate of change of biotic structure and ecosystem processes and can lead to strong differences over relatively small spatial extents. The pattern of plant species occurrence is related strongly to position along the catena within tens of meters of forest streams (Scatena and Lugo 1995). Plant species richness, community composition, and physiognomy change substantially over 700 m of vertical elevation from the forest boundary to the mountain tops (Weaver and Murphy 1990; Barone et al. 2008). Consequently, the biotic structure is quite distinct between the extremes of this elevational gradient (Waide et al. 1998) (figure 8-8). At mid-elevations, landform and landscape gradients interact to produce an interdigitation of forest communities, with

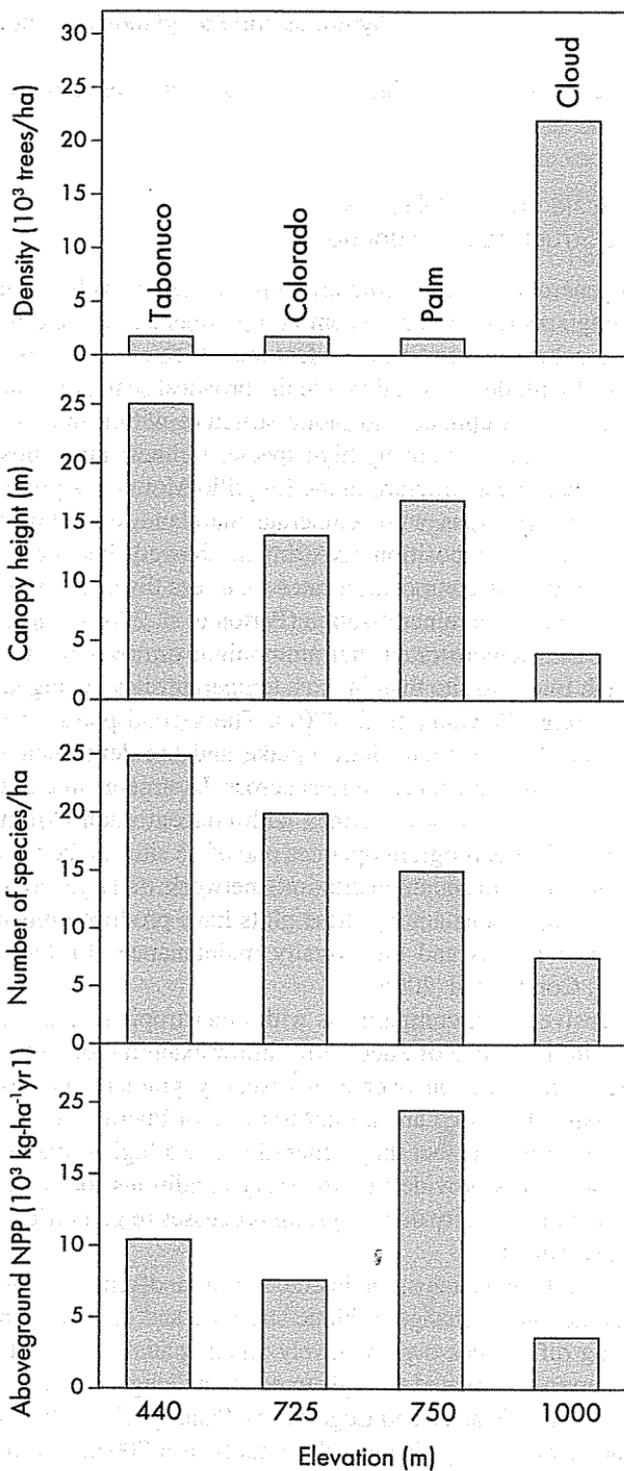


Figure 8.8 Changes in forest structure and net primary productivity (NPP) with elevation in the Luquillo Mountains, Puerto Rico. Data are from Weaver and Murphy (1990) and references therein. Elevations (in meters above sea level) are those at which particular studies were conducted; full elevational ranges of forest types are indicated in the text.

lower elevation species sometimes occupying ridgetops and higher elevation species occurring in the valleys (Odum 1970). We know less about changes in ecosystem processes (e.g., decomposition, primary production) across scales, and even less about the traits of organisms that might modulate these processes (but see González and Zou 1999; González and Seastedt 2001; González 2002). Therefore, the study of the correspondence of changes in biotic structure and ecosystem function across scales is a research priority.

Chapin (2003) presents a framework with which to predict which plant traits (and therefore which species) have the strongest effects on ecosystem processes. This framework incorporates five state factors that determine the characteristics of ecosystems (climate, parent material, potential biota, topography, and time) (Jenny 1941) and five interactive controls (functional types of organisms, resources, modulators [e.g., temperature, pH], disturbance, and human activities) (figure 8-9) that mediate the effects of state factors. Interactive controls respond to changes in state factors, and both affect and are affected by other interactive controls. As a result, state factors have both direct and indirect effects that must be measured (or controlled) in order to assess the effect of species traits on ecosystem processes. For example, Grace et al. (2007) employed a multivariate statistical model to assess the relationship between species diversity and biomass production while controlling for the effects of other integrative factors. The interplay among fluctuating interactive

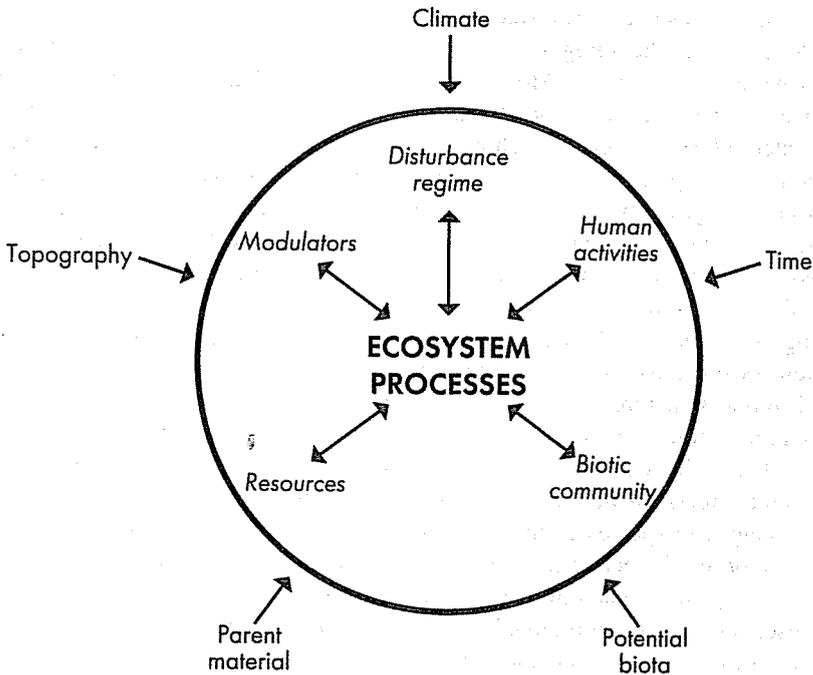


Figure 8.9 The relationship between state factors (listed outside the circle), interactive controls (listed inside the circle), and ecosystem processes. The circle represents the boundary of the ecosystem. (Modified from Chapin et al. 2002 and Chapin 2003.)

controls regulates ecosystem dynamics in the context of broader-scale changes in state factors (Chapin 2003). Species traits are most likely to have strong effects on ecosystem processes when they alter the interactive controls on those processes (Chapin et al. 2002). For example, differences in litter quality among plant species can alter resource supply rates by influencing rates of nutrient cycling (Chapin 2003).

Factors that affect the interactive controls of ecosystem processes (species identity, community composition, and physiognomy) (Chapin 2003) all vary with elevation in the Luquillo Mountains (Brown et al. 1983). However, a lack of critical information impedes our ability to use Chapin's (2003) framework to predict the effect of changing species, community characteristics, and physiognomic factors with elevation. Although functional traits and species identities are related closely (Chapin 2003), we do not know whether the distribution of species and functional traits are congruent in the Luquillo Mountains, or whether species replacements result in the continuity of functional traits with elevation. Moreover, we lack the knowledge to determine a priori which traits have the strongest effects on processes in Luquillo ecosystems or how these effects are exerted on interactive controls. The response of ecosystem processes to changes in functional traits might be linked to diversity at particular trophic levels. For example, primary productivity depends on the number and functional diversity of producers, whereas decomposition might be more closely linked to the functional diversity of microbial consumers (Chapin 2003). Our knowledge of the functional diversity of producers in the Luquillo Mountains is substantially stronger than our knowledge of the functional diversity of microbial consumers. The spatial and temporal dynamics of ecosystems along the elevational gradient might be subject to cross-scale interactions that create nonlinear patterns (see above). Moreover, anthropogenic changes in state factors are likely to increase the likelihood of nonlinear responses (Chapin et al. 2000; Ives and Carpenter 2007). Further research is needed to address these issues in the Luquillo Mountains, and particularly to determine whether the responses of ecosystem processes to changes in biotic structure at different scales are nonlinear.

Because the many factors that alter biotic structure often change in tandem across space and time, an integrated understanding of the nature and pace of ecological change requires a conceptual framework that includes the interactions among the elements of biotic structure (Willig and Walker 1999). This conceptual framework must also accommodate differences in spatial and temporal scales at which biotic structure changes (Peters et al. 2007a, 2007b; Willig et al. 2007). Substantial evidence exists that the state factors affecting ecosystems are changing at a global scale (Chapin 2003) and that these global changes have potentially important effects on biomes (Millennium Ecosystem Assessment 2005). However, changes in species composition at landform or landscape scales might be more important for ecosystem functioning than are global changes in the atmospheric composition and climate (Chapin et al. 2002). Moreover, rapid changes in land use, acting through regional climate shifts or alterations in the species pool, might have more immediate landform or landscape effects on ecosystem function than do slower global changes. The hurricane-dominated disturbance regime of the Luquillo Mountains interacts with global and regional climate changes operating as press disturbances. The development of a conceptual framework that

incorporates changes at multiple spatial and temporal scales is one of the most important challenges facing researchers in the Luquillo Mountains.

Food Webs Link Forests and Streams following Disturbances

Research in the Luquillo Mountains can make valuable contributions toward an understanding of the food web connecting terrestrial and aquatic portions of tropical ecosystems. Our research uses an integrated analysis of stream and riparian food webs to allow us to understand responses to different types of disturbance. These disturbances remove biomass and alter dominance relationships of species, with significant consequences to the food web structure. In order to understand the spatial and temporal dynamics of stream food webs and their responses to disturbances, it is important to examine (1) the underlying physical structure of the drainage basin (e.g., steepness of slopes, locations and sizes of waterfalls, and depths of pools that together affect distributions of species); (2) the disturbance history of the watershed (e.g., effects of recent and past landslides, hurricanes, extreme floods and droughts, and land uses); (3) the life history characteristics of the freshwater species and their adaptations to extremely variable flows; and (4) the distributions and diversity of riparian trees, including the phenology of leaf fall, leaf chemistry, and patterns of wood inputs and shading that influence sources of energy in different locations within the drainage basin. These factors interact in a hydrological and ecological network in which horizontal and vertical flow paths of various strengths determine food web structure and function. Landslides and treefalls from riparian forests and steep hillslopes have significant long-term effects on stream environments by altering sources of nutrients and energy, as well as by changing rates of deposition of sediments and modifying pool depths and channel configurations. All these interactions can affect food web dynamics through food limitations (e.g., sediments that cover leaf litter and algae), increased vulnerability to predators (e.g., shallow pools have few refuges), and the physical removal of stream organisms to downstream or overbank locations. Moreover, inputs ("subsidies") to streams of terrestrially derived nutrients and organic matter link riparian and aquatic food webs (Covich 1988b, 2006b; Crowl et al. 2006). The movement of stream-produced nutrients and organic matter (e.g., emergent aquatic insects, shrimps, and amphibious crabs) into the terrestrial food web (e.g., spiders, bats, anolis lizards, and wading birds) is another important connection between food webs. Rates of runoff and groundwater inputs from the surrounding hillslopes greatly affect the concentrations of dissolved nutrients and sediments that, in turn, influence species distributions and abundance in the rivers of the LEF (Covich and McDowell 1996).

Physical Habitat and Succession Affect Food Web Composition

Stream food webs on islands such as Puerto Rico are characterized by relatively low species richness as a result of the combined effects of biogeography and disturbance history (chapter 3). Distances from mainland to insular rivers, as well as the ages and geological origins of tropical islands, greatly influence the geographic distributions

of freshwater species and food web structure (Craig 2003; Smith et al. 2003; Covich 2006a; Boulton et al. 2008; Kikkert et al. 2009; Hein et al. 2011). Insular food webs are characterized by a high degree of connectivity among species because of the presence of dominant omnivorous species. This complex structure results in multiple energy pathways and the potential for rapid rates of biotic responses to disturbance that appear to be characteristic of many insular headwater streams. In addition to modifying the light and temperature environment, riparian forest communities along headwater streams provide important inputs of leaf litter and wood (Pyron et al. 1999), as well as other energy subsidies (e.g., dead insects) that sustain complex food webs (Crowl et al. 2001; Covich et al. 2006; Crowl et al. 2006).

Tropical insular streams generally differ from mainland streams by having smaller and more linear drainage basins, as well as fewer freshwater and riparian species. These relatively narrow basins result in the rapid rise and fall of high discharges that influence the downstream transport of food resources (leaf litter and algae) and which constitute important pulsed disturbances (Wohl and Covich, unpublished data). These events further limit the number of species that are adapted to these extremely high flows. Some species are able to migrate upstream and recolonize headwaters following disturbances (Covich and McDowell 1996; Fievet et al. 2001; Pyron and Covich 2003; Blanco and Scatena 2006). Many insular species evolved from marine species and adapted to low salinities. However, even those species that are adapted to migrate upstream to feed and reproduce must return to higher salinities during some phase of their life history. In general, the steep terrain and extremes in rainfall and runoff act as filters for the colonization of headwater streams, so that only a subset of potential colonists reaches the highest elevations. The resulting distribution of species along elevational gradients constitutes a hierarchical series of nested food webs composed of subsets of the riverine community (Covich 1988b; Greathouse and Pringle 2006; Kikkert et al. 2009; Hein et al. 2011).

Although montane streams on tropical islands are subject to many of the same types of disturbances and geologic processes as their mainland counterparts, the biotic responses to changes are often more evident on islands because they can occur rapidly over a large proportion of the watershed and are observed readily in steep terrain with high numbers of streams per unit area. For example, primary stream succession in relatively small insular watersheds is initiated when new channels are created on steep slopes by erosional processes over long periods of time (decades), as well as by the rapid (hours, days) removal of materials during major landslides. Some older channels and deep pools are filled with sediments and disappear during large landslides. Such rapid changes in the physical structure (depth, volume, flow velocity, turbidity, turbulence, and sizes of substrata) of pool habitats cause frequent turnover in the species composition and food web structure. Consequently, over decadal scales, the Luquillo Mountains provide numerous opportunities for examining how riparian and aquatic food webs are linked to successional dynamics throughout the watershed.

The steep terrain of the LEF contains numerous small streams. Importantly, these streams constitute a hierarchical network that ultimately comprises a few larger channels. Each location in the drainage network has distinct types and sizes of pools, runs, and waterfalls (Pyke 2008). As in all forested montane watersheds,

headwater tributaries contain small, shallow pools and fast-flowing riffles that retain sediments and organic matter (Church 2002; Benda et al. 2004; Richardson and Danehy 2007). Larger rivers have deeper pools and longer segments of rapids in downslope locations, often with longer retention times than are typical of headwater streams (Thorp and Delong 1994; Townsend 1996; Fisher et al. 1998; Rice et al. 2001).

Pulsed Flows in Drainage Networks Affect Food Web Resilience

Pulsed additions of nutrients and organic matter from hurricanes, landslides, and land use practices affect stream nutrient cycling and retention in riparian zones (McDowell 2001). These additions result from extreme flow events, from treefalls in the riparian zone, and from bank erosion, as well as from larger scale, often repetitive landslides on steep slopes. Frequent natural, small-scale disturbances (e.g., treefalls, local bank erosion, and landslides) produce scattered inputs of nutrients that are relatively transient. However, infrequent, large disturbances contribute significant pulsed inputs of fine and coarse sediments that affect the stream channel substrata for long periods. A dynamic series of disturbances with short-term and long-term effects influences the community composition over time because species respond to changes in substrata-related resources (e.g., retention of leaf litter by roots, stable rock surfaces for algal growth, and crevices for protective cover from predators).

Intense tropical rainstorms result in extreme flows (Wohl and Covich, unpublished data). Such variability affects the distribution of species and the retention of leaf litter in montane streams. High-flow events displace some individuals to considerable distances downstream. A series of these events homogenizes distributions of detritivores, as well as leaf litter and other food resources in headwater tributaries. The downstream transport of highly turbid water to wide, well-illuminated channels decreases light penetration and algal growth, an important source of food for herbivores and omnivores.

In years with only brief, low-intensity rainfall events, stream flows do not produce pulses of organic matter and nutrients. Under these low-flow or no-flow conditions, spatial distributions of different riparian trees within the drainage network can be important in determining the quality of local habitats and species abundances. These differences in litter inputs are especially significant during periods of prolonged drought, when leaf fall increases and is retained locally in pools and riffles (Covich et al. 2003, 2006). If the periods between large storm flows are sufficiently long (several months), then local conditions in pools and riparian influences can dominate food web composition and dynamics.

Continuous inputs of leaf litter throughout the year, as well as pulsed inputs after storm events, provide important sources of energy in forested headwater streams. Daily inputs of leaf litter differ among riparian tree species. Some (e.g., *Prestoea montana*, *Casearia arborea*, and *Dacryodes excelsa*) produce a relatively continuous supply of dead leaves to the stream throughout the year. Others (e.g., *Buchenavia tetraphylla*) produce a pulse of leaf input during February and March (Thompson et al. 2002). The input of wood and the accumulations of leaf litter (especially large

palm leaves) in debris dams result in the retention of organic matter until the debris dams are disrupted by larger floods. Such retention increases the reliability of energy supplies to detritivores and provides structural habitats for many species during periods of low and high stream flows.

Intense winds and rainfall associated with hurricanes and other tropical storms affect the composition and structure of riparian forests (and constituent tributaries) over timescales as short as hours or as long as several decades. Intense tropical hurricanes remove the riparian canopy, resulting in increased sunlight and nutrient availability in headwater streams. These physical and chemical changes enhance rapid growth by algae and aquatic grazers. At the same time, aquatic detritivores benefit from a large pulsed input of leaf litter, so that these riparian connections are especially strong. Thus, posthurricane conditions lead to several months of high biological productivity within the headwater tributaries.

Downstream connections within the entire drainage network are important because these channels distribute sediments, nutrients, and other materials. These connections provide corridors for upstream and downstream movements of migratory species. Debris dams and other large accumulations of organic matter associated with bank-side roots and in-channel rocky substrata reduce peak flows of water and the downstream transport of suspended sediments and dissolved nutrients. However, extreme peak flows of water transport significant amounts of nutrients and suspended sediments into larger rivers along the coast and, ultimately, into marine ecosystems.

Biotic Responses to Disturbances

Stream species respond to disturbances in different ways depending on their mobility and life history characteristics. Many are well adapted to avoid extreme floods by seeking small side channels, slow-moving waters along streambanks, or undercut banks and burrows. Often, they rapidly recolonize upstream habitats from these refuges after extremely high flows. Some species (highly mobile fishes and larger species of shrimp) are well adapted to move rapidly upstream after being displaced downstream or onto flood plains and into lateral pools along the main channels at lower elevations. Because of their mobility (e.g., swimming and crawling by fishes, many decapods, and gastropods, or flying by most adult aquatic insects), stream animals are resilient to natural disturbances and often return rapidly to their pre-disturbance food web structure (e.g., species composition, relative abundance).

Increasingly, stream ecologists examine the responses of food webs to drought or other disturbances (Covich et al. 1991, 1996, 2006; Power and Dietrich 2002; Romanuk et al. 2006). Responses are often rapid but seasonal in temperate-zone ecosystems (Wallace and Hutchens 2000; Nakano and Murakami 2001; Power and Dietrich 2002; Power 2006). In tropical ecosystems, flow-mediated disturbance events can occur frequently and at any time of year. Some disturbances produce long-lasting legacies by changing the species composition and dominance of riparian forest trees (Heartsill-Scalley 2005; Lecerf et al. 2005). Moreover, disturbances that lead to the establishment of nonnative riparian tree species can have long-lasting effects on the quality, quantity, and temporal distributions of leaf litter,

as well as on shading. For example, since its introduction several decades ago, non-native bamboo has come to dominate many riparian zones in the Luquillo Mountains, affecting leaf-litter production and breakdown by microbes and benthic invertebrates (O'Connor et al. 2000). Similar effects occur in other insular tropical streams where nonnative trees are introduced, such as *Hibiscus tiliaceus* L. (Larned et al. 2003).

Tropical Stream Food Webs in a Landscape Perspective

Long-term studies of food web structures are critical for understanding the direction and magnitude of net flows of energy or nutrients between terrestrial and aquatic ecosystems and among different elevational zones. Particular species in these food webs determine the directions of movement for energy and nutrients. For example, spiders and bats in the riparian corridor increase connectivity between freshwater and terrestrial food webs when they consume emerging aquatic insects from headwater streams. Adult freshwater crabs move from the stream channel to the forest floor as they forage in the leaf litter and thus link terrestrial and freshwater components of food webs (Zimmerman and Covich 2003). These amphibious adult crabs return to the stream to reproduce, and thus transfer nutrients into headwater pools from the forest floor (up to 50 m from the stream). In addition, the upstream movement of numerous postlarval shrimps, snails, and fishes transports nutrients and energy from coastal lagoons to headwaters (Covich and McDowell 1996; March et al. 2001; March and Pringle 2003; Pyron and Covich 2003; Blanco and Scatena 2006). Despite movements of matter and energy associated with animal activity, the large amount of water flowing downslope from higher elevations produces a net downstream transport of dissolved and suspended materials. At lower elevations, the movement of water from river channels onto the flood plains transfers large amounts of organic and inorganic materials into these habitats (Ballinger and Lake 2006).

Detrital Processing in Stream Food Webs

The breakdown rates of leaf litter are affected by changes in riparian tree species richness and composition, in the composition of microbial and macroinvertebrate communities, and, especially, in species that shred leaves (Crowl et al. 2001, 2006; Lecerf et al. 2005; Wright and Covich 2005a, 2005b). However, relatively little is known regarding the distributions of freshwater detritivores, changes in the rates of litter processing, and species-specific relationships in tropical stream ecosystems that differ greatly in the seasonality of rainfall and phenology of riparian leaffall (Boulton et al. 2008). Factors controlling rates of leaf-litter processing in tropical streams might differ regionally. For example, the relative importance of physical, microbial, and invertebrate-based processing of leaf litter seems to differ between insular streams and those on the mainland, where more invertebrate species occur and shred leaf litter. Some of the fastest rates of leaf breakdown have been reported for shredders in the Luquillo Mountains, where freshwater shrimp (*Xiphocaris elongata*) rapidly shred leaf litter (Crowl et al. 2006). The importance of rapid leaf shredding by invertebrates is demonstrated in streams in some locations but not

others (Cheshire et al. 2005; Gonçalves et al. 2006; Rincón and Martínez 2006; Rueda-Delgado et al. 2006; Wantzen and Wagner 2006).

Most stream research has been done in northern temperate regions, where many programs focus research on food webs and ecosystem processes. The value of concepts developed in these temperate-zone ecosystems for understanding tropical ecosystems remains uncertain (Graça et al. 2001; Mathuriac and Chauvet 2002; Iwata et al. 2003; Greathouse and Pringle 2006; Boulton et al. 2008). Research in Puerto Rico has highlighted some of the most fundamental differences (e.g., continuous inputs of leaf litter and wood, high diversity of riparian forests, high frequency of extremely high-flow events) and similarities (e.g., importance of detrital inputs and shading from closed canopies, functions of extreme high and low flows, and significance of cumulative effects) among ecosystems at different latitudes. Such geographic comparisons are important for understanding how types, intensities, and frequencies of disturbances affect food webs in tropical streams relative to those in other regions (Covich et al. 2006; Crowl et al. 2006; Wantzen and Wagner 2006; Boulton et al. 2008). Recent research on riparian and stream connections in temperate-zone ecosystems has focused on the diversity of connections among terrestrial and stream communities at one or more elevations (Nakano and Murakami 2001; Power and Deitrich 2002; Sabo and Power 2002; Allan et al. 2003; Decamps et al. 2004; Baxter et al. 2005; Naiman et al. 2005; Ballinger and Lake 2006; Paetzold et al. 2006). Studies in Puerto Rico have emphasized that gradients of biodiversity and food web structure (figure 8-10) in stream communities arise because of the locations of differently sized waterfalls and the steepness of the channels. Patterns of species distribution result from (1) the types and timing of disturbance events, (2) different distances of upstream migrations of freshwater invertebrates (*Macrobrachium* and *Atya* [shrimps] and *Neritina* [snails]) into headwaters, and (3) limited upstream migrations of predatory mountain mullet (*Agonostomus monticola*) and eels (*Anguilla rostrata*) related to geomorphic barriers. The limited upstream migrations of predatory eels affect prey populations of shrimp differently from those of mountain mullet, because eels are more common at lower elevations (Lamson et al. 2006; Covich et al. 2009). Studies of invertebrate migrations and their effects on food webs have not been emphasized for temperate streams. However, studies of river shrimp (*Macrobrachium ohione*) in the lower Mississippi River are underway (Bauer 2004). The results of these studies will provide a basis for comparative analyses of migratory pathways with several species of *Macrobrachium* from Puerto Rico, as well as with those of other low-latitude locations.

At smaller scales, vertical gradients within sediment-filled river channels characterize subsurface flows through groundwater and porous sediments within channels (the hyporheic zone). Inflows of groundwater to channels enhance the persistence of those stream segments during prolonged drought, when runoff is not available. Several locations become important refuges for species that lack adaptations for living in intermittent streams. In many streams, these vertical gradients of upwelling and lateral inflows create highly complex subsurface flow paths (Boulton et al. 1998; Poole 2002; Fisher et al. 2004). These subsurface waters provide dissolved nutrients, organic matter, and refuge for benthic invertebrates and microbes.

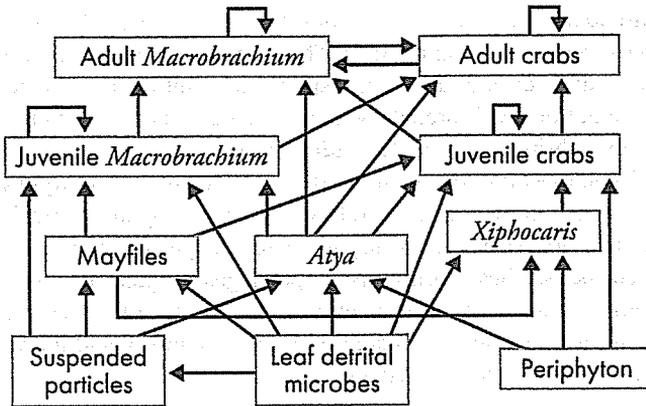


Figure 8.10 Headwater food webs in the Luquillo Mountains are dominated by omnivorous decapods (shrimps [*Atya*, *Macrobrachium*, and *Xiphocaris*] and crabs) that occupy habitats that lack fish predators. Riparian trees provide leaf litter (energy subsidies) that represents important food resources for detritivores (microbes, invertebrate shredders, and filter feeders) and determine light regimes that influence instream algal production (periphyton) for grazers. Arrows denote the flow of energy between food web compartments. Recursive arrows identify cannibalistic, intraspecific predation (i.e., food loops).

Up-welling waters from the subsurface zone typically contain dissolved nutrients that increase algal production at the channel surface. Down-welling zones generally transport dissolved oxygen and organic matter to depths where microbial and invertebrate communities process materials. These complex gradients are well studied in temperate-zone rivers (Fisher et al. 1998, 2004; Poole 2002; Lowe et al. 2006) but are just beginning to be considered in the tropics.

Gradients and Organization of Food Webs

Studies on linear profiles and gradients are used widely for forecasting the distributions of functional feeding groups of invertebrates (primarily aquatic insects as detritivores, grazers, and predators) along rivers (Vannote et al. 1980). In many forested watersheds, inputs of leaf litter from riparian trees represent energy sources for detritivores in small, narrow tributaries of first- and second-order streams (Cummins 1974; Henderson and Walker 1986). Grazers typically dominate communities in wider channels where sunlight is the main source of energy. Predators occur at lower elevations where herbivorous prey are abundant. The pattern of organic-matter processing in headwaters results from species (shredders) that break down coarse leaf material into fine suspended particulates that are consumed by downstream filter-feeding species. These processing chains in forested headwaters depend on adequate flow and turbulent transport. The biotic linkages (from shredders to filter feeders) represent flow-mediated ecosystem processing that is drought sensitive in both temperate-zone (Heard and Richardson 1995; Whiles and Dodds 2002) and tropical (Crowl et al. 2001; Covich et al. 2003; Wright and Covich 2005a, 2005b) streams. For example, filter-feeding shrimp (e.g., *Atya lanipes*) and

leaf-litter shredders (e.g., *Xiphocaris elongata*) constitute detrital processing chains when both co-occur in flowing habitats. These species alter their rates of consumption of food (leaf litter and algae) in response to combinations of flow velocities and biotic interactions with predatory fishes such as eels and mountain mullet and larger, predatory shrimps such as *Macrobrachium carcinus* (Covich 1988a, 1988b; Crowl and Covich 1994; Crowl et al. 2001; Covich et al. 2009). Atyid shrimp function as grazers when flow rates are too low to suspend organic particulates for filter feeding (Covich 1988a). Their grazing increases the productivity of algae growing on submerged rocks. These shrimp use appendages adapted for both filtering and grazing (cheliped fans composed of many setae) to remove overlying sediments during feeding, which results in increased light availability and nutrient recycling (Pringle et al. 1993; March and Pringle 2003).

Geomorphic Network Approaches to Food Webs

Important insights for understanding entire drainage basins have emerged from observational and experimental analyses of species responses to disturbances within riparian and stream communities of Puerto Rico. These studies illuminate how species-specific interactions, such as processing chains of detritivores that function as shredders and filter feeders, respond to different riparian inputs (Covich and McDowell 1996; Crowl et al. 2001, 2006) and to disturbance events such as floods and droughts (Covich et al. 1991, 1996, 2003). Previous agricultural land uses modified the physical terrain and soils, consequently altering the plant species composition. This legacy has persistent and significant effects on riparian tree species and the composition of stream food webs (Beard et al. 2005; Zimmerman and Covich 2007). Extreme floods, landslides, and erosion of stream banks continue to alter the sediment composition and habitat quality for many riparian tree species and stream invertebrates. These physically driven disturbances create patchiness that alters species distributions in different locations of drainage networks.

Early studies of temperate stream ecosystems established that terrestrial inputs of water and nutrients affect the diversity of detritivores and the productivity of aquatic food webs along stream profiles (Cummins 1974; Hynes 1975; Vannote et al. 1980). More recent studies established that drainage network connections (Gomi et al. 2002; Benda et al. 2004; Fisher et al. 2004) and the geomorphic template are critical for understanding how changes in land use or climate alter the structure and functioning of drainage basins (Church 2002; Likens 2004). Recent studies in the Luquillo Mountains provide tropical comparisons in which the degree of patchiness is high as a consequence of 2 decades of natural disturbances (e.g., Hurricanes Hugo and Georges). Agricultural clearing and other human land uses resulted in legacies that produced a complex mosaic of habitats and riparian tree distributions that still influences stream food webs. Flows of water and materials connect forest and stream food webs in ways that accelerate responses to frequent disturbances and create a high degree of food web resiliency.

Recognition that aquatic and terrestrial habitats are highly interconnected by hydrologic processes is critical for understanding ecosystem dynamics and managing riparian areas. Because drainage networks link land-based nutrients to stream

food webs, effective land use policies require an ecosystem-level approach for controlling nutrient availability (Meyer and Wallace 2001; Power and Dietrich 2002; Pringle 2003; Thoms and Parsons 2003; Freeman et al. 2007; Meyer et al. 2007). Hydrologic connections link stream food webs across a wide range of elevations within a drainage basin (Lewis et al. 2001; Junk and Wantzen 2004). These hydrologic and ecological connections are especially important during prolonged droughts, because habitats with sustainable stream inflows become refuges for species adapted to persistent stream flows (Covich et al. 2003, 2006). Ecologists continue to explore linkages among aquatic and terrestrial ecosystems (Kling et al. 2000; Hershey et al. 2006; Richter et al. 2006) that integrate biotic distributions relative to the physical terrain and long-term variability in flow regimes. Research on tropical stream ecosystems is needed in order to document the importance of anticipated extremes in flow that arise from climatic changes and the increased diversion of water for human needs (Covich et al. 2004a, 2004b; Giller et al. 2004; Malmqvist et al. 2008).

Introduced Species in Ecological Perspective

The effect of introduced species invasions on native species composition and on ecosystem functioning and services is of critical concern to society (Ewel et al. 1999). Unfortunately, the ecological consequences of introduced species invasions are unclear. Some connect introduced species invasions to native species extinctions (Allendorf and Lundquist 2003; Lodge and Shriver-Frechette 2003), homogenized landscapes (McKinney and Lockwood 2001), or even the genetic alteration of native species through hybridization (Lockwood and McKinney 2001). Others consider the level of native species extinctions resulting from invasions to be exaggerated (Case 1996; Vermeij 1996) and perceive the landscape to be diversified as a result of enrichment with introduced species (Davis 2003). Because importance values or rank-abundances of species (*sensu* Whittaker 1970) change after invasions, and because an altered species composition affects the rates of ecosystem processes and the magnitudes of state variables, extreme caution must be exercised before advocating or introducing species into new environments (Ewel et al. 1999).

Research in the Luquillo Mountains and elsewhere in Puerto Rico has documented the presence and some of the ecological roles of introduced plant and animal species. This research provides a basic understanding upon which to build an ecological perspective of introduced species invasions in tropical environments ranging from primary to urban forests. We briefly present 10 observations from studies involving introduced species and conclude with a discussion of implications for biodiversity science and management. The first observation focuses on primary and mature native forests and excludes anthropogenically disturbed sites (e.g., roadsides, recreation areas, tree plantations). The second observation includes experimental disturbances of mature native forests. The remaining eight involve sites subjected to anthropogenic disturbances.

First, many introduced animal species and one introduced tree species have been reported in the otherwise mature or primary forests of the Luquillo Mountains

Table 8.1 Examples of naturalized introduced species within mature or primary forests of the Luquillo Mountains

Scientific name	Common name	Source
Animals		
<i>Mus musculus</i>	House mouse	Odum et al. 1970a
<i>Rattus rattus</i>	Roof rat	Odum et al. 1970a; Weinbren et al. 1970; Snyder et al. 1987
<i>Rattus norvegicus</i>	Wharf rat	Weinbren et al. 1970; Snyder et al. 1987
<i>Herpestes auropunctatus</i>	Mongoose	Weinbren et al. 1970; Snyder et al. 1987
<i>Felis catus</i>	Cat	Weinbren et al. 1970; Snyder et al. 1987
<i>Bufo marinus</i>	Common toad	Odum et al. 1970b
<i>Apis mellifera</i>	Honeybee	Snyder et al. 1987
<i>Aedes aegypti</i>	Mosquito	Weinbren and Weinbren 1970
Trees		
<i>Syzygium jambos</i>	Pomarosa	Smith 1970
<i>Calophyllum calaba</i>	María	Thompson et al. 2007
<i>Genipa americana</i>		Thompson et al. 2007
<i>Simarouba glauca</i>		Thompson et al. 2007
<i>Swietenia macrophylla</i>	Caoba	Thompson et al. 2007

(table 8-1). Some of these species have been present in the forest for centuries and maintain stable, but low, population densities. For example, active honeybee (*Apis mellifera*) hives have an average density of 1 per 3.4 ha at upper elevations (Snyder et al. 1987). Rat (*Rattus rattus*) density ranges from 32 to 40 ha⁻¹ (Odum et al. 1970b) and fluctuates annually (Weinbren et al. 1970). Introduced plant species such as bamboo (*Bambusa vulgaris*) or African tulip tree (*Spathodea campanulata*) are common in some areas and provide food (leaves and seeds) to native shrimp in reaches of streams for which there are no records of historical deforestation by humans.

Second, experimental disturbance (cutting and gamma irradiation) of mature tabonuco forest resulted in the establishment of introduced plant taxa such as *Swietenia* (Duke 1970) and eight species from roadsides (Smith 1970) that do not survive conditions of canopy closure. Twenty-three years after irradiation, regeneration in the experimental area was only by native species (Taylor et al. 1995), a finding recently corroborated by Thompson et al. (2007).

Third, introduced tree species occur in mature forest sites that were logged selectively over 60 years ago (e.g., the Luquillo Forest Dynamics Plot [LFDP]), but densities are low, and local ranges are not expanding (Thompson et al. 2007). After a hurricane, the invasive introduced tree species *Spathodea campanulata* germinated but failed to establish beyond the sapling stage as a consequence of canopy closure. Most introduced species on the LFDP occur on a sector that had been farmed and logged, and fewer occur on the sector that was not farmed or where the canopy has been closed at least since 1936 (Thompson et al. 2007).

Fourth, in some areas of the Luquillo Mountains, pastures dominate after deforestation, agricultural use, and abandonment. In instances where introduced species were planted as monocultures in these pastures, forest cover was restored, but

Table 8.2 Examples of Puerto Rican taxa with increased numbers of species resulting from the introduction and naturalization of species.

Taxon	Number of species			Source
	<i>Native</i>	<i>Introduced</i>	<i>Total</i>	
Plants			3,126	Liogier and Martorell 2000
Trees	547	203	773	Little et al. 1974
Orchids	137	6	143	Ackerman 1992
Ferns			408	Proctor 1989
Birds	240	87	327	Biaggi 1997
Earthworms	18	11	29	Borges 1996
Ants	<i>a</i>		<i>a</i>	Torres and Snelling 1997

**a* Surveyed Puerto Rico and 44 adjacent islands over an 18-year period and found 31 extinctions and 146 new colonizing species. In all but two cases, the number of ant species increased.

native species quickly invaded plantation understories (Lugo 1992) and eventually dominated the canopy (Silver et al. 2004). Introduced species remain, but with low dominance after 60 years of forest succession (Silver et al. 2004). Native species reinvade the site at a rate of one species per year (Lugo et al. 1993).

Fifth, hurricanes can destroy plantations of introduced species and accelerate the establishment of native tree species (Wadsworth and Englerth 1959; Liegel 1984). In other instances, mechanical injury by hurricanes to forests with mixed species composition (introduced and native) was more a function of tree growth rate (faster growing trees experienced greater effects than did slower growing ones) or location relative to wind direction than of the biogeographic origin of the species (Ostertag et al. 2005).

Sixth, the conversion of forest to pastures results in the invasion of introduced earthworms and the local extinction of native earthworms (González et al. 1996). The abandonment of pastures and their subsequent recovery results in a community comprising both introduced and native earthworm species, in which introduced species dominate in terms of numbers but not biomass (Sánchez de León et al. 2003).

Seventh, as a result of the introduction of species into Puerto Rico, the species richness of many areas has increased (table 8-2). These increases were not associated with native species extinctions, which are low in Puerto Rico, at least for plants (Lugo 1988; Figueroa Colón 1996) and birds (Brash 1984; Biaggi 1997). The large increase in bird species richness as a result of introductions led Biaggi (1997) to state that any future compendium on birds requires attention to the introduced species, because they increase in number on a daily basis (p. 327). He listed 87 introduced bird species from Puerto Rico, compared to 116 native resident bird species and 92 migratory ones.

Eighth, island-wide forest inventories document that introduced species of trees dominate most of the Puerto Rican landscape, particularly in regions with high anthropogenic disturbance (Lugo and Brandeis 2005). One introduced species, *Spathodea campanulata*, is the most common tree on the island. The abundance of introduced species was greatest in moist life zones that had been deforested, farmed, and abandoned, and it was lowest in dry and wet life zones and in regions with

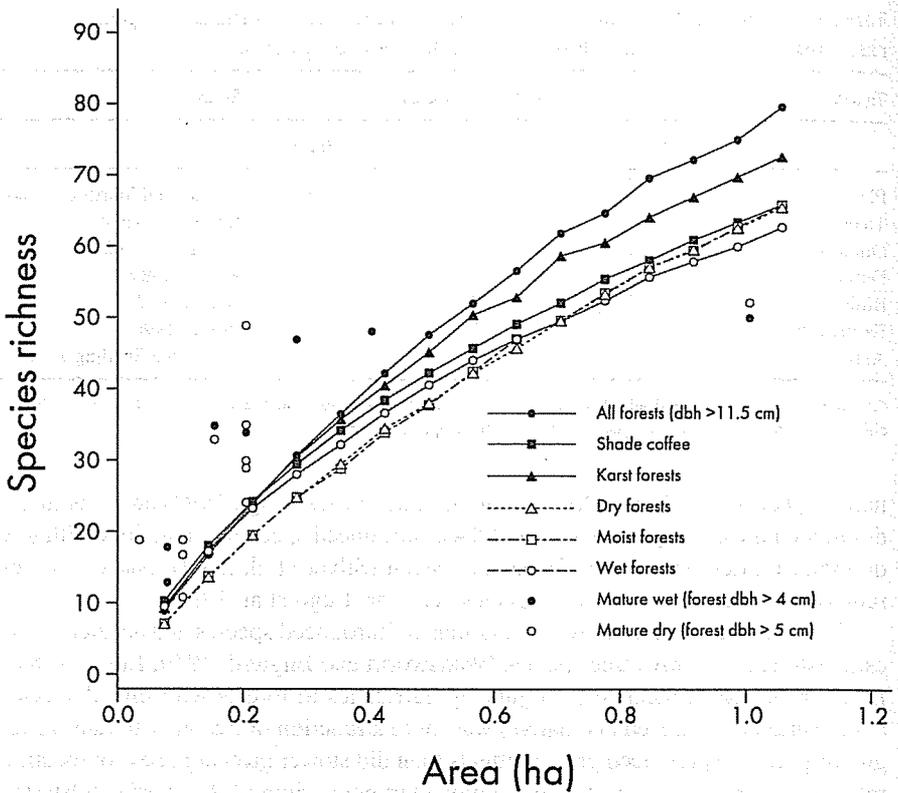


Figure 8.11 Species-area curves for undisturbed mature native dry and wet forests (point data) and new forest types dominated by introduced species (data connected by lines). The data for new forest types are from an island-wide forest inventory and cover different types of forests; there also is a combined curve for all forests (Lugo and Brandeis 2005). Note the differences in the minimum diameter at breast height (dbh), which result in different amounts of underestimation in the number of species in the emerging new forests. Native forests in Puerto Rico saturate at about $60 \text{ species ha}^{-1}$ (Lugo 2005), but the emerging forests have higher species densities.

mature or undisturbed native forests. Rather than causing forests to become depauperate, the presence of introduced species augmented species density (figure 8-11).

Ninth, urban forests had the highest proportion of introduced species in Puerto Rico (Lugo and Brandeis 2005). Sixty-six percent of the importance value (an index that reflects abundance, frequency of occurrence, and biomass) in urban forests was attributed to introduced species.

Tenth, the dominance of introduced species in Puerto Rican forests declines over time. Native species grow under the canopies of nonnative species and regain dominance in more mature forests that support combinations of introduced and native species (Wadsworth and Birdsey 1983; Lugo 2004b; Lugo and Helmer 2004).

Ecological research on introduced species contributes to the emerging fields of conservation biology and conservation biogeography (Lomolino 2004). The Puerto Rico case study offers empirical evidence about a situation in which intense and chronic human activity created environmental havoc through deforestation, fragmentation, conversion to agriculture, and abandonment after centuries of soil-degrading activity. From this scenario emerged a natural recolonization of abandoned lands by trees, mostly introduced species. Some 60 to 80 years after abandonment, forests that do not resemble the original ones in terms of species composition cover almost half of the island (Lugo and Helmer 2004). They contain a considerable proportion of introduced species, as well as native and endemic elements of the flora.

At the same time, species extinctions in Puerto Rico have been negligible relative to predictions of island-biogeographic theory or ideas about fragmentation of forest cover (Lugo 1988). These methods for estimating species extinctions do not consider recovery mechanisms after deforestation and abandonment and assume linear or exponential relationships between the percentage of area deforested and the percentage of the species pool that becomes extinct. Island-wide deforestation of > 90 percent should have resulted in large losses of species in Puerto Rico and a depauperate biota. However, extensive extinctions did not occur, and current forests are diverse and functional (Lugo 2004a). By "functional," we mean that ecological processes in these emerging forests (e.g., rates of primary productivity, nutrient cycling, and decomposition rates) compare favorably with those in native, undisturbed ones (Lugo 1992).

Documenting and understanding the consequences of massive deforestation and subsequent invasion by introduced species advances ecological understanding and provides insights to guide the restoration and conservation of tropical forests. Introduced species invasions and establishment in Puerto Rico occur naturally in response to anthropogenic disturbances. In the absence of anthropogenic disturbances, only a few introduced species become established in native forests; where they function as rare specialists.

The consideration of species invasion from the perspective of ecological space is consistent with the deconstructive approach to species richness favored by Marquet et al. (2004). They argued that understanding patterns of species richness requires the consideration of evolutionary (extinction/speciation dynamics), environmental (external properties and states), and physiological or life history characteristics (internal properties and states). This approach is particularly important in a disturbance-mediated system because ecological characteristics continually change across geographic space and along time sequences at the same geographic location. Indeed, disturbance and subsequent succession alter the environmental characteristics associated with geographic space, providing dynamic opportunities for many species to establish or go locally extinct, potentially influencing the species composition and richness at multiple scales. Knowledge of the physiological and life history characteristics of species is thus essential if one is to understand the acclimation, adaptation, and even evolution of species to new ecological conditions, including the novel ones that emerge because of human activity.

Understanding the dynamics of species assembly in tropical forests, including mechanisms that favor or retard invasion, is critical for the development of policies

concerning the conservation of biodiversity. This is particularly true because human activity is accelerating changes in the composition of species, either through the introduction of new species or by altering site conditions and redirecting succession. Regardless of the identity of the factors that cause changes in the species composition, conservation scientists need to understand how communities reassemble, self-organize, and form new ecosystems after disturbance or invasion by introduced species (chapter 7).

In summary, tropical environs can be quite resilient to anthropogenically induced habitat loss and fragmentation. Moreover, invasion by introduced species frequently does not lead to the loss of native species or to significantly altered ecosystem services. The challenge for the future is to understand the circumstances that lead to resilience and to inform restoration and reclamation efforts by articulating a mechanistic approach to guide successional trajectories to endpoints consistent with societal goals of sustainability.

Emerging New Forest Types on the Tropical Landscape

Research in the Luquillo Mountains has illuminated the nature of emerging new forest types. The paleoecological and biogeographical literature is replete with examples of changes in forest types as a consequence of environmental change (Behrensmeyer et al. 1992; Colinvaux 1996; Jackson 2004). Modifications to the biota that result in different types of ecosystems are a matter of historical record (Graham 2003a, 2003b) and characterize the natural spatiotemporal dynamics of ecosystems. Alterations in species composition and ecosystem processes that result from global change are a growing concern, especially as they become connected more clearly to human activities (Mack et al. 2000). At least four legitimate issues arise concerning future changes in species composition in contemporary ecosystems: (1) the potential loss of endemic species, (2) spatial homogenization of the biota as a result of the spread of introduced species and the extinction of native species, (3) the loss of ecosystem services, and (4) uncertainty regarding long-term consequences (Mack et al. 2000; Lockwood and McKinney 2001). Such issues are best considered in the context of emerging new forest ecosystems.

An emerging new forest ecosystem is one with a species composition (e.g., distribution of importance values among species) that is novel for the landscape on which it occurs (Lugo and Helmer 2004). This process is a natural one; the emergence of new forest ecosystems occurs because species invade, establish, and interact, even in the absence of human intervention. This differentiates emerging new forest ecosystems from those purposefully established by humans (e.g., plantations). An emerging new forest is different from a forest with no known history of anthropogenic disturbance in that it results from human activities that were *not* executed in order to achieve biotic change per se. Rather, new forests emerge at severely modified sites at which the succession of native species failed to reestablish a native forest. Emerging new forest ecosystems are characterized by three key elements. First, they occur mostly on sites that were modified severely by humans and which are incapable of sustaining many native tree species. Second, they become established through natural processes of dispersal, establishment,

and species interaction. Third, they involve novelty; that is, they encompass a combination of species that is different from what is typical for a particular landscape.

In emerging new forests in Puerto Rico, introduced species are dominant components of the flora (Lugo and Helmer 2004). Over the long term (~80 years), introduced species share dominance with native and endemic species that reinvade subsequent to initial colonization by introduced species (Lugo 2004b). Generally, emerging new forests in Puerto Rico occur on sites that support dry, moist, or wet forests and on calcareous, volcanic, or alluvial substrates. They are ubiquitous wherever humans have modified the ecological characteristics of geographic space significantly. Compared to native forests, the notable characteristics (Lugo and Helmer 2004) of emerging new forests in Puerto Rico are that they (1) have a small complement of endemic species, (2) are young (<100 y), (3) originate in highly fragmented landscapes, (4) are structurally simple (low basal area and low species richness), (5) contain few large trees (≥ 30 cm diameter at breast height), (6) arise on soil with low organic matter and high soil bulk density, (7) exhibit high temporal turnover of species, and (8) are similar in canopy structure and physiognomy to each other as well as to native forests.

The degree of difference in the species composition between new emerging forests and native forests with no known historical record of anthropogenic activity is a function of the type and intensity of disturbance. Disturbances of all types (natural or anthropogenic) offer opportunities for invasions and the reassembly of species (chapter 5). However, undisturbed tropical forests remain resistant to invasion even when subjected to natural disturbances (Denslow and DeWalt 2008), and emerging forests must cope with natural disturbances. The synergy between natural and anthropogenic disturbances, many of which produce novel combinations of ecological characteristics, predisposes sites to support emerging forests. The type and intensity of disturbance are thus responsible for changes in species composition, especially the distribution of importance values among species in forests. Forest responses to combined natural and anthropogenic disturbance can be characterized into four states:

1. When a natural disturbance (e.g., a hurricane) affects a mature or primary forest, the change in species composition is minimal, particularly in the long term (Crow 1980). In the short term, secondary forest species can become abundant, but primary forest species remain dominant. Introduced species are rare or absent.
2. When a natural disturbance (e.g., a hurricane) affects a mature forest that was deforested previously and used for agriculture (Scatena et al. 1996; Thompson et al. 2002), changes in the species composition and the distribution of importance values among species persist. Introduced species are rare or absent.
3. The abandonment of intensively used agricultural fields (Lugo and Helmer 2004) gives rise to species compositions that are different from those of native forests. Introduced species dominate early in succession and remain present in forests at maturity (Lugo 2004b).

4. The abandonment of highly degraded land leads to arrested succession and an herbaceous system in which trees fail to grow. Tree planting is required in order to restore forest conditions, and the early species composition is determined by the identities of planted species (Parrotta 1995; Silver et al. 2004). Over time, and without further human intervention, a new combination of species emerges, including native and introduced species.

Research in Puerto Rico (e.g., Lugo and Brandeis 2005) suggests that ecologists need to recognize variant ecosystem types (from pristine to artificial) associated with a gradient of human activity. Within this gradient, successional processes lead to particular combinations of species with familiar physiognomy and structure. These floras generally function in a manner comparable to that of native forests. However, the evaluation of various ecosystem functions is considerably less advanced than the description of the structure and species composition of these new forests. Once ecologists recognize the reality of emerging new forest ecosystems, the level of research concerning their functional characteristics will increase, thereby helping to resolve the current debate about the role of introduced species in a human-dominated environment.

Comprehensive study of the emergence of new forest ecosystems will provide new perspectives and avenues of investigation regarding four ecological issues. First, populations of some endemic species have an opportunity to flourish in emerging new forests, as has occurred in Puerto Rico (Lugo and Brandeis 2005). This happens as new forests mature and conditions for increased species diversity develop through restored soil fertility and microclimate.

Second, homogenization of the biota by the spread of introduced species and the extinction of native species (McKinney and Lockwood 1999) is not consistent with observations from Puerto Rico, as relatively few extinctions have been caused by introduced species, and when forests recover after deforestation, both native and introduced species generally persist (Lugo 2004a). However, during the early stages of establishment of emerging forests, species diversity is low, weedy species predominate, and rare species are absent. These trends reverse over time. Consequently, homogenization has a temporal trajectory that requires additional study. Moreover, the potential hybridization of introduced and native species (Ellstrand and Schierenbeck 2000) is a possibility that requires new research.

Third, little research has focused on the functionality of emerging ecosystems and the ecosystem services that they provide to society. This is an area in urgent need of comprehensive research, especially in light of the contention that ecosystem services are not compromised during the establishment of emerging new forest systems (Lugo and Helmer 2004).

Finally, uncertainty and surprise are fundamental characteristics of the behavior of complex systems, especially those containing an appreciable number of species that did not evolve in syntopy. Because novelty is a fundamental aspect of emerging new forests, uncertainty and surprise regarding successional trajectories, functionality, and ecosystem services are unavoidable. The only avenue by which to advance the understanding of this issue is long-term research on the properties of tropical ecosystems that span the gradient of anthropogenic disturbance.

The Integration of Social and Natural Sciences in Understanding and Forecasting Ecological Change

In the Luquillo Mountains and elsewhere, the integration of social and natural sciences is critical to a comprehensive understanding of pressing environmental issues that face society in the 21st century. After decades of focusing research on pristine areas of the tropics, ecologists now recognize that the principal influence on many processes in tropical ecosystems, including the pristine ones, is the activity of a growing human population (Turner et al. 1990; Clark 1996; Foster et al. 1998; Hall 2000; Watson et al. 2001; Lambin et al. 2003; LeClerc and Hall 2007). Initially, studies of human effects in the tropics focused on the effects of deforestation on biodiversity and global biogeochemical cycles (Gómez-Pompa et al. 1972; Detwiler and Hall 1988; Turner et al. 1990). In addition, the economic development of the tropics has been of interest to social scientists since the 1950s. However, few linked that development with environmental effects, even though a clear association exists between economic development and land use change (Hall and Ko 2005; Hall 2006). The outright conversion of tropical forests is only one of many aspects of human-induced ecological change in the tropics; less intensive development that leaves large proportions of forests standing still affects such environmental attributes as biodiversity, hydrology, and meteorology (Bonnell and Bruijnzeel 2004). As has been documented widely in the temperate zone as well (e.g., Foster et al. 1998), the general pattern of initial colonization, deforestation, and land degradation in the tropics often is followed by generalized economic development and industrialization, associated in turn with rural-to-urban migration and the abandonment of agriculture in economically marginal areas (Hall 2000; Rudel et al. 2002; United Nations 2002). In other words, as the basis for the economy shifts from solar to fossil energy, pressure on the land is reduced. In a few tropical regions, this has led to the establishment of large areas of secondary forest; Puerto Rico is the best documented case of this (Grau et al. 2003). As urbanization continues, these secondary forests might themselves be deforested as suburban areas expand away from urban centers (e.g., Thomlinson and Rivera 2000). All of these processes are underway on a large scale in Puerto Rico (Grau et al. 2003).

Future long-term research in the Greater Luquillo Ecosystem (the Luquillo Mountains and environs) should consider two important questions. First, to what degree are changes in forest cover, and the socioeconomic factors driving these changes, a general feature of other regions in the tropics (i.e., to what degree might Puerto Rico be a model for the rest of the tropics)? If the situation in Puerto Rico is unique, then perhaps there is little value in studying this aspect of the Greater Luquillo Ecosystem. We argue, however, that it is not. Instead, the situation in Puerto Rico, where the net effect is reforestation, illustrates a general relation between humans and tropical forests that is driven by the changing characteristics of tropical economies, especially the degree to which they become industrialized at the expense of land-intensive labor. Second, to what degree is it necessary to understand and account for human ecology in explaining ecosystem change? In other words, how complex are human interactions with the environment? We contend that such interactions are best understood in an integrated socioecological context

that explicitly defines the connections between humans and other components of nature (Hall 2000; Hall et al. 2001; Pickett et al. 2001; Hall and Klitgaard 2006; LeClerc and Hall 2007). Because Puerto Rico is small with a steep topography, its social and ecological systems are tightly coupled, presenting an excellent opportunity to address complex human-environmental dynamics. We address generality and complexity, and we outline a strategy for integrating human dynamics into the long-term study of the Greater Luquillo Ecosystem, as has been done for similar programs in the mainland United States (Gragson and Grove 2006).

The traditional view of human dynamics in the tropics is that of an unavoidable pattern of an expanding human population, growing out along newly created roads into tropical wilderness areas, leading to deforestation and destruction (Gómez-Pompa et al. 1972; Barbier 2005). In large part, this perspective has been correct. Many tropical countries have lost, and continue to lose, much of their forest cover (Turner et al. 1990; Hall 2000; Watson et al. 2001; Lambin et al. 2003). However, a few exceptions to this pattern currently exist in the tropics in places where economic growth, principally fueled by fossil fuels, has resulted in the growth of secondary forest, paralleling a pattern first seen in the United States and Western Europe (e.g., Andre 1998; Foster et al. 1998). Clear examples include some Caribbean islands (including Puerto Rico), northwestern Costa Rica, (Janzen 2000, 2002), Taiwan, peninsular Malaysia, and portions of the Andes (Rudel et al. 2002; Grau et al. 2003). One controversial viewpoint argues that these patterns apply to the entire tropics, which would guarantee that human development will not lead to a catastrophic loss of tropical biodiversity (Wright and Mueller-Landau 2006).

Grau et al. (2003) presented a detailed assessment of such an ecodemographic transition in Puerto Rico. During the first half of the 20th century, the population of Puerto Rico increased from 1 million to just over 2 million inhabitants, and forest cover was reduced to approximately 5 percent of the island (much of this in shade coffee). However, Puerto Rico was one of the earliest parts of the tropics to be developed explicitly for industrial manufacturing, as a result of close ties with the United States; the desire of many in the United States to take advantage of the relatively well-educated, inexpensive, and compliant labor force; and the success of the program "operation bootstrap," initiated in 1948 (Dietz 1987). Although the population almost doubled again during the second half of the century, forest cover increased from 5 to 35 percent, such that much of the island now supports secondary forest (figure 8-12). These changes were initiated by the abandonment of marginal agricultural lands in mountainous regions and a concentration of the human population in urban areas (Rudel et al. 2000) concomitant with a dramatic increase in the portion of the economy devoted to manufacturing and an increase in oil consumption from a very low level to about 70 million barrels per year in 2000. The rural population in Puerto Rico actually decreased during the second half of the 20th century, even though the overall population was growing quite rapidly (Grau et al. 2003).

Grau et al. (2003) were careful not to extrapolate the results from Puerto Rico too broadly, because much of the economic dynamics that drove the change in land use might result from the special political relationship between Puerto Rico and the United States. Some recent data suggest, however, that increased free trade and

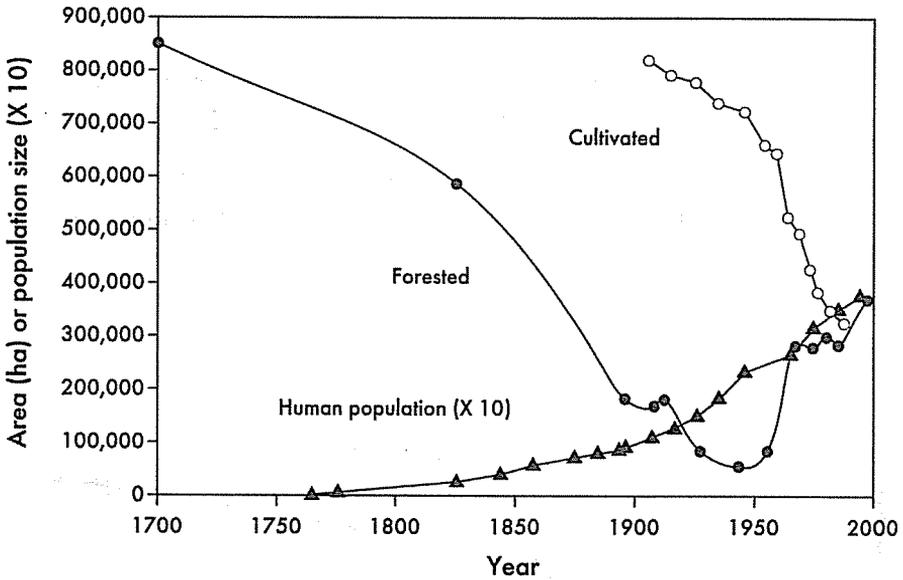


Figure 8.12 Temporal trends in land cover and human population size in Puerto Rico over 3 centuries.

other aspects of globalization, including the continued expansion of fossil-fuel-based economic activities, allow Puerto Rico to serve as a model for other parts of the tropics. An example can be drawn from patterns of urbanization. As revealed by a recent United Nations Population Division study (United Nations 2002), the current proportion of the human population in urban areas in Puerto Rico, and projected increases in coming decades (figure 8-13), are similar to such patterns throughout the tropical countries of the Americas (Wright and Mueller-Landau 2006). Levels of urbanization (i.e., the proportion of the entire population living in urban areas) in the American tropics range from 60 to 85 percent, bracketing the current value in Puerto Rico (72 percent). These values are very different from those of central Africa and Southeast Asia, where current levels of urbanization are about 35 percent and are not expected to exceed 60 percent by the year 2030. Guyana is the only tropical American country that currently has such a low level of urbanization (33 percent). The high levels of urbanization in most countries of tropical America offer hope that future effects of the growth of human populations, which will occur predominantly in urban areas, will minimize the anthropogenic modification of forests and other native habitats in rural areas and lead to an increase of secondary forest, as occurred in Puerto Rico (Grau et al. 2003). The important point arising from this crude assessment is that Puerto Rico, in the context of the Neotropics, has followed a pattern similar to those of many other countries.

Levels of urbanization, of course, are only one dimension of socioeconomic change in developing economies. For example, the level of urbanization in Brazil is higher than that in the United States (figure 8-13), but no one would claim that the standard of living or the effect of the Brazilian citizens on their forests and environment are the

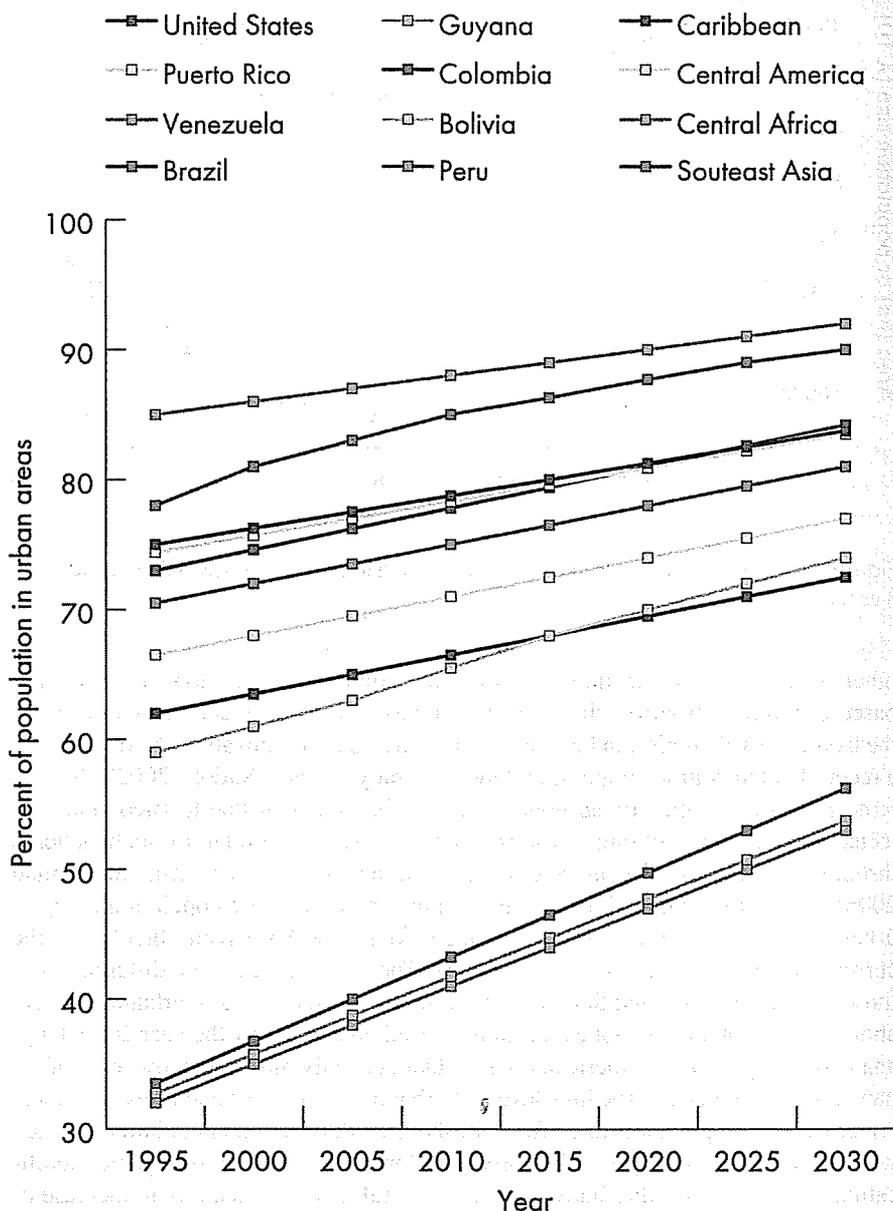


Figure 8.13 Predicted percentage of human population in urbanized areas for various tropical countries or regions. Puerto Rico (included both individually and pooled with all Caribbean countries) and the United States serve as references. The order of population projections for 2030 (highest to lowest) corresponds to that of countries (associated symbols) in the legend.

same as those in the United States. To understand such differences, one must delve deeper into the relationship between economic development and human influences on the environment. The reversal in forest losses with development, as observed in Puerto Rico (Rudel et al. 2000) and elsewhere, is of particular interest to those seeking to understand the relationship between human activities and land use change, and it might reflect a more general phenomenon of human ecology. Forest cover does not necessarily decrease monotonically with increasing human population in the developing tropics. Rather, human effects on the environment are nonlinear and complex. In particular, it is critical to understand and assess the relationship between population growth and the degree of industrialization, because the real driver of deforestation probably is the degree to which the human economy depends directly on the quantity of solar energy intercepted and used by agriculture, pastures, and other solar, non-forest-based economic activities. Because there has been a trend in parts of the tropics to displace these solar-based economies with fossil-fuel-based economic activities such as manufacturing, tourism, and even ecotourism, there exists, for some regions, the possibility of continued growth of the human population and the economy with a concomitant decrease in the use of land-based resources. Whether the environmental effects stemming from the use of fossil fuels are greater than the effects of deforestation is for others to ponder. Moreover, human perceptions of the value and meaning of nature and the manner in which government policies and regulations drive patterns of development deserve additional study and consideration from the perspective of sustainability (Pickett et al. 2001).

The initial loss of forest cover but subsequent gain with increasing economic development has been called the "forest transition" (Rudel 1998; Rudel et al. 2002; Perz and Skole 2003). If real and, more important, general, this forest transition could be an example of an environmental Kuznets curve (EKC) (Kuznets 1955; Dinda 2004), an empirical observation that the degradation of the environment increases with economic development until, at some point, further development leads to a decline in human effects. A common example is the pollution of air and water, which generally increases initially with development but then often decreases (at least locally) with continued development. The actuality, degree, mechanisms, and value of EKCs have been widely debated, with biophysical (e.g., declining soil quality), demographic (e.g., rural-urban migration), economic (e.g., capital scarcity, transitions from agrarian to industrial to service-based industries), political (strong democratic traditions), and sociological (e.g., demand for a cleaner environment) factors prominent among the many explanations proffered (Rudel 1998; Ehrhardt-Martínez et al. 2002; Perz and Skole 2003; Dinda 2004; Khanna and Plassman 2004). It is clear that different environmental factors have different Kuznet curves (Khanna and Plassman 2004), with the change in forest cover being one of the earliest and, therefore, key transitions (Rudel 1998; Ehrhardt-Martínez et al. 2002). However, recently there have been claims that the manner in which development now proceeds in tropical countries might be so different from the way in which their temperate counterparts developed that the forest transition concept (Klooster 2003) and EKCs in general might not apply (Stern 2004). Most critical, the reliance of most economies on fossil fuels, which generate CO₂ pollution and lead to global warming (IPCC 2007), is the most important EKC, and one for which

modern economies are nowhere near the turning point, as energy use and release of CO₂ show no sign of decreasing for most countries. More generally, and contrary to the viewpoint of Wright and Mueller-Landau (2006), increased urbanization and economic development in tropical countries must lead to a larger ecological footprint for these cities, with concomitant demands for increased resources and increasing local and global pollution (e.g., Hall 2000).

A separate issue is the degree to which present models, including economic models, are adequate to represent in a comprehensive and integrative way the changes that are taking place in Puerto Rico and that are expected to take place in the future. In particular, contemporary economic models might not be adequate to represent or guide the future (Hall 2000; Hall and Klitgaard 2006; LeClerc and Hall 2007). Instead of, or in addition to, neoclassical models, a more biophysical approach might be necessary in order to understand economics and the effect of humans on the environment. An example is the identity of the real drivers that allowed the reforestation of Puerto Rico. The standard explanation is that Puerto Rico has changed from a principally agriculturally based economy to an increasingly urban manufacturing- and service-based economy. Another way to view this, which is more aligned with a biophysical perspective, is that the energy basis of the Puerto Rican economy has shifted from a solar basis early in the 20th century to a fossil-fuel-based one today. Thus it is (only) the availability of cheap oil that has allowed the development of today's economy, which in turn has allowed the forests to regenerate. Given increasing evidence for "the end of cheap oil" (e.g., Campbell and Leharrère 1998) and the very large dependence of Puerto Rico on oil as a basis for its manufacturing and service economy, it is not clear that this approach (increased use of fossil fuels) will remain feasible for a great deal longer. If not, a resurgence of intensive deforestation in Puerto Rico and other such areas might be forthcoming.

How would a detailed understanding of human ecology in Puerto Rico improve our understanding of the Greater Luquillo Ecosystem? A conceptual diagram illustrates the key factors for the development of an integrated perspective on human and natural systems in the Luquillo area (figure 8-14). This model distinguishes human, geomorphic, and ecological processes and proposes that the most significant interactions among these processes are regulated by the disturbance regime. External drivers, such as long-term climate change, are important in regulating the disturbance regime (e.g., increased sea surface temperatures might cause an increased frequency of severe hurricanes [Emanuel 2005; Webster et al. 2005]). The key integrating feature of this model is that ecosystem services feed back from geomorphic and ecological processes to the human component.

There are a number of ways that this conceptual approach can lead to an integrative understanding of human and natural systems. These include several areas of current interest, focusing on how increasing urbanization (1) feeds back on the climate and (2) is regulated by geomorphology, and (3) how this in turn feeds back on agricultural production and the provision of ecosystem services.

The feedback of human processes (i.e., the expansion of the urban zone) on local climate is illustrated by an "urban heat island" associated with San Juan, where city temperatures are higher by about 2°C (usually) to as much as 10°C (occasionally in

Integrating human and natural systems in the greater Luquillo ecosystem

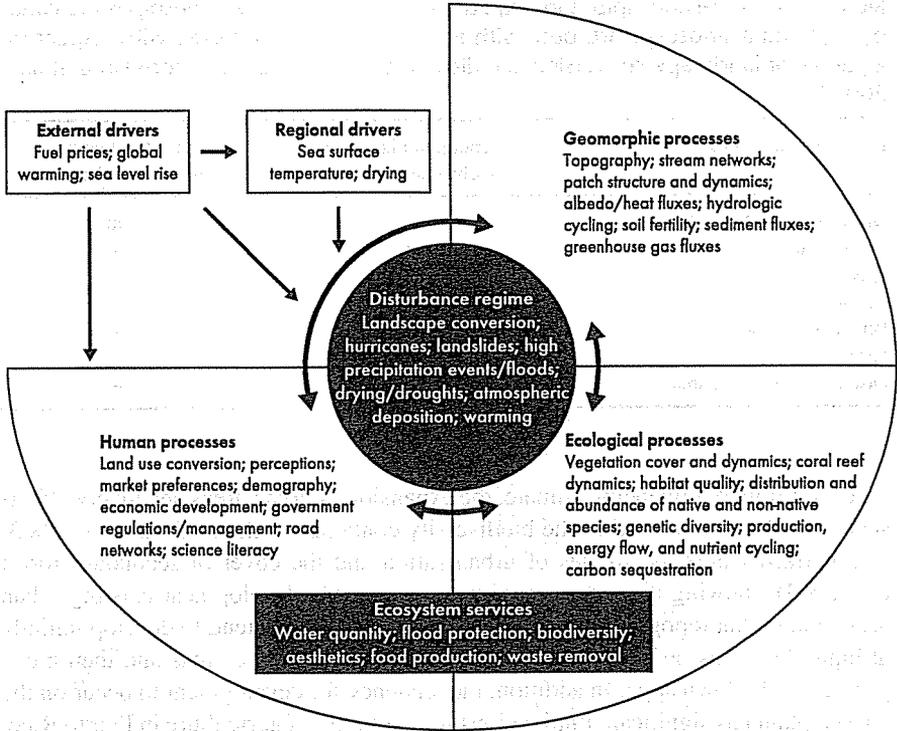


Figure 8.14 A conceptual diagram for the integration of human and natural systems in understanding and forecasting long-term change in the greater Luquillo ecosystem (the Luquillo Experimental Forest and adjacent urban areas, including San Juan). The entire ecosystem is divided into three interacting components: human, geomorphic, and ecological processes. “Disturbance regime” is placed at the center of the three interacting components to emphasize the degree to which disturbance regulates these interactions. Similarly, ecosystem services are a critical feedback between ecological/geomorphic processes and human processes. External drivers emphasize prices (particularly liquid fuel) and local and regional climate.

the dry season) because of the existence of the urban construction itself (e.g., Velázquez-Lozada et.al. 2006; Murphy 2007). The transition from the forested to the suburban environment has as great an effect on meteorological characteristics as that between the urban and the suburban environment (A. Chen and D. Murphy, personal observation). Thus, development to the east of San Juan is extending the urban heat island toward the Luquillo Mountains, a major source of municipal water. This is an important concern because global climate models predict drying of the Caribbean region (Neelin et al. 2006). Urban heat islands such as that associated with San Juan might be expected to exacerbate the effect of global climate change, both locally and in adjacent forest (Velázquez-Lozada et al. 2006). As possible evidence of this interaction, Wu et al. (2007) recently found that the proportion of rainfall leaving the Fajardo watershed as streamflow is decreasing.

Table 8.3 Influence of landscape attributes on changes in land cover in Puerto Rico. A positive relationship is indicated by "+," a negative relationship is indicated by "-", and a landscape attribute with effects that were not tested with respect to a particular landscape conversion is indicated by "nt." (Modified from Grau et al. 2003.)

Landscape attributes	Agricultural land lost to urban development	Agricultural land lost to secondary forest
Distance to existing urban areas	+	nt
Population	nt	-
Elevation	-	+
Distance to roads	-	+
Percentage of slope	-	+
Farm size	nt	-
Distance to reserved area	-	+

In addition to influencing climate, the expansion of urban areas negatively affects secondary forests, as well as the biodiversity contained in them. Grau et al. (2003) summarized landscape studies of urbanization and the cover of secondary forest (table 8-3), showing that urban areas most commonly develop near existing urban areas and on flat topography. In contrast, secondary forests tend to develop initially at high elevations on steep topography near existing reserve areas and then move progressively downslope. In addition, the tendency for development to occur on the coastal plain has significant implications for the future of agriculture in Puerto Rico. Much of the development takes place on what were once prime agricultural lands, implying difficulties for feeding people should the current, petroleum-based economy become less viable. As a point of concern, Puerto Rico lost 6 percent of its prime agricultural lands to urbanization between 1977 and 1994 (López et al. 2001).

Human actions also feed back on the ecological connectivity of streams. Dams and water withdrawals strongly influence the biotic structure of the island's streams, strongly affecting migratory species (e.g., Greathouse et al. 2006a, 2006b). As such, there might be significant economic benefits to maintaining free-flowing streams (González-Cabán and Loomis 1997). This has led to an ongoing effort to develop an integrated understanding of stream and road networks (NSF Biocomplexity Project 2009) that should provide a firm basis for developing a wider understanding of the socioecological system of the Greater Luquillo Ecosystem.

Each of these examples emphasizes the influence of land cover change on climate, rainfall, and biodiversity, as modified by the geomorphic setting. What is clearly lacking is a detailed understanding of the dynamics of the human system and how ecological systems feed back to them. For the immediate future, an integrated research strategy should focus on the human population (including institutions and perceptions), biodiversity, and water as key elements in tropical ecosystems. The goal of the strategy should be to develop a series of validated models, the integration of which would facilitate the prediction of human population density and distribution, forest cover, and the biodiversity of key taxa, as well as water quality, quantity, and biodiversity in streams flowing through the landscape. Other factors deemed to be of

importance (e.g., NPP, soil fertility) should be measured, modeled, and integrated into this strategy. The models should incorporate three characteristics:

1. A spatially explicit land use model would allow us to predict land cover and effect on aquatic resources under a variety of development scenarios. A number of good candidates for modeling approaches currently exist (Hall et al. 1995; Acevedo et al. 2001; Engelen and Gutiérrez 2003; Veldkamp and Verburg 2004). The model should combine biophysical factors (e.g., using the watershed approach [Pickett et al. 2001]) with key sociological, economic, and political factors. With respect to political considerations, an important issue in Puerto Rico would be the degree to which the promulgation and enforcement of public planning could guide future urban development. That is, the model should be relevant not only to biophysical and social scientists, but to regional planners as well (e.g., Engelen and Gutiérrez 2003).
2. A model should link land use cover to spatial patterns of and changes in local temperature and precipitation, the latter being a key driver of aquatic systems. Wu et al. (2006, 2007) have developed a series of models for the Luquillo Mountains that predict cloud cover, evapotranspiration, and stream flow as a function of land cover. Such models could be adapted readily to a larger scale. A model has been developed for the entire island of Puerto Rico that indicates that deforestation will reduce annual precipitation (van der Molen 2002). The development of a model integrating regional and local climate changes and their effects at the scale of the Greater Luquillo Ecosystem might be a challenge. However, if this were possible, then, in combination with global climate models for the northern Atlantic region (Neelin et al. 2006), it would facilitate the prediction of stream water quantity through time. The integration of a land use model with a precipitation and hydrology model would be used to predict water quality, which in turn would be used to predict the biodiversity of key taxa.
3. The diversity of secondary forests and some key terrestrial taxa (e.g., terrestrial arthropods) in Puerto Rico is well described (summarized in Grau et al. 2003), and studies of other key taxa are underway. Land use cover could be combined with these data in a model that incorporates life zone (determined predominantly by temperature and precipitation [Ewel and Whitmore 1973]) or environmental gradients (Hall et al. 1992) straightforwardly in order to predict terrestrial biodiversity. A forest model also would have to incorporate factors controlling the distribution of trees and other key taxa along the elevational gradient in the Luquillo Mountains (Abbott-Wood 2002; Wang et al. 2002). In this way, one could predict changes in forest zonation caused by long-term drying of the climate in Puerto Rico owing to reduced forest cover or global climate change.

We now accept that humans are the principal agents of change in most tropical ecosystems. Accordingly, the Luquillo LTER is beginning to integrate this perspective explicitly into a number of facets of its research program. We propose that this can be achieved by developing models that incorporate human effects on the environment, as long as effects from social factors in the human population are given

sufficient weight. A wild card in our analysis would be the longer term effects associated with "the peaking of oil." This peak, and its presumed accompaniment, "the end of cheap oil," is likely to have enormous effects on land use in Puerto Rico as, perhaps, the tourism industry contracts, the cost of commuting increases, and the need for locally grown food increases. It might be likely that these processes will be dominant forcing functions for future land use in Puerto Rico (e.g., Hall 2000; Hall and Klitgaard 2006). A long-term strategy for understanding ecosystem dynamics in the Greater Luquillo Ecosystem (specifically, land use, biodiversity, and aquatic resources) must consider both direct and indirect effects of human populations. Once constructed, such a model could be used to guide local decision making (e.g., land use planning) and serve as a rubric for understanding the potential for human effects on ecosystems of other Neotropical countries.

Concluding Remarks

Long-term associations among scientists with multiple disciplinary backgrounds, as well as the inclusion of young scientists with fresh perspectives, contribute to the vigor and productivity of the Luquillo LTER Program. As such, the program acts as an incubator for new research ideas that emerge from the in-depth understanding of complex ecological systems within the context of evolving theory about populations, communities, and biogeochemical processes. Our divergent perspectives challenge dogmatic assumptions and expand the frontiers of ecological understanding in an integrated, innovative, and synthetic fashion.

Following in this tradition, it is clear that research in the program will continue to expand our understanding of geographic and ecological gradients of Puerto Rico via synoptic approaches, more intimately incorporate social and natural science perspectives, explore larger scale manipulative and observational experiments to produce a mechanistic understanding of responses to disturbance and successional change, and assume greater relevance to society by addressing important issues that are central to management, conservation, and policy. At the same time, our future likely will continue to leverage our strengths as (1) the hot and wet environmental anchor of the U.S. LTER Network, (2) a portal for network research to engage tropical issues, and (3) a complex, disturbance-mediated ecological system that is sensitive to modifications arising from global change.

Summary

Research in the Luquillo Mountains has documented the variety of ways in which the biota responds to disturbance and the way in which the biota influences the frequency, magnitude, and intensity of disturbances. Disturbance increases the complexity of interactions (i.e., macro- and microclimatic, biogeochemical, biotic) that control the flow of energy and the cycling of materials through ecosystems. It affects the life history and demographic parameters of species at fine spatial scales and creates a mosaic of patches at large spatial scales that, together, influence the

dispersal of individuals among patches (i.e., the degree of connectedness) in a species-specific fashion. Such a cross-scale perspective provides a spatially explicit framework for understanding the assembly of species in disturbance-mediated environments. Moreover, differences in biodiversity affect ecosystem processes through species complementarity, organismal traits, and trophic interactions. Soil microorganisms, as well as the timing, quantity, and quality of litter deposition, play a critical role in affecting the dynamics of carbon and nutrient cycling over short and long temporal scales. These effects are mediated by scale, ultimately determining the resistance and resilience of ecosystems to disturbance.

Within this context, environmental gradients provide a platform for contrasting the role of particular species with respect to resilience and resistance during the interplay between disturbance and succession. In addition, multiple or sequential disturbances have complex spatial and temporal linkages, especially in riparian and stream communities, where species that connect freshwater and marine communities with those in headwater tributaries and riparian forests provide pathways for pulsed flows of energy and materials. From a terrestrial perspective, anthropogenic disturbance facilitates invasions by introduced tree species, sometimes culminating in the emergence of new forest communities dominated by introduced taxa. In mature forests not subject to intense anthropogenic degradation, introduced species might occur sporadically as rare species in hurricane-induced gaps, but these populations rapidly decrease in number after canopy closure. Thus, the development of new emerging forests does not necessarily result in the loss of native species or a reduction in species richness. The recognition and study of emerging new forests are important for understanding how organisms respond to anthropogenic disturbances, including global climate change. Finally, forecasting change requires the integration of biophysical and social science perspectives, an approach we have developed for studying interconnected ecosystems of the greater Luquillo region of Puerto Rico, extending from ridgetop to coastal environments.

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A Caribbean Forest Tapestry

*The Multidimensional Nature of
Disturbance and Response*

Edited by

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