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Management Implications and Applications of Long-Term Ecological Research

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Key Points

- Uses and conservation of tropical forests reflect the economic and social circumstances of their associated human populations.
- Conservation efforts in the Luquillo Mountains have benefited from research activity since the 1920s.
- Early research in Puerto Rico focused on descriptions of flora and fauna, tree nurseries and plantation establishment, tree growth, and forest products, whereas recent research focuses on ecosystem functioning and services, climate change, landscape scale patterns, disturbances, and land use legacies.
- Ecological information from both aquatic and terrestrial ecosystems facilitates the sustainable use of natural resources while informing methods for conserving ecosystems and their services.
- Results from research also help in the interpretation of environmental change and in the design of resource conservation strategies in the face of uncertainty.
- A new era of conservation based on ecological knowledge is emerging. Conservation is increasingly based on sustainable development goals and implemented in collaboration with citizens. Management in this era will be more flexible in outlook and adaptable to a continuously changing environment.
- We give examples of surprise events for which we have no explanation, and which we did not have the means to anticipate. These examples collectively demonstrate that the management of complex ecosystems requires continuous long-term research.

Introduction

In this chapter, we highlight the contributions of long-term ecological research (LTER) activity to tropical forest conservation issues. We begin by reviewing the context for management activities in the Luquillo Experimental Forest (LEF), including both the historical changes in forest cover and the research activity that resulted from these changes. We then review what management is and its relationship to disturbances and conservation, and we follow with a discussion of the implications of long-term research in current conservation issues in the tropics. To do this, we use four examples from the Luquillo LTER. Next we describe applications of LTER results for tropical conservation and provide six examples. Finally, we address the question of how the research conducted in the LEF has informed and challenged past paradigms developed in the tropics, and we finish the chapter with what we consider to be our future research needs and priorities. Our approach in this chapter is to be illustrative and synthetic, rather than to provide a comprehensive review of the implications and applications of our research.

Management in the Luquillo Experimental Forest

The LEF, also known as the El Yunque National Forest (previously the Caribbean National Forest), constitutes the core of forests in the Luquillo Mountains and is a site where management and research are concentrated. Currently, between 38 and 58 percent of the LEF is considered primary forest (Lugo 1994). Primary forests are areas where forest cover has existed continuously for centuries. The rest of the LEF experienced changes in forest cover owing to human activities (Scatena 1989; García Montiel and Scatena 1994; Foster et al. 1999; Thompson et al. 2002; Lugo et al. 2004). Aerial photography, available since 1936, allows quantification of changes in the forest cover of the LEF. In 1936, 34 percent of the current LEF was deforested or secondary forest, and 49 percent had >80 percent cover (Foster et al. 1999). In 1989, more than 97 percent of the LEF had continuous forest cover. By 2002, the LEF was almost 100 percent forested. Outside of this forest boundary, however, land cover had changed significantly, mostly transitioning from agriculture to forest and urban landscapes (Lugo et al. 2004).

Between 1936 and 1995, the landscape outside the periphery of the LEF experienced a cycle of fragmentation and consolidation (Lugo 2002), while the economy changed from an agricultural, solar-based economy to one based on fossil fuels. During a period of intense agricultural use (early 20th century), most of the land surrounding the LEF was being managed for agriculture. During this time, there were small urban fragments and patches of forest cover. In satellite images of the area, fragments were defined as groups of pixels comprising homogeneous land cover such as forest, agriculture, or urban. Landscape fragmentation reached a peak in the 1980s following the abandonment of agricultural lands (Lugo 2002). This peak coincided with the increasing dominance of small patches of regenerating forests throughout the region, as well as patches of urban cover. Increases in forest and urban land cover types were generally at the expense of low-lying agricultural lands, a process that contributed most significantly to the higher rates of fragmentation recorded during this period. More recently, these urban and forest patches have coalesced, resulting in a smaller number of larger patches of both forest and urban areas (i.e., less fragmentation).

The products and services required by the socioeconomic system in the communities surrounding the LEF changed dramatically from the time of small-scale agricultural activities of indigenous peoples to the extractive period of the Spanish government, to the agricultural period of the 20th century that was dominated by coastal sugar cane plantations, to the present with the current high-energy urban system. For example, indigenous peoples introduced fire as an ecological factor in Puerto Rico and locally modified valleys and flood plains for agriculture (Scatena 1989; Burney and Burney 1994). The Spanish mined rivers and exploited existing natural capital by inventorying and cutting valuable trees (chapter 1). Their main interest was using, rather than conserving, resources, but they also established guidelines to protect riparian zones and control erosion (Wadsworth 1949, 1970; Scatena 1989). During the early 1900s, land managers in Puerto Rico were influenced by a "the world is my garden" mentality and were keen to restore significantly altered landscapes to their previous condition. To improve conditions and even improve upon nature, they planted what they thought were the most desirable trees, as well as those that offered economic returns. Forest managers also seeded streams with fish species (i.e., trout that were highly valued in temperate zones but which did not do well in Puerto Rico [Erdman 1984]), built dams to harness stream power, and sought to improve tree growth. The ecological impacts of natural disturbances were not considered because the focus was on improving the dire livelihood of humans in Puerto Rico (Murphy 1916; Zon and Sparhawk 1923; Roberts 1942). Recreation was a luxury for most people at this time and involved making trips to the city, not to the forest.

In response to the need to improve the living conditions of the rural population on the island, research related to resource uses and improving the harvesting of products became a prominent activity in the LEF after the 1930s. Over the next 65 years, research in the Luquillo Mountains evolved from its initial focus on reforestation, forest products, and increasing land productivity to an emphasis on the maintenance of ecosystem functions and services (Wadsworth 1970, 1995; Lugo and Mastroantonio 1999). The research history in the LEF shows that adding new lines of research did not preclude the continuation of older lines of research, emphasizing the building of fundamental knowledge supporting forest conservation. For example, the first decade of U.S. Department of Agriculture (USDA) Forest Service research (1939 to 1949) identified 17 lines of scientific inquiry for its research agenda. At present, there are 69 active lines of research. They include all but one of the lines of inquiry identified during the first decade (figure 7-1). From the outset, Forest Service research was mechanistic and empirical, as was management, which used a top-down approach in which technical people provided the research agenda to those implementing the research on the ground. However, by the 1950s, Forest Service research had begun to consider input from farmers and adapt project implementation based on local knowledge. It employed local people in reforestation projects, road maintenance, and other public works. Analysis of the research productivity of Forest Service scientists and collaborators shows that all lines of research ultimately contribute to forest conservation (table 7-1).

Until the 1980s, much of the research in the Luquillo Mountains was based on repeated field observations and typically involved little more than measuring tapes, field books, and physically strenuous work. Scientists established plots in areas selected to represent the region and recorded changes in the structure and species

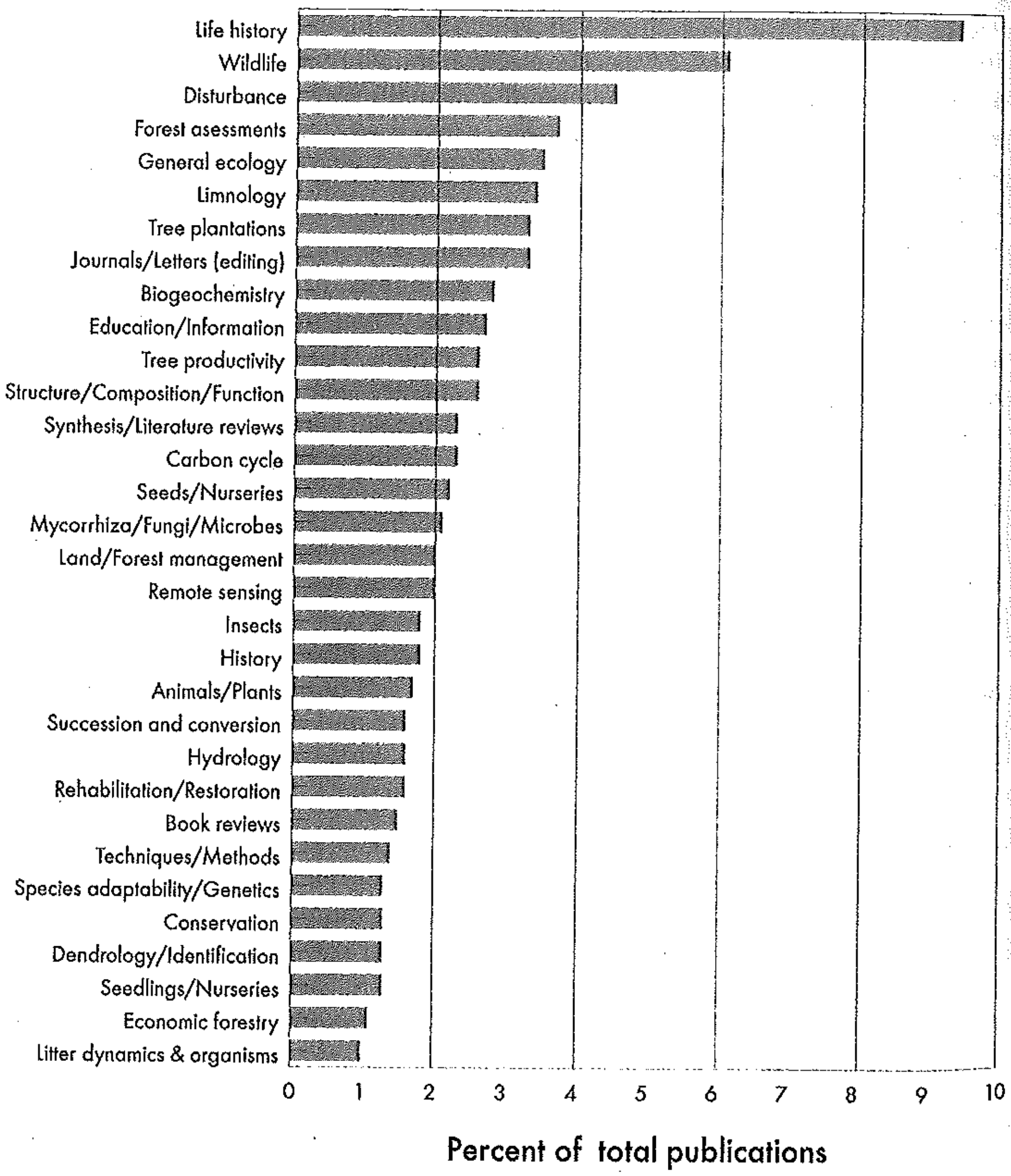

Figure 7.1 Number of publications of the International Institute of Tropical Forestry according to topic of research. The total number of publications represented is 2,000 over a period of 65 years. Data by decade of research are available from the senior author. For each publication, only the dominant topic or topics were recorded.

composition over time. Since the 1980s, there have been major advancements in the tools for research, but the goal is similar: to understand changes in ecological space over time. Although researchers continue to study many of the research plots and plantations that were established in the 1940s and 1950s, technology now allows for a greater scope of field research, with an increased capacity for data collection, storage, and analysis.

Table 7.1 Twenty topics of research in the Luquillo Mountains and their relevance to conservation

Topic	Relevance
Tree and vine identification	Increases fundamental knowledge for conservation activities
Parrot recovery	Prevents the extinction of a species
Tree species selection for different sites	Increases the effectiveness of reforestation
Reforestation techniques	Ensures the success of tree planting programs
Tree nursery techniques	Ensures the effectiveness of developing trees for reforestation and planting programs
Urban tree plantings	Allows the establishment of green areas in urban settings
Silvicultural treatment for cutover and volunteer forests	Allows the management of secondary forests for multiple uses
Properties of Caribbean woods, drying, and preservative treatments	Provides knowledge in support of wood-using industries
Rehabilitation of landslides	Allows the reestablishment of forests and the stabilization of hazardous slopes
Wood production via plantations	Increases the productivity of the land and reduces pressure on native forests
Techniques for the long-term monitoring of tree growth, tree turnover, and wildlife abundance	Saves time and increases the effectiveness of biodiversity-monitoring programs
Restoration of biodiversity on degraded lands	Returns degraded lands to productive use
Vegetation surveys and forest inventories	Assesses biodiversity and contributes criteria for the sustainability of development
Understanding tropical forests	Increases knowledge of forests (the main land cover of these regions and the principal providers of ecological services to people)
Safe water yields from watersheds	Assesses the amount of clean and abundant water for society
Chemical content and composition of plant, soil, water, and air in the tropics	Increases understanding of the functioning of forests and helps estimate their role in cleaning air and water
Understanding tropical forest function	Increases knowledge of the services provided by forests to people
Understanding forest disturbances such as land cover change, hurricanes, global change, and ionizing radiation	Increases knowledge about strategies for managing change
Understanding how silvicultural practices influence wildlife populations, soil fertility, greenhouse gas emissions, and water yield	Increases knowledge needed in order to maintain biodiversity while managing stands
Site effects on tree growth	Provides strategies for maintaining tree growth in spite of land cover changes

Management, Disturbances, and Conservation

Management is a regime of human-motivated interventions that can be understood within the context of disturbance ecology. Many management practices associated with agriculture and forestry alter ecological space in order to create a state that enhances the production of valued, often introduced or domesticated species such as ornamentals, crops, timber, or livestock. In these schemes, management retards natural secondary succession via the selective application of system-specific activities that ideally mimic natural disturbances (e.g., burning, canopy opening) or their effects. Alternatively, management might represent intervention by humans in an existing anthropogenically disturbed site (e.g., mines, clearcuts, and abandoned pastures). In this case, the intent is to increase resiliency; hasten succession toward a particular goal; or restore biodiversity, the productive capacity of the ecosystem, and ecosystem services. If the goal is to manage those sites so that they achieve a state with desired functional characteristics such as forest productivity or the production of clean water, without regard for the biotic composition or structure, then rehabilitation (*sensu* Brown and Lugo 1994) is the focus of activities. If the goal is to manage the system such that its state is within defined boundaries of the predisturbance condition with respect to the biotic composition, structure, and function, then restoration is the focus. The pervasive nature of anthropogenic disturbance often means that natural ecosystems become reduced in their extent and highly fragmented, with altered climatic and environmental conditions (Wiens 1976; Sala et al. 2000). This approach often increases the likelihood of localized species extinction, as well as decoupled ecosystem processes and services. Ecosystem-based management techniques attempt to design local environments in order to reduce the likelihood of species extinction and ensure the continued provision of ecosystem services.

Anthropogenic disturbances have been occurring for millennia in Puerto Rico and elsewhere (Crosby 1986; Perlin 1989). Signatures of these disturbances remain in forest landscapes and modify the current ecosystem structure and function at varying spatial scales across continents (Diamond 2005; Mann 2005). Past human disturbances have modified ecosystems at equally broad temporal scales, so that it has become difficult to identify what is a "natural" ecosystem (Cronon 1996). Thus, recent management activities often occur in ecosystems that have already been modified by humans. The changes that have occurred in the forests of Puerto Rico are a testament to the dynamic nature of ecosystems in the face of human and natural disturbances (see chapters 1 and 4).

Given the objectives of management activities discussed above, it is critical to link management with conservation. We believe that management and conservation must be synonymous. Considering them as conflicting activities is a false dichotomy that hinders the protection of biodiversity and ecosystem services. The importance of considering management and conservation as facets of each other became apparent early in the management of tropical forests because many tropical economies are extraction-based. Because many hot spots of biodiversity in the world are also located in tropical areas that have high poverty rates and political instability, significant challenges in implementing conservation projects exist in these regions (Wilshusen et al. 2002).

However, not until the early 1990s did the scientific community and resource managers outside the tropics recognize these challenges and acknowledge that the successful implementation of conservation projects requires the simultaneous linking of management activities with conservation efforts and the inclusion of the constraints imposed by society (Wells and Brandon 1992; Vogt et al. 2000, 2002b).

A new discipline, Conservation Biology, developed in the 1980s with three guiding principles (Meffe and Carroll 1997) that conservation is based on: (1) evolutionary change, (2) dynamic ecology, and (3) the human presence. These principles orient conservation activities toward the stewardship of natural biodiversity through sustainable development. Thus, the aims of conservation are the same as those of resource management. Aldo Leopold said it best (Meine 1987:148) in an observation about the use of land by farmers:

> This paper proceeds on two assumptions. The first is that there is only one soil, one flora, one fauna, and hence only one conservation problem. Each acre should produce what it is good for, and no two are alike. Hence a certain acre may serve one, or several, or all of the conservation groups. The second [assumption] is that economic and aesthetic land uses can and must be integrated, usually on the same acre. The ultimate issue is whether good taste and technical skill can both exist in the same land owner.

The importance of linking conservation and sustainable development is widely accepted by the scientific community and conservation practitioners. However, formally linking these concepts in order to produce a mechanistically based tool with which to assess the sustainability of resource uses and conservation has been difficult in complex human landscapes (Wells and Brandon 1992; Vogt et al. 1997, 2002b). In this book we treat "conservation" as synonymous and interchangeable with "management," because in principle their goals are the same: to "save all the parts" (*sensu* Leopold 1953) and to satisfy human needs sustainably, using the best science available, within the social and cultural context of the people that depend upon the products and services of an ecosystem. Both management and conservation include the goal of the preservation of wilderness by excluding humans. But conservation or management actions are more likely to succeed if they incorporate human needs and activities (Salwasser 1997). A preservation-only agenda usually fails, as would an agenda that excluded preservation.

Implications of Luquillo Long-Term Ecological Research

This book's synthesis of LTER at the LEF has led to a series of broad generalizations that are useful guidelines for forest managers dealing with management issues at various scales of organization from populations to watersheds and life zones. In this section, we present four examples that demonstrate particular conservation actions and strategies. These four examples include an examination of the implications of ecological space for choosing management units, species life histories in relation to disturbances, the limits of forest resilience, and the notion of ecosystem self-organization. These four examples have helped us develop an approach to and understanding of particular management situations that are common in the tropics.

Ecological Space and Management Units

Shifts in ecological space (chapter 2), whether from local or global change, influence the species composition and rates of ecological processes in affected sites. Depending upon the causal force of the change, the movement in ecological space can be cyclical or directional. Hurricane Hugo, for example, caused a large but temporary change in ecological space across the Luquillo Mountains; after a decade or so, the species composition at a scale of hectares returned to prehurricane conditions (chapter 5). In sites where human-induced change of ecological space altered soil structure and chemistry, species shifts have lasted decades and appear irreversible (Thompson et al. 2002; Lugo 2004; Lugo and Helmer 2004), challenging the concept of "recovery to the original state."

Shifts in ecological space have significant implications for conservation and for the ability of managers to achieve the desired outcomes or management objectives. In this context, the selection of boundaries for conservation units becomes critical to the effectiveness of the conservation activity, and therefore we begin our discussion with the issue of management units.

The initial step for forest management is to identify management units in geographical space. Traditionally, foresters subdivide forests into compartments, and compartments into stands. These are spatial units with similar objectives and management tools, and the long-term objective is to produce similar ecological conditions across the compartment. The criteria for compartment identification usually include geography (delimited by roads or other geographic features), history (past treatments or uses of the compartment), and the purpose for which the compartment is to be managed. Stands are smaller spatial units within compartments with similar species composition, tree age, or structure. The criteria for compartment and stand identification are subjective, and these designations have practical value to foresters because of their flexibility.

Management and conservation activities occur in geographic space. The success of these activities depends upon our understanding of ecological phenomena and our ability to manipulate ecological space constrained by past and future land uses and disturbances. Thus, managers or conservationists who do not understand ecological space and focus their attention solely on geographic space are in danger of failing to achieve their objectives, or they might create long-term conflicts. For example, managers might select the boundaries of their management units based on logistical requirements (e.g., road access, land ownership, etc.). However, such spatial mapping tends to produce ecologically heterogeneous compartments. Soil conditions, drainage, and topography vary within a stand or compartment, and this environmental heterogeneity translates into variable responses to management or natural disturbances. Moreover, the boundaries of a particular stand or compartment might overlap different watersheds and/or parts of watersheds, which would limit their usefulness for managing aquatic resources.

Catena and Watershed Management Units

Catenas and watersheds are geographical or spatial units that coincide with ecological units of function and, as such, provide a logical means to integrate spatial and ecological approaches to management. In a watershed, for example, it is possible to simultaneously manage terrestrial and aquatic ecosystems while also maximizing the effects on water resources. Given the importance of water resources to humans and the need to conserve the biodiversity of aquatic systems, watersheds are sound units of forest management for conservation purposes. However, variability in the response to management within a watershed is a confounding factor. In large or complex watersheds, it is necessary to stratify the watershed by life zone (*sensu* Holdridge 1967), geology, soil type, and land cover in order to identify environmental conditions that are as similar as possible and which are likely to respond uniformly to natural or management disturbances. Such an approach will identify legacies of land uses and vulnerability to future disturbances that affect the function and structure of the management unit. In short, by identifying homogeneous units of ecological function, the heterogeneous and less predictable responses of complex watersheds to natural or anthropogenic disturbances are minimized (Lugo et al. 1999a, 1999b).

Within any hillslope in the watershed, the catena is a practical and ecologically valid spatial unit for stratifying the watershed (Weaver 1987; Scatena and Lugo 1995). A catena is a topographic continuum from ridge to slope to valley (figure 7-2) that is interconnected by the mass transfer and exchange of water and material, resulting in distinct edaphic and geomorphic conditions at each level. In general, soil properties (e.g., moisture, grain size, nutrient and carbon content) and forest attributes (e.g., tree density and basal area, rates of tree mortality and primary productivity, species richness) differ in a predictable manner among levels of the catena in any given watershed. For example, stands located on ridges behave differently from those found growing on slopes or in valleys. In the LEF, stands located in valleys within the Luquillo Mountains have more access to nutrients and water and exhibit faster turnover of biomass, whereas those found on ridges have slower biomass turnover rates and accumulate more biomass (Scatena and Lugo 1995). When ridge areas are modified by management or disturbance, the effect will be the transport of materials to adjacent slopes and valleys by downslope movement. The convergence of ecological function, environmental conditions, and biotic responses to these conditions according to the level of the catena—that is, ridges, slopes, or valleys—translates into a higher likelihood that the responses of stands to management interventions will be similar and have low variability within a topographic sector of the catena.

Although a catena is useful for categorizing different ecological conditions between ridges, slopes, and valleys, catenas with different elevations, aspects, or underlying geology can behave differently. In addition, the patterns of variation along catenas in the Luquillo Mountains (discussed above) do not necessarily occur in catenas in other locations. The important management guideline is the need to recognize and group similar ecological conditions within watersheds so that management actions will be as effective as possible by targeting the treatments to the capabilities of the sites. Hillslope catenas can provide one framework for defining ecological conditions.

A watershed contains many catenas, and a watershed approach to conservation allows a focus on the interaction between land and water resources, rather than the

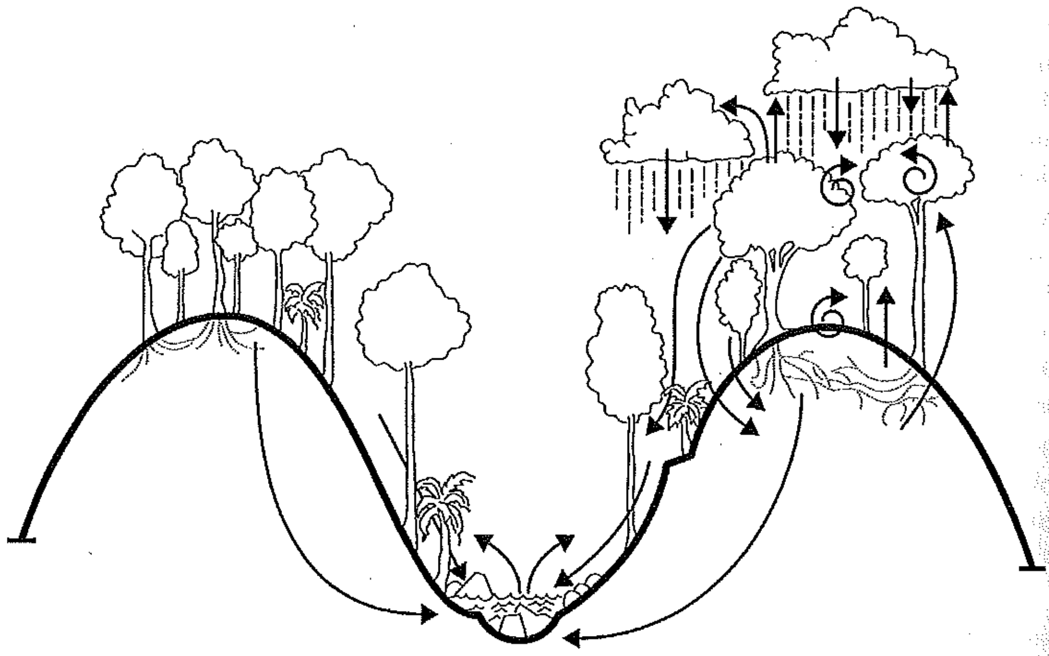

Figure 7.2 A catena in the Luquillo Experimental Forest illustrating variation in vegetation physiognomy and the fluxes of mass and nutrients (from Lugo and Scatena 1995).

consideration of each as a separate ecosystem. The importance of a watershed approach to understanding land-water relations has been well established in other LTER sites, such as Hubbard Brook (Likens and Bormann 1995). The land-water connectivity is observed clearly when rainfall produces a connective water surface layer, rivers flood over flood plains, materials are leached from terrestrial to aquatic systems, or organisms move between the land and the water. The movement of waters from terrestrial to aquatic systems influences the food supply and water quality for stream organisms. The movement of stream waters over flood plains influences the nutrient status and productivity of terrestrial ecosystems. Understanding this connectivity and its effects on the biota leads to insights into watershed management. In addition to watershed processes that feature water moving downstream from headwaters to coastal waters, the movement of organisms uphill during annual migrations contributes to downstream-upstream connectivity (Pringle 2000b).

A terrestrial example that illustrates one of the threats to upland forests from events in the lowlands is the movement of introduced species and terrestrial wildlife from adjacent urban systems into the Luquillo Mountains. This is the case with *Syzygium jambos*, an introduced tree species that is spreading upstream into the riparian areas of montane streams, and even into the mature forest (Brown et al. 2006). The movement of the Pearly-eyed Thrasher (*Margarops fuscatus*) from the lowlands to the uplands of the Luquillo Mountains (Arendt 2006) and that of the roof or black rat *Rattus rattus* (Odum et al. 1970a; Weinbren et al. 1970) are examples for animal populations.

The movement of organisms is a pathway of influence to upland systems through their surrounding interfaces (land-water, land-land, and land-air). For example, wildlife from the Luquillo Mountains supplement their diets in the lowlands. Puerto Rican parrots fly to agricultural fields in search of food (Snyder et al. 1987), as secondary forests within and outside the Luquillo Mountains have higher fruit production than do mature forests within the mountains (Lugo and Frangi 1993). Perhaps a landscape mosaic of forest types and ages is important for the support of native wildlife in the Luquillo Mountains.

Turbulence at the Interfaces within Management Units

Management unit connections with adjacent ecosystems and the atmosphere must be taken into account when designing conservation activities. It is helpful to visualize a management unit as a multidimensional volume having multiple interfaces with adjacent ecosystems and the atmosphere. The interfaces are surfaces where two ecosystems or sectors of ecosystems meet and interact through the exchange of materials, energy, and information. A sharp environmental gradient occurs at an interface, or, in some cases (as in the aerobic-anaerobic interface), there is a discontinuity in ecological space. As we show below, high flux rates and, at times, high turbulence characterize many of the processes at the interfaces. The dynamics of interfaces are best exemplified by atmospheric gas and wind interactions with forest canopies at the atmosphere-canopy interface. Gaseous diffusion between leaf surfaces and the atmosphere controls ecosystem productivity, and strong winds dissipating energy against the canopy transfer biomass to the forest floor and represent a major disturbance of Caribbean forests. Tropical forest management must attend to the processes at the interfaces of management units, including their coupling to climatic and atmospheric circulation patterns (Lugo and Scatena 1992).

In chapter 3, we document three of many possible interfaces within individual ecosystems where ecological processes occur at particularly rapid rates. These are the terrestrial-aquatic, aerobic-anaerobic, and canopy-atmosphere interfaces. The terrestrial-aquatic and the canopy-atmosphere interfaces are spatial interfaces (as is the interface between a stream and the groundwater), but the aerobic-anaerobic interface is a functional interface that can occur at any place (including spatial interfaces) and any time depending on environmental conditions (McClain et al. 2003). Thus, aerobic-anaerobic interfaces can occur within the canopy, within the soil, in wetlands, or at the edges of streams and other aquatic ecosystems. Managing ecosystems requires that managers be alert to the shifting positions of interfaces both in time and in space. The aerobic-anaerobic interface gains importance as well, given its significance to the production of methane and other greenhouse gases.

At the terrestrial-aquatic interface, or riparian zone, at the lower end of catenas, McDowell et al. (1992, 1996) documented dramatic changes in both the form and the total concentration of inorganic nitrogen and dissolved organic matter across redox gradients. Decades of research on temperate watersheds have shown that the maintenance of a vegetated buffer zone is critical to maintaining water quality in forested and agricultural landscapes (Peterjohn and Correll 1984; Simmons et al. 1992; Triska et al. 1993; Lowrance et al. 1997; Naiman et al. 2005). More recent work in an urban setting shows that even in heavily managed landscapes, the role of the riparian zone in reducing nutrient loading to surface waters can be critical (Groffman et al. 2002).

Data from the LEF and the Amazon basin suggest that in humid tropical climates, riparian processes are especially important in maintaining water quality (McDowell et al. 1992, 1996; McClain et al. 1994). In both sites, remarkable transformations of nitrogen (N) occur in the riparian flood plain (nitrate [NO_3-D] loss and ammonium [NH_4^+] accumulation), and a significant N loss (40 percent or more) occurs at the narrow groundwater-stream interface. These plot-scale studies have been expanded to a reach-scale analysis in the Río Icacos basin of the Luquillo Mountains. Chestnut and McDowell (2000) found, by comparing upslope groundwater and stream chemistry, that the stream export of N would be six to eight times as high in the absence of N losses at the stream-groundwater interface. The export of dissolved organic carbon was reduced fourfold by passage through the riparian zone.

The management implications of these results are striking. Riparian zones (the terrestrial-aquatic interface) represent biogeochemical "hot spots" that have a disproportionate effect on watershed nutrient losses relative to their spatial area (McClain et al. 2003). They are also critical for maintaining aquatic habitat (Heartsill-Scalley and Aide 2003) and aquatic food webs (Covich and McDowell 1996). When maintained in a vegetated state, riparian zones maintain water quality and terrestrial and aquatic species diversity in humid tropical environments. They are critical and priority areas of tropical landscape management (McDowell 2001). Luquillo LTER research on the structure and composition of riparian zones has provided insight into how land managers can define the appropriate width for riparian zones based on local ecological conditions (Scatena 1990).

Silver et al. (1999) demonstrated the importance of the aerobic-anaerobic interface in soils when they discovered periodic anaerobic conditions in all forest types of the Luquillo Mountains. They found high rates of methane production during oxygen-free periods. This finding in turn led to the discovery of a new pathway of the N cycle associated with the aerobic-anaerobic interface (Silver et al. 2001). Because the dissimilatory reduction of NO_3^- to NH_4^+ without oxygen is a N-conservation pathway that favors N immobilization by plants, these aerobic-anaerobic interfaces will feed back to regulate plant growth rates by affecting the nutrient supply and root respiration rates. The aerobic-anaerobic interface will also influence the vegetative community composition, as only plants adapted to periodic anaerobic conditions will survive. Survival requires specialized structures such as aerenchymatous tissue, pneumatophores, lenticels, stilt roots, etc. (Benzing 1991). Management of the aerobic-anaerobic interface is possible using a variety of approaches. One is the manipulation of water levels and water turnover. Slowing down water turnover or increasing water levels favors anaerobic conditions, and the opposite actions favor aerobic conditions. Other management mechanisms involve manipulating vegetation in riparian zones and wetlands or the alteration of river channels or the topography.

Recognition of the high rate of fluxes at ecosystem interfaces is of paramount importance to forest conservation (Hunter 1990; Saunders et al. 1991; Silver et al. 1996b). In Puerto Rico, Silver et al. (1996a) focused attention on the capture, retention, transfer, and recapture of nutrients at the atmospheric-terrestrial, biotic (organism-organism), plant-soil, and terrestrial-hydrologic interfaces. Organisms or attributes of forests at these interfaces included epiphytes and nitrogen-fixing organisms in the atmospheric-terrestrial interface; live plant tissue and dead plant tissue in biotic interfaces; root mats, fine roots, mycorrhizae, and symbiotic nitrogen fixers in the plant-soil interface; and coarse woody debris, roots, and soil microbes in the terrestrial-hydrologic interface. Many disturbance forces dissipate energy at these interfaces, thereby affecting critical sectors of the ecosystem. For example, hurricane winds directly interact with the canopy-atmosphere interface, and floods affect riparian and aerobic-anaerobic interfaces (chapter 6). Interactions between disturbance forces and the inherent high rates of fluxes at ecosystem interfaces mean that these are places where the biota are especially active and continually adjusting to turbulent environmental conditions (Silver et al. 1996b).

Another aspect of the functioning of interfaces within particular ecosystems is their spatial extent in terms of area or volume. For example, cloud penetration in forests can either be limited to the upper canopy or encompass the whole volume of the ecosystem down to the soil surface. This affects the distribution of epiphytes, which in colorado forests can extend their habitat from the canopy to the forest floor. The riparian zone, as well as the area involving aerobic-anaerobic interfaces, can expand significantly after heavy and prolonged rainfall (or contract with drought), with concomitant changes in aeration, nutrient distribution, and mechanical effects on the forest floor.

Disturbances and Species Life Histories

An understanding of the natural history of tree species is fundamental to species conservation. Information about natural history traits such as time to first reproduction, light tolerance, growth rates, regeneration potential, fecundity, and germination rates is required in order to propagate species, reforest lands, establish tree plantations, and successfully grow a tree crop. Research on the subject of tree life history in the Luquillo Mountains has been a priority, as evidenced by the 189 publications on this subject (figure 7-1). A manual with life history information for 101 tree species that grow in Puerto Rico (Francis and Lowe 2000) has been instrumental in supporting land management activities in Puerto Rico and throughout the Caribbean. Specialized manuals on the life history of urban trees (Schubert 1979) or best management practices (Wadsworth 1997; Ruiz 2002) have also been widely used. In spite of the importance and applicability of past life history research for plantation management and degraded land rehabilitation, such applications have traditionally not considered large and infrequent disturbances (*sensu* Dale et al. 2001).

Traditionally, the selection of tree species for plantations and reforestation has been based on their growth and yield potential rather than on their resistance to disturbances such as wind events. However, Liegel (1982, 1984) found that there were differences among species in their resistance to high winds. When planted together in mixed-species plantations, individuals of *Pinus oocarpa* exhibited six times the mean blowdown and twice the survival and structural effects of individuals of *P. caribaea*. Not surprisingly, after Hurricane Hugo, pine plantations in the Luquillo Mountains were destroyed beyond repair, demonstrating the importance of understanding the role of disturbances when collecting life history information. Life history attributes also proved relevant to the response to hurricane winds of pioneer and nonpioneer tree species in the LEF (Zimmerman et al. 1994) and urban trees in San Juan and Florida (Duryea et al. 2006). In short, life history traits help us understand the mechanisms for species-specific responses to disturbances and allow managers to anticipate which species will cope better with conditions before and after the disturbance.

The life history traits of trees and other organisms exposed to large and infrequent disturbances include common characteristics that make organisms adaptive to surviving under a particular disturbance regime. For example, some tree species from hurricane-prone regions have relatively short life spans, an early age of first reproduction, leaf heterophylly (ability to grow both shade-tolerant and shade-intolerant foliage and to change quickly between the two types), advanced regeneration, conspicuous sprouting, tree unions, and low ratios of crown to stem area (Lugo and Zimmerman 2002). These adaptations by species to environmental conditions might or might not be special adaptations to hurricanes, but they underscore the importance of understanding ecological rhythms (discussed later) and the life history characteristics of species that are targeted by managers.

Understanding the Limits of Forest Resilience

The forests of the Luquillo Mountains have been disturbed experimentally with ionizing radiation, chemical defoliants, clearcutting, selective cutting and planting, canopy removal, the manipulation of wood input, and fertilization (chapter 4). Scientists have also documented the effects of wind, rainfall, landslides, the conversion to different types of agriculture, and road construction (chapter 5). After each of these events, much of the forest cover and structure has returned to predisturbance conditions, but at different rates, and with different species composition (Lugo et al. 2000; Lugo 2004; Lugo and Helmer 2004). Despite the differences, however, generalizations about the resilience (*sensu* Holling 1973; Carpenter et al. 2001) of these ecosystems, even if tentative, are possible.

At least three aspects of resilience need attention from a conservation perspective. The first is the level of resilience, which differs among the components of a particular ecosystem (Zimmerman et al. 1996). For example, after Hurricane Hugo and experimental harvests, tabonuco forests at the watershed scale exhibited high resilience in leaf area index, litterfall, and root production, but lower resilience in species composition (Ewel 1977; Devoe 1989; Silver 1992; Scatena et al. 1996; Lugo et al. 2002; Beard et al. 2005). At the catena level within a watershed, however, litterfall recovered at a slower rate in the riparian zone than in the ridge and mid-slope areas (Vogt et al. 1996). At the watershed scale, biomass and basal area resilience were intermediate in response to hurricane disturbance. The resilience of biomass after a hurricane differed depending on the legacies or residuals existing at each site, with biomass recovering rapidly in areas with legacies of higher soil N from past land uses (Beard et al. 2005). Second, the state of the ecosystem relative to legacies and the level of maturity influences its resilience. For example, the resilience of forest biomass differs with the type of prior land use (Silver et al. 2000) or nutrient legacies from prior land uses (Beard et al. 2005). Biomass accumulated slowest after pasture abandonment, at a medium rate after abandoned agricultural crops, and fastest for prior coffee plantations (Silver et al. 2000). The resilience of forests on sites previously occupied by coffee plantations was attributed to high levels of soil N from nitrogen-fixing trees (*Inga* spp.) planted to provide shade to coffee trees (Beard et al. 2005). Finally, the level of resilience is influenced by the nature of the disturbance in relation to a particular disturbance event. For example, given the same conditions and timing, a forest might exhibit high resilience to wind disturbances but low resilience to landslides, because landslides remove soil and significantly delay succession (Walker 1999), whereas wind mostly knocks down biomass. Similarly, different places within a landslide are differentially resilient because of the distribution of organic residuals (chapter 5).

Each ecosystem structural component has a particular time scale at which it cycles (Scatena 1995). For example, leaf biomass cycles within a year, whereas woody biomass turns over at a scale of decades, and certain soil carbon fractions cycle much more slowly. The evaluation of resilience involves both slow and fast response variables (Carpenter et al. 2001), which have distinct effects on ecosystem resilience. Fast variables allow for a rapid response to disturbance and quick readjustment. Slow variables exhibit less of a short-term response but are critical for the long-term persistence of ecosystems. The rate of turnover of ecosystem compartments is a function of ecological space. In general, for a given compartment, tropical ecosystems have faster rates than temperate ecosystems, and within the tropics moist forests have faster rates than dry forests (Brown and Lugo 1982).

Soils in the tabonuco forest, for example, are not permanently affected by the formation of a single experimental canopy gap, as the regrowth of biomass is extremely rapid (Silver 1992). After chronic use of the same soil in agriculture and pastures, however, land degradation produces arrested succession and a shift in the ecosystem state (Silver et al. 2000). In the Luquillo Mountains, it took 6 decades of forest development to convert pastures into mature species-rich closed-canopy forests (Silver et al. 2000, 2004). Returning forest cover to sites such as pastures with arrested succession requires the repair of the soil structure and fertility (slow variables), which can be accomplished through the planting of selected tree species effective at ameliorating soil chemical characteristics (Parrotta 1995, 1999).

Rates of ecosystem processes are useful measures of resilience, but they can be deceiving when used to compare systems. Based on differences in net primary productivity and response to fertilization, Waide et al. (1998) concluded that low-elevation forests had greater resilience to hurricanes than high-elevation forests (table 7-2). However, because the biomass of high-elevation forests is lower than that in low-elevation forests, the ratio of primary productivity to biomass is similar in the two forests (0.053 and 0.044), suggesting similar rates of biomass turnover (19 to 22 y) and therefore resilience (table 7-2). If a forest failed to recover a sufficient level of biomass between hurricanes, it would not persist in the disturbance regime of the Luquillo Mountains over time.

Table 7.2 Biomass, productivity, and potential resilience of low- and high-elevation forests in the Luquillo Experimental Forest. Time for aboveground biomass turnover is the ratio of aboveground biomass to net aboveground biomass production. Values are estimated at approximately steady-state conditions. After disturbances, biomass decreases and rates are assumed to increase at both elevations, leading to roughly equal resilience (rate of return to predisturbance biomass). All data are from Weaver and Murphy (1990)

Parameter	Low-elevation forest	High-elevation forest
Net aboveground biomass production (Mg ha^{-1} y^{-1})	10.5	3.7
Litterfall (Mg ha^{-1} y^{-1})	8.6	3.1
Aboveground biomass (Mg ha^{-1})	198.0	83.0
Time for aboveground biomass turnover (y)	19	22

The estimate of biomass recovery in table 7-2 supports the notion that these forests are capable of restoring the biomass of mature states in about 20 to 25 years, or less than the 60 years available between successive hurricanes. Sixty years is the average return rate for direct hurricane hits in the Luquillo Mountains (Scatena and Larsen 1991). Therefore, at the current rate of primary productivity, these forests have sufficient time to reestablish the biomass expected of mature forests in the hurricane belt. This also implies that although the biomass and primary productivity of the lowlands and uplands of the Luquillo Mountains are different, both forest types are able to bounce back between disturbance events. This is to be expected, as both forest types have occurred under the same disturbance regime for millennia, and are therefore likely to contain species that have evolved to reach some level of biomass maturity in the average time interval between natural disturbance events (Lugo et al. 2002). Those species incapable of reproducing between disturbance events are unlikely to persist.

After a large and infrequent disturbance, what one sees is the devastation caused by the hurricane, landslide, fire, or volcanic explosion. The inherent tendency of forest managers is to restore the damaged forest or somehow accelerate succession in order to avoid further site degradation. The tangles of weeds that naturally invade affected sites immediately after the disturbance event do not appear sufficient in relation to a restoration goal. If one understands and considers the limits to resilience as discussed in this section, or nature's self-organization capacity (next section), a different management strategy emerges. When restoring landslides in the Luquillo Mountains, the Forest Service learned that those slides that were seeded with introduced herbaceous plants recovered at a slower rate than those allowed to regenerate through natural succession. Vegetation recovery after the eruption of Mount St. Helens (Dale et al. 2005) and littoral recovery after the *Exxon Valdez* oil spill (Parker and Wiens 2005) followed the same principle. A critical management strategy involves recognizing when to intervene and when not to. This requires some understanding of the ecological condition of sites after a disturbance and evaluating whether natural resilience mechanisms will restore the original ecosystem, or whether resilience capacity somehow has been lost and, therefore, management interventions are required. As with all management interventions, the management objectives and underlying ecological assumptions play a critical part in deciding what to do (Parker and Wiens 2005).

Self-Organization

Self-organization is the sorting of species through a variety of replacement mechanisms after a disturbance event. It occurs at all scales of size and complexity, from the small fragmented patch within an urban environment to large landscapes responding to a variety of natural and anthropogenic disturbances. Self-organization is a component of ecosystem resilience (Gunderson 2000) because it allows the system to reform and continue to function in a particular state (e.g., forest or pasture). After a disturbance or large shift in ecological space, many plant species will germinate, and organisms of all types will arrive at a site via either natural or artificial vectors. These species will compete for space and resources with species that survived the disturbance event. In the absence of human management, environmental conditions result in some species establishing, growing, and reproducing while competition eliminates less well-adapted species. Positive species interactions (facilitation) can also influence species composition (Callaway and Walker 1997). The resulting mix of species at the site emerges from interspecific interactions in the context of new environmental and structural conditions. The process is known as self-organization because the systems that prevail are self-reinforcing and might be different from those of the past (Odum 1988, 1989).

There are numerous examples of self-organization in the Luquillo Mountains. For example, after Hurricane Hugo devastated whole forest stands, thickets of weeds and vines covered hectares of land, and the expectation was that it would be difficult for the forest to regenerate through such a tangle of vegetation (Chinea 1999). But trees did grow through the weeds (many of which were introduced species), and a closed-canopy forest emerged with a species composition similar to that of the prehurricane forest (Scatena and Lugo 1995; Scatena et al. 1996).

Self-organization also occurs after human intervention with succession. In the 1930s to 1950s, the Forest Service planted introduced and native tree species in many degraded sites, and these plantations were allowed to develop with minimal management after the first decade (Marrero 1950). Today, mature forests occur in these former degraded lands, but their species composition is different from the original and from that of adjacent native forests of similar age (Lugo 1992; Silver et al. 2004).

When allowed to proceed unhindered, self-organization is an effective conservation tool because it is powered by natural forces rather than by the costly subsidies required for human intervention (Odum et al. 2000). Self-organization allows natural forces to determine the trajectory of ecosystem change at no cost to managers other than time. The challenge is to recognize when to allow self-organization to continue unabated ("rolling with the punches") and when to nudge it one way or another in order to meet conservation or economic goals (Lugo 1988).

Applications of Long-Term Ecological Research

Research in the Luquillo Mountains has been instrumental in developing management systems for tropical forests within and outside Puerto Rico. Long-term ecological research adds new information and insight to the body of knowledge concerning tropical forest dynamics. Hereafter, we use all available information (LTER and non-LTER) to illustrate applications of research to six tropical forest conservation issues: ecosystem services, restoring land to productivity, restoring biodiversity to deforested sites, water abstraction and conservation of biodiversity, the management of roads and landslides, and living with environmental change. This information and its application are of universal value and are not limited to the insular conditions of the Luquillo Mountains. Sites in particular systems might differ in terms of landscape types, disturbance forces, ecological cycles, or species being managed. However, regardless of the geographic location, the scientific principles and their applications to management or conservation do not change.

Ecosystem Services

Ecosystems have always provided people with products and services, but the market system focused on the value of products (e.g., wood, meat, fruit) while assuming services (e.g., clean water and air) were free externalities to economies. Ecosystem services include those that are species dependent and those that are whole-ecosystem dependent. The cleaning of rocks in streams by shrimp (discussed below) or the aeration of soils by earthworms are ecosystem services that are species dependent. In contrast, clean water at the bottom of a watershed is a service provided by the whole ecosystem, and the species composition within the watershed is not as critical. Today, ecosystem services are increasingly recognized as important to the quality of life and the functioning of economies (Daily and Ellison 2002; Scherr et al. 2004). Moreover, many believe that the ability of an ecosystem to deliver services is limited or that it might change when ecosystem states change, making the "free externality" an uncertainty for many economies. As a result, the importance of nonmarket economics is gaining importance in the analysis of economic development (Costanza and Daly 1987). Unfortunately, no agreement exists concerning ways to quantify the value of nonmarket services of ecosystems to the economy.

EMERGY Evaluation

Managing a complex system with multiple objectives and constraints, such as a national forest, requires an integrated assessment and decision-making tools. A diversity of metrics is required in order to assess ecosystem processes, impacts, and services that occur over a wide range of time scales. EMERGY analysis (Odum 1996) has been developed as a tool for quantifying and clarifying the relationships between environmental services and their effects on ecological space over different time scales. EMERGY, an energy-based measure of resource contribution and influence, is defined as the solar energy required in order to produce a flow or storage of another type of energy. EMERGY evaluation evolved from the need to develop a system of economic analysis in which market and nonmarket products and services are measured with the same units (Odum 1996). It uses a systems approach to the analysis of energy and dollar flow through natural and economic systems (figure 7-3).

Using figure 7-3, one can estimate the relative importance of natural energy inputs to the watershed (left side of the diagram) and the energy inputs to a watershed that cost money (i.e., purchased energy) (right side of the diagram). In this example (units of sej ha^{-1} y^{-1} $\times$ 10^{12}), the ratio of natural (2,765) to purchased (2,447) energy input is 1:1. In addition, one can compare the sum of all the outputs of watershed services (bottom right; 8,336) and compare that with the sum of all inputs (natural plus purchased = 5,212). This results in a ratio of 1.6. The ratio would be 3.4 if one compared outputs in services (8,336) to human investment in purchased energy inputs (2,447). In summary, figure 7-3 shows a watershed in which the contribution of natural energy to its functioning and value to society is higher than that of the purchased energy. It also shows that the return of the investment for management is positive (between 1.6 and 3.4 times).

This systems-based approach, which was developed by H. T. Odum (1971), partly from his research on energy and mass flows in the Luquillo Mountains, can be used to evaluate the flows and storages within a defined ecosystem boundary. The synthesis requires an inventory of all forms of energy and all types of materials in every flow within the system and their expression in units of solar EMERGY or EMdollars (EM$). "EMdollars" refers to the proportion of the system's buying

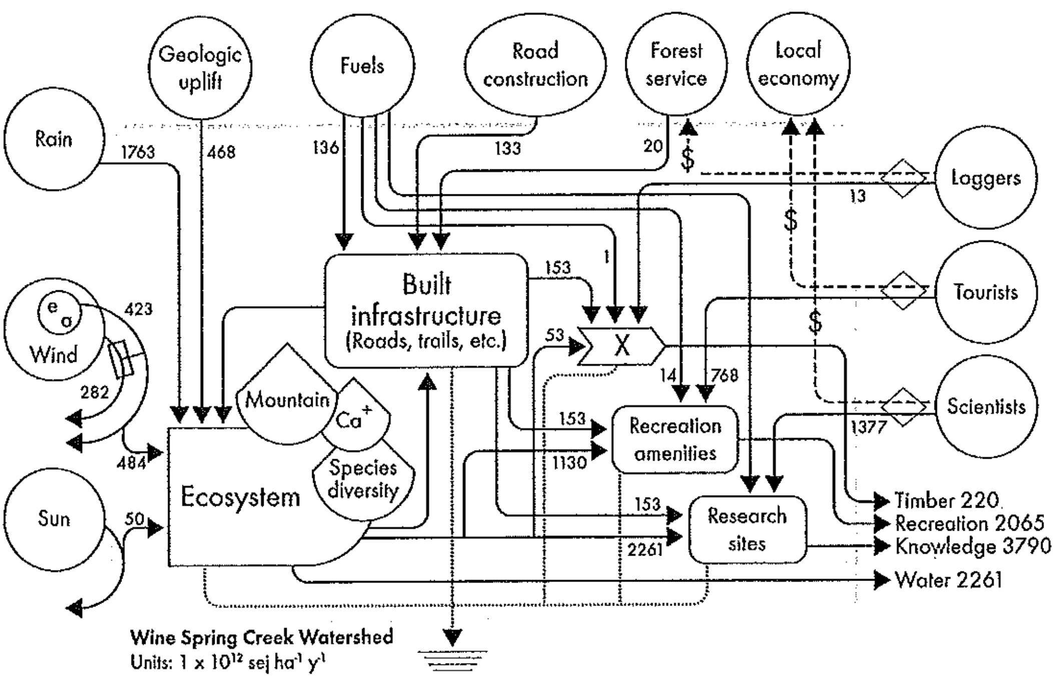

Figure 7.3 Systems diagram of the ecological-economic interface of the Wine Spring Creek watershed, North Carolina (from Tilley and Swank 2003). Circles represent outside inputs to the watershed. Symbols are according to Odum (1996). More details can be found in the text.

power that is supported by the system's solar EMERGY and is a standard way of expressing a monetary value of services and storages not traditionally accounted for in standard economics. Examples of natural values or services are carbon sequestration, the provision of water quality, transpired moisture, photosynthetic production, and forest biomass. Any transaction involving market or nonmarket economics is expressed in EMERGY units in order to ensure that the human and natural economies are measured with common units.

Two examples of the application of EMERGY analysis to forestry issues are those of Odum et al. (2000) and Tilley and Swank (2003). Odum et al. (2000) showed that natural reforestation in Puerto Rico returned a net benefit with an accumulation of national wealth 15 to 25 times the money invested over the 10 to 20 years required for canopy closure. Tilley and Swank used EMERGY analysis to evaluate alternative uses of forested watersheds in the southern Appalachian Mountains and found that ecosystem services were worth 40 times the amount of money invested in their management. The public value of annual forest production in southern Appalachia is compared to that in the LEF in table 7-3. Odum (1996) offers many more examples of these values.

In the Luquillo Mountains, EMERGY analysis has been used to analyze the forest as a system coupled to the larger ecologic-economic system of Puerto Rico (Scatena et al. 2002). This analysis indicates that rainfall and tectonic uplifting are the largest environmental inputs to the forest. The interaction between these inputs produces an erosional landscape in which the EMERGY of biological processes are less than the EMERGY associated with the physical and chemical sculpturing of the landscape. This erosional landscape undergoes a systematic shift from physically

Table 7.3 EMERGY values associated with ecological processes and human activities in the Luquillo Mountains of Puerto Rico and the Wine Spring Creek watershed in North Carolina.

Parameters	Luquillo Mountains	Wine Spring Creek
Ecological processes		
Precipitation, chemical	2,128	1,603
Precipitation, geopotential	1,372	525
Transpiration	744	440
Stream discharge, chemical potential	2,128	2,055
Net primary productivity, live biomass	744	982
Human activities		
Research information	685	3,445
Recreation	3,451	2,065
Annual road maintenance (EM$ km^{-1} y^{-1})	22,323	4,136
EMERGY indices		
Social flows/environmental flows	3.5	1.03
EM$ ratio, 1992 (sej $dollar^{-1}$)	1.64×10^{12}	1.12×10^{12}

Based on Tilley and Swank (2003) and Scatena et al. (2002). Except where indicated, units are in EM$ ha^{-1} y^{-1}. EMERGY is the available energy of one kind, previously used—either indirectly or directly—to make a product or service. EMERGY dollars (EM$) is the total amount of dollar flow generated in the entire economy supported by a given amount of solar EMERGY input. The unit sej is solar emjoules, an energy flow unit corrected for its solar energy equivalence (Odum 1995).

to biologically dominated EMERGY flows with decreasing elevation (Scatena et al. 2002). The lower elevations are relatively efficient at accumulating biomass, and the upper elevations are relatively efficient at accumulating soil organic matter.

A similar analysis done for a watershed in North Carolina allows a comparison with the Luquillo Mountains (table 7-3). The comparison shows that the wet Luquillo Mountains have greater physical and chemical erosion rates and support a considerable amount of recreation. One result of the differences in the ecological characteristics of the two locations is that the cost of maintaining roads in the highly erosive Luquillo Mountains is over five times that in the Wine Spring Watershed in North Carolina.

In the Luquillo Mountains, about 59 percent of the total annual EMERGY flows are from human activities. Most of this is from tourism. This relatively high level of human activity reflects the high value that society places on the national forest. However, the amount of environmental work that was required over millennia in order to build the natural capital of the forest was 9 to 50 times the current market value of property adjacent to the Luquillo Mountains (Scatena et al. 2002). This underestimated value of the land surrounding the Luquillo Mountains is one reason for the tremendous urban pressure on them (Lugo et al. 2004). The analysis also indicated that the environmental effect of extracting water is almost 300 times that of building roads, in large part because the effects of downstream releases of treated sewage are almost nine times those associated with water removal. Natural and artificial wetlands and the reduced use of artificial channels and other structures that promote runoff at the expense of recycling water might conserve water resources and offset these effects of treated sewage (Kent et al. 2000).

Species-Dependent Ecosystem Services

Tropical forest managers face the challenge of dealing with species-rich ecosystems, usually with little information about the ecological role that each species plays in the functioning of the ecological system. The traditional solution has been to focus attention only on those species with known commercial value (usually a few tree species). As research reveals the ecological importance of individual species or groups of species, managers must pay attention to a greater fraction of the species components of forests. One approach is to use life history information to help focus management activities (see above). As we show below, life history information for species other than timber trees is rapidly accumulating for the Luquillo Mountains. Some groups of species draw the attention of managers based on their native/nonnative status. Here we discuss the role of species in providing desired ecological services as another criterion for identifying species that might require the attention of managers. We end this section with a few guidelines for managing species for ecological services.

Freshwater shrimp species provide many ecosystem services for recreational users within the Luquillo Mountains and for residents and users of surrounding ecosystems. Recreational shrimp harvesting is one example that has been studied by Luquillo LTER scientists (Kartchner and Crowl 2002). Palaemonids (i.e., shrimp such as *Macrobrachium* spp.), which reach lengths > 230 mm, are a particularly prized catch in recreational freshwater shrimp fisheries. Atyid and xiphocaridid shrimps, with small maximum lengths (<100 mm), are also caught but are viewed as less challenging and exciting to capture and eat. Although shrimping provides an ecosystem product, the primary purpose of most shrimping in the Luquillo Mountains is recreation. Interviews with fisherman who harvest Luquillo shrimps reveal that shrimp harvesting is a relaxing hobby, a family tradition, or a means of interacting with nature.

Providing an opportunity for recreational shrimping might be the service that is most obvious to visitors of the Luquillo Mountains. However, shrimp also provide an additional service relevant to recreation, as revealed by basic research on stream ecology. The feeding activities (scraping and brushing) of atyid shrimp rapidly remove sediment, organic matter, and algae that accumulate on rock surfaces between storms and provide the service of water and habitat cleansing (Pringle and Blake 1994; Pringle et al. 1999; March et al. 2002; see chapter 6) (figure 7-4). After one storm, 440 to 620 g m^{-2} of dry mass accumulated on rocks where shrimp had been excluded, whereas shrimps in control treatments removed the sediment within 30 hours. To those visiting the Luquillo Mountains streams, this service contributes to the aesthetics of montane rivers (i.e., clean boulders and clear water). This service might also contribute to safety. If the stream bottom is visible and less slick after algae and organic matter are removed from rock surfaces, hiking in the streams is less treacherous.

In mountain streams outside the Luquillo Mountains, shrimp provide similar cleaning services, but over a wider range of conditions resulting from human effects. Survey work combined with *in situ* shrimp exclosure and enclosure experiments have shown that atyid shrimp are able to clean rock surfaces even in streams with relatively high percentages of agricultural land cover in the catchments (15 to 45 percent) and, consequently, high levels of dissolved nutrients (up to 1500 μg nitrate-N L^{-1}) (Greathouse 2006b). This indicates that shrimp foraging can reduce or prevent algal blooms in mountain streams that drain mixed land uses.

In mid- and low-elevation stream ecosystems immediately surrounding the Luquillo Mountains, grazing by goby fish (E. Greathouse, personal observation) and snails (March et al. 2002; Blanco and Scatena 2005) can provide rock-cleaning services, replacing the function of shrimp foraging observed at high elevation. However, in mid- and low-elevation rivers and estuaries, freshwater shrimps still provide important food resources for predatory fishes (e.g., mountain mullet [*Agonostomus monticola*], sleepers [e.g., *Gobiomorus dormitor*], and American eel [*Anguilla rostrata*]), which are important for both recreational and commercial fisheries (Covich and McDowell 1996; Nieves 1998; March and Pringle 2003). The "freshwater" larval shrimps pass through the estuaries and river as they migrate to saltwater, and they return to freshwater as juveniles (March et al. 1998). Larval shrimps are an important food source for estuarine fishes (Freeman et al. 2003), judging from the prevalence of shrimp larvae in the guts of fish collected from an estuary prior to the construction of a low-head dam (Corujo Flores 1980). The low-head dam now removes an estimated 34 to 62 percent of drifting larval shrimp (Benstead et al. 1999). The results of recent Luquillo LTER studies in the same estuary indicate that despite the reduction in shrimp availability, juvenile

Figure 7.4 Shrimp exclusion in the Quebrada Sonadora at El Verde, Luquillo Experimental Forest, Puerto Rico. The electric treatment (rear hoop) excludes shrimps and fishes and contains high levels of benthic particulate material, as evidenced by the dark brown depositional layer. In contrast, the unelectrified control treatment (the hoop in the foreground) has no visible particulate material because of shrimp foraging activities. (Photograph by Catherine M. Pringle.)

freshwater shrimps are still a key food resource for estuarine fishes, including fishes of commercial importance such as *Bairdiella* spp. and *Centropomus* spp. (Smith 2008).

Long-term ecological research has also shown that the ecological services provided by freshwater shrimps have significant implications for stream ecosystem function (chapter 6). Humans benefit from these functions because they are part of the regulating services of ecosystems (Millennium Ecosystem Assessment 2005). When shrimp are present, levels of benthic inorganic sediments, organic material, carbon, and nitrogen in streams are lower and less variable than when shrimp are absent. Moreover, higher rates of leaf decomposition and export of fine particulate organic matter at base flow occur in the presence of xiphocaridid shrimps. Through these effects, shrimps influence the availability of nutrients to other trophic levels. We are still elucidating the linkages between shrimps and ecosystem components and services of high practical and aesthetic value. For example, what are the effects of shrimp foraging on aquatic insect emergence or on terrestrial predators, including Puerto Rico's flagship species, coquí frogs (*Eleutherodactylus portoricensis*)?

Research in the Luquillo Mountains has discovered other examples of species-dependent services—for example, the roles of (1) ferns in the stabilization of soil and the reduction of downstream sedimentation (Walker 1994; Shiels and Walker 2003), (2) coquís in accelerating plant growth and decomposer activity after hurricanes (Beard et al. 2002, 2003), (3) earthworms and other soil fauna in accelerating litter decay or aerating soils (González and Seastedt 2000, 2001), and (4) *Cecropia* in the restoration of forest conditions after disturbances (Brokaw 1998).

The examples presented above illustrate that individual species or functional groups of species perform important ecological services. People benefit from these services by obtaining food or fiber products, clean water and air, aesthetics, etc. Thus, managers must attend to the sustainability of these species and species groups and not focus only on trees with economic value. In the Luquillo Mountains, life history information on shrimp species has suggested practices that help sustain these populations. For example, as we discuss below, water abstraction schedules and the location of intakes are designed to sustain shrimp populations. Proposals for stream channel modification, which affects habitats and migration routes, must take into consideration and mitigate any effects on migrations of aquatic fauna. Similarly, the reproductive success of coquís could be enhanced with properly located artificial nesting sites (Stewart and Woolbright 1996). Finally, managers now have justification for the protection of specialized habitats such as roosting sites for bats, wet locations for earthworms, or riparian zones that harbor a disproportionate concentration of species that deliver ecological services.

Managing Time: The Relevance of Ecological Cycles and the Time Tax

Ecological processes, and thus their associated ecosystem services and products, are time dependent. The reliable functioning of complex ecosystems such as those of the Luquillo Mountains depends on numerous cyclic and noncyclic processes that occur at different time steps ranging from nanoseconds to millennia (Scatena 1995). Those processes that occur rapidly are said to involve rapid variables because the variables have a fast turnover rate; this is the case with photosynthetic or respiration rates or leaf turnover. There are processes that take decades or centuries to unfold, and they are said to involve slow variables; the recovery of soil nutrient and organic matter supplies after degradation is an example of this. There is a need to be aware of the types of variables manipulated by managers because there is less risk when fast variables are manipulated than when the manipulation involves slow variables (Crépin 2007). A mistake takes longer to rectify when dealing with a slow variable than when manipulating a fast one. In essence, time management is a critical component of ecosystem management because conservation actions are time dependent, as they require the manipulation of ecological processes with different time steps. Human activity influences ecological processes that are either too fast (less than days) or too slow (over centuries) for effective management. For example, the lunar-controlled changes in plant secondary chemistry that affect herbivory rates on palm leaves occur at scales of weeks (Vogt et al. 2002a). The harvesting of palms (as nontimber forest products) can therefore affect herbivore population dynamics. Opportunities for management differ with the time step involved, with particular challenges when dealing with time intervals that are too short or too long.

EMERGY analysis, which uses time as a source of embodied value, and concepts of ecological space are useful in defining and evaluating natural resource management problems. However, managers need operating rules to explicitly address the problems. One method, developed directly from the time-sequence approach suggested by Scatena (2001), is to coordinate management activities with ecological cycles, which are defined broadly as biological or environmental processes that repeatedly occur at definable intervals. These cycles are commonly related to climate (e.g., phenological patterns), daily processes (e.g., diel or circadian cycles), life histories (e.g., reproduction or feeding behavior), disturbance (e.g., successional cycles), and physical and biogeochemical cycles (e.g., tides).

Knowledge of ecological cycles in the Luquillo Mountains has been applied in order to enhance the conservation of endangered species such as the Puerto Rican Parrot, allocate water supply to municipal watersheds, satisfy recreational demands, and boost productivity of natural forests and plantations (table 7-4). Although the timing of management activities with the ecological cycles has definable benefits, this type of dynamic management is not without costs or tradeoffs. It requires knowledge of the response of ecosystems and organisms to environmental

Table 7.4 Examples of ecological rhythms used in natural resource management in the Luquillo Mountains. (From Scatena 2001.)

Ecological cycle or life history trait	Management objective	Management guidelines	Source
Annual reproductive cycle and daily foraging behavior	Protect endangered Puerto Rican Parrot	Limit management activity by season and time of day	USDA, FS Southern Region 1997, Snyder et al. (1987)
Diurnal habitat preference	Define instream flow requirements for resident biota	Develop nighttime and daytime instream flow requirements	Johnson and Covich (2000)
Diurnal and seasonal larval release	Maintain migratory aquatic biota	Restrict water withdrawals by night and season	Benstead et al. (1999)
Weekly and seasonal recreational-use patterns	Maintain aquatic recreation downstream of water intakes	Restrict water withdrawals during summer weekends	Scatena (2001)
Diurnal and seasonal dissolved oxygen cycles	Minimize eutrophication by sewage plant effluent	Reduce releases during nighttime and low-flow periods	Scatena (2001)
Annual growth rates and light responses	Improve timber yields	Selective thinning by density and species	Wadsworth (1997)
Regeneration in natural tree fall gaps	Sustain timber resources	Harvesting that mimics natural gaps	Odum (1996)
Annual phenology and response to canopy opening	Sustainable mahogany plantations	Limited harvesting during seed set, thinning after canopy disturbances	Wang and Scatena (2003)

conditions; institutional memory; and an administrative commitment to long-term environmental monitoring, data analysis, and synthesis.

In some instances, time constrains the achievement of conservation goals. This might happen if the conservation goal requires the completion of ecological processes that take longer than the time that is available or desirable for the manager. When this happens, managers attempt to accelerate the process, such as with the establishment of plantations to increase the rate of wood production, or when artificial reforestation accelerates natural forest reestablishment. Sometimes it is impossible to accelerate processes because of specific conditions of natural or anthropogenic origins. The "time tax" is a symbolic way of expressing the idea that when we affront nature—eroding the soil, for example—a certain amount of time is required in order to rehabilitate productive conditions or at least overcome degradation (Lugo 1988). Often, if the disturbance is sufficiently intense, the system flips (or bifurcates, *sensu* Ludwig et al. [2002]) to a different state further removed from the familiar or desirable state (Crépin 2007). For example, the vegetation on a site that was deforested and farmed does not return to forest after abandonment but becomes permanent pasture or grassland. When the forest fails to redevelop, succession is arrested, and the pasture system might persist for decades with less structural development than the original forest ecosystem.

Restoring Degraded Lands to Productivity

Deforestation is an acute anthropogenic disturbance that, when followed by crop production or livestock grazing, results in a chronic condition that lasts as long as farmers or ranchers perceive a net benefit from their efforts. In many tropical areas of high rainfall and heavily leached or thin soils, farming is not sustainable without significant inputs of fossil fuels (Hall et al. 2000). Consequently, farmlands in these regions are abandoned relatively quickly (years to decades) when there is no access to external subsidies. Abandoned lands are usually degraded to some degree; they are eroded, and remaining soils are compacted or nutrient depleted. Without human intervention, they might slowly return to forest cover or remain as pastures in a state of arrested succession. The establishment of secondary forests following the abandonment of agricultural lands is a pantropical phenomenon responsible for the current era of secondary vegetation that characterizes the tropics (Brown and Lugo 1990). In many places, where human-induced fires or cattle grazing prevent forest reestablishment, the burning and grazing activities exacerbate land degradation, and the vegetation does not return to a forest physiognomy after abandonment (Goldammer 1992; Laurance et al. 1997). Therefore, the restoration of forest productivity requires an understanding of the types and intensities of past and present disturbances on the sites of interest.

The first step in restoring degraded lands to productive forest in the tropics is to limit chronic disturbances such as fire and cattle grazing that hinder forest succession. Many sites will gain forest cover in the absence of cattle and fire, whereas others will not recover because soils might be eroded, compacted, or nutrient depleted, or there might be less soil water available. Some organisms also might be affected by conditions such as high temperatures and low humidity in disturbed sites. Seed predators might consume the few available tree propagules, or distances might preclude effective seed rain to the site. In short, ecological space will have shifted to nonforest conditions, weakening or destroying the resilience of the original system.

Tree planting might be required in order to reestablish forests on sites with ecological conditions that have caused the persistence of pastures. The success of tree planting as a management strategy has been pantropical and includes the recovery of forests on pastures dominated by *Imperata*, a grass thought to prevent forest reestablishment once it gains hold of a site (Kosonen et al. 1997). Determining which tree species to plant and where to plant them requires scientific knowledge. In Puerto Rico, foresters planted both native and introduced tree species for timber and restoration purposes (Marrero 1950). During decades of study, nearly 500 native and introduced tree species were tested before it was determined that 32 species (mostly introduced species) were best for timber production (Wadsworth 1995). Today in the Neotropics, the use of tree plantations of native tree species for the sole purpose of establishing forest conditions has gained popularity and success (Butterfield and Fisher 1994).

In the LEF, forest cover was restored through a combination of tree planting on pastures (Silver et al. 2000, 2004), line plantings in degraded forests (Weaver and Bauer 1986), tree planting in agricultural fields (taungya system) (Weaver 1989), and natural succession (Lugo 1992). Initial plantings of tree species were designed to increase wood production by establishing tree species with high timber yields (e.g., pines, mahogany, *Eucalyptus*) (Francis 1995). This approach was successful in establishing high-yielding forest plantations (Lugo 1992) and productive secondary forests (Silver et al. 2000, 2004) that improved the soil organic matter content and nutrient accumulation (Lugo et al. 2004). Many of these positive results occurred over 6 decades (Silver et al. 2004) at the La Condesa site within the LEF (table 7-5). This site, which was planted with introduced and native species, was a carbon source for several decades before becoming a carbon sink (Silver et al. 2004). The loss of soil carbon originating from pasture soils was initially faster than carbon gain by plantation trees. These secondary forests and others in the vicinity support wildlife, improve soil conditions, and protect water supplies and watershed values. The data in table 7.5 also show that the forest stand at La Condesa had more aboveground biomass and productivity but less root biomass than a nearby native forest of similar age.

Rates of succession after pasture abandonment are variable in sites where secondary succession advances without human intervention (Zimmermann et al. 1995; Aide et al. 1996; Silver et al. 2000). The land cover at the time of abandonment influences the speed of succession. More rapid succession and accumulation of biomass characterized sites that were less disturbed at the time of abandonment, as opposed to sites that were pastures or bare soil at the time of abandonment. Succession in heavily disturbed sites was slower than in native forests after a natural disturbance (Aide et al. 1995; Silver et al. 2000). Such differential rates of succession and biomass accumulation in relation to past land use represent the time tax mentioned above. Learning when to enter the successional cycle in order

Table 7.5 Characterization of a 55-year-old subtropical moist forest restored through the planting of 13 tree species on a degraded pasture at La Condesa, Luquillo Experimental Forest, Puerto Rico.

Parameter	La Condesa	Mature tabonuco
State variable: Mg ha^{-1}		
Soil organic matter	204	161
Aboveground biomass	160	80
Fine root biomass	2.5	9.0
Annual rates		
Accumulation of tree species	1 species y^{-1}	1 species y^{-1}[a]
Accumulation of aboveground biomass	2.8	2.6
Litterfall	10.6 to 12.9	9.7 to 11.3
Aboveground net primary productivity	14.9	12.3
Fine root productivity	0.3	—[b]
Net primary productivity	15.4	—
Soil organic matter accumulation	1.8	—
Net soil organic matter sink	1.1	—

Data are from Silver et al. (2004). Data are based on trees > 9.1 cm in diameter at breast height and a forest area of 4.64 ha. Roots were sampled to a depth of 10 cm, and soil to 1 m. Mature tabonuco data are from Lugo (1992) for a native stand > 50 y at a similar elevation.
[a] Mean for native secondary forest succession (Lugo et al. 1993).
[b] No data.

to promote recovery is an example of managing with ecological cycles, and it requires an understanding of the rates of succession under different ecological conditions.

Of social interest is the role that *parceleros* (farmers who lived on LEF lands at the time of land acquisition by the Forest Service) played in the restoration of lands in the Luquillo Mountains (Wadsworth 1995). The Forest Service allowed *parceleros* to continue planting crops in their fields as long as they also planted and cared for trees selected by the Forest Service. This tree-planting method is known as the taungya system, and it is effective in plantation establishment (Weaver 1989). When planted trees reached heights that prevented farming, the Forest Service acquired lands for the *parceleros* outside the boundaries of the LEF, and the *parceleros* moved. This partnership allowed the agency to reforest larger areas at a faster rate than would have been possible otherwise. It also gave local communities the opportunity to adjust to the new ecological space, and it provided *parceleros* with continuous access to areas of ecological space suitable for farming via geographic relocation.

Restoring Biodiversity to Deforested Sites

The first critical step in restoring biodiversity to deforested sites is to reestablish forest cover. The expectation is that with the reestablishment of forest cover, other components of biodiversity (understory plants, soil organisms, and fauna) will follow. The reestablishment of forest cover can be accomplished by allowing tree regeneration to proceed naturally or by planting native or introduced trees (Lugo

1997; Lugo and Helmer 2004). Once trees are established, the next critical step is canopy closure. A fundamental change in the microclimate of the forest occurs following canopy closure. A closed-canopy forest is effective in attracting seed vectors and other organisms that require shade and cooler temperatures for reproduction and growth. The species richness of the understory in a young forest is higher than in the canopy, and many understory species will enter the stand's canopy in the future (Wadsworth and Birdsey 1983; Lugo 1988, 1992). In Puerto Rico, the number of tree species per hectare increases at a rate of one tree species per year of succession (Lugo et al. 1993), so that within 5 decades or so the number of tree species per unit area approaches the level for undisturbed stands (50 to 60 species per hectare; Lugo et al. 2002). Similar rates have been observed in landslides (Guariguata 1990; Myster and Walker 1997).

In the La Condesa site, the Forest Service planted 13 tree species on an abandoned pasture. Fifty-five years after the original planting, this site supported 70 tree species with diameter at breast height (dbh) ≥ 9.1 cm in an area of 4.64 ha; the tree species consisted of a new mixture of native and introduced taxa (Silver et al. 2004). The processes of tree species enrichment—through planting followed by natural secondary succession, or by secondary succession following abandonment of sites—is common in Puerto Rico, where the abandonment of agricultural lands is widespread (Lugo and Helmer 2004; Lugo and Brandeis 2005).

Ways in which reforestation restores ecosystem functions are shown in table 7-5, in which La Condesa is compared with a nearby native forest of similar age. At La Condesa the forest ecosystem is operating at rates comparable to those of mature native forests. In fact, most measures of ecosystem function in restored sites at the Luquillo Mountains show little if any differences compared to native forests of similar age (Lugo 1992).

The establishment of tree cover and the succession of species that follow alter site conditions such as the microclimate or the quantity and chemistry of organic inputs to soils (Zou and González 1997). These alterations accelerate the establishment of other types of organisms at the site. As a result, the overall site biodiversity is enhanced. The change through succession in species composition, biomass, and the function of earthworms is particularly well documented in the Luquillo Mountains (González et al. 1996; Zou and González 1997; González and Zou 1999; Liu and Zou 2002; Sánchez de León et al. 2003). With the conversion of pastures to forests, the richness of earthworm species increases owing to the presence of both introduced and native earthworms. The restoration of earthworm species after tree establishment is an example of how restoring tree cover affects other components of forest biodiversity. A similar pattern is known for the restoration of understory plant species (Lugo 1992) and birds (Cruz 1987, 1988).

Water Supply and Conservation of Freshwater Biota

In the early 1990s, approximately half of the water draining the Luquillo Mountains was diverted on a daily basis for human consumption (Naumann 1994). At the time, this amount of water supplied the needs of about 22 percent of the island's population. By 2005, daily withdrawals accounted for 70 percent of median daily water flow (Crook et al. 2007). However, owing to poor maintenance of the delivery infrastructure, nearly half of the water is lost in transmission or stolen before it is delivered to customers, and the actual population served is only about 11 percent (Ortiz Zayas and Scatena 2004).

The method most commonly used for harvesting water from rivers and streams is to dam the main channel and extract water for as long as is necessary or possible (figure 7-5). Many streams in the Luquillo Mountains are pumped dry by this procedure, particularly during dry periods and extended droughts (Naumann 1994; Crook et al. 2007). Moreover, streams and rivers in Puerto Rico and the rest of the Caribbean have been modified heavily with structures such as concrete channels, dams, or water intakes (figure 7-6) (Pringle and Scatena 1999a, 1999b; March et al. 2003; Greathouse et al. 2006a). Dam construction is an increasing conservation problem of global proportions, particularly in developing countries (figure 7-7) (Pringle et al. 2000a). Damming and overharvesting of river water are fundamentally incompatible with the conservation of stream biota because dewatering streams or converting them to ponds and reservoirs changes the nature of the stream ecosystem, with consequent negative effects on the survival of native freshwater biota. However, the application of a combination of science-based measures and technology offers hope for the conservation of stream biota.

Important animals (shrimps, snails, fishes) within river ecosystems of the Luquillo Mountains are migratory, with most of the migrations occurring at night (March et al. 1998; Benstead et al. 1999; Johnson and Covich 2000). Adults reproduce in freshwater, and larvae drift downstream to estuaries. Juveniles later return

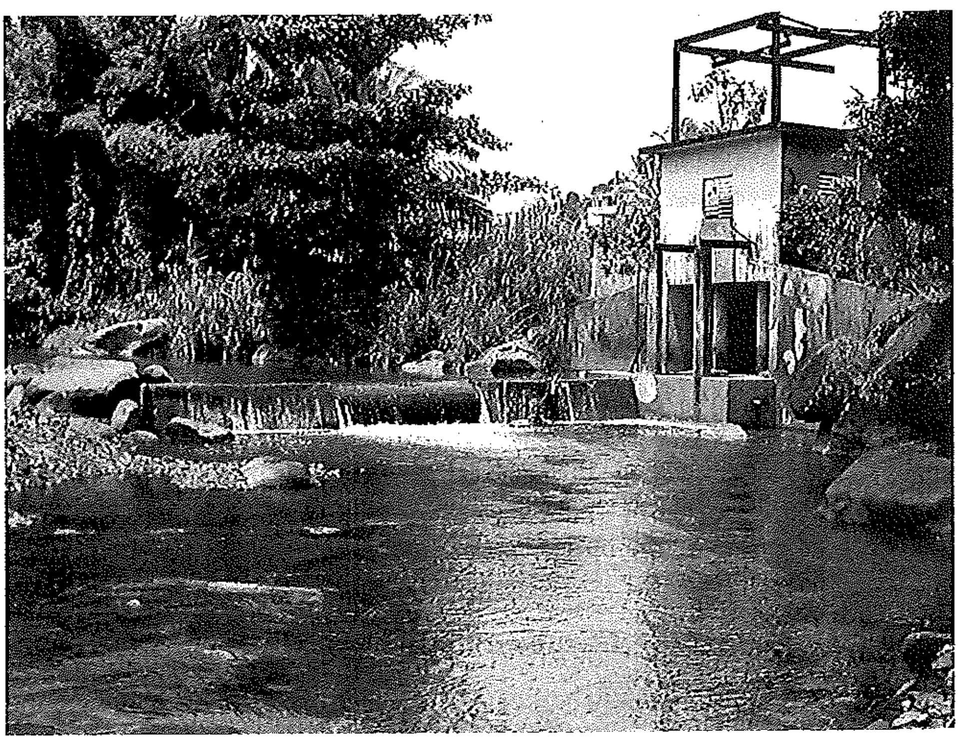

Figure 7.5 The low-head dam on the Río Fajardo. Low-head dams can cause mortality of drifting larval freshwater shrimps. (Photograph by Kelly Crook.)

to freshwater (Benstead et al. 2000). Dams obstruct these migrations, facilitate predation on sensitive life stages, reduce biodiversity above the dam, and favor the establishment of introduced species. High dams without releases of water over their spillways are impenetrable barriers that prevent migration and eliminate native fish and shrimp from upstream reaches (Holmquist et al. 1998), with cascading effects on food web dynamics and ecosystem-level processes (Greathouse et al. 2006b). Furthermore, as dams and water abstraction reduce stream flow, saltwater intrusion from the ocean reaches 2 to 3 km upstream, with concomitant predation on freshwater species by saltwater fish (Pringle 1997). Because of the migratory life cycles of many stream organisms, such impacts in the lowlands are transmitted upstream, affecting not only lowland river and estuarine reaches but also the biota of headwater systems such as those in the Luquillo Forest (Pringle 1997).

Issues of water quality compound the conservation problem associated with water supplies. Industrialization often produces new compounds (such as pesticides and fertilizers) that are introduced into tropical aquatic systems, where they are novel to the biota and might be toxic (Meybeck et al. 1989). In Puerto Rico and

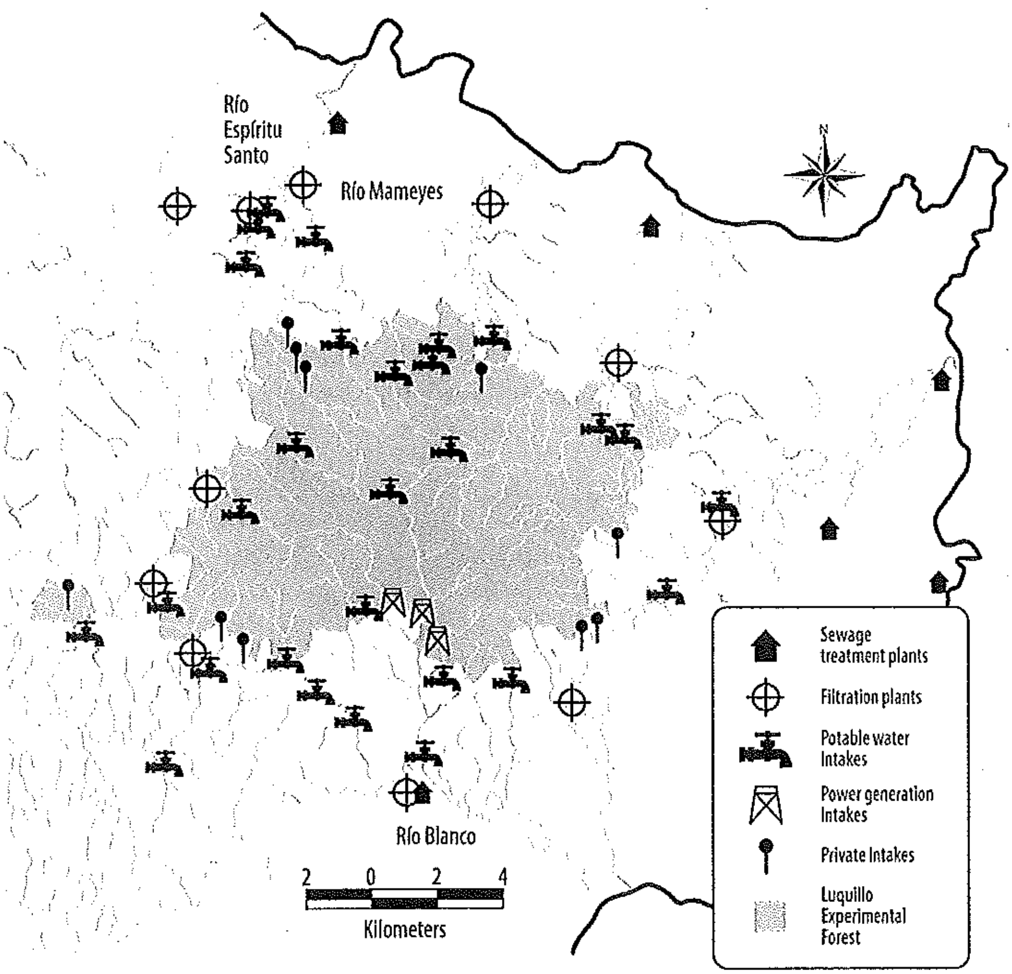

Figure 7.6 Sites of water withdrawals (intakes for potable water, power generation, and private), sewage treatment plants, and filtration plants in the Luquillo Experimental Forest. (Modified from Pringle 2000b.)

much of the tropics, the input of raw sewage into aquatic systems poses a severe water-quality problem (Hunter and Arbona 1995; Jobin 1998). This situation is exacerbated by water intakes, which reduce the capacity of river flow to dilute sewage by reducing freshwater runoff. The dire environmental situation of tropical rivers can prevent the use of rivers and coastal estuaries for tourism and recreation (Pringle and Scatena 1999b). With the singular exception of the Luquillo Mountains (Pringle and Scatena 1999a, 1999b), the scientific understanding needed in order to conserve water supplies and maintain quality in streams of the Caribbean is generally lacking. However, our research in the Luquillo Mountains is relevant to the management and conservation of streams and rivers not only in the Caribbean and Latin America but also in the temperate zone (Pringle 2000a, 2000b, 2001; Pringle et al. 2000a, 2000b; Postel and Richter 2003).

Earlier, we suggested that an understanding of ecological cycles and ecological life histories was important for ecosystem management. This is best illustrated by research on shrimp that showed that predictable temporal cycles characterize reproduction and migration. These predictable ecological cycles allow the development of pumping schedules that minimize the entrainment of biota. Larval shrimp drift during the night, with a nocturnal peak slightly after dusk (March et al. 1998). Water abstraction entrains larvae, juveniles, and even adults, significantly reducing population levels (Pringle 1997; Benstead et al. 1999). For example, in the lower Río Espíritu Santo, water abstraction caused 42 percent mortality of drifting first-stage

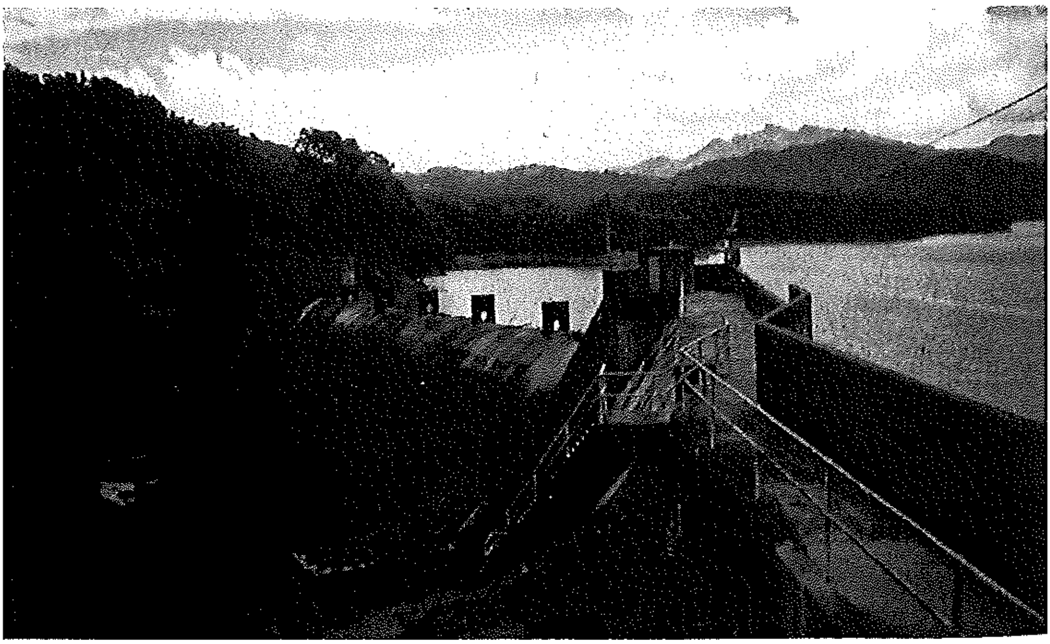

Figure 7.7 The Lago Guayo dam, a large structure that blocks shrimp and fish migration and causes the upstream decimation of native shrimp and fish populations in Puerto Rico. (Photograph by Effie A. Greathouse.)

shrimp larvae via entrainment during downstream migration (figure 7-8). All drifting larvae were killed during the dry season (Benstead et al. 1999). By stopping water abstraction for 5 hours during peak migration periods, larval mortality due to entrainment can be reduced to only 11 to 20 percent (Benstead et al. 1999).

The effects of dams can also be mitigated by fish ladders and the maintenance of a minimum flow over the dam (March et al. 2003). However, all dams alter riverine conditions. This problem can be averted through alternative water intake designs. A different design of the water intake pipes at the Río Mameyes eliminated the need to use dams, and thus allowed water abstraction without changing the free-flowing nature of the river. The new intake design was supplemented with administrative actions based on hydrological estimates, coupled with life-history information of organisms. Studies calculated the minimum flows required in order to maintain the ecological functioning of streams (Scatena and Johnson 2001). The enforcement of minimum flows would facilitate ecosystem functioning during drought periods and ensure a sustainable balance between human use and conservation of the biota, in addition to attendant ecosystem services. Recently, some new water storage reservoirs in Puerto Rico have been constructed off the river channel so as to avoid damming the river and exposing the reservoir to excessive sedimentation.

Roads and Landslides

Roads and landslides are land covers in which the soil is either covered by pavement (roads) or lost to such a degree that the saprolite or deep soil strata are exposed. The conditions resulting from both types of disturbance are inhospitable to plant growth (Walker 1999). Roads and landslides cover about 1 percent of the surface of

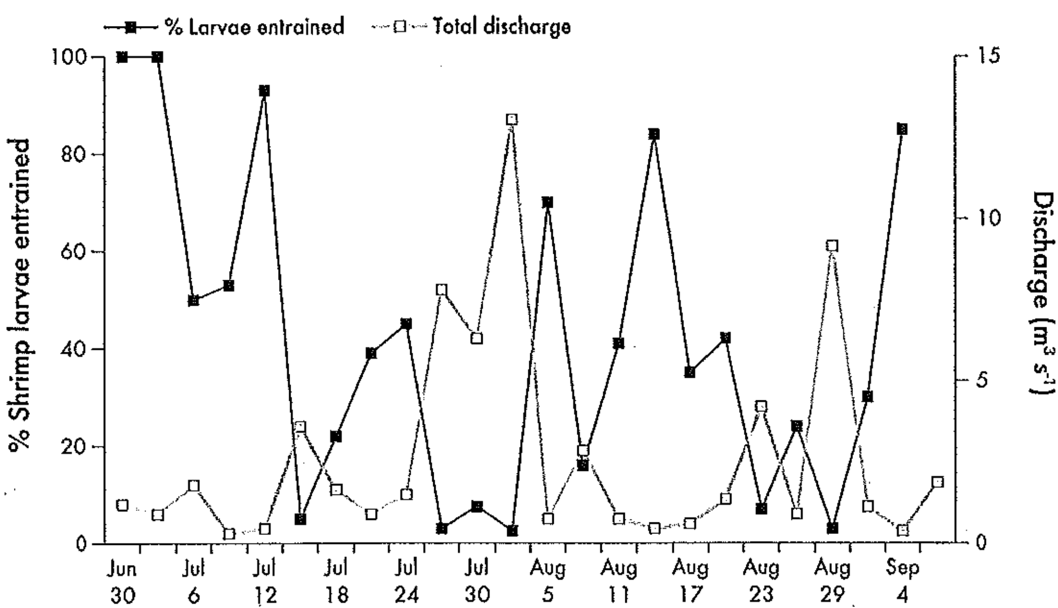

Figure 7.8 Percentage of larval entrainment by a major water intake on the Espíritu Santo River (left axis) and discharge over the dam (right axis) during the period of June 30 to September 4, 1995. (Modified from Benstead et al. 1999.)

the Luquillo Mountains (Larsen and Torres-Sánchez 1992) but are the most severe disturbances in the forest because of the burial or removal of all organic matter (Walker et al. 1996). Landslides potentially redistribute nutrients in the Luquillo Mountains, as phosphorus-rich mineral soil is exposed or added to streams, and carbon- and nitrogen-rich organic matter is buried to varying depths. However, such redistributions have yet to be quantified. Studying ecosystem recovery on roads and landslides provides valuable insights about primary succession, ecosystem assembly, and revegetation that are applicable to many severe disturbances, including in urban areas, construction zones, mined areas, or flooded areas (Walker and del Moral 2003; Walker et al. 2007). Contrasts between secondary succession on abandoned farmlands and in hurricane-affected forests in Puerto Rico and primary succession on roads and landslides clarify the role of soils and surviving vegetation in recovery following disturbance.

Road construction and poor maintenance enhance the likelihood of landslides, as >80 percent of landslides in the Luquillo Mountains occur along road corridors (Larsen and Parks 1997). Roads also act as corridors for the movement and establishment of introduced species (Walker and Boneta 1995), although little spread of introduced grasses into adjacent forests has been detected in the upper Luquillo Mountains (Olander et al. 1998). Successional changes on abandoned paved roads at lower elevations in the Luquillo Mountains occur quickly. Within 11 years of road abandonment, the litter mass, soil bulk density, soil moisture, soil organic matter, and total soil nitrogen reached adjacent forest levels (Heyne 2000). At higher elevations, changes were slower on road fill (Olander et al. 1998) and differed from those noted in a study conducted at a lower elevation by Heyne (2000). The species composition, however, did not resemble that of adjacent forests in any of the forests in the 60-year chronosequence studied (Heyne 2000).

Plant succession on landslides is governed by slope stability and nutrient availability (Guariguata 1990; Walker et al. 1996). Upper slip faces are often unstable and low in nutrients, so only climbing ferns that spread vegetatively can survive (Walker 1994). The middle chute zone of landslides is generally more nutrient rich but very unstable, so shrubs and trees might grow but often reslide. The deposition zone is the most stable and fertile zone, and succession to forest can occur there within 50 years (Zarin and Johnson 1995a, 1995b; Myster and Walker 1997). Fern thickets can inhibit tree colonization (Walker 1994), and seed dispersal can be slow from landslide edges (Walker and Neris 1993). Large landslides are generally slower to revegetate than narrow or small landslides that are affected by local slumping of residual forest soil and short-distance propagule dispersal. Frequent resliding, limitations in nutrient and propagule dispersal (Fetcher et al. 1996; Shiels et al. 2006), and growth inhibition can delay forest recovery for centuries (Walker et al. 1996).

Landslide management requires the application of knowledge from the ecological, engineering, and geological sciences, as each makes a significant contribution to the others. The first conservation alternative for dealing with landslides is to prevent them, because once they occur, the time tax of recovery can be long. Once the landslide occurs, the management options include stabilizing the landslide and either (1) allowing succession to proceed naturally or (2) accelerating natural succession or revegetating the slide through planting.

Because most landslides are associated with roads, their prevention is best achieved through better road design and maintenance, and especially improved drainage design. The management of landslides in roadless areas involves forecasting which conditions are likely to create them. Larsen and Simon (1993) suggested that landslides in the Luquillo Mountains are triggered by storms that exceed 100 to 200 mm of rain. Shallow landslides result from storms of short duration, whereas longer storms result in much deeper landslides.

Efforts to stabilize landslides in the LEF include minimal treatments with mulches, silt fences, and fertilizer to encourage plant growth. Also used are contouring, plantings, and jute cloth coverings. Greater interventions include the use of gabions and the redirection of water flow along lined channels (M. Ortíz and P. Ríos, USDA Forest Service, personal communication, 1999). The long-term success of such efforts depends largely on stochastic factors such as rainfall and the rate and direction of succession that result in a stabilizing vegetative cover.

Sometimes landslides involve massive land movements, such as the 300,000 m^3 landslide that bisected State Road 191, the main road that traverses the Luquillo Mountains. Given the importance of the road, government efforts to stabilize the landslide and restore the road were undertaken at a cost of millions of dollars. In this particular case, it was impossible to stabilize the slopes with the resources available, and the restoration efforts had to be abandoned after several years. Today, some 30 years later, the road remains closed, and natural succession has taken over the site of the landslide. The example illustrates the limits of human manipulation of natural phenomena.

The prediction and manipulation of succession on landslides is still problematic. Adding perches that attract birds onto landslides facilitates propagule and seed arrival (Shiels and Walker 2003). Fertilizers can increase plant growth (Fetcher et al. 1996) but might promote a dense cover of ferns or grasses, which hamper tree establishment and prevent the longer-term landslide stabilization provided by trees (Walker et al. 2010). Natural stabilization by thicket-forming ferns appears to be the best long-term path to forest recovery on landslides. Sloughing of nutrient-rich forest soil (Shiels et al. 2006) and the decomposition of pioneer tree ferns and *Cecropia* trees (Shiels 2006) eventually lead to forest development on landslides in the Luquillo Mountains. Tree planting can speed primary succession and is most successful when proper soil and symbionts such as mycorrhizae are provided (Lodge and Calderón 1991; Myster and Fernández 1995). Matching plant species to appropriate microsites and layering exposed surfaces with moss to provide better germination sites for seeds might aid landslide recovery (Myster and Sarmiento 1998). Also, the redirecting of roads can reduce the angle of the slope and thus the potential for landslides.

The experience in the Luquillo Mountains and elsewhere in Puerto Rico raises the issue of the inevitability of the association of roads and landslides. In the karst region, for example, chronic landslides raised the cost of constructing 1 km of road to over $30 million. Despite this expenditure of funds and decades of roadwork, PR 10 remains unstable (Lugo et al. 2001). Given these experiences, planners and road builders have two main options when dealing with wet, steep terrain. First, they need to select road alignments carefully and arrive at realistic cost-benefit analyses in order to avoid the costly surprises of PR 10. Second, they can opt to avoid building the road altogether, as was decided in the Luquillo Mountains with the repair of PR 191.

Regardless of the choices made, roads will continue to be ubiquitous components of landscapes and present problems to managers. Lugo and Gucinski (2000) proposed a unified approach to the management and analysis of the function and effects of roads on forested rural landscapes. The approach is based on considering roads as ecosystems (techno-ecosystems) and conducting analyses of road ecology prior to making policy or management decisions. An ecosystem approach to road issues has four advantages: (1) it allows for the analysis of all types of roads, irrespective of geographic location; (2) it provides a holistic framework for analyzing all aspects of roads, from their alignment to their operation and decommissioning, as well as all road functions, irrespective of value judgments; (3) it provides a holistic focus to road management; and (4) it supplements landscape management approaches based on spatial concepts. Lugo and Gucinski (2000) recommended five precautions when evaluating road ecosystems:

1. Identify the type of road under consideration.
2. Differentiate the effects and conditions of individual road segments from those of road networks.
3. Be explicit about to which phase of road development the argument applies, because different phases of development have different effects on the landscape.
4. Ascertain the age of the road and evaluate the degree of landscape adjustment to the road, and vice versa.
5. Do not prejudge human-induced changes in landscapes as automatically good or bad for the ecology or economy of a region.

Figure 1 in their work (Lugo and Gucinski 2000) is a useful model of a road ecosystem that applies to most tropical conditions.

Living with Environmental Change

The emergence of humans as the dominant agents of change on Earth was one of the most biologically significant consequences of the Industrial Revolution. As an example of the extent to which humans influence the biosphere, Sanderson et al. (2002) quantified the human footprint on the planet and found that humans directly influence 83 percent of the land surface and 98 percent of the area where it is possible to grow rice. In contrast, protected areas represent less than 10 percent of the land surface of Earth, and it is obvious that protected areas alone cannot resolve environmental problems facing the world. The most practical alternative for achieving a sustainable future for humans is to learn to cope with environmental change and apply conservation measures to all lands and waters of the planet. In this section we present examples of the consequences of environmental change in the Luquillo Mountains and assess the usefulness of these examples for informing management beyond the Luquillo Mountains.

Current and future agents of environmental change in the Luquillo Mountains include natural disturbances, urbanization, land cover change, and climate change.

These agents of change are interconnected and known to influence the ecological space and development of the ecosystems of the Luquillo Mountains. For example, after Hurricane Hugo, when much of the forest in the Luquillo Mountains was defoliated, the forest experienced a drought because of the change in the cloud level over the forest (Beard et al. 2005; Heartsill-Scalley et al. 2007). Cloud level and associated water inputs are also influenced by urbanization in the lowlands and on the periphery of the mountains (van der Molen 2002). Urbanization creates a heat island that influences the elevation to which air must rise in order to form clouds (Malkus and Stern 1953). Climate change has affected and will continue to affect the Luquillo Mountains (Scatena 1998), but we do not know with certainty the magnitude or direction of the change. We can formulate scenarios of likely outcomes of environmental change using current knowledge. Here, we provide two likely scenarios that are already in progress in the Luquillo Mountains.

The first likely scenario is a progressive change in the species composition of forests and aquatic ecosystems. Changes in the species composition of ecosystems owing to introduced species are a ubiquitous result of environmental change in the Luquillo Mountains. The recent natural invasion of the Luquillo Mountains by an ecotype of Africanized bee (*Apis mellifera scutellata* [Ruttner]) is one example. Africanized bees have competitively displaced the preexisting (as well as introduced) honeybee species (*Apis mellifera*) in places without any obvious change in environmental conditions. Other progressive changes in species composition include the loss of amphibian species (Joglar 1998) and the spread of the invasive tree *Syzygium jambos* (Brown et al. 2006).

Ecologists argue about the role and causes of species invasions (Vermeij 1996; Lodge and Shrader-Frechette 2003; Lugo and Brandeis 2005), but they agree on the fact that the presence of introduced species increases with increasing anthropogenic disturbances. High dams are an example for aquatic systems. The dams create new aquatic environments, made by people, where introduced aquatic plant species such as *Eichornia crassipes* dominate. In streams above large reservoirs, migration failures cause reductions of native aquatic biota, which allow the spread of introduced aquatic species (Holmquist et al. 1998).

These progressive changes in species composition can lead to the emergence of new ecosystems that perform desired ecological services and support economic development (Lugo 1996; Lugo and Helmer 2004). The process is notable in degraded sites, but it also occurs, at a slower rate, in less disturbed conditions. Tropical plant and animal species, both native and introduced, have the capacity to invade most ecosystems and, through self-organization, form terrestrial and aquatic ecosystems of species mixtures that are new to the island (Lugo and Brandeis 2005). This "creativity" and adaptability of the biota in the face of significant environmental change provides examples and experiences that will be useful to other tropical countries where landscapes have not yet reached the levels of modification seen in Puerto Rico.

The second likely scenario deals with ecosystem-level adjustments that are likely in an environment with an increased frequency of disturbances and change (Lugo 2000). For example, an increased level of disturbances such as hurricanes would lead to the following outcomes:

- A larger fraction of the natural landscape will be set back in successional stage (i.e., there will be younger ecosystems). For example, modeling different hurricane intensities and frequencies showed that a range of forest types are possible, from mature forests with large trees in areas of low hurricane frequency to areas in which forest trees are not allowed to mature when hurricane frequencies are high (O'Brien et al. 1992).
- Forest aboveground biomass and height will decrease because vegetation growth will be interrupted more frequently or will suffer greater impact.
- Combinations of familiar species will change as species capable of thriving under disturbance conditions increase in frequency at the expense of species that require long periods of disturbance-free conditions in order to mature.

The mitigation of environmental change requires global measures because of the magnitude of the forces that regulate climate and land use. At local scales, individual countries have control over the management of land cover (Lugo 2002), which influences climate at mesoscales. Land cover management should pursue those options that reduce changes in atmosphere–land interactions and are more amenable to the movement of species into desirable and appropriate habitats as change proceeds. Thus, landscape management is a regional approach to mitigating the consequences of global environmental change.

Future Directions for Tropical Ecology

The tropics contain most of the world's biodiversity (Wilson 1988) and ecosystem types (Lugo and Brown 1991). The moist tropics alone support half of the world's population (Gladwell and Bonell 1990). Four-fifths of the world's population increase will occur in the tropics (Pereira 1989). The resulting mosaic of social and natural ecosystems is one of enormous complexity and interdependence. For tropical ecology, this scenario presents a formidable challenge. It requires a new vision and era of conservation. We need new ways to evaluate the increasingly intimate relationship between humans and their environment. In response to this reality, scientific societies are proposing new approaches to ecological research (Bawa et al. 2004; Palmer et al. 2004). These approaches, coupled with changes taking place in civil society, are harbingers of a new era of conservation.

A New Era of Conservation

The new era of conservation taxes our knowledge, understanding, and imagination. Understanding how ecosystems function and are assembled is the key to conservation success, a success best ensured through LTER of the type presented in this book. Aldo Leopold (1953) wrote that the first rule of intelligently tinkering with nature is to save all the parts, a task that is made more difficult with increasing human pressure on the biota. In order to prevail, we must do our utmost to avoid species extinctions. One strategy is the maintenance of global and regional interconnected systems of reserves (Andelman and Willig 2003). This solution is compromised by climate change, which shifts environmental conditions and can strand reserves in the wrong climatic setting. Climate change, for example, might convert moist forests to dry forests, thus endangering moist-forest species that cannot adjust to the reduction in water availability. Global change also endangers small reserves. Reserves with a large perimeter-to-area ratio are more vulnerable to invasion and edge effects.

A reduction in the pressures occurring on reserves is possible if we concentrate human activity in small areas (Lugo 1991). Such a solution currently requires increased supplies of fossil fuels to power the intense level of human activity and transport the vital materials needed to sustain urban systems (Odum and Odum 2001). However, the sustainability of fossil fuel supplies for powering urban systems is uncertain (Hubbert 1968; Campbell 1997). At the same time, we must be ready to deal with the consequences of increased concentrations of atmospheric carbon dioxide (CO_2) produced by the combustion of fossil fuels. Regardless of how we elect to arrange humans on the landscape, all lands and waters require conservation attention in order to sustain human activity and protect ecosystems and species.

The conservation of the biota is leading to new areas of scientific activity such as ecological engineering (Mitsch and Jørgensen 1989), ecological economics (Maxwell and Costanza 1989; Hall et al. 2001), and restoration ecology (Jordan et al. 1987). In all these new fields of science, a common denominator is the use of designed ecosystems to obtain needed products and services. No longer do we deal with natural ecosystems in the search for ecological solutions to human problems; we now manipulate and create new ecosystems for specific purposes, such as with the use of microbes and wetlands for treating sewage and cleaning water. The biota serves as a reservoir of genetic information; each species contains genetic combinations that allow it to function under particular sets of environmental conditions. Therefore, the biota has functional capabilities that humans can use judiciously in the design of new ecosystems. We could use a green infrastructure in cities, such as a vegetation wall to absorb sound, rather than the current inanimate, gray infrastructure built of concrete or steel. For flood control, flood plains or wetlands function as well as, or better than, concrete canals and reservoirs. New ecosystems, often containing introduced species, have been designed to repair degraded lands such as abandoned mines (Parrotta et al. 1997). Green infrastructure provides aesthetic and pollution-control services to cities, lowers the heat island effect, is self-maintaining, provides open green spaces that provide connectivity between natural habitats for the movement of organisms, and reduces pressure on native ecosystems. In short, the new era of conservation should be an era of the protection of biodiversity and intelligent tinkering for products and services and for coping with constant global change. This new era of conservation will require novel ways of evaluating ecosystems and their services and functions.

Uncertainty and Surprise

Uncertainty and surprise are inevitable aspects of the future that sometimes help, but usually derail, conservation plans. Natural ecosystems and anthropogenic landscapes are too complex to permit accurate forecasting based on current knowledge, but this does not mean that all surprises will be negative. In Puerto Rico, we were surprised by several ecological events that no one had predicted (listed below). Usually, once revealed, the surprise is easily explained, but in other examples, such as the extinction of frogs (see below), the explanation is still elusive. The lesson for conservation is to work on managing uncertainty while expecting surprises, with the understanding that the changes they entail are not necessarily detrimental to conservation objectives. The strategy must be to first assess the nature of the change, before making judgments about its value, and then be ready to adapt to the change, incorporating new knowledge into the conservation activity.

The following examples of surprises are presented in rough chronological order.

- The linking of tabonuco trees by root grafts, as revealed by the failure of tree poisoning in tabonuco trees, was a surprise to foresters employing the standard technique of poisoning selected trees in order to thin stands. At the time, it was not known that root grafts connect tabonuco trees (Lugo and Scatena 1995), and that nonpoisoned trees in the tree union could keep the poisoned trees and logged stumps alive for decades. The poisoning of root-grafted trees is no longer a management option.
- The high resistance of the rain forest to high levels of ionizing gamma radiation (Odum et al. 1970b) was a surprise, as pine forests in the United States had proven to be sensitive to this treatment (Woodwell and Rebuck 1967). This was one of the first experimental indications of the resilience of tropical forests.
- The development of species-rich understories under plantations of introduced pines was surprising because it was previously thought that monocultures of introduced species would inhibit understory development (Lugo 1992). This led to the use of introduced-species tree plantations to restore native tree species to degraded sites.
- The sudden increase in reproductive effort by wild populations of Puerto Rican Parrot after Hurricane Hugo was a surprise. Long-term study of these birds had consistently shown a low reproductive output in the wild (Snyder et al. 1987), but somehow the hurricane reversed the trend and mitigated to some extent the losses of birds during the storm. This observation provided clues for managing parrot reproduction in the aviary.
- The endangerment and local extinction of amphibians in places where the habitat has not changed (Joglar 1998) is a surprise with negative consequences, because species might be lost for reasons we still do not understand. The outcome has been to increase the monitoring of amphibian populations in undisturbed sites.
- Researchers had not anticipated the importance of the legacy of tree species' spatial distribution in response to past land uses (Thompson et al. 2002). Before this study we had not fully understood that knowledge of past land use history is a requirement for the interpretation of species distribution data.
- Life history studies yield many surprises regarding the adaptations of organisms to ecological space—for example, the 40-plus-year-old and woody

seedlings of *Manilkara bidentata* that suddenly responded to canopy opening by a hurricane (You and Petty 1991), or the extremely slow upstream migrations and age-size distributions of snails that reflected old age groups in such small organisms (Blanco and Scatena 2005). These surprises underscore the importance of slow variables to ecosystem management and illustrate biological responses (seedling growth) tuned to low-frequency environmental signals (hurricanes).

- Predictions of land cover change did not anticipate the collapse of agricultural activity (Lugo 2002), and thus forest cover increased island-wide in spite of increased population density. This surprise underscores our inability to predict the direction of major land use/land cover processes.
- The dominance of introduced tree species in the secondary forests of Puerto Rico was unexpected. Although introduced species have always been part of the flora and were known to compose 28 percent of the tree flora, scientists were not aware that introduced species were forming and dominating new forest types until island-wide inventories starting in 1980 demonstrated this (Birdsey and Weaver 1982). This finding led to the realization that natural processes of self-organization are already integrating the forest composition with past land uses and current environmental changes.
- The similarity of the turnover rates of biomass in elfin and tabonuco forests in spite of their differences in structure and productivity (table 7-2) explained how low-productivity forests can survive in environments with high levels of natural disturbances.

Adaptive management is the best way to deal with uncertainty and a surprise (Bormann et al. 1999). The core idea behind the concept of adaptive management is that we need to learn from and adapt to changes in ecological space. Conservation activities should be conducted as if they were an unfinished experiment. For example, as part of management, a disturbance is applied to a system with a purpose and an expectation of a product. The response of the system is not always as expected, and thus it has to be monitored and evaluated against the expectations. Long-term study and monitoring, as well as the scientific process, are critical for understanding those human activities that occur on large scales and impact ecosystems for a long time. Such types of study require institutions and procedures, such as sound data management and record keeping, that provide continuity to the study regardless of the turnover of people.

What Is Next?

Tropical science will continue to be challenged by the complexity of tropical ecosystems. This complexity compounds most research problems that we attempt to solve. The future requires more and better science in support of management and conservation policy. Such science needs to monitor the effects of human activities on the planet's ecosystems. In order for science to be effective in future ecosystem management, scientists must increasingly use the scientific approach to focus on the synthesis of knowledge and communicate its relevance to society. Scientists and managers must produce materials that are easy for nonscientists, such as policymakers and the public, to understand. More important, scientists must work in closer collaboration with nonscientific citizens (figure 7-9). According to Ludwig (2001), the era of management is over. He believes that the problems of resource conservation facing society are so complex that they cannot be solved by scientists alone or by any one sector of society. Instead, "scientists must be prepared to share their advisory and decision-making roles with a variety of interested parties and participate with them on equal footing" (Ludwig 2001:758). This has been put in practice in the Luquillo Mountains in the development of the land management plan for the El Yunque National Forest, with positive outcomes. During this effort, scientists maintained their objective approach to understanding and developed a relationship of mutual respect with forest managers. The persistence of humans and the ecosystems on which they depend requires a new global coalition with long-term

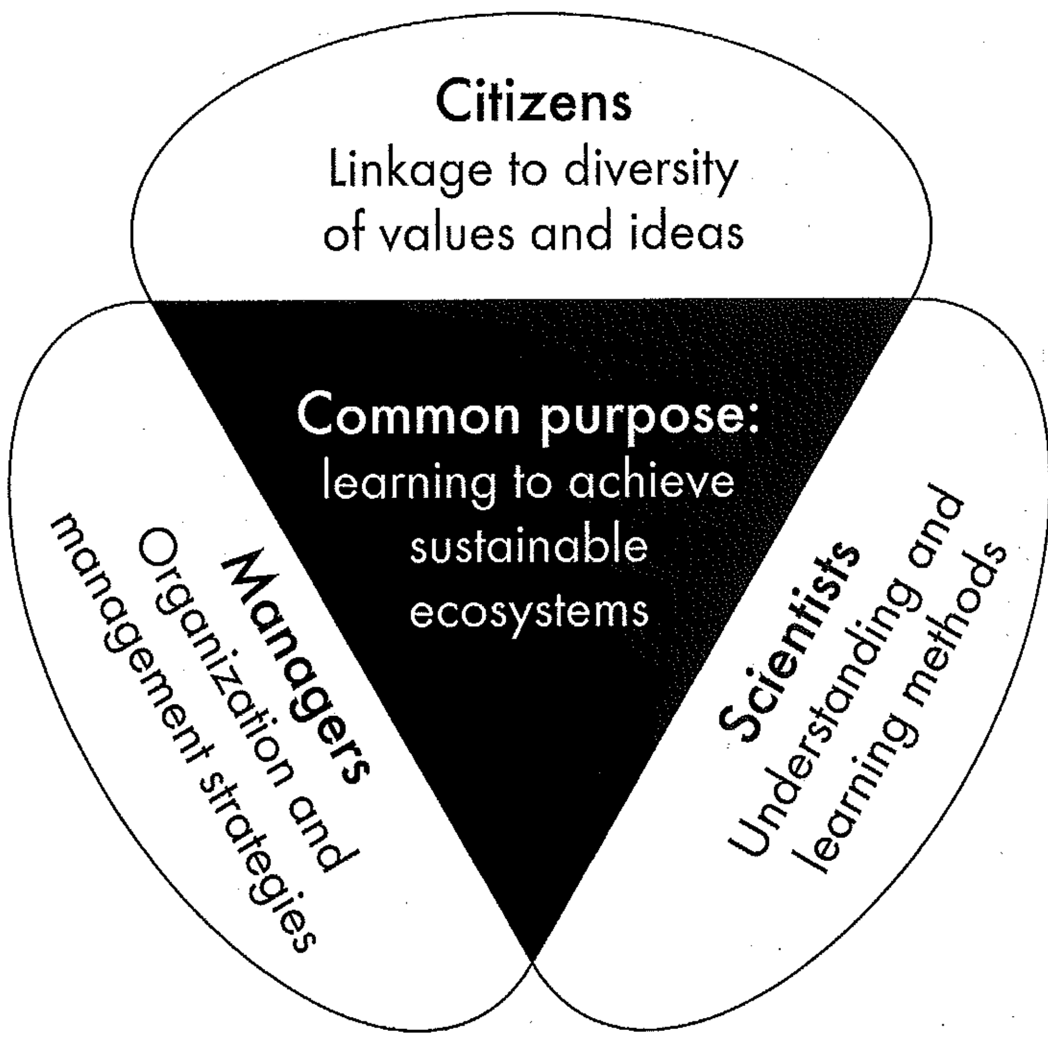

Figure 7.9 Learning as a common ground for building new, mutually beneficial relations among citizens, managers, and scientists in order to achieve sustainable ecosystems (Bormann et al. 1999).

understanding of contemporary systems and the mechanisms that support them. If this is achieved, a humane balance between use and preservation can be sustained for future generations in the face of risk and uncertainty.

Summary

Research in the Luquillo Experimental Forest has made significant contributions to the conservation and management of tropical forests and watersheds. The research has focused on species life histories and ecosystem processes at three levels of spatial organization over the long term. These spatial levels are the catena, the watershed, and the interfaces between different ecosystem components, such as the leaf–atmosphere, terrestrial–aquatic (riparian), or aerobic–anaerobic substrates. We discuss six examples of how research results have contributed to the addressing of specific management situations. These examples include the management of forests for ecosystem services, restoring degraded lands to productivity, restoring biodiversity to degraded lands, sustaining water supplies while conserving aquatic biodiversity, the management of roads and landslides, and living with environmental change. Moreover, the Luquillo LTER has contributed to changes in paradigms in the field of tropical ecology, particularly in terms of the importance of disturbances and the resilience of tropical forests as a result of both natural and anthropogenic disturbances. Future avenues of research activity will have to deal with novel environmental conditions, biotic surprises, and uncertainty. Managing under these conditions requires flexibility and support from cutting-edge research activity, which foresees a new era of conservation.

Literature Cited

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

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

Andelman, S. J., and M. R. Willig. 2003. Present patterns and future prospects for biodiversity in the Western Hemisphere. *Ecology Letters* 6:818–824.

Arendt, W. J. 2006. Adaptation of an avian supertramp: Distribution, ecology, and life history of the Pearly-Eyed Thrasher (*Margarops fuscatus*). General Technical Report IITF-GTR-27. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Bawa, K. S., W. J. Kress, and N. M. Nadkarni. 2004. Beyond paradise—Meeting the challenges in tropical biology in the 21st century. *Biotropica* 36:276–284.

Beard, K., A. K. Eschtruth, K. A. Vogt, D. J. Vogt, and F. N. Scatena. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 19:607–617.

Beard, K. H., K. A. Vogt, and A. Kulmatiski. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* 133:583–593.

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

Benstead, J. P., J. G. March, and C. M. Pringle. 2000. Estuarine stages and upstream migration of freshwater shrimps in two tropical rivers, Puerto Rico. *Biotropica* 32:545–547.

Benstead, J. P., J. G. March, C. M. Pringle, and F. N. Scatena. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications* 9:656–668.

Benzing, D. H. 1991. Aerial roots and their environments. Pages 867–886 in Y. Waisel, A. Eshel, and U. Kafkafi, editors, *Plant roots: The hidden half.* New York: Marcel Dekker, Inc.

Birdsey, R. A., and P. L. Weaver. 1982. The forest resources of Puerto Rico. Resource Bulletin SO-85. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station.

Blanco, J. F., and F. N. Scatena. 2005. Floods, habitat hydraulics and upstream migration of *Neritina virginea* (Gastropoda: Neritidae) in northeastern Puerto Rico. *Caribbean Journal of Science* 41(1):55–74.

Bormann, B. T., J. R. Martin, F. H. Wagner, G. W. Wood, J. Alegría, P. G. Cunningham, M. H. Brookes, P. Friesema, J. Berg, and J. R. Henshaw. 1999. Adaptive management. Pages 505–534 in W. T. Sexton, A. J. Malk, R. C. Szaro, and N. C. Johnson, editors, *Ecological stewardship. A common reference for ecosystem management.* Oxford, England: Elsevier.

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

Brown, S., and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161–187.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1–32.

Brown, S., and A. E. Lugo. 1994. Rehabilitation of tropical lands: A key to sustaining development. *Restoration Ecology* 2:97–111.

Brown, K. A., F. N. Scatena, and J. Gurevitch. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. *Forest Ecology and Management* 226:145–152.

Burney, D. A., and L. P. Burney. 1994. Holocene charcoal stratigraphy from Laguna Tortugero, Puerto Rico and the timing of human arrival on the island. *Archaeological Science* 21:273–281.

Butterfield, R. P., and R. H. Fisher. 1994. Untapped potential: Native species for reforestation. *Journal of Forestry* 92:37–40.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.

Campbell, C. J. 1997. Depletion patterns show change due for production of conventional oil. *Oil and Gas Journal Special* 29(Dec):33–37.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4:765–781.

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

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

Corujo Flores, I. N. 1980. A study of fish populations in the Espíritu Santo River estuary. M.S. thesis. University of Puerto Rico-Río Piedras, PR.

Costanza, R., and H. E. Daly. 1987. Toward an ecological economics. *Ecological Modeling* 38:1–7.

Covich, A. P., and W. H. McDowell. 1996. The stream community. Pages 433–460 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

Crépin, A. S. 2007. Using fast and slow processes to manage resources with thresholds. *Environmental & Resources Economics* 36:191–213.

Cronon, W. 1996. The trouble with wilderness; or, getting back to the wrong nature. Pages 69–90 in W. Cronon, editor, *Uncommon ground: Rethinking the human place in nature*. New York: W.W. Norton.

Crook, K. E., F. N. Scatena, and C. M. Pringle. 2007. Water withdrawn from the Luquillo Experimental Forest, 2004. General Technical Report IITF-GTR-34. Rio Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Crosby, A. W. 1986. *Ecological imperialism: The biological expansion of Europe, 900–1900*. Cambridge, England: Cambridge University Press.

Cruz, A. 1987. Avian community organization in a mahogany plantation in a Neotropical island. *Caribbean Journal of Science* 23:286–296.

Cruz, A. 1988. Avian resource in a Caribbean pine plantation. *Journal of Wildlife Management* 52:274–279.

Daily, G. C., and K. Ellison. 2002. *The new economy of nature. The quest to make conservation profitable*. Washington, DC: Island Press.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate change and forest disturbances. *BioScience* 59:723–734.

Dale, V. H., F. J. Swanson, and C. M. Crisafulli, editors. 2005. *Ecological responses to the 1980 eruption of Mount St. Helens*. New York: Springer.

Devoe, N. N. 1989. Differential seeding and regeneration in openings and beneath closed canopy in subtropical wet forests. Doctor of Forestry dissertation. Yale University, New Haven, CT.

Diamond, J. 2005. *Collapse. How societies choose to fail or succeed*. New York: Viking Penguin Group.

Dirzo, R. 2001. Tropical forests. Pages 251–276 in O. E. Sala, F. S. Chapin III, and E. Huber-Sannwald, editors, *Global biodiversity in a changing environment: Scenarios for the 21st century*. New York: Springer-Verlag.

Duryea, M. L., E. Kampf, R. C. Littell, and C. D. Rodríguez-Pedraza. 2006. Hurricanes and the urban forest: II. Effects on tropical and subtropical tree species. *Arboriculture and Urban Forestry* 33:98–112.

Erdman, D. S. 1984. Exotic fishes in Puerto Rico. Pages 162–176 in W. R. Courtenay, Jr., and J. R. Stauffer, Jr., editors, *Distribution, biology and management of exotic fishes*. Baltimore, MD: Johns Hopkins University Press.

Ewel, J. J. 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* 1:103–117.

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

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

Francis, J. K. 1995. Forest plantations in Puerto Rico. Pages 210–223 in A. E. Lugo and C. A. Lowe, editors, *Tropical forests: Management and ecology*. New York: Springer-Verlag.

Francis, J. K., and C. A. Lowe, editors. 2000. Silvics of native and exotic trees of Puerto Rico and the Caribbean islands. General Technical Report IITF-GTR-15. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Freeman, M. C., C. M. Pringle, E. A. Greathouse, and B. J. Freeman. 2003. Ecosystem-level consequences of migratory faunal depletion caused by dams. Pages 255–266 in K. E. Limburg and J. R. Waldman, editors, *Biodiversity, status and conservation of the world's shads*. Bethesda, MD: American Fisheries Society.

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

Gladwell, J. S., and M. Bonell. 1990. An international programme for environmentally sound hydrological and water management strategies in the humid tropics. Proceedings of the International Symposium on Tropical Hydrology and Fourth Caribbean Islands Water Tesources Congress. Technical Publication Series TPS-90-2. Denver, CO: American Water Works Association.

Goldammer, J. G. 1992. Tropical forests in transition. Ecology of natural and anthropogenic disturbance processes—An introduction. Pages 1–16 in J. G. Goldammer, editor, *Tropical forests in transition*. Basel, Switzerland: Birkhäuser Verlag.

González, G., and T. R. Seastedt. 2000. Comparison of the abundance and composition of litter fauna in tropical and subalpine forests. *Pedobiologia* 44:545–555.

González, G., and T. R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82:955–964.

González, G., and X. Zou. 1999. Earthworm influence on N availability and the growth of *Cecropia schreberiana* in tropical pasture and forest soils. *Pedobiologia* 43:824–829.

González, G., X. Zou, and S. Borges. 1996. Earthworm abundance and species composition in abandoned tropical croplands: Comparison of tree plantations and secondary forests. *Pedobiologia* 40:385–391.

Greathouse, E. A., C. M. Pringle, and J. G. Holmquist. 2006a. Conservation and management of migratory fauna: Dams in tropical streams of Puerto Rico. *Aquatic Conservation-Marine and Freshwater Ecosystems* 16:695–712.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006b. Indirect upstream effects of dams: Consequences of migratory consumer extirpation in Puerto Rico. *Ecological Applications* 16:339–352.

Groffman, P. M., N. J. Boulware, W. C. Zipperer, R. V. Pouyat, L. E. Band, and M. F. Colosimo. 2002. Soil nitrogen cycling processes in urban riparian zones. *Environmental Science and Technology* 36:4547–4552.

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

Gunderson, L. 2000. Ecological resilience in theory and application. *Annual Review of Ecology and Systematics* 31:425–439.

Hall, C. A. S., C. Leon, W. Ravenscroft, and H. Wang. 2000. Temporal and spatial overview of Costa Rican agricultural production. Pages 349–401 in C. A. S. Hall, G. Leclerc, and C. L. Perez, editors, *Quantifying sustainable development: The future of tropical economies*. San Diego, CA: Academic Press.

Hall, C., D. Lindenberger, R. Kümmel, T. Kroeger, and W. Eichhorn. 2001. The need to reintegrate the natural sciences with economics. *BioScience* 51:663–673.

Heartsill-Scalley, T., and T. M. Aide. 2003. Riparian vegetation and stream condition in a tropical agricultural-secondary forest mosaic. *Ecological Applications* 13:225–234.

Heartsill-Scalley, T., F. N. Scatena, C. Estrada, W. H. McDowell, and A. E. Lugo. 2007. Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. *Journal of Hydrology* 333:472–485.

Heyne, C. M. 2000. Soil and vegetation recovery on abandoned paved roads in a humid tropical rain forest, Puerto Rico. M.S. thesis. University of Nevada, Las Vegas, NV.

Holdridge, L. R. 1967. *Life zone ecology.* San José, Costa Rica: Tropical Science Center.

Holling, C. S. 1973. Resiliency and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.

Holmquist, J. G., J. M. Schmidt Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. *Conservation Biology* 12:621–630.

Hubbert, M. K. 1968. Energy resources. Pages 157–242 in *Resources and man.* San Francisco, CA: National Academy of Science and W.H. Freeman.

Hunter, J. M., and S. I. Arbona. 1995. Paradise lost: An introduction to the geography of water pollution in Puerto Rico. *Social Science & Medicine* 40:1331–1355.

Hunter, M. L. 1990. *Wildlife, forests and forestry: Principles of managing forests for biological diversity.* Upper Saddle River, NJ: Prentice Hall.

Jobin, W. 1998. *The Caribbean region.* Pages 201–214 in W. Jobin, editor, *Sustainable management for dams and waters.* Boca Raton, FL: Lewis Publishers.

Joglar, R. L. 1998. *Los coquíes de Puerto Rico. Su historia natural y conservación* [*The coquís of Puerto Rico. Their natural history and conservation*]. Río Piedras, PR: Universidad de Puerto Rico.

Johnson, S. L., and A. P. Covich. 2000. The importance of night-time observation for determining habitat preferences of stream biota. *Regulated Rivers: Research and Management* 16:91–99.

Jordan, W. R., M. E. Gilpin, and J. D. Aber. 1987. *Restoration ecology. A synthetic approach to ecological research.* Cambridge, England: Cambridge University Press.

Kartchner, S. C., and T. A. Crowl. 2002. Recreational use of montane streams of the Puerto Rico rainforest. Luquillo LTER REU Program Report. Logan: Utah State University.

Kent, R., H. T. Odum, and F. N. Scatena. 2000. Eutrophic overgrowth in the self-organization of tropical wetlands illustrated with a study of swine wastes in rainforest plots. *Ecological Engineering* 16:255–269.

Kosonen, M., A. Otsamo, and J. Kuusipalo. 1997. Financial, economic and environmental profitability of reforestation of *Imperata* grasslands in Indonesia. *Forest Ecology and Management* 99:247–259.

Larsen, M. C., and J. E. Parks. 1997. How wide is a road? The association of roads and mass-wasting in a forested montane environment. *Earth Surface Processes and Landforms* 22:835–848.

Larsen, M. C., and A. Simon. 1993. A rainfall intensity-duration threshold for landslides in a humid-tropical environment, Puerto Rico. *Geografiska Annaler* 75A:13–23.

Larsen, M. C., and A. J. Torres-Sánchez. 1992. Landslides triggered by Hurricane Hugo in eastern Puerto Rico, September 1989. *Caribbean Journal of Science* 28:113–120.

Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de-Morena, C. Gaston, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118.

Leopold, L. B., editor. 1953. *Round River: From the journals of Aldo Leopold.* Oxford, England: Oxford University Press.

Liegel, L. H. 1982. Growth, development and hurricane resistance of Honduras pine in Puerto Rico. Pages 28–48 in J. González-Liboy and J. Figueroa, editors, *Noveno simposio de recursos naturales*. San Juan, PR: Departamento de Recursos Naturales de Puerto Rico.

Liegel, L. H. 1984. Assessment of hurricane rain/wind damage in *Pinus caribaea* and *Pinus oocarpa* provenance trials in Puerto Rico. *Commonwealth Forestry Review* 63:47–53.

Likens, G. E., and F. H. Bormann. 1995. *Biogeochemistry of a forested ecosystem*. New York: Springer-Verlag.

Liu, Z. G., and X. M. Zou. 2002. Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications* 12:1406–1417.

Lodge, D. J., and F. J. Calderón. 1991. Distribution of plant species in landslides can be explained by their dependency on VA-mycorrhizal fungi and responsiveness to high phosphorus availability. *Bulletin of the Ecological Society of America* 72:178.

Lodge, D. M., and K. Shrader-Frechette. 2003. Nonindigenous species: Ecological explanation, environmental ethics, and public policy. *Conservation Biology* 17:31–37.

Lowrance, R., L. S. Altier, J. D. Newbold, R. R. Schnabel, P. M. Groffman, J. M. Denver, D. L. Correll, J. W. Gilliam, J. L. Robinson, R. B. Brinsfield, K. W. Staver, W. Lucas, and A. H. Todd. 1997. Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. *Environmental Management* 21:687–712.

Ludwig, D. 2001. The era of management is over. *Ecosystems* 4:758–764.

Ludwig, D., B. H. Walker, and C. S. Holling. 2002. Models and metaphors of sustainability, stability, and resilience. Pages 21–48 in L. H. Gunderson and J. L. Pritchard, editors, *Resilience and the behavior of large-scale systems*. Washington, DC: Island Press.

Lugo, A. E. 1988. The future of the forest. Ecosystem rehabilitation in the tropics. *Environment* 30:16–20, 41–45.

Lugo, A. E. 1991. Cities in the sustainable development of tropical landscapes. *Nature and Resources* 27:27–35.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs* 62:1–41.

Lugo, A. E. 1994. Preservation of primary forests in the Luquillo Mountains, Puerto Rico. *Conservation Biology* 8:1122–1131.

Lugo, A. E. 1996. Caribbean island landscapes: Indicators of the effects of economic growth on the region. *Environment and Development Economics* 1:128–136.

Lugo, A. E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99:9–19.

Lugo, A. E. 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenario. *The Science of the Total Environment* 262:243–251.

Lugo, A. E. 2002. Can we manage tropical landscapes? An answer from the Caribbean perspective. *Landscape Ecology* 17:601–615.

Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment* 2:265–273.

Lugo, A. E., J. S. Baron, T. P. Frost, T. W. Cundy, and P. Dittberner. 1999a. Ecosystem processes and functioning. Pages 219–254 in R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. *Ecological stewardship: A common reference for ecosystem management*. Oxford, England: Elsevier Science.

Lugo, A. E., and T. J. Brandeis. 2005. A new mix of alien and native species coexist in Puerto Rico's landscapes. Pages 484–509 in D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley, editors, *Biotic interactions in the tropics: Their role in the maintenance of species diversity*. Cambridge, England: Cambridge University Press.

Lugo, A. E., and S. Brown. 1991. Comparing tropical and temperate forests. Pages 319–330 in J. Cole, G. Lovett, and S. Findlay, editors, *Comparative analysis of ecosystems: Patterns, mechanisms, and theories.* New York: Springer-Verlag.

Lugo, A. E., S. L. Brown, R. Dodson, T. S. Smith, and H. H. Shugart. 1999b. The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. *Journal of Biogeography* 26:1025–1038.

Lugo, A. E., J. Figueroa Colón, and F. N. Scatena. 2000. The Caribbean. Pages 593–622 in M. G. Barbour and W. D. Billings, editors, *North American terrestrial vegetation.* Cambridge, England: Cambridge University Press.

Lugo, A. E., and J. L. Frangi. 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 25:73–84.

Lugo, A. E., and H. Gucinski. 2000. Function, effects, and management of forest roads. *Forest Ecology and Management* 133:249–262.

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

Lugo, A. E., T. d. M. López, O. Ramos, and L. L. Vélez. 2004. Urbanización de los terrenos en la periferia de El Yunque [Urbanization of lands in the periphery of El Yunque]. General Technical Report IITF-66. Washington, DC: USDA Forest Service, International Institute of Tropical Forestry.

Lugo, A. E., and L. Mastroantonio. 1999. Institute of Tropical Forestry: The first fifty years. General Technical Report IITF-GTR-7. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Lugo, A. E., L. Miranda-Castro, A. Vale, T. d. M. López, E. Hernández-Prieto, A. García-Martinó, A. R. Puente-Rolón, A. G. Tossas, D. A. McFarlane, T. Miller, A. Rodríguez, J. Lundberg, J. Thomlinson, J. Colón, J. H. Schellekens, O. Ramos, and E. Helmer. 2001. Puerto Rican karst—A vital resource. General Technical Report WO-65. Washington, DC: USDA Forest Service.

Lugo, A. E., J. A. Parrotta, and S. Brown. 1993. Loss in species caused by tropical deforestation and their recovery through management. *Ambio* 22:106–209.

Lugo, A. E., and F. N. Scatena. 1992. Epiphytes and climate change research in the Caribbean: A proposal. *Selbyana* 13:123–130.

Lugo, A. E., and F. N. Scatena. 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. Pages 59–108 in A. E. Lugo and C. Lowe, editors, *Tropical forests: Management and ecology.* New York: Springer-Verlag.

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

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

Malkus, J. S., and M. E. Stern. 1953. The flow of a stable atmosphere over a heated island. *Journal of Meteorology* 10:30–41.

Mann, C. C. 2005. *1491: New revelations of the Americas before Columbus.* New York: Alfred A. Knopf.

March, J. G., J. P. Benstead, C. M. Pringle, and F. N. Scatena. 1998. Migratory drift of larval amphidromous shrimps in two tropical streams, Puerto Rico. *Freshwater Biology* 40:1–14.

March, J. G., J. P. Benstead, C. M. Pringle, and F. N. Scatena. 2003. Damming tropical island streams: Problems, solutions, and alternatives. *BioScience* 53:1069–1078.

March, J. G., and C. M. Pringle. 2003. Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. *Biotropica* 35:84–93.

March, J. G., C. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. *Freshwater Biology* 47:377–390.

Marrero, J. 1950. La reforestación de tierras degradadas de Puerto Rico. *Caribbean Forester* 11:16–24.

Maxwell, J., and R. Costanza. 1989. An ecological economics for ecological engineering. Pages 57–77 in W. J. Mitsch and S. E. Jørgensen, editors, *Ecological engineering. An introduction to ecotechnology*. New York: John Wiley & Sons.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301–312.

McClain, M. E., J. E. Richey, and T. Pena Pimental. 1994. Groundwater nitrogen dynamics at the terrestrial-lotic interface of a small catchment in the central Amazon basin. *Biogeochemistry* 27:113–127.

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

McDowell, W. H., W. B. Bowden, and C. E. Asbury. 1992. Riparian nitrogen dynamics in two geomorphologically distinct tropical rain forest watersheds—Subsurface solute patterns. *Biogeochemistry* 18:53–75.

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

Meffe, G. K. and C. R. Carroll, editors. 1997. *Principles of conservation biology*, 2nd ed. Sunderland, MA: Sinauer Associates, Inc.

Meine, C. 1987. The farmer as conservationist: Aldo Leopold on agriculture. *Journal of Soil and Water Conservation* 42:144–149.

Meybeck, M., D. Chapman, and R. Helmer. 1989. *Global freshwater quality. A first assessment*. Oxford, England: Basil Blackwell.

Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Synthesis*. Washington, DC: Island Press.

Mitsch, W. J., and S. E. Jørgensen, editors. 1989. *Ecological engineering: An introduction to ecotechnology*. New York: John Wiley & Sons.

Murphy, L. S. 1916. Forests of Puerto Rico: Past, present, and future and their physical and economic environment. Bulletin 354. Washington, DC: U.S. Department of Agriculture.

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

Myster, R. W., and F. O. Sarmiento. 1998. Seed inputs to microsite patch recovery on two tropandean landslides in Ecuador. *Restoration Ecology* 6:35–43.

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

Naiman, R. J., H. Décamps, and M. E. McClain. 2005. *Riparia: Ecology, conservation, and management of streamside communities*. San Diego, CA: Elsevier.

Naumann, M. 1994. A water-use budget for the Caribbean National Forest of Puerto Rico. Special Report. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Nieves, L. O. 1998. Ecological study of the freshwater stream fishes of the upper Mameyes River (Bisley) in the Luquillo Mountains of Puerto Rico. Ph.D. dissertation. George Mason University, Fairfax, VA.

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

Odum, H. T. 1971. *Environment power and society*. New York: Wiley.

Odum, H. T. 1988. Self-organization, transformity, and information. *Science* 242: 1132–1139.

Odum, H. T. 1989. Ecological engineering and self-organization. Pages 79–101 in W. J. Mitsch and S. E. Jørgensen, editors, *Ecological engineering*. New York: Wiley.

Odum, H. T. 1995. Tropical forest systems and the human economy. Pages 343–393 in A. E. Lugo and C. Lowe, editors, *Tropical forests: Management and ecology*. New York: Springer-Verlag.

Odum, H. T. 1996. *Environmental accounting: EMERGY and environmental decision making*. New York: John Wiley & Sons.

Odum, H. T., S. J. Doherty, F. N. Scatena, and P. A. Kharecha. 2000. EMERGY evaluation of reforestation alternatives in Puerto Rico. *Forest Science* 46:521–530.

Odum, H. T., G. Drewry, and E. A. McMahan. 1970a. Introduction to Section E. Pages E3–E15 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

Odum, H. T., P. Murphy, G. Drewry, F. McCormick, C. Schinham, E. Morales, and J. McIntyre. 1970b. Effects of gamma radiation on the forest at El Verde. Pages D3–D75 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

Odum, H. T., and E. C. Odum. 2001. *A prosperous way down: Principles and policies*. Boulder, CO: University Press of Colorado.

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

Ortiz Zayas, J. R., and F. N. Scatena. 2004. Integrated water resources management in the Luquillo Mountains, Puerto Rico: An evolving process. *Journal of Water Resources Development* 20:387–398.

Palmer, M. A., E. Bernhardt, E. Chornesky, S. Collins, A. Dobson, C. Duke, B. Gold, R. Jacobson, S. Kingsland, R. Kranz, M. Mappin, M. L. Martinez, F. Micheli, J. Morse, M. Pace, M. Pascual, S. Palumbi, O. J. Reichman, A. Simons, A. Townsend, and M. Turner. 2004. Ecology for a crowded planet. *Science* 304:1251–1252.

Parker, K. R., and J. A. Wiens. 2005. Assessing recovery following environmental accidents: Environmental variation, ecological assumptions, and strategies. *Ecological Applications* 15:2037–2051.

Parrotta, J. A. 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science* 6:627–636.

Parrotta, J. A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia, Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management* 124:45–77.

Parrotta, J. A., O. H. Knowles, and J. M. Wunderle. 1997. Development of floristic diversity in 10-year-old restoration forests on a bauxite mined site in Amazonia. *Forest Ecology and Management* 99:21–42.

Pereira, H. C. 1989. *Policy practice in the management of tropical watersheds*. San Francisco, CA: Westview Press.

Perlin, J. 1989. *A forest journey: The role of wood in the development of civilization*. Cambridge, MA: Harvard University Press.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology* 65:1466–1475.

Postel, S., and B. Richter. 2003. *Rivers for life: Managing water for people and nature*. Washington, DC: Island Press.

Pringle, C. M. 1997. Exploring how disturbance is transmitted upstream: Going against the flow. *Journal of the North American Benthological Society* 16:425–438.

Pringle, C. M. 2000a. River conservation in tropical versus temperate regions. Pages 367–379 in P. J. Boon, B. Davies, and G. E. Petts, editors, *Global perspectives on river conservation: Science, policy and practice*. New York: John Wiley & Sons.

Pringle, C. M. 2000b. Threats to U.S. public lands from cumulative hydrologic alterations outside of their boundaries. *Ecological Applications* 10:971–989.

Pringle, C. M. 2001. Hydrologic connectivity and the management of biological reserves: A global perspective. *Ecological Applications* 11:981–998.

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

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000a. Regional effects of hydrologic alterations on riverine microbiota in the New World: Tropical-temperate comparisons. *BioScience* 50:807–823.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. *Ecology* 80:1860–1872.

Pringle, C. M., and F. N. Scatena. 1999a. Factors affecting aquatic ecosystem deterioration in Latin America and the Caribbean. Pages 104–113 in U. Hatch and M. E. Swisher, editors, *Tropical managed ecosystems: The Mesoamerican experience*. New York: Oxford University Press.

Pringle, C. M. and F. N. Scatena. 1999b. Freshwater resource development: Case studies from Puerto Rico and Costa Rica. Pages 114–121 in U. Hatch and M. E. Swisher, editors, *Tropical managed ecosystems: The Mesoamerican experience*. New York: Oxford University Press.

Pringle, C. M., F. Scatena, P. Paaby, and N. Nuñez. 2000b. River conservation in Latin America and the Caribbean. Pages 39–73 in P. J. Boon, B. Davies, and G. E. Petts, editors, *Global perspectives on river conservation: Science, policy and practice*. New York: John Wiley & Sons.

Roberts, R. C. 1942. Soil survey of Puerto Rico. USDA Series 1936, No. 8. Washington, DC: U.S. Department of Agriculture.

Ruiz, B. I., editor. 2002. Manual de reforestación para América tropical [Reforestation manual for tropical America]. General Technical Report IITF-GTR-18. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.

Salwasser, H. 1997. Conservation biology and the management of natural resources. Pages 9–10 in G. K. Meffe and C. R. Carroll, editors, *Principles of conservation biology*. Sunderland, MA: Sinauer Associates, Inc.

Sánchez de León, Y., X. Zou, S. Borges, and A. Honghua Ruan. 2003. Recovery of native earthworms in abandoned tropical pastures. *Conservation Biology* 17:999–1006.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. A. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18–32.

Scatena, F. N. 1989. An introduction to the physiography and history of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico. General Technical Report 72. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station.

Scatena, F. N. 1990. Selection of riparian buffer zones in humid tropical steeplands. Pages 328–337 in R. R. Ziemer, C. L. O'Loughlin, and L. S. Hamilton, editors, *Research needs and applications to reduce erosion and sedimentation in tropical steeplands.* AISH Pub. No. 192. Louvain, Belgium: International Association of Hydrological Sciences.

Scatena, F. N. 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane forest of Puerto Rico. Pages 103–111 in J. E. Costa, A. J. Miller, K. W. Porter, and P. Wilcock, editors, *Natural and anthropogenic influences in fluvial geomorphology*. Monograph 89. Washington, DC: American Geophysical Union Press.

Scatena, F. N. 1998. An assessment of climate change in the Luquillo Mountains of Puerto Rico. Pages 193–198 in *Third international symposium on water resources. Fifth Caribbean islands water resources congress.* San Juan, PR: American Water Resources Association.

Scatena, F. N. 2001. Ecological rhythms and the management of humid tropical forests: Examples from the Caribbean National Forest, Puerto Rico. *Forest Ecology and Management* 154:453–464.

Scatena F. N., S. J. Doherty, H. T. Odum, and P. Kharecha P. 2002. An EMERGY evaluation of Puerto Rico and the Luquillo Experimental Forest. General Technical Report IITF-GTR-9. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Scatena, F. N., and S. L. Johnson. 2001. Instream-flow analysis for the Luquillo Experimental Forest, Puerto Rico: Methods and analysis. General Technical Report GTR-11. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

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

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

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

Scherr, S., A. White, and A. Khare. 2004. For services rendered. The current status and future potential of markets for the ecosystem services provided by tropical forests. ITTO Technical Series No. 21. Yokohama, Japan: International Tropical Timber Organization.

Schubert, T. H. 1979. *Trees for urban use in Puerto Rico and the Virgin Islands.* General Technical Report SO-27. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry.

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

Shiels, A. B., and L. R. Walker. 2003. Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology* 11:1–9.

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

Silver, W. L. 1992. Effects of small-scale and catastrophic disturbance on carbon and nutrient cycling in a lower montane subtropical wet forest in Puerto Rico. Ph.D. dissertation. Yale University, New Haven, CT.

Silver, W. L., S. Brown, and A. E. Lugo. 1996a. Biodiversity and biogeochemical cycles. Pages 49–67 in G. Orians, R. Dirzo, and J. H. Cushman, editors, *Biodiversity and ecosystem process in tropical forests*. Heidelberg, Germany: Springer-Verlag.

Silver, W. L., S. Brown, and A. E. Lugo. 1996b. Effects of changes in biodiversity on ecosystem function in tropical forests. *Conservation Biology* 10:17–24.

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

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

Silver, W. L., A. E. Lugo, and M. Keller. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44:301–328.

Silver, W. L., R. Ostertag, and A. E. Lugo. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology* 8:394–407.

Simmons, R. C., A. J. Gold, and P. M. Groffman. 1992. Nitrate dynamics in riparian forests—Groundwater studies. *Journal of Environmental Quality* 21:659–665.

Smith, K. L. 2008. Managing freshwater inflow to estuaries in northeastern Puerto Rico: Ecological and institutional considerations. Ph.D. dissertation. Department of Ecology, University of Georgia, Athens.

Snyder, N. F. R., J. W. Wiley, and C. B. Kepler. 1987. *The parrots of Luquillo: Natural history and conservation of the Puerto Rican Parrot*. Los Angeles, CA: Western Foundation of Vertebrate Zoology.

Stewart, M. M., and L. L. Woolbright. 1996. Amphibians. Pages 273–320 in D. P. Reagan and R. B. Waide, editors, *The food web of a tropical rain forest*. Chicago: University of Chicago Press.

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

Tilley, R. D., and W. T. Swank. 2003. EMERGY-based environmental systems assessment of a multi-purpose temperate mixed-forest watershed of the southern Appalachian Mountains, USA. *Journal of Environmental Management* 69:213–227.

Triska, F. J., J. H. Duff, and R. J. Avanzino. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream: Examining terrestrial-aquatic linkages. *Freshwater Biology* 29:259–274.

U.S. Department of Agriculture, Forest Service. 1997. Revised land and resource management plan: Caribbean National Forest, Luquillo Experimental Forest, Puerto Rico. Management Bulletin R8-MB 80G. Atlanta, GA: USDA Forest Service Southern Region.

van der Molen, M. K. 2002. *Meteorological impacts of land use change in the maritime tropics*. Amsterdam, The Netherlands: Vrije Universiteit.

Vermeij, G. 1996. An agenda for invasion biology. *Conservation Biology* 78:3–9.

Vogt, K. A., K. H. Beard, S. Himmann, J. O. H. Palmiotto, D. J. Vogt, F. N. Scatena, and B. P. Hecht. 2002a. Indigenous knowledge informing management of tropical forests: The link between rhythms in plant secondary chemistry and lunar cycles. *Ambio* 31:485–490.

Vogt, K. A., J. Gordon, J. Wargo, D. Vogt, H. Asbjornsen, P. A. Palmiotto, H. Clark, J. O'Hara, W. S. Keeton, T. Patel-Weynand, and E. Witten, editors. 1997. *Ecosystems: Balancing science with management*. New York: Springer-Verlag.

Vogt, K. A., M. Grove, H. Asbjornsen, K. Maxwell, D. J. Vogt, R. Sigurdardottir, B. C. Larson, L. Schibli, and M. Dove. 2002b. Linking social and natural science spatial scales. Pages 143–175 in L. Jianguo and W. M. Taylor, editors, *Integrating landscape ecology into natural resource management*. Cambridge, England: Cambridge University Press.

Vogt, K. A., O. Schmitz, K. H. Beard, J. O'Hara, and M. Booth. 2000. Conservation biology—Contemporary issues. Pages 865–881 in S. Levin, editor, *Encyclopedia of biodiversity*. New York: Academic Press.

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

Wadsworth, F. H. 1949. The development of the forest land resources of the Luquillo Mountains of Puerto Rico. Ph.D. dissertation. University of Michigan, Ann Arbor, MI.

Wadsworth, F. H. 1970. A review of past research in the Luquillo Mountains. Pages B33–B46 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

Wadsworth, F. H. 1995. A forest research institution in the West Indies: The first 50 years. Pages 33–56 in A. E. Lugo and C. Lowe, editors, *Tropical forests: Management and ecology*. New York: Springer-Verlag.

Wadsworth, F. H. 1997. Forest production for tropical America. Agriculture Handbook 710. Washington, DC: USDA Forest Service.

Wadsworth, F. H., and R. A. Birdsey. 1983. Un nuevo enfoque de los bosques de Puerto Rico [A new focus to the forests of Puerto Rico]. Pages 12–27 in *Puerto Rico Department of Natural Resources ninth symposium on natural resources*. San Juan, PR: Puerto Rico Department of Natural Resources.

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

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

Walker, L. R., editor. 1999. *Ecosystems of disturbed ground*. Amsterdam, The Netherlands: Elsevier.

Walker, L. R., and W. Boneta. 1995. Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. *Journal of Tropical Ecology* 11:473–479.

Walker, L. R., and R. del Moral. 2003. *Primary succession and ecosystem rehabilitation*. Cambridge, England: Cambridge University Press.

Walker, L. R., F. H. Landau, E. Velazquez, A. B. Shiels, and A. D. Sparrow. 2010. Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides. *Journal of Ecology* 98:625–635.

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

Walker, L. R., J. Walker, and R. J. Hobbs, editors. 2007. *Linking restoration and ecological succession*. New York: Springer.

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

Wang, H. H., and F. N. Scatena. 2003. Regeneration after hurricane disturbance of big-leaf and hybrid mahogany plantations in Puerto Rico. Pages 237–257 in A. E. Lugo, J. C. Figueroa Colón, and M. Alayón, editors, *Big-leaf mahogany: Genetics, ecology, and management*. New York: Springer-Verlag.

Weaver, P. L. 1987. Structure and dynamics in the colorado forests of the Luquillo Mountains of Puerto Rico. Ph.D. dissertation. Michigan State, East Lansing, MI.

Weaver, P. L. 1989. Taungya plantings in Puerto Rico. *Journal of Forestry* 87:37–41.

Weaver, P. L., and G. P. Bauer. 1986. Growth, survival and shoot borer damage in mahogany plantings in the Luquillo Forest, Puerto Rico. *Turrialba* 36:509–522.

Weaver, P. L., and P. G. Murphy. 1990. Forest structure and productivity in the Luquillo Mountains of Puerto Rico. *Biotropica* 22:69–82.

Weinbren, M. P., B. M. Weinbren, W. B. Jackson, and J. B. Villella. 1970. Studies of the roof rat (*Rattus rattus*) in the El Verde forest. Pages E169–E181 in H. T. Odum and R. F. Pigeon, editors, *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge, TN: U.S. Atomic Energy Commission.

Wells, M., and K. Brandon. 1992. *People and parks: Linking protected area management with local communities*. Report to The International Bank for Reconstruction and Development (World Bank), Washington, DC.

Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81–120.

Wilshusen, P., S. Brechin, C. Fortwangler, and P. West. 2002. Reinventing a square wheel: Critique of a resurgent "protection paradigm" in international biodiversity conservation. *Society and Natural Resources* 15:17–40.

Wilson, E. O. 1988. The current state of biological diversity. Pages 3–18 in E. O. Wilson and F. M. Peters, editors, *Biodiversity*. Washington, DC: National Academy of Sciences.

Woodwell, G. M., and A. L. Rebuck. 1967. Effects of chronic gamma radiation on the structure and diversity of an oak-pine forest. *Ecological Monographs* 37:53–69.

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

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

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

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

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

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

Zon, R., and W. N. Sparhawk. 1923. *Forest resources of the world*. New York: McGraw-Hill.

Zou, X., and G. González. 1997. Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. *Soil Biology and Biochemistry* 29:627–629.

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The Multidimensional Nature of Disturbance and Response

Edited by

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