Tropical Forests in Transition
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A Research Perspective on Disturbance and Recovery of a Tropical Montane Forest

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Abstract

Studies of disturbance in tropical forest ecosystems have been important in developing the new paradigm that views these ecosystems as dynamic in structure and function rather than constant. Long-term investigations in the Luquillo Experimental Forest in Puerto Rico are designed to evaluate the relative importance of the four principal types of disturbance within the forest and to analyze the importance of the biota in restoring the ecosystem after disturbance. Puerto Rico is an excellent site to conduct such investigations because of the availability of long-term weather and growth records, the detailed understanding of historical land use, and the long tradition of ecosystem research.

Research is driven by the concept that the response of an ecosystem to disturbance is a function of the type, intensity, periodicity, and extent of the disturbance. Recovery is influenced by a complex interaction among the soil, biota, hydrosphere, and atmosphere, but we hypothesize that the biota plays a key role in conditioning the return to the previous level of productivity after disturbance. With increasing severity of disturbance, the role of the biota becomes more important.

A patch dynamics model is being used to guide research on disturbance and regeneration at the ecosystem level. Results from this work are being linked to the landscape level of organization through simulation models generalized to each cell of a geographic information system covering the forest.

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Introduction

Studies of response of forested ecosystems to disturbance have been historically important in ecology and have contributed to a developing view of forest systems as dynamic in structure and function. Forest ecosystems are subject to a variety of disturbances, differentiated along scales of severity, spatial extent, frequency, and duration (e.g., Karr & Freemark 1985; White & Pickett 1985; Jordan 1985; Lugo *et al.* 1986; Foster 1988a and b). Many studies of forest disturbance and its consequences have been undertaken, some with a long-term perspective; however, relatively few such studies have occurred in the humid tropics. Extending studies of forest disturbance to the tropics is potentially valuable because: (1) comparison of a wider variety of ecosystems will assist in forming generalizations about disturbance, (2) tropical forests are different from temperate forests in many aspects that may affect response to disturbance, such as type of soil, amount and half-life of organic matter, and community complexity, and (3) anthropogenic disturbance is occurring widely in tropical forests.

Most investigations of disturbance in tropical forests focus on a limited subset of the broad spectrum of ecosystem disturbances, partly because most tropical research is short-term due to logistic difficulties and lack of long-term institutional support. Long temporal series of observations are necessary to unravel short- from long-term responses to events with complex return frequencies. Hence, long-term research is a necessary tool for the eventual understanding of tropical forests. The National Science Foundation's Long-Term Ecological Research (LTER) program provides an ideal framework for examining ecological events that occur on a temporal scale of decades or centuries.

We are conducting long-term studies of the relationship between disturbance regime and forest structure in the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 1). Our objectives are (1) to investigate the relative importance of different types of disturbance within the four life zones (Ewel & Whitmore 1973) constituting the landscape of the LEF, and (2) to analyze the importance of the biota in restoring ecosystem productivity after different types of disturbance within representative watersheds in one of these life zones.

The history of disturbance in the LEF is well known through measurements of long-term plots, although ecosystem responses have not been well studied for each type of disturbance (Brown *et al.* 1983). Frequent human-related and natural disturbances to the forest have created a mosaic of areas in various stages of succession. The major forms of disturbance in this humid tropical forest are natural treefalls, landslides, hurricanes, and selective cutting. The integral role of disturbance in the LEF was shown by Doyle's (1982) close simulation of actual relative abundances of tree species, using a forest dynamics model that incorporated treefalls and hurricanes (Fig. 2).

Components of the current research include examination of:

1. Pattern, frequency, and intensity of disturbance in the LEF (e.g., treefalls, landslides, and hurricanes).
2. Environmental properties that are expected to vary with disturbance size, age, and origin (e.g., light, nutrient availability, moisture, temperature, and soil organic matter).

3. Biological properties that are expected to vary with environmental properties (e.g., species composition, growth, nutrient dynamics, reproductive success, carbon fixation, and food web structure).
4. System properties that emerge from the effects of disturbance pattern and frequency on the mutual interaction of abiotic environment and biota (e.g., nutrient cycling, phases of recovery, rates of recovery, and displacement from and return to steady state).

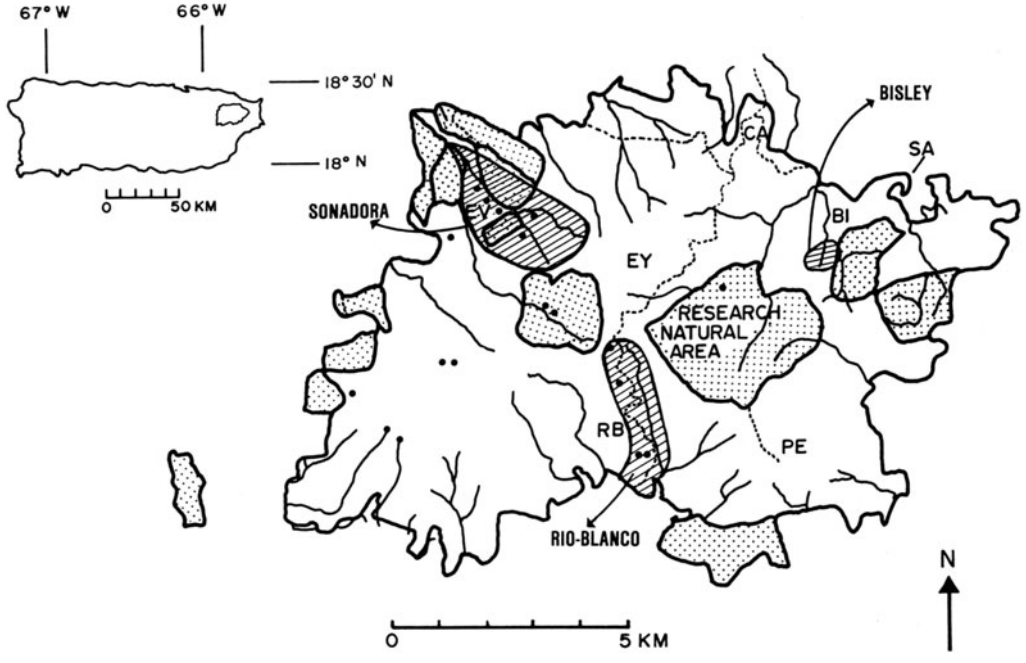

Fig. 1. Map of the LEF showing (1) 12 reserved research tracts (dotted areas), (2) the Bisley, Sonadora, and Rio Blanco watersheds (shaded areas), (3) long-term growth plots under study by the Institute of Tropical Forestry (points), and (4) other sites for which long-term data sets exist (EV = El Verde, CA = Catalina, BI = Bisley, SA = Sabana, EY = El Yunque, RB = Rio Blanco, PE = Pico del Este). The inset shows the location of the LEF in Puerto Rico

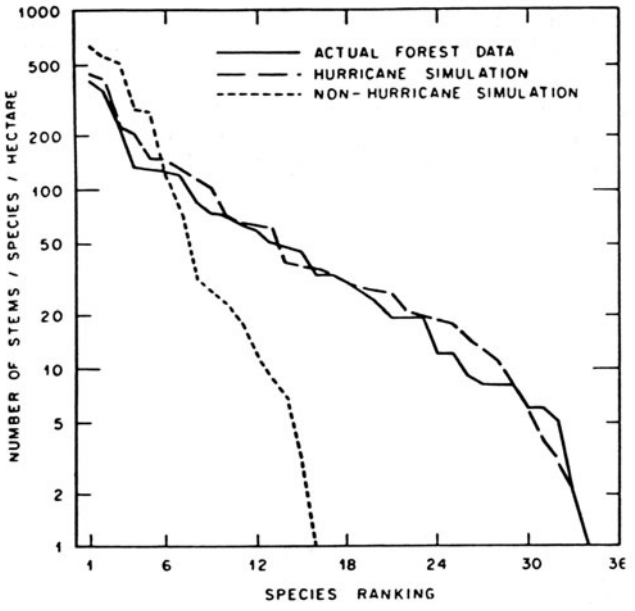

Fig.2. Dominance-diversity curves for model simulations with and without hurricane effects compared to tabonuco (*Dacryodes excelsa*) forest data. Species rank ranges from most abundant (1) to least abundant (36). Species abundance is represented as the total number of stems (> 4 cm dbh) per hectare (Doyle 1982)

The new Paradigm of Disturbance in Tropical Ecology

Speciation and hence high biotic diversity in the tropics is driven by "environmental challenges" that, according to Dobzhansky (1950), stem chiefly from "the intricate mutual relationships among the inhabitants." This quotation reflects a central idea of tropical ecology, namely, that the benign and relatively constant tropical environment allows biotic interactions to be the dominant factor in determining the structure and function of forest ecosystems (Giller 1984). This view has led to impressive progress in evolutionary tropical biology and has resulted in particular emphasis being given to the importance of predation, competition, pollination, and fruit dispersal (Leigh *et al.* 1982; Janzen 1983; Giller 1984; den Boer 1986).

This traditional paradigm of tropical ecology, however, is now under close scrutiny (Ho *et al.* 1986). For example, Sousa (1984, p. 338) stated: "There is a growing realization that disturbance may play as great a role in community dynamics as do biological interactions such as competition and predation, which have received far more empirical and theoretical attention from ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organization and spatial patterning of natural communities." Several types of evidence have triggered alternative interpretations of the driving factors of ecosystem structure and function in the tropics.

For example: (1) the possibility that extraterrestrial forces caused mass species extinctions (Alvarez *et al.* 1980) and that such extinctions follow recurrent cyclic patterns (Fischer 1981) has stirred considerable debate over traditional thinking about speciation and extinction in the tropics (Raup 1984, Spepkoski & Raup 1986, Officer *et al.* 1987); (2) the debate over the existence of species refugia in the tropics (Haffer 1982, Benson 1982, Endler 1982) has challenged the assumption that the tropics were not affected by glaciations; (3) the formulation of a "new concept" in ecology ("patch dynamics"; Pickett & White 1985) and the realization of the importance of canopy gaps for the regeneration of canopy tree species (Whitmore 1975, Hartshorn 1978, Brokaw 1982) has caused a re-evaluation of the way tropical ecologists view forest succession; and (4) the recent fire that burned millions of hectares of tropical moist forest in Borneo (Leighton 1984; Goldammer & Seibert 1990), the discovery of charcoal in the soil profiles at La Selva, Costa Rica, San Carlos, Venezuelan Amazon, and many other locations (Sanford *et al.* 1985; Goldammer & Seibert 1989), and paleoecological data from lake sediments (Covich 1978; Deevey 1984) have forced a re-examination of the concept of what a primary tropical forest is or is not.

Parallel to this change in paradigms, and implicit in the evidence that motivates the change, is the realization that disturbances are stressors that operate at many scales, frequencies, and intensities (Fig. 3). Scale can vary from very local (e.g., the small area affected by a falling branch) to global disturbances (e.g., biomes affected by meteorite impacts [Raup 1984] or human deforestation of the tropics [Lanly 1982]).

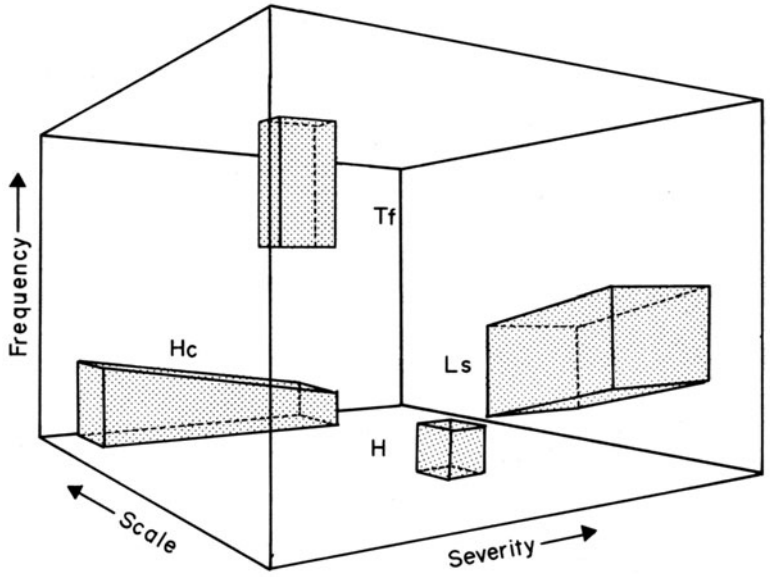

Fig.3. Conception of the relationship of four common types of disturbance in the LEF along dimensions representing disturbance severity, scale, and frequency. Tree fall (Tf), landslides (Ls), hurricanes (Hc), and harvest (H) are the four kinds of disturbance. In this figure, the relationships among the disturbance types can be seen. For instance, tree falls are frequent, but low in severity and scale, while hurricanes are infrequent (especially severe hurricanes), have moderate to very severe effects, and act on a large scale. The effects of these disturbances and the responses of ecosystems should be equally dissimilar

Severity of disturbance (the impact of the stressor on the ecosystem; Lugo 1978; White & Pickett 1985; Jordan 1985) may or may not be related to scale. For example, a tree fall gap is a less severe stress than a landslide of similar size because only structure is removed from the system and the productive capacity of the soil is unaffected (Lugo 1978). The evaluation of the impact of a given type of disturbance event is complicated further by the frequency of return of the event. Usually, less severe events have higher frequencies of return than do more severe ones (Fig. 3). A less severe disturbance, however, could be highly stressful to a system if its period of return is sufficiently frequent. The challenge to ecologists is to unravel the mechanisms of ecosystem response to disturbances that differ in scale, frequency, and severity of action.

Most tropical research in the area of disturbance ecology is focusing on systems dominated by small gaps whose frequency of occurrence is high (Denslow 1980; White & Pickett 1985; Denslow 1987). Although small gaps are important in maintaining diversity in certain forest types, this situation represents only one end of a continuum of disturbance severity and frequency. Tropical forests comprise large numbers of species that must face natural disturbances of all scales and intensities, each with a different frequency of return, yet relatively little is known about the effects of infrequent, large-scale disturbance. Forest response to small-scale, low-severity disturbance with a frequency of 10 years is likely to be much different from response to large-scale, high-severity disturbance with 100-year frequency.

Treefalls are the most common form of natural disturbance in tropical forests. Landslides also occur in many tropical forests, but differ in their importance based on geology and topography. In the Caribbean, southeast Asia, Australia, and some parts of Central America, hurricanes are the disturbance events that operate at scales and intensities that are most conducive to long-term ecological research and that offer an opportunity to answer questions about the mechanisms of action of physical forces relative to long-term behavior of the biota. Hurricanes occur in the Caribbean with predictable frequencies (Fig. 4), on the order of centuries for hurricanes with very severe effects and on the order of several decades, decades, or years for lesser storms (Weaver 1986).

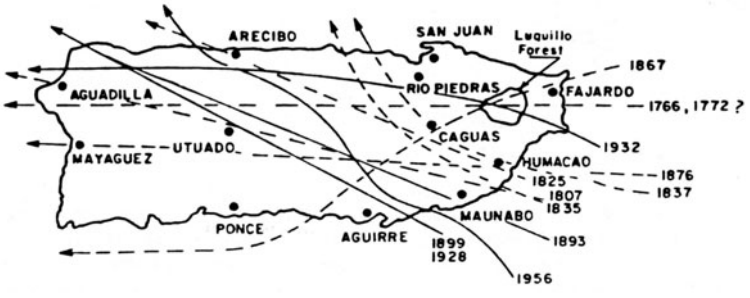

Fig.4. Paths of severe hurricanes over Puerto Rico from 1700 to 1960. Solid lines are known trajectories and dashed lines are assumed trajectories based on literature descriptions (Weaver 1986)

Tropical forestry research in Puerto Rico has already produced observations that suggest certain patterns of biotic response to both large- and small-scale phenomena. For example, the estimated age of large colorado trees (*Cyrilla racemiflora*; Fig. 5) and palms (*Prestoea montana*; Fig. 6), can be related to hurricanes in 1867 and 1932, respectively (Weaver 1986; Lugo & Rivera-Battle 1987). Studies show that frequently measured forest parameters such as biomass, tree density, number of tree species, basal area, wood volume, wood density, above ground primary productivity, and complexity index will change in predictable patterns over periods of 40 years following a hurricane (Crow 1980; Weaver 1986; Fig. 7).

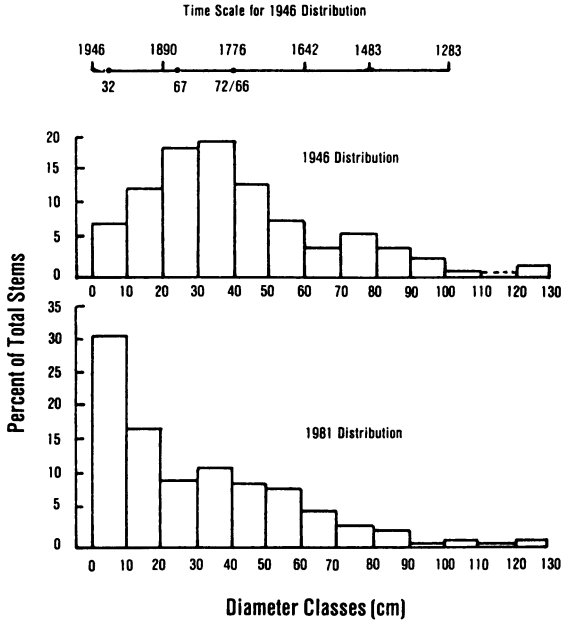

Fig.5. Diameter class distribution of *Cyrilla racemiflora* on undisturbed long-term research plots within the colorado forest of the Luquillo Mountains in two different years. The time scale indicates the years to which the diameter class corresponds as well as the years that severe storms passed directly over the LEF (Weaver 1986)

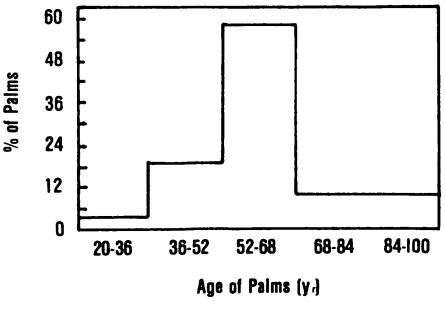

Fig.6. Age of palms (*Prestoea montana*) in the LEF. Individuals in the dominant age class were seedlings at the time of passage of the 1932 hurricane (from Lugo and Rivera-Battle 1987)

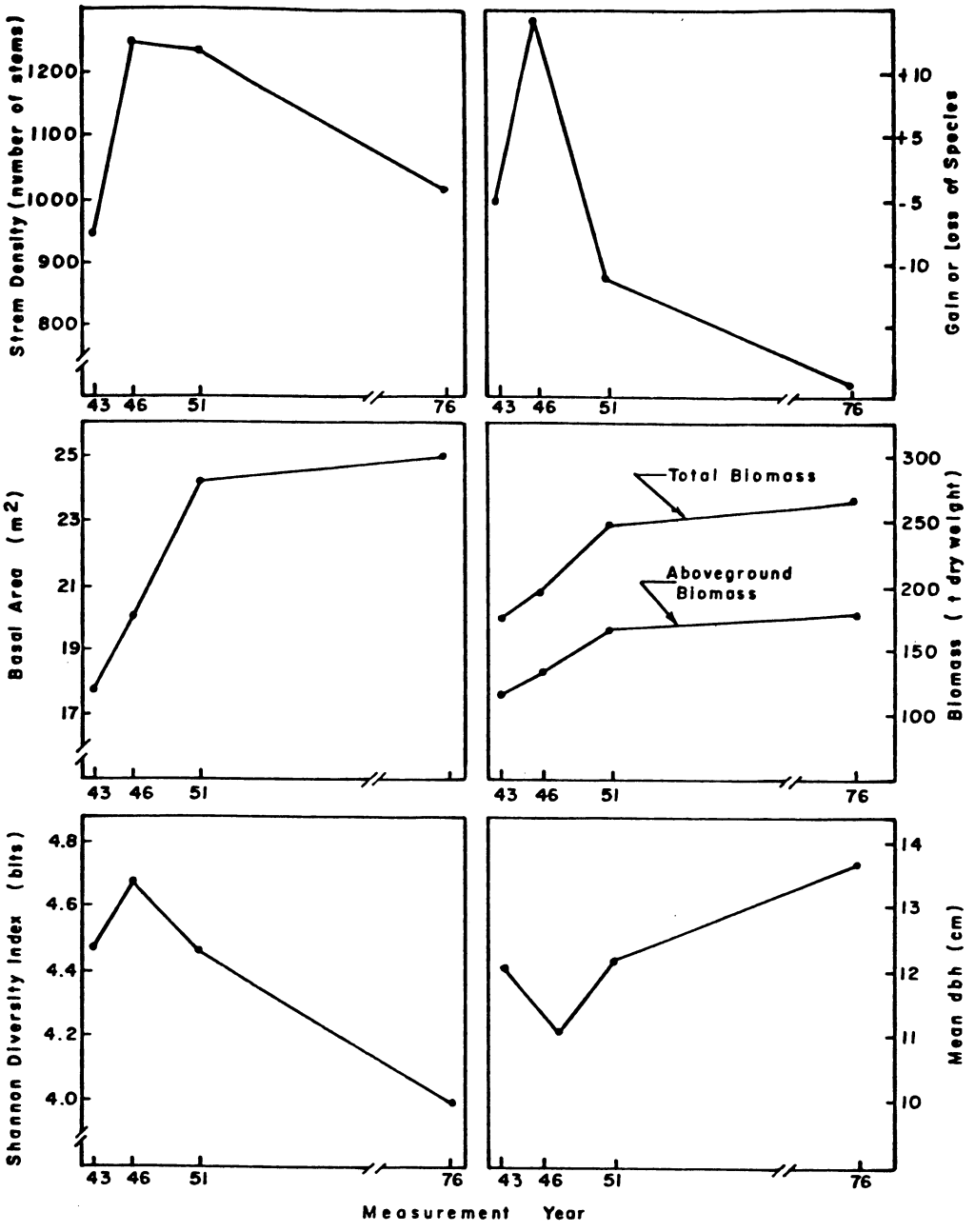

Fig.7. Changes in stand characteristics for the El Verde plots during the period 1954-1976. Measurements are based on all trees with dbh > 4 cm in a 0.75 ha plot (Crow 1980). The graphs show patterns of increasing biomass, basal area, and mean dbh and decreasing stem density, species richness, and diversity, reflecting recovery from hurricanes that struck the LEF in 1928 (San Felipe), 1931 (San Nicholas), and 1932 (San Ciprian)

Variation in annual rainfall that is unrelated to hurricane events can also elicit biotic responses since periods with more frequent and higher rainfall increase the probability of landslides and can result in a doubling of annual stream runoff (Fig. 8). Because hydrologic fluxes are critically important to many ecosystem processes (Lugo 1986), infrequent but large fluctuations in rainfall will have significant effects on ecosystem functions such as organic matter export (Lodge & Asbury 1988), nutrient cycling, and productivity. Long-term records are necessary to measure and understand infrequent events (Fig. 8). Clearly, both time and spatial scale are critical factors in the design of any ecological research in tropical forests subjected to such types of disturbances. The LEF offers significant background understanding and sufficient records of long-term ecosystem processes to permit the formulation of specific hypotheses for long-term ecological research (Brown *et al.* 1983).

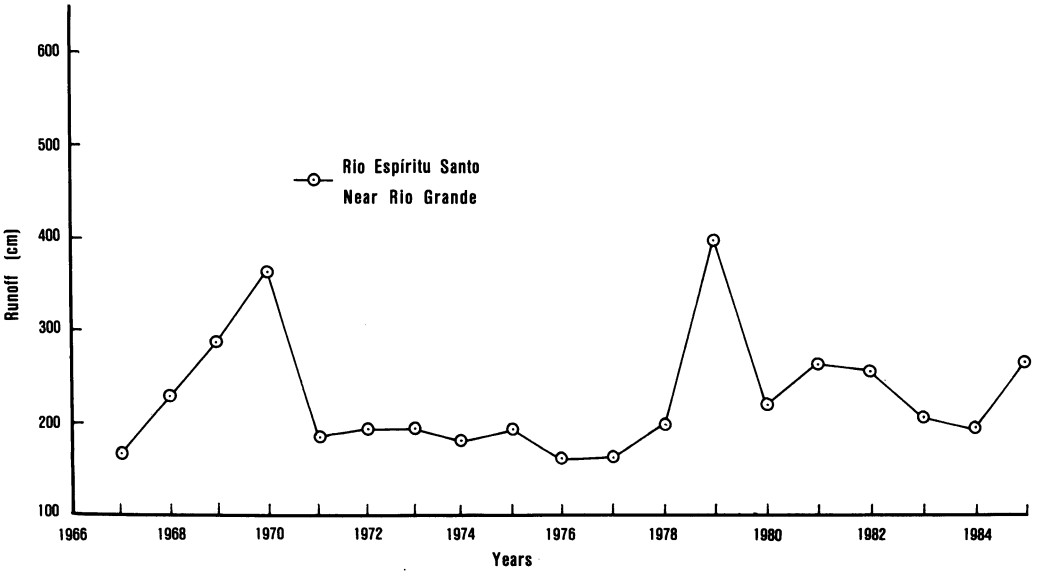

Fig.8. Long-term records of annual runoff in the Espiritu Santo River show recurrent peaks (1970 and 1979) separated by eight years of low flow. This pattern occurs in other gaged rivers in the forest (Brown *et al.* 1983). This record illustrates the need for long-term data collection in this forest which is greatly affected by infrequent meteorological events (data are from US Department of the Interior)

Long-Term Ecological Research in the Luquillo Mountains

The Luquillo Experimental Forest

Four life zones occur in the LEF (subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest; Ewel & Whitmore 1973), and four major vegetation types occupy these life zones (Table 1). Below 600 m the dominant tree is the tabonuco (*Dacryodes excelsa*), which is best developed on protected, well-drained ridges. Above the average cloud condensation level (600 m), palo colorado (*Cyrilla racemiflora*) is the dominant tree except in areas of steep slope and poorly drained soils, where the sierra palm (*Prestoea montana*) occurs in nearly pure stands. The dwarf forest occupies ridge lines and is composed of dense stands of short, small diameter trees and shrubs that are almost continually exposed to winds and clouds. Both the palm and dwarf forests are dominated by only a few plant species.

Tab.1. Distribution of forest types within the Luquillo Experimental Forest (adapted from Brown *et al.* 1983)

	Approximate area (ha) of each forest type*					
SITE	1	2	3	4	5	TOTAL
Higher elevation (600-1,070 m)	5,868					5,868
Medium elevation (300-600 m)	59	1,076	2,499	215	76	3,925
Lower elevation (100-300 m)		56	1,094	163	125	1,438
Increasing human disturbance	---------->					
Total	5,927	1,132	3,593	378	201	11,231

*
1. Colorado, palm, and dwarf forest
2. Old growth tabonuco forest
3. Secondary tabonuco forest
4. Plantations
5. Deforested

The tabonuco forest has been the subject of the most extensive ecological studies of any of the four forest types. Long-term studies of forest growth have been conducted by Wadsworth (1951) and represent a 40 year record of tabonuco forest dynamics. In addition, the tabonuco forest has been the subject of studies of tree growth (Crow & Weaver 1977) and community composition (Crow & Grigal 1979), and the extensive data base has served in the development of simulation models of forest regeneration (Doyle 1981; Doyle *et al.* 1982).

The most detailed study of the tabonuco zone was the Rain Forest Irradiation Project of the U. S. Atomic Energy Commission, which took place from 1963 to 1968 (Odum & Pigeon 1970). The principal goals of this project were to determine the effects of gamma irradiation on a rain forest ecosystem, to examine the cycling of fallout elements, and to develop an understanding of vertical and horizontal forest structure and various system processes including nutrient cycling, energy flow, and forest regeneration mechanisms.

The Center for Energy and Environment Research (CEER) has continued to conduct studies of nutrient cycling and energy flow in tabonuco forest since the end of the Rain Forest Project in 1968. This research has been sponsored by the U. S. Department of Energy (AEC, ERDA) and the University of Puerto Rico. The initial phase of the current Rain Forest Cycling and Transport Project (1980-83) concentrated on the structure of terrestrial and aquatic food webs and their possible roles in the biotic control of ecosystem processes. The current phase examines nutrient import, export, and immobilization, decomposition, primary productivity, and forest regeneration as well as continuing work on food webs. The accumulated work of 50 years makes the tabonuco forest the best known of the four forest types in the Luquillo Mountains and probably the best known site in the tropics. In addition, the El Verde Field Station and research area has served as a focus for local and mainland ecologists, whose work has greatly enhanced knowledge of forest processes.

Research opportunities in the LEF

Unique scientific opportunities result from the size of the island of Puerto Rico, its mountainous topography, and its location relative to the trade wind belt and hurricane trajectories. For example, rainfall ranges from 500 to 5,000 mm in ecosystems separated by a three hour drive; within the LEF rainfall ranges from about 2,000 mm to 5,000 mm along a 1,000 m elevational transect. The diversity of rainfall conditions, complex topography, and variety of soil types in the LEF support a rich array of ecosystems with contrasting diversity of species and functional attributes that cannot be matched in continental sites where distance and access limit comparative research. The range of mature vegetation available for research in Puerto Rico is representative of many environments in tropical America. Using the life zone system of Holdridge as a guide, the six life zones in Puerto Rico (4 in the LEF) represent 40% of the land area in Central America (Budowski 1965).

Periodic visits by hurricanes and tropical depressions in the Caribbean and their interaction with steep topography offer an opportunity to study long-term responses of complex ecosystems to natural disturbance, which is greatly enhanced in the LEF by the

existence of long-term observation plots established by the Forest Service in the 1940's. These plots have changed dramatically in species composition and growth rates during the 30-40 yr since the last major disturbance (Crow 1980; Brown *et al.* 1983; Weaver 1986).

Scientific opportunities are enhanced by the fact that the island of Puerto Rico as a whole (including much of the lowlands of the LEF but not its uplands) was deforested early in this century (to about 10% forest cover) and has since recovered naturally to about 35% forest cover (Birdsey & Weaver 1982). Critical questions about succession, ecosystem recovery from human devastation, and the issues of how tropical diversity responds to human disturbance and management can be addressed in an island where research sites can be protected over long time periods. The intensive management of lands by the U.S. Forest Service in the LEF adds another dimension to the scientific opportunity at the site. Beginning in 1933 over 2,300 ha of plantations of dozens of exotic and native tree species were established in the LEF. Today the LEF has some of the oldest research plantations in the American tropics as well as an arboretum with over 100 tree species planted. Twenty mahogany provenances from central America (NW Mexico to Panama) and the West Indies are preserved in the arboretum. Seed collections are available and knowledge of tree establishment is much more advanced in Puerto Rico than in any other tropical research site (e.g., 412 tree species, including 100 native ones, have been tested; Marrero 1947).

In the LEF, the availability of long-term weather and growth records, an understanding of land use change, and a complex mix of ecosystems provide unique opportunities to study tropical moist forests under natural conditions, disturbed by periodic hurricanes, responding to previous human impacts, and managed with the purpose of restoring the land to production. Nowhere else under the U. S. flag is there such a mix of opportunity and background understanding for long-term ecological research. Furthermore, forest lands such as those in the LEF are the ones that are most likely to be deforested and used for agricultural production. Understanding montane moist tropical ecosystems should have priority if ecological research is to be of relevance to resolving the fiber and water needs of the growing human populations in the tropics.

Importance of Disturbance in the Luquillo Mountains

We are using a combination of experimental and observational studies to address questions about the response of the terrestrial and aquatic biota to disturbances of different scales, severities, and frequencies in five watersheds in the Luquillo Mountains. By response we mean both the impact of disturbance as well as the feedback from the biota to site quality following disturbance. The main questions addressed are:

- What is the distribution of different disturbance types within the landscape of the LEF, and how does the disturbance regime at a given site affect the structure and function of the ecosystem?

- What is the response of the biota to disturbances differing in scale, severity, and frequency, and how does this response affect a site's recovery toward mature forest?

These questions stem from the observation that the end results of secondary succession after different types of disturbance in the LEF are virtually indistinguishable despite quite different initial conditions. The type of disturbance that initiated succession at a site is difficult or impossible to determine through examination of the regenerated mature forest. We base our approach on the hypothesis that the mode of resistance of an ecosystem to disturbance is a function of the stressor (intensity, periodicity, sector of the ecosystem that it affects, and area affected). After disturbance of any severity, the path of site recovery is influenced by the physical and chemical properties of the soil, water, and atmosphere, by the activity of the biota, or by a complex interaction among all four (soil, biota, hydrosphere, and atmosphere).

The Role of the Biota in Recovery After Disturbance

Most tropical research has concentrated on interactions within the biota or the effect of environment on the biotic community. However, the biota's effect on site characteristics is also a key component in the post-disturbance recovery process. We hypothesize that the potential for a return to the previous level of productivity after disturbance is conditioned by the biota. This follows from the premise that different types of disturbance produce different types of environments conducive to different rates and pathways of recovery. Our research focuses on that period of time when the biota exerts its main influence over the physical environment (the recovery phase; *sensu* Bormann & Likens 1979). We expect that with increasing severity of disturbance the feedback function of the biota becomes more critical to the recovery process.

Some examples of biotic feedbacks that act during recovery illustrate the point: (1) The capacity of plants to retranslocate nutrients from senescent leaves prior to leaf fall affects litter quality, decomposition rates, and nutrient availability in the soil. Plants in some environments have high rates of retranslocation while those in others have low rates, and these are reflected in the ratio of nutrient use efficiency proposed by Vitousek (1982, 1984). Plants that exhibit high use efficiency ratios enhance nutrient recirculation and minimize potential losses due to leaching. Studies in Puerto Rico (Frangi & Lugo 1985) and Venezuela (Cuevas & Medina 1988) suggest that high efficiency ratios are associated with degraded sites and sites exposed to high leaching potential (Frangi & Lugo 1985). (2) Increasing complexity of root morphology, root functions, and spatial distribution of roots significantly increase the availability of nutrient pools to plants, enriching many substrates with organic matter, and improving the aeration and physical properties of soils. (3) Increased interception of rainfall by developing vegetation reduces soil erosion, leaching, and overland runoff. (4) The range of decomposition constants of complex biochemical materials (wood, bone, and shell) spreads nutrient releases over time. This provides stability to nutrient cycles in terms of storage and slow steady release. (5) As food web complexity increases through successional time, system resilience decreases (Pimm 1982). DeAngelis (1980) has shown theoretically that system resilience is inversely related to the "tightness" of nutrient cycling. Hence, as food web resiliency decreases during succession, the probability of retaining vital nutrients in biotic circulation increases (Odum 1969; Pimm 1982). High rainfall areas such as the LEF (average = 3775 mm/yr; Lugo 1986) are subjected to the mechanical impact of rain

drops and winds, potential land movements, and constant leaching of nutrients. These potential stressors, if unchecked, can deplete soil nutrients, remove soil from the site, and lower site productivity. To the extent that the biota mitigates such a series of events, it represents a collection of mechanisms that conserve soil and nutrients and maintain the capability of the site to support biological productivity (Budowski 1965). Successional species are known to grow rapidly, bind nutrients in biomass, protect soil by closing the forest canopy, and moderate forest microclimates (Odum 1969; Budowski 1965; Marks 1974; Ewel 1980). However, these generalizations do not address the more important question of how the complexity of an ecosystem is rebuilt from different initial conditions. This issue can be addressed only through long-term study of specific sites that have been subjected to different severity, frequency, or scale of disturbance.

Conceptual Models for Ecosystem Study

In designing the Luquillo LTER program, we have taken advantage of the extensive research history of the forest by combining new approaches to ecosystem study with those that have traditionally proven effective in the LEF. A conceptual model of the main forcing functions and subsystems of a watershed in tabonuco (*D. excelsa*) forest provides a unifying focus for the proposed research (Fig. 9). The forcing functions of this ecosystem model are hurricanes, climate (including heavy rainfall events and resultant landslides), solar energy, geological substrate, and human management. The main subsystems are vegetation, animals, and soil and associated microbiota. The processes within the system include hydrologic flows, biotic interactions, and energy and nutrient fluxes, all of which are subject to disturbances generated by the forcing functions. Forcing functions, disturbances, subsystems, and flows are being studied as part of the LTER program. However, the measurements and experiments underway range widely in scale and detail depending of the hypothesis being tested.

We are using a patch dynamics model (Doyle 1982), as recommended for comparative studies of disturbance (Pickett & White 1985), to guide our research on disturbance and regeneration in the tabonuco forest. This model describes disturbance-mediated ecosystem processes by taking into account: (a) the frequencies, dispersion, and environmental characteristics of all types and sizes of disturbances; and (b) the recovery rates from all types and sizes of disturbances. The basic premises of the model are adapted from Levin & Paine (1974):

1.The community is a mosaic of different patch types, many of which originate as disturbances.

2.The patch is the fundamental unit of ecosystem structure. When recovery within individual patches is coupled to events generating patches, a bridge is built between patch processes and ecosystem processes.

The frequency, scale, and severity of disturbances affect the recovery process because there is a "continuum of biogeochemical, hydrological, and radiant energy responses at the forest floor, depending on the scale of the disturbance" (Bormann &

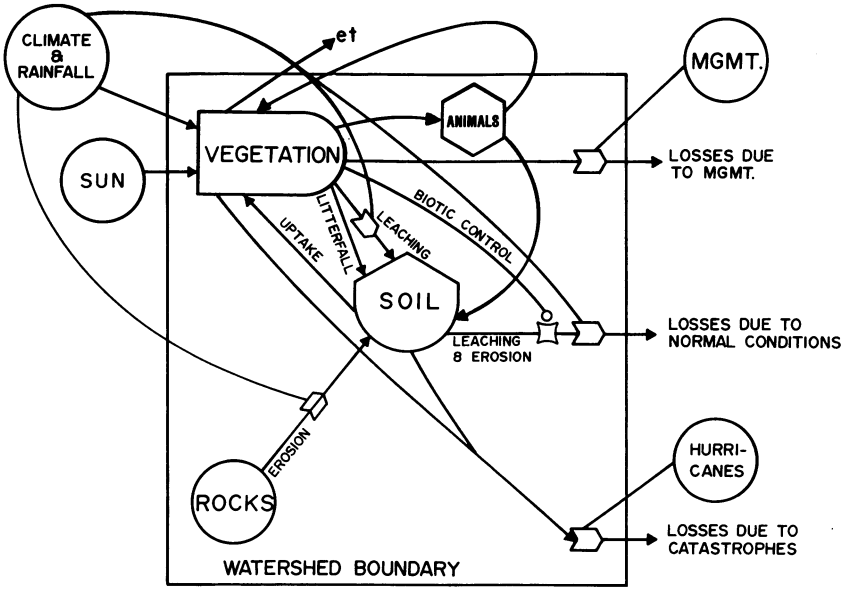

Fig.9. Conceptual model of watershed dynamics in tabonuco forest. Symbols in the watershed model are after Odum (1983). Management is abbreviated **MGMT**, and evapotranspiration is abbreviated **et**

Likens 1979). This environmental continuum among disturbances induces a corresponding continuum of biological responses, which in turn influence the environment and ecosystem state (Bormann & Likens 1979) of recovering patches.

Our ultimate goal is to use our knowledge of these properties to predict the frequency and size-class distribution of different states - reorganization, aggrading, transition, steady state (Bormann & Likens 1979) in the forest mosaic, thus leading to an understanding of the structure and function of the system as a whole (Levin & Paine 1974).

Scaling up from the Ecosystem to the Landscape

The component investigations being conducted in the LEF are linked to the landscape level of ecosystem organization through a landscape model generalized to each cell of a geographic information system (GIS) covering the LEF. Whereas there is a relatively rich literature available for modeling forest stands (Shugart 1984; Dale & Gardner 1986), most of these models are based on growing a series of individual species in plots of

about 0.1 hectare. There does not exist to our knowledge an explicit transfer of this approach to a geographically complex system except to solve the initial equations for one site vs. another (Shugart, personal communication). We have developed an explicit scheme for translating geographical information, derived from geographical space, into model parameter space (equivalent to ecological space) using a gradient approach (Whitaker 1975; Austin *et al.* 1984). For example, we can now predict micrometeorological conditions for many locations in the LEF landscape by integrating a GIS physical-specifications system with a statistical analysis that predicts meteorological data as a function of site location and related topographical characteristics (Wooster 1989). The parameters derived from this analysis plus other GIS-derived physical and biotic parameters that act as forcing functions operating on the ecosystem are being used to predict the behavior of individuals, populations, and ecosystems throughout the entire landscape.

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