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LONG-TERM ECOLOGICAL RESEARCH ON THE LUQUILLO EXPERIMENTAL FOREST III

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Long-Term Ecological Research on the Luquillo Experimental Forest III

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PROJECT SUMMARY

The Luquillo Experimental Forest (LEF) Long-Term Ecological Research Program began in 1988 with the goal of integrating studies of disturbance regime and forest structure and dynamics with a landscape perspective. Two central research questions addressed 1) the relative importance of different disturbance types within the four tropical rain forest life zones of the

LEF and 2) the importance of the biota in restoring ecosystem productivity after disturbance. The long-term monitoring program initiated as part of the LEF-LTER was critical to the evaluation of the immediate effects of Hurricane Hugo, which struck Puerto Rico in 1989, and the long-term response of the forested ecosystems of the LEF to that severe disturbance. Monitoring of the effects of several less-severe storms and a subsequent hurricane (Hurricane Georges in 1998) has resulted in the LEF-LTER being in the position of the most thoroughly studied forested ecosystem subject to repeated hurricane disturbance. Important strides also have been made in determining the spatial and temporal patterns of other natural disturbances (landslides, treefalls, floods, and drought).

The LEF-LTER also has been instrumental in establishing the predominant importance of human disturbance in molding the structure and functioning of tropical ecosystems. In the LEF, legacies of human disturbance dating from before the 1930's appear in present times as important sources of variation in forest structure and species composition. Human disturbance affects natural disturbance regimes by making particular events more likely to occur (e.g., landslides are most common near roads) or increasing their severity (e.g., hurricane damage to forests is more severe in areas recovering from agriculture).

The long-term experiments and measurements initiated in 1988 will remain the central focus of the LEF-LTER. Emphasis on the impacts of hurricanes and human disturbances on ecosystem dynamics of the LEF will continue. Further attention will be directed at deciphering interactions among the biota and their impact on critical ecosystem variables that determine responses to natural disturbances. New initiatives will expand the comprehensive analysis of disturbance and ecosystem response to include elevations up to the summit of the Luquillo Mountains.

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LIST OF ABBREVIATIONS

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BOM - Benthic Organic Matter
CENTURY - Biochemical cycling model
DBH - Dioameter at breast height
DOC - Dissolved Organic Carbon
EXPOS - Topographic exposure model
FACET - Relief sensitive gap model

HURRECON - Hurricane meteorologu model
LEF - lUquillo Experimental Forest
LFDP - Luquillo Forest Dynamic Plot
LTER - Long-term Ecological Research
MEL - Multiple Element Limitation model
MOSAIC - Spatial extension of a gap model
PAR - Photosynthetically Active Radiation
PI - Principal Investigator
REU - Research Experience for Undergraduates
SEMAPAR - Landscape model
SGER - Special Grants for Exploratory Research
SOM - Soil Organic Matter
SORTIE - Forest Dynamics model
UPR - University of Puerto Rico
USDA - United State Department of Agriculture
ZELIG - Gap-based stand dynamics model

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RESULTS FROM PRIOR NSF SUPPORT

Long-Term Research In The Luquillo Experimental Forest II; NSF Grant DEB-9411973 and DEB-9705814, Oct. 1994 Nov. 2000 ($3,600,000).

The Luquillo Experimental Forest (LEF) LTER program was initiated in 1988 and continued with renewed funding in 1994. The program includes researchers at the University of Puerto Rico, USDA Forest Service International Institute of Tropical Forestry, and numerous collaborators. By focusing research on issues central to understanding tropical forest structure and function, the LTER program is a catalyst for studies that cut across disciplines. The long-term nature of the program has provided the means to conduct measurements and experimental studies at time scales relevant to ecological phenomena in the tropics and to provide major new insights in conceptualizing tropical forest dynamics.

The primary goal of the LEF-LTER program is to **understand the interaction of disturbance, physical parameters, and the tropical biota from population, community, biogeochemical, and landscape perspectives.** Two central questions guided our research on the tabonuco (*Dacryodes excelsa* Vahl.) forest (Fig. 1) during the first 12 years of our program (LTER 1 and LTER 2):

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 recovery toward mature forest?

To address these questions, we examined four issues: 1) the pattern, frequency, and intensity of disturbances in the LEF (e.g., hurricanes, human activities, landslides); 2) environmental properties (light, nutrients, moisture, temperature, and soil organic matter[SOM]) that vary with disturbance size, age, and origin; 3) biological properties that are expected to vary with environmental properties (e.g., population density, species composition, growth, nutrient dynamics, reproductive success, carbon fixation, and food web structure); and 4) system-level properties that emerge from the effects of the disturbance regime on the mutual interaction of abiotic environment and biota (e.g., nutrient cycling, resilience).

During LTER 2 we more completely conceptualized our approach to disturbance by considering how disturbance affects key abiotic variables (Hall et al. 1992, Willig & Walker 1999) and how these, in turn, affect the response of the biota, particularly pivotal species thought important to ecosystem structure and function. These concepts are treated more fully in the body of the current proposal and are the subject of a book we are currently preparing (Crowl, Brokaw, Lugo, McDowell, Waide & Willig, in preparation; see http://luq.lternet.edu/pulicat/book2000/proy2kbo.htm for outline). This conceptualization is important because it allows us to extend our focus beyond tabonuco forest to include the entire elevational gradient of vegetation in the LEF as well as to other tropical forests.

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Research Accomplishments

Hurricane Hugo, a severe hurricane (maximum sustained winds, 120 mph) that struck the site in September 1989, dominated research efforts during LTER 1. Much of our research focused on documenting the response of the tabonuco forest ecosystem to hurricane disturbance (Walker et al. 1991, 1996a, Boose et al. 1994) while maintaining our goals of understanding other aspects of the disturbance regime, e.g., treefalls (Alvarez & Willig 1993, Woolbright 1996) and landslides (Fetcher et al. 1996, Walker et al. 1996b). Our goal in LTER 2 was to: 1) more fully address the role of human disturbance in tabonuco forest and; 2) obtain a more mechanistic understanding of the response of tabonuco forest to disturbance. A second severe hurricane, Hurricane Georges, struck the site in September 1998 (110 mph), providing the opportunity to refine our understanding of how hurricanes regulate forest structure and function. The effects of successive hurricanes demonstrated that the frequency, intensity and directionality of hurricanes are critical in determining how resilient the forest and streams are to successive disturbances.

Disturbance Regime The most important types of disturbance affecting the LEF are hurricanes, past agricultural activities and other human disturbances, landslides, droughts, and treefalls

(Waide & Lugo 1992). Hurricane Georges struck our site only nine years after Hurricane Hugo. Prior to Hurricane Hugo, the site had not been visited by a similar magnitude storm since 1932, and thus the forest was in a less mature state when Georges struck than when Hugo struck. Before the LEF was purchased and protected by the USDA Forest Service in the 1930's and 40's much of the area that would have supported tabonuco forest was in agriculture or had been severely disturbed by humans (Foster et al. 1998: Fig. 2c). The interaction between historical land use and recent disturbances is now one of the most important foci of the LEF-LTER. During LTER 1 and 2, we reached the following conclusions regarding the disturbance regime in the LEF:

- Human disturbance was strongly evident in aerial photographs from 1936 in areas of tabonuco forest (Foster et al. 1998; Fig. 2c) while much of the upper elevations of the LEF remained unaffected. Recovery of canopy cover between 1936 and 1989 demonstrated the resilience of tropical forest to pre-1936 human disturbance in terms of forest cover. However, legacies of human disturbance are evident in the species composition of the forest (Fig. 3; Garcia-Montiel & Scatena 1994; Aide et al. 1995, 1996, Zimmerman et al. 1995a, Willig et al. 1996, Olander et al. 1998, Reed 1998, Thompson et al. submitted).
- Patterns of forest cover in 1936 showed no obvious correlation with the 1932 hurricane (Foster et al. 1998) suggesting that human disturbance was the predominant effect on vegetation patterns at that time and that the forest exhibits a high resilience to hurricane disturbance. Secondary tree species are more susceptible to hurricane disturbance than are primary species (Zimmerman et al. 1994). On a local scale, human disturbance affects spatial patterns of hurricane disturbance through effects on distributions of species (Everham 1996).
- Reconstruction of the spatial and temporal patterns of hurricane impacts for Puerto Rico between 1886 and 1996 showed that hurricane frequency and intensity decreased from southeast to northwest across the island, although all areas were subject to repeated damage by hurricane-intensity winds (Boose et al. in preparation; Fig. 4)
- In addition to Hurricanes Hugo and Georges, several other recent hurricanes passed near the LEF with varied levels of impact (Fig. 5). This variability has allowed us to document the severity of hurricanes of differing intensities on forest canopies, litterfall, and tree damage.

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- Intense rainstorms associated with hurricanes and other storms create numerous landslides. Landslides are most common near roads and on granitic diorite substrates in the LEF (Guariguata 1990, Larsen & Simon 1993, Larsen 1995, Walker et al. 1996b, Myster et al. 1997, Larsen & Parks 1997). Landslides affect 0.8 to 1.1% of the LEF landscape per century, similar to other areas of the Caribbean (Walker et al. 1996b). The major factors affecting regeneration on landslides (during the first 5 years) are: seed dispersal, germination (availability of microsites) and competition for light and soil nutrients (Myster 1997).

- Droughts are a disturbance type that had been relatively unappreciated in the LEF. Severe droughts in 1989, 1994 and 1999 (Fig. 5) underscored the importance of this type of disturbance in wet forest (Waide 1991, Parrotta & Lodge 1991, Silver & Vogt 1993, Covich et al. 1996, Silver et al. 1996, Vogt et al. 1996, Woolbright 1996, Covich et al. 1999).
- Severe floods associated with hurricanes and other severe rainstorms alter litter inputs and storage in streams, have no negative impacts on stream organisms (e.g., decapods, Covich et al. 1991, 1996, Johnson et al. 1998, Pyron et al. 1999, Johnson & Covich 2000) but can have important impacts on streamside plant populations (e.g., Sharpe 1997).
- Human impacts on streams are cumulative over time and space such that the effects of natural variability in rainfall and river discharge are sometimes exacerbated. These impacts are often localized at critical points along river corridors. Water diversions and dams on rivers draining the LEF have important effects on organisms that regularly migrate along stream corridors as a part of their life histories (Pringle et al. 1997, March et al. 1998, Benstead et al. 1999, Pringle et al. 1999, Scatena & Johnson 2000).

Response to Disturbance Regeneration depends on the biotic and abiotic conditions at the onset of succession. At local scales, patches dominated by the effects of recent disturbances are aggregated with patches reflecting previous disturbance to form complex mosaics. At landscape scales, topography and other factors may affect the severity and spatial extent of disturbance, in turn affecting the long-term response. Experiments and measurements during LTER 1 and 2 provided the following insights into the response of tabonuco forest to disturbance:

- Responses to hurricane disturbance can be negative, positive or neutral, depending on the temporal scale of observation and the organisms under study (Zimmerman et al. 1996, Willig & McGinley 1999). The five-year response of the tabonuco forest ecosystem to Hurricane Hugo (Fig. 7) showed that forest floor litter and some stream nutrients exhibited rapid, transient increases following the hurricane (Scatena et al. 1996, McDowell et al. 1996, Crowl et al. 2000a). Frogs and snails, which take advantage of increased forest floor structure and resources, and freshwater shrimp, which utilize increased detritus in streams, showed significant increases for several years following the hurricane (Covich et al. 1991, 1996, Woolbright 1991, Willig et al. 1998). Some soil nutrients and animal populations decreased only to rise above pre-hurricane levels within a five years post-hurricane period (Silver et al. 1996, Willig et al. 1998). Some populations remained low after Hurricane Hugo. Walking sticks (*Lamponius portoricensis* and two frog species (*Eleutherodactylis richmondi* and *E. portoricensis*, which were very abundant prior to Hugo, have not yet reached their previous numbers (Zimmerman et al. 1996, Woolbright 1997).
- The response to Hurricane Georges has so far been less dramatic than the response to Hurricane Hugo (e.g., stream water chemistry, frog densities; Fig. 8, 9). The differences apparently occurred for two reasons: 1) the forest was still recovering canopy wood biomass following Hurricane Hugo, with the result that deposition of coarse woody debris was less in Georges than Hugo (Zimmerman et al. 1995b, Zou et al. unpublished data) and; 2), the intensity of Georges to the

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LEF focal study sites, El Verde and Bisley (Fig. 5) was less than that caused by Hugo because of the direction of oncoming winds (N to E vs. NW to NE) relative to the orientation of the mountainous terrain.

- At the stand level, the forest community appeared stable with respect to hurricane disturbance (Fig. 10). In the census 6 years after Hugo the abundance of stems ò10 cm DBH of most species were only slightly reduced compared to the number present before Hugo struck. The pioneer species *Cecropia schreberiana* was a significant exception and increased in abundance by 800 %. *Cecropia schreberiana* was identified as a pivotal species in the response of the forest to hurricane disturbance because it is the first species to establish a canopy in the most severely disturbed areas (Brokaw 1998) and because it functions to retain nutrients at the ecosystem level (Scatena et al. 1996).
- Community stability with respect to hurricane disturbance may be maintained by life history trade-offs among component species (Zimmerman et al. 1994). Focusing on 12 key species, we continue to analyze trade-offs in growth, recruitment, and mortality (Fig. 10), herbivory defense (Angulo-Sandoval and Aide 2000), seed rain (Zimmerman et al., in preparation), seedling shade tolerance (Fernandez and Zimmerman, in preparation). Projects on nutrient uptake dynamics and mycorrhizal associations are to be completed in the coming year.
- Using multivariate analyses, Secrest et al. (1996) showed that despite distinct differences in the severity of hurricane damage at Bisley and El Verde (Boose et al. 1994), snail populations at the two sites responded to environmental gradients in the same fashion in part because the hurricane-induced changes did not disrupt the pattern of correlation among key environmental characteristics.
- Removal of aboveground biomass in tropical forests does not necessarily lead to a loss of soil nutrients (Silver et al. 1996). Seven years after clearing all aboveground biomass in two experimental plots at Bisley, most nutrient pools were similar to or greater than initial values. Belowground nutrient conservation mechanisms included maintenance of soil organic matter pools, high fine root biomass, and slow root decomposition. Rapid aboveground regrowth also helped maintain ecosystem nutrient stocks and minimize nutrient and C losses.

Synthesis and Modeling Accomplishments - Results of the LEF-LTER program have been summarized in three books (Lugo & Lowe 1995, Reagan & Waide 1996, Walker 1999) and in two special issues of the journal Biotropica (Walker et al. 1991, 1996a). We currently are preparing a contribution to the LTER Oxford series of books which will provide an integrated treatment of the results obtained during LTER 1 and 2 (http://www.ites. upr.edu sunceer/publicat/ book2000/proy2kbo.htm). In addition, LEF-LTER researchers took a lead role in an effort to use published data from LTER and other sites to investigate the relationship between primary productivity and species richness (Waide et al. 1999, Gross et al. 2000, Scheiner et al. 2000) and effects of large, infrequent disturbances on ecosystems (Dale et al.

1999). Simulation modeling has been used as a tool to both integrate and guide research (e.g., Sanford et al. 1991, Boose et al. 1994, Zimmerman et al. 1995b, Buzby 1998, Crowl et al. 2000b):

- The HURRECON and EXPOS models allow prediction of hurricane damage to the LEF (Fig. 2d) and Puerto Rico (Fig. 5) . These models have been used to investigate interactions between human and hurricane disturbance (Zimmerman et al. 1995a, Aide et al. 1996).
- We have recently completed landscape models that predict solar exposure and photosynthesis in the Mameyes watershed (Marley 1998) and soil C over the entire LEF (Fig. 11 ; Wang et al. submitted).

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- Efforts are being made to develop a version of the SORTIE forest community model (Pacala et al. 1993, 1996) for tabonuco forest. The development of this model is taking advantage of damage caused by Hurricanes and Georges to integrate our understanding of the role of hurricanes in tropical forest community dynamics.
- Sabat and Fetcher (in preparation) have developed a model for the sierra palm (*Prestoea montana*), the most common tree in the LEF, that shows that the palm would disappear from tabonuco forest if not for the repeated canopy opening caused by hurricanes.
- By analyzing data from the LEF with respect to models of canopy rainfall interception, Schellekens et al. (1999) have shown that an important source of interception loss in maritime tropical climates is the high rate of evaporation from wet canopies. This distinguishes these areas from continental sites where interception losses are much less.
- A bioenergetic model for streams in the LEF (Crowl et al. 2000b) was developed to explore the potential role of decapods in limiting aquatic insect production through top-down control.
- Using long-term discharge and shrimp population data, instream flow models were developed to aid in managing water resources in the area surrounding the LEF (Scatena & Johnson 2000; Fig. 12).

Relationship of past research to proposed research - During LTER 3 we will extend the geographical scope of our research from tabonuco forest to the entire LEF landscape. This expansion of the application of our conceptual model will encompass forest types (Fig. 1) that become progressively shorter, more dense, less species rich, and of lower productivity as one reaches the mountain summits (Weaver and Murphy 1990, Waide et al. 1998, Fig 13). Previous research has addressed the variation in composition of forest within identified forest types (Fig. 1; Smith 1970, Crow & Grigal 1979, Weaver 1991), but no study has sampled the entire elevational gradient to determine whether forest types represent true, distinct communities or whether species are organized in a continuous or hierarchical fashion (Whittaker 1951, Curtis 1959, Collins et al. 1993, Hoagland & Collins 1997). Silver et al. (1999) have shown that soil oxygen can become depleted in soils of higher elevation forests for prolonged periods and suggested that low soil oxygen content likely induces plant stress and may be responsible for patterns in species composition, productivity, and biodiversity along rainfall and soil moisture gradients. The expansion of research effort to higher elevation forests will sample ecological conditions that are cloudier, wetter, and cooler. Thus, the link between disturbance and the response of the biota to disturbance will be investigated under a broader range of ecological conditions.

Human Resource Development

Under the current proposal, 30 students have completed doctoral or masters degrees (see List of Publications for student names). In addition, 18 students (15 Hispanic) have been involved in summer Research Experience for Undergraduates (REU) projects funded either by Long-Term Studies or from a site grant to UPR-Rio Piedras (we are currently working to establish a second site grant at El Verde Field Station). Also, to conduct the most recent census of the Luquillo Forest Dynamics Plot (LFDP), we paid for travel and board for 38 student volunteers to assist technicians in field work. Most of these students were from the mainland US and the three-month volunteer position was their first introduction to tropical biology. This grant also supports one research associate, Jill Thompson. v

LEF-LTER PUBLICATIONS

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INTRODUCTION

When we established the Luquillo Experimental Forest Long-Term Ecological Research Program (LEF-LTER) in 1988, we proposed to examine the roles of disturbance and the biota's response to disturbance as fundamental factors determining the structure and function of tabonuco (*Dacryodes excelsa*) forest in Puerto Rico (Waide & Lugo 1992; Fig. 14). Beginning six years ago (LTER 2), we sought to integrate responses to disturbance into a theoretical framework that considered how disturbance affected gradients in abiotic variables that were important for understanding the response of the biota to disturbance (ecological space; Hall et al. 1992, Everham 1996, Willig & Walker 1999). We suggested that by recognizing differences in geographical space and ecological space, particular shifts in species' occurrences with respect to disturbance could be interpreted conceptually. We have also sought to understand how pivotal species thought important to community dynamics and ecosystem functioning provide a basis for understanding biotic responses to disturbance (Reagan & Waide 1996, Walker et al. 1996a, Brokaw 1998).

We now have an improved understanding of many aspects of the disturbance regime. We know that forests and streams in the Luquillo Experimental Forest (LEF) are affected by recurrent episodic disturbances due to hurricanes (Walker et al. 1991, 1996a). We have a good record of the impacts of Hurricane Hugo (1989) and Hurricane Georges (1998), which passed directly over the LEF (Fig. 5). The occurrence and distribution of landslides are now well understood (Guariguata 1990, Scatena & Larsen et al. 1991, Walker et al. 1996b, Myster et al. 1997). We have documented the legacy of previous human disturbance on the forest, illustrating the strong imprint that it imparts on the biotic landscape (Garcia-Montiel 1994, Zimmerman et al. 1994, 1995, Everham 1996, Willig et al. 1996, Foster et al. 1999, Thompson et al., submitted). We have recorded the effects of drought (e.g., Covich et al. 1999, 2000) and have begun to appreciate the impacts of floods on terrestrial vegetation (e.g., Sharpe 1997).

During LTER 3, we will continue to refine our understanding of the response of the biota to disturbance, focusing on the effects of Hurricane Georges (September 1998) to test observations and ideas generated by Hurricane Hugo (Research Theme 1; Table 1). We will also continue to document the dynamics of forests with differing land-use histories. We will build on these observations to further develop the idea that dissimilar disturbances can be understood by their impact on gradients of environmental variables. We will also expand our previous emphasis on food webs and pivotal species to include species richness and other community attributes as important factors providing a mechanistic context for understanding the biotic responses to disturbance (Research Theme 2).

As part of LTER 3, we will expand the scale of our research to the entire elevational gradient of the LEF and the different forest communities that occur along this gradient (Fig. 1; Brown et al. 1983, Weaver & Murphy 1990, Garcia-Bermudez, 1995, Alvarez 1997, Cox 1999, Richardson 1999). This expansion (Research Theme 3) will test the idea that factors that are important to the functioning of tabonuco forest and the response to disturbance may not be the same in forests where the climate is colder, wetter, and cloudier. This expansion in scale is a major modification of the scope of the LEF-LTER program that will continue well beyond LTER 3.

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THEORETICAL FOUNDATIONS FOR LTER 3

Our conceptual model of the Luquillo Experimental Forest (Hall et al. 1992, Willig & Walker 1999) considers the disturbance regime to represent forcing functions that affect the biota both directly and indirectly via their effects on abiotic environmental gradients (Figure 13). We start with a geophysical template of the forest, including latitude, longitude, elevation, topography, and geology; features which change only over exceptionally long temporal scales. Such attributes of the physical template have distinctive influences on the biota through their impact on basic physiological drivers (i.e., temperature, water, light, and nutrients). When these abiotic characteristics are superimposed on the physical template, they represent environmental gradients. More specifically, these abiotic drivers are the primary gradients of the fundamental resources or conditions that organisms require for survival and reproduction. The distribution of organisms in geographical space is determined by their species-specific optima with respect to these critical abiotic variables. Consequently, biotic components of the LEF populations, functional groups, and communities of species exhibit heterogeneous distributions with respect to the physical template and environmental gradients. Moreover, the biota can affect primary gradients by altering ecosystem processes such as nutrient uptake, litter production, decomposition and nutrient mineralization, soil oxygen consumption, and weathering.

Disturbance plays a critical role in the forest because it modifies the physical template, alters environmental gradients, and changes the abundance and distribution of species (Fig. 15; Research Theme 1; Table 1 and below). Building on the foundation of research from LTER 1 & 2, we integrate the concepts of disturbance and the biota's role during secondary succession by quantifying the impacts of disturbance on resource gradients over the physical template (Keddy 1991, Hall et al. 1992, Gosz 1992) and associating them with subsequent changes in the composition of the biota. The premises to this approach are as follows:

1) Biotic components of the LEF and associated rates of ecosystem processes are related to primary gradients of environmental factors, which in turn are affected by the physical template of a landscape. A focus on primary gradients facilitates development of process-based hypotheses and models (Research Theme 2), and leads to mechanistic understanding of patterns of structure and function across the landscape of the LEF (Willig & Walker 1999).

2) A given geographic location on the landscape can be characterized by its position along each important environmental gradient and the environmental gradients together define the abiotic space (Research Theme 3 and Monitoring). Each species will be found only over a particular range of environmental conditions and will tend to be most abundant and have its highest productivity within a subset of that range. Biotic space is based on the composition of species, and may reflect either presence/absence data or measures of species abundance. Abiotic space is based on the concentrations and quantities of essential nutrients and water, as well as light and temperature.

3) Disturbance has the direct effect of changing the abundance of organisms by causing mortality and displacement in a site-specific fashion. In addition, disturbance alters the environmental conditions associated with the site. Together, these two effects of disturbance regulate subsequent trajectories of change in the biota during response to disturbance (Research Theme 1 and Monitoring).

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4) Our gradient approach thus facilitates comparison of different elements of the disturbance regime (e.g., hurricanes, previous agricultural activities, treefalls, landslides, and droughts) by allowing us to quantify differences in the intensity of response as the length of the vector of net change in multi-dimensional biotic or abiotic space (Research Theme 1 and Monitoring).

5) Response to disturbance can be quantified as the rate of return to a previously specified reference state in multi-dimensional space. Changes in biotic or abiotic conditions at a site that result from additional disturbances can be depicted as continued displacement to new and unique positions in multi-dimensional space, preventing recovery toward the original reference position. Legacies are reflected as a displacement to a new reference state (Research Theme 1).

6) This gradient approach leads to a direct understanding of system resistance and resilience. Resistance can be measured as the inverse of displacement in abiotic or biotic space, whereas resilience is the time required to return to a reference state (or the instantaneous rate of return in that direction). Theory and observation suggest that resistance and resilience are inversely related (Holling 1973, Grimm 1996; Herbert et al. 1999a).

7) Changes in the biota may affect primary gradients. The biota can: 1) modify the abiotic space of a particular site (e.g., an expanding tree canopy shades the forest floor, reducing temperature and light and influencing local position in ecological space; 2) influence resistance (in terms of gradient space) to a given disturbance; and 3) influence resilience by controlling the speed and direction of response. These effects can be investigated by focusing on pivotal species and groups of species thought important to the response to disturbance (Research Theme 2).

8) Community patterns can be predicted using this approach (Fig. 16; Research Theme 3). Geographical space (sites arranged along an elevational gradient) translates into ecological space as a function of primary gradients (e.g., temperature and moisture). Using a null model approach, where species niches (ellipses) are randomly placed in ecological space, most species overlap at intermediate values of the primary gradients. This results in a peak in species richness at intermediate elevations (Willig and Lyons 1998), and the absence of distinctive community types (based on species composition) along any particular gradient (Hofer et al. 1999).

PROPOSED RESEARCH

Our research plan for LTER 3 consists of continued monitoring directed toward understanding long-term impacts of disturbance and climatic phenomena, as well the development of three inter-related Research Themes (Table 1). Research Theme 1 continues our studies begun in LTER 1, but focuses on the cumulative effects of Hurricane Hugo and Georges and legacies of human disturbance. Research Theme 2 is directed at the biota, focusing on food webs and the processing of organic matter. Research Theme 3 considers the complex gradient of environmental factors resulting from the interactions between disturbance and abiotic factors governing the distribution of organisms in the entire LEF. This undertaking comprises the first step in our long-term goal to extend our work beyond tabonuco forest and to develop an understanding of the disturbance regime and biotic response across the entire LEF. Each research theme is discussed below by describing the background to the problem and our general approach. Specific hypotheses are presented within each Research Theme, indicating the rationale and workplan for testing each hypothesis. Additional details on methodology for each hypothesis are presented at our website

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(http://luq.lternet.edu/publications/prop2000/propy2k.htm). Table 8 provides information on the affiliations of scientists involved in LTER 3 (also see http://luq.lternet.edu/publications/prop2000/associates.htm).

Monitoring of Spatial-Temporal Patterns

The foundation of any LTER program is the monitoring of populations and key ecosystem parameters, which together provide a means of evaluating the effect of the infrequent, episodic, or gradual events that are the focus of long-term research (Fig. 17). In addition, the existence of long-term records provides a spatio-temporal context for short-term measurements and experiments. Our monitoring program is primarily based at two focal study sites in the LEF, El Verde and Bisley (http//www.ites.upr.edu/sunceer/publicat/prop2000/monitoring.htm).

The occurrence of Hurricane Hugo in 1989 provided an immediate test of the monitoring program developed under our initial proposal. On the basis of our experience with Hugo, we modified and expanded the parameters being monitored, adding flowering phenology, canopy openness, and seedling dynamics. Moreover, in 1990 we initiated studies in the 16 ha Luquillo Forest Dynamics Plot (LFDP), located at El Verde, to provide detailed information on the response of 139 woody plant species to disturbance. Over 130,000 stems > 1 cm DBH have been marked, measured , or mapped (only trees $\geq$ 10 cm DBH) in the LFDP. Because previous studies of the effect of the 1932 hurricane on the LEF (Crow 1980) missed the first 11 years of succession, data from the LFDP filled an important gap in knowledge. The second survey of the LFDP was completed just before Hurricane Georges struck the LEF in September 1998 (Fig. 10). Information from this survey and from annual measurements of forest plots in Bisley (Scatena et al. 1996) provided an immediate opportunity to assess damage to thousands of individual trees and to compare the effects of the two hurricanes in less than 10 years. More important, LTER permanent plots provide opportunities to study the cumulative effects of additional, sequential disturbances.

Plant populations In preparation for LTER 3, we have conducted an evaluation of our monitoring program. As in LTER 2, we will continue to support the extensive monitoring of key populations and environmental conditions in the Bisley watersheds and the LFDP at El Verde (Table 4). The principal objectives of these monitoring efforts are: 1) to quantify the rate of recovery of biomass and ecosystem nutrient capital after disturbance; 2) to establish successional trajectories and changes in species composition over time after disturbance. Population data on over 120 woody plant species are monitored in these two locations through surveys conducted once a year at Bisley and once every five years in the LFDP. Surveys at Bisley provide a means of assessing annual dynamics whereas measurements in the LFDP provide sample sizes adequate to evaluate the population dynamics of rare species. The long-term records from these plots have been invaluable in quantifying the longer-term impacts of hurricanes (Walker et al. 1996a), determining life-history traits (Zimmerman et al. 1994), and defining the ecological space of animal and microbial communities (Secrest et al. 1996, Huhndorf & Lodge 1997, Reed 1998, Willig et al. 1998).

Responses to other kinds of natural and anthropogenic disturbance are monitored in permanent plots established for this purpose. We have measured vegetative responses in three landslides annually and 17 landslides less frequently since LTER 1, resulting in over 20 publications (summarized in Walker et al. 1996b). Succession, aboveground biomass, and soil nutrient pools have been monitored in two clear cuts at Bisley since 1989 (Silver et al. 1993, Silver & Vogt 1993, Silver 1994, Silver et al.1996).

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In LTER 2, permanent plots were established to monitor revegetation after abandonment of pasture and coffee plantation and after the creation of artificial canopy gaps through harvest of single trees. The response of riparian areas to periodic flooding will be initiated in LTER 3 by establishing monitoring programs for three species, a fern, an orchid, and a bromeliad (see http://luq.lternet.edu/publications/prop2000/methods/ methoy2k.htm#riparianstudies for details).

Animal populations - Monitoring of animal populations is coordinated with plant surveys in the LFDP and Bisley. Standard methods are used to measure abundances of decapods, birds, frogs, and lizards. In addition, we monitor intensively 19 focal species (http:///www.ites.upr.edu/sunceer/publicat/prop2000/monitoring.htm) selected on the basis of numerical density in their particular trophic guild. Data from these studies have been essential in assessing the response of animal populations to changes in ecological space resulting from disturbance (e.g., Alvarez & Willig 1993, Covich et al. 1996, Gannon & Willig, 1997, Pyron et al. 1999, Reed 1998, Scatena & Johnson 2000, Secrest et al. 1996, Willig et al. 1998, Willig & Gannon 1996, Woolbright 1996). Following Hurricane Georges, we initiated long-term sampling of arthropods at four localities in areas of closed and open canopy (Fig. 18).

Biogeochemistry - The dynamic nature of the LEF has allowed us to sample a wide range of environmental conditions and biogeochemical responses in a relatively short period. During the previous LTER funding cycles, biogeochemical monitoring demonstrated the resilient nature of nutrient cycles to hurricane disturbances (Scatena et al. 1996, Silver et al.1996, McDowell et al. 1996, Schaefer et al. 2000), the influence of topography and riparian zone morphology on nutrient cycling (Silver et al. 1994) and trace gas emissions (Bowden et al. 1992, McDowell et al. 1992, Cox 1999, McSwiney 1999), and the effects of individual plant species on local biogeochemical conditions (Bloomfield et al. 1993, Vogt et al. 1996, Gonzalez & Zou 1999). During LTER 3 we propose to continue basic biogeochemical monitoring at Bisley and El Verde and expand the spatial extent of sampling along an elevation gradient under Research Theme 3.

Environmental variables - Measurements of primary gradients are central to the description of ecological space at any point in geographical space. In LTER 1 and 2, we emphasized meteorological measurements at multiple sites (Table 4) conforming to LTER level 3 weather stations. Data from these stations and historical records were extrapolated to the whole LEF using mechanistic models (Wooster et al. 1989, Hall et al. 1992). These permanent stations were augmented by short-term measurements of environmental variables associated with specific experiments. In LTER 3, we propose to expand and refine our understanding of primary gradients by developing an intensive micrometeorological program associated with Research Theme 3 (see below). This program will take advantage of state-of-the-art wireless technology being implemented in the LEF under a separate grant.

Synthesis of Monitoring Data - Synthesis of long-term monitoring data is an ongoing process at the LEF-LTER, feeding back into the design of new experiments and measurements. During LTER 3, we will devote special emphasis to the synthesis and publication of two long-term data sets accumulated during the first 12 years of the LTER. We will complete synthesis of the 10-year record of biogeochemical changes in the Bisley Experimental Watersheds following Hurricane Hugo. Data analysis and synthesis of the vegetation and biogeochemistry data will be completed and published during LTER 3. Measurements of environmental variables and plant and animal abundance on the LFDP has produced a large body of data that requires further analysis and synthesis from the perspective of measures of dispersion and correlation.

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Long-Term Experiments

A number of long-term experiments that were initiated during LTER 1 and 2 will be continued during LTER 3 (Table 3). The long-term measurements associated with these experiments constitute a core activity of the LEF-LTER and are integrated into Monitoring or the Research Themes discussed below. During LTER 3, we will continue a manipulative experiment on the effect of supplemental nutrients and hurricane disturbance on forest productivity (Walker et al. 1996c), a project begun in 1989 with funds from UPR's Center for Research Excellence in Science and Technology. An additional experiment takes advantage of treefalls, created to study the impacts of coarse woody debris on ecosystem processes (Hypothesis 1B), to study the dynamics of the understory vegetation.

Research Theme 1: Cumulative Effects of Disturbance Hurricanes Hugo and Georges and Legacies of Human Land Use (Continuation of LTER 2)

Background - Studies in Research Theme 1 are continuations of long-term measurements or new measurements with a long-term perspective that relate directly to concepts developed in LTER 2.

Specifically, they address how the predominant disturbance factors in the LEF, hurricanes and humans, impact abiotic factors presumed to affect the community response to disturbance or lead to semi-permanent changes in levels of abiotic variables or forest community composition (legacies).

Hurricane Disturbance - Hurricanes impact tropical forests by removing much of the canopy (Zimmerman et al. 1994) and moving it to the forest floor. This canopy removal causes increases in light levels on the forest floor (Fernandez & Fetcher 1991), which strongly affects the dynamics of the understory (Scatena et al. 1996). Decomposing woody debris has the potential to immobilize nutrients, which can temporarily retard forest productivity (Zimmerman et al. 1995b). Soil pits created by uprooted trees provide access to light levels and nutrients that promote the establishment of pioneer tree species, particularly *Cecropia schreberiana* (Brokaw 1998, Walker 2000). Thus, following a hurricane, ecological space, (changes in light levels and in soil nutrient availability and distribution) becomes remapped on geographic space causing a spatial reorganization of the plant community.

Anthropogenic legacies - In LTER 2 we introduced into our research program the concept of legacies of anthropogenic disturbance. These are distinguishable features that remain on the landscape for long periods after these disturbances. In the LEF, we have identified the legacies of roads (Olander et al. 1998, Heyne 1999), coffee plantations, pastures and clear-cut logging on plant, animal, and bacterial community composition (Zimmerman et al. 1995a, Willig et al. 1996, Willig et al. 1998, Thompson et al., submitted; Fig. 3). In LTER 3 we will expand upon this concept by examining the effects of legacies on ecosystem-scale carbon dynamics following reforestation of pastures and nitrogen cycling following reforestation of coffee plantations. The well documented history of land use in the LEF allows us to investigate the degree to which human disturbance alters ecological space in unique ways and how human and natural disturbance thus differ in their impacts on the ecosystem.

Approach We describe four projects that take advantage of established monitoring programs or the documented history of human land use in the LEF to determine 1) how repeated hurricane disturbance affects tropical forest community dynamics in a large, gridded plot; 2) how repeated additions of coarse woody debris caused by hurricanes affects nutrient cycling; 3) the

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dynamics of soil carbon following pasture abandonment and; 4) the long-term impact of coffee cultivation on nitrogen cycling and forest composition following abandonment.

Hypothesis 1A: Stability in tree composition in the tabonuco forest is a result of niche-based partitioning of light environments following hurricane disturbance (Thompson, Brokaw, Zimmerman, Waide).

Rationale Using data from the 2000 census of the 16 ha Luquillo Forest Dynamics Plot (LFDP), we will test two general hypotheses that explain diversity in species-rich tree communities (Connell 1978, Denslow 1980, Hubbell 1998). The equilibrium hypothesis (Connell 1978), as Hypothesis 1A postulates, is that tree species partition resources and occupy different ecological niches. If the forest is disturbed, the equilibrium hypothesis predicts that it eventually returns to the pre-disturbance state of species composition and relative abundances. Furthermore, disturbance can promote diversity in the community by maintaining heterogeneous conditions that favor a variety of species (e.g., light demanding vs. shade tolerant). Thus, in the context the theoretical foundations of our research program, changes in forest community following a disturbance such as a hurricane can be predicted by species-specific tolerances of low light levels. In contrast, the non-equilibrium hypothesis (Connell 1978) ignores species-specific adaptations to light level. Here, the composition and relative abundances are determined by chance, and there can result any number of new combinations of relative abundances of species after the same disturbance. Under these non-equilibrium conditions, diversity can be maintained if there is recruitment limitation (Hubbell et al. 1999). This operates if seed dispersal or seedling establishment is so limited that particular tree species do not have access to all potential recruitment sites, allowing inferior competitors to occupy sites by default and remain in the community.

Workplan The LFDP will be resurveyed in 2000, two years after Hurricane Georges, the approximate time of maximum understory development following a hurricane (Scatena et al. 1996). The fate of all shrubs and trees >1 cm DBH recorded in the 1995/6 census will be determined, and the distribution of trees compared with results from the initial census before Hurricane Hugo (Zimmerman et al. 1994). Different from previous censuses, we will map trees and shrubs 1-10 cm DBH to the nearest 0.5 m within the plot (previously they were only located within a 5x5 m subquadrats). These detailed spatial data will provide a basis for testing whether self-thinning that occurs as the forest canopy re-establishes itself is nonrandom, as suggested by Hubbell et al. (1999) for tropical forest in Panama. The canopy of the plot is currently being mapped to record the location of gaps caused by Hurricane Georges and a series of 150 1x2 m seedling plots has been established which will assess recruitment limitation.

Aspects of the impact of Hurricane Georges have been incorporated into a version of the SORTIE model (Pacala et al. 1993, 1996) for the LFDP using separate funding. Focusing on 12 species differing in life-history characteristics (http://luq.lternet.edu/publications/prop2000/keytrees.htm), we use SORTIE to synthesize LFDP data on forest community dynamics. SORTIE is an empirically based model that uses species-specific curves relating growth and mortality to light availability to understand how tree mortality and recruitment respond to variation in storm frequency and intensity. Thus, by addressing the influence of a key abiotic variable, light, on forest community dynamics, this model specifically incorporates the basic assumptions of the theoretical foundations of our research program into a predictive model of long-term changes in forest composition.

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Hypothesis 1B: The decomposition of coarse woody debris differentially controls the recovery of tree species by regulating the availability of critical nutrients in the soil (K. Vogt, D. Vogt, Lodge, Covich).

Rationale - Coarse woody debris can be a major contributor to ecosystem level carbon and nutrient cycles in forests (Harmon et al. 1986, Zimmerman et al. 1995b, Vogt et al. 1996). During LTER 2, experimental additions and removals of coarse woody debris in plots located in three watersheds were used to simulate hurricane impacts and identify biogeochemical processes associated with wood decomposition. Initial results suggest that decomposing coarse wood controls the growth rates of trees and palms (*Prestoea montana*) differentially, by controlling the availability of limiting nutrients that were required by plants and by soil/litter microbes.

Workplan

- In LTER 3 we will continue monitoring the experimental treatments begun in LTER 2 to determine the effect of coarse woody debris on soil-carbon sequestration, nitrogen leaching below the rooting zone, plant productivity, and plant species diversity. Coarse woody debris deposited during Hurricane Georges has been removed from wood removal treatments and randomly placed on the wood-addition treatments. In LTER 3 we will initiate starch amendments to the coarse wood input treatment at rates equivalent to aboveground litterfall. Specific questions to be addressed include: 1) does the amount of coarse wood control available plant nutrients by regulating the pools and fluxes of nutrients in the soil through its decomposition; and 2) does coarse wood increase the availability of specific nutrients (e.g., Ca) required by some plant species such that species-level net primary production changes differentially with wood addition leading to changes in forest community composition?

Hypothesis 1C: The reforestation of tropical pastures will lead to an increase in surface soil carbon derived from forest vegetation, but this will be offset by a loss of pasture soil carbon from deeper soil depths. Over time, the amount of soil carbon lost from the previous land use will approximate the amount of soil carbon gained through reforestation (Silver, Lugo).

Rationale - This hypothesis addresses the legacy of human disturbance on the dynamics of soil carbon in tropical soils. The storage of C in tropical forest soils plays an important role in the global C cycle (Lugo & Brown 1980, Houghton et al. 1993). Deforestation generally decreases soil C pools, and pasture establishment can increase (Chone et al. 1991) or decrease soil C pools

(Detwiler 1986, Veldkamp 1994). We know very little about the effects of reforestation on soil C pools in tropical forests. In plantations established on old sugar cane fields, there was a net C deficit after 11 yr of tree growth (Bashkin & Binkley 1998). Because secondary forest land area currently exceeds land area in mature forests in the tropics (FAO 1993), an understanding of the legacies of pasture on forest soil C pools is essential to better understand C sequestration in tropical forests.

Workplan - We will use stable carbon isotopes to determine the legacy of pasture carbon in secondary forests in the LEF. In the tropics, most pastures are dominated by species that use the C4 photosynthetic pathway, whereas most trees use the C3 pathway. Plants with the C3 pathway discriminate against 13CO2 during photosynthesis, causing the 13C/12C ratios of their phytomass to be depleted of 13C (i.e., a more negative d13C) relative to those of C4 plants (Smith & Epstein 1971). The isotopic composition of soil organic C reflects the plant material from which it is derived, with relatively minor isotopic fractionation as it undergoes decomposition (Dzurec et al. 1985). Therefore, the introduction of vegetation with a different

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photosynthetic pathway provides an *in situ* label that allows us to approximate the net input rate of C from the new source. The LEF offers a unique opportunity to examine the long-term trends in reforestation of tropical pastureland. In the mid 1930's, the USDA Forest Service began reforesting pastures by planting a mix of native and exotic species plantations among trees that had already colonized the abandoned pastures. Using 15 long-term permanent plots and adjacent 65 year old pastures, we will quantify the amount of C3 carbon gained since reforestation, and estimate the amount of C4 carbon lost from pastures. Pastures in this region are not fertilized, and grazing intensity has been low throughout the 65-year time period (Marerro 1947, J. Melendez pers. com).

Hypothesis 1D: Differences in the forest composition of abandoned coffee plantations and other land uses is maintained by higher levels of nitrogen availability in soils related to the use of legumes as shade trees (Zimmerman, Herbert, McDowell, Zou).

Rationale - Differences in historical land uses affect the abiotic conditions controlling reforestation and result in permanent changes in forest composition. Abandoned coffee plantations maintain a unique species composition over 60 years after their abandonment (Zimmerman et al. 1995a). In the LEF, as in much of the tropics, coffee was planted under nitrogen fixing tree species (*Inga vera* in the LEF, Zimmerman et al. 1995a) to provide shade and (presumably) increase the availability of nitrogen in the soil. *Inga vera*, a relatively short lived species, disappears from abandoned coffee plantations as the forest becomes reestablished and the stand becomes dominated by *Guarea guidonia*. After hurricane disturbance, fast-growing, nutrient-demanding species such as *Cecropia schreberiana* also dominate for a period of time (Zimmerman et al. 1995a). *Guarea guidonia* exhibits particularly high growth under conditions of high light and nitrogen availability (Fernandez 1997), suggesting its dominance also may be the result of interactions between previous land use and hurricane disturbance.

Workplan - We will use the old coffee plantation which surrounds the El Verde Field Station (abandoned in 1928; Gerhardt 1934) because its borders are readily identifiable from 1936 aerial photographs (Foster et al. 1998). Six replicate transects, 100 m in length, will be placed perpendicular to the coffee plantation border extending 50m into the plantation and, in the opposite direction, into the adjacent secondary forest. Canopy trees, understory trees and shrubs, and seedlings will be located along the transects using transect widths of 25 m, 5 m, and 1m, respectively. Comparison of seedling and tree distributions along the transects will determine the degree to which secondary forest species are invading adjacent coffee plantations following hurricane disturbance, and vice versa. Determinations of soil N-availability, N-mineralization rate, SOM, and production of nitrous oxide gases along transects will determine the degree to which soils in the abandoned coffee plantation are still influenced by the history of growing coffee shade trees. Shifts in species composition and associated changes in carbon and nutrient storage and fluxes will be examined mechanistically with the Multiple Element Limitation (MEL) model (Rastetter & Shaver 1992, Rastetter et al. 1997, Herbert et al. 1999b). MEL is particularly useful in this context because of the recent incorporation of autotrophic and heterotrophic nitrogen fixation with species-specific effects (Herbert et al.1999b).

Research Theme 2: The Role of the Biota in Controlling Community and Ecosystem Processes that Affect Nutrient Availability and Organic Matter Processing

Background - In Research Theme 2 we describe short-term measurements and experiments designed to illuminate the manner in which individual species (pivotal species) or groups of organisms (e.g., biodiversity) regulate key environmental variables,

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particularly soil nutrient availability or organic matter content (Fig. 18). These factors can, in turn, feedback on succession and food web interactions. Biota can directly impact environmental variables or have an indirect impact through trophic cascades. Deciphering these mechanisms is critical before we can understand fully the effects of disturbance on the ecosystem. We will focus on three types of biotic effects on community and ecosystem processes: top down versus bottom up control (Carpenter & Kitchell 1988, Osenberg & Mittelbach 1996), impacts of diversity on function (Grime 1997, Hooper and Vitousek 1997, Chapin et al. 1997), and single species influences (e.g., facilitation; Callaway & Walker 1997, Covich et al. 1999, Crowl et al. 2000a).

All of these interactions can be influenced by disturbance and affect the response of the tabonuco forest ecosystem to disturbance.

Approach - We propose five key manipulative experiments to address the role of biotic control on nutrient availability or organic matter processing: 1) the cascading effect of secondary consumers on detritivores and rates of decomposition; 2) the relative role of algae, detritus, and predators in determining patterns of carbon flow in stream ecosystems; 3) the role of species composition of litter substrate and fungi on leaf decomposition; 4) the pivotal role of earthworms in soil phosphorus dynamics; and 5) the influence of pioneer vegetation in landslides on soil properties that affect subsequent successional change.

Hypothesis 2A. Consumer populations in tabonuco forest are limited by predation. Exclusion of predators will have cascading effects on the abundance of herbivores and detritivores and rates of decomposition and nutrient cycling. (Waide, Willig, Belovsky).

Rationale - Strong (1992) suggested that top-down control of food webs is less important in species-rich communities where the effects of consumption are spread over many prey species. However, in tabonuco forest, where vertebrate and invertebrate species richness is more similar to temperate than mainland tropical forests, evidence exists for both top-down and bottom up regulation of populations. Dial (1992) removed *Anolis* lizards from isolated treetops in tabonuco forest and found a subsequent increase in insect populations that influenced the rate of herbivory. Fertilization of 20 x 20 m plots at El Verde led to increases in litterfall, leaf area index, seedling growth, and abundance of ants, termites, flying insects, and spiders (Waide unpublished data). In LTER 2, we initiated an experiment to examine the influence of predation on prey populations, herbivory rates, and plant species composition. We propose to expand this ongoing experiment through a modeling approach linking populations, trophic webs, energy flow, nutrient cycling, and disturbance.

Two separate approaches to the study of trophic networks, the biogeochemical and bio-demographic, employ the food web as the unit of study (Winemiller and Polis 1996). These two perspectives are embodied today in the process-functional and population-dynamic approaches to the study of ecosystems (O'Neill et al. 1986). The dynamics of populations and the structure of food webs comprising these populations both depend on the availability of energy and nutrients, and at the same time influence the rates and pathways of energy and material flow (Oksanen et al. 1981, Carpenter et al. 1985, DeAngelis et al. 1989). Thus, food webs represent an important link among the fields of population, community, and ecosystem ecology. However, ecologists seldom integrate consumer (trophic) perspectives with nutrient cycling (ecosystem) perspectives, especially in terrestrial ecosystems.

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Parallel with exclosure experiments, we will develop a model linking trophic interactions, disturbance, and nutrient availability in the soil. The model (Fig. 21) is presented qualitatively, but each arrow represents consumption or uptake of nutrients which depends upon differential equations that can take various forms (DeAngelis 1992). In the model, release of nutrients from dead herbivores, excrement, and leaf leachates (the Fast Cycle) are distinguished from the decomposition of plant material (the Slow Cycle) because of large differences in the rates at which nutrients are made available to plants (Pastor et al. 1988, Pastor & Naiman 1992). The model also distinguishes between fast- and slow-decomposing plants (e.g., pioneer vs. nonpioneer vegetation) whose relative abundances 1) represent changes in species composition resulting from disturbance and subsequent secondary succession, and 2) affect the rate of nutrient release. Disturbance affects all components of the model by altering predator and herbivore populations, changing the proportion of fast- and slow-decomposing plants, modifying available nutrient pools, and shifting the proportion of energy and nutrients processed by herbivores compared to detritivores. Consequently, the model accounts for shifts in proportion of nutrients released by Fast versus Slow Cycles, which may change nutrient availability to plants and modify plant production and species composition. Thus, this particular model provides the capacity to distinguish the effects of plant species composition and herbivore and predator abundance on nutrient availability to plants.

Workplan - The food web in tabonuco forest is characterized by the absence of large consumers and predators and an abundance of small vertebrate predators, principally *Anolis* lizards and *Eleutherodactylis* frogs (Reagan & Waide 1996). Our exclosure study investigates how variation in the abundance of lizards and frogs in the understory affects litter arthropod abundance, herbivory, and rates of litter decomposition. We have established 40 exclosures, 3.3 m in each dimension, which have been dispersed among 8 blocks in tabonuco forest with a history of little human disturbance. Four treatments are represented in each block: 1) frogs and lizards at usual densities (exclosure effect), 2) frogs at usual post-hurricane densities (Woolbright 1991) with *Anolis gundlachi* excluded, 3) *A. gundlachi* at usual densities (Reagan 1991) with frogs excluded and 4) both frogs and lizards excluded. Currently, we are investigating the impact of variation in predator densities on abundance of invertebrates and herbivory on a fast-growing shrub (*Piper glabrescens*) and seedlings of a slow-growing tree (*Manilkara bidentata*). During LTER 3, we will use the exclosures as an experimental arena to determine cascading effects of predators on litter decomposition.

Our model will be used to examine the effects of disturbance on the dynamics of the tabonuco trophic web. Information from measurements of herbivore populations, herbivory, and decomposition rates from the exclosure study, the effect of plant quality and diversity on decomposition (see H2C below), previous fertilization experiments (Waide unpublished), long-term monitoring of plant and animal populations, and new measures of nutrient availability in the exclosures will allow us to parameterize the model. The model will subsequently be used to examine the effect of different kinds of disturbance on trophic dynamics and to identify further experiments that need to be performed to evaluate the respective strengths of top-down and bottom-up control of populations and nutrient and energy dynamics. Finally, the model will be used to compare terrestrial and aquatic trophic dynamics using data from H2B (below).

Hypothesis 2B. Wind damage to tree canopies changes ecological space by increasing light availability above streams, causing a shift from allochthonous riparian leaf litter to autochthonous algal production. However, the

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extent and duration of the increased accrual of algal standing crop varies as a function of top-down control of stream food webs by predatory fishes. (Crowl, Covich, McDowell, Pringle).

Rationale - Energy flow in stream food webs in forested catchments largely is controlled by the availability of light, nutrients, and inputs of riparian leaf litter. These bottom-up parameters are dynamic in response to disturbances, especially hurricanes and other severe wind storms. Shading by riparian tree species and associated leaf-litter inputs are well known to affect the species composition of stream communities and related ecosystem processes such as decomposition and nutrient cycling, as synthesized in the River Continuum Concept (Vannote et al. 1980, Cummins et al. 1995, de la Rosa 1995, Covich & McDowell 1996, Johnson & Covich 2000). The River Continuum Concept emphasizes detrital inputs and *in situ* primary productivity. Consequently, it assumes that interconnected stream habitats and the biodiversity of stream consumers are organized by energy flow (i.e., bottom up). Although this approach has been useful for comparisons of stream communities, it does not effectively incorporate potential food-web regulation by top predators such as fishes. In some streams these top-down effects may occur simultaneously with bottom-up effects depending on physical conditions of the habitat over time. Our experiments will focus on how changes in ecological space influence foodweb composition and function.

Workplan - Since the recent impact of Hurricane Georges, we have identified large, persistent riparian gaps that allow us to test new hypotheses regarding both detrital and algal resource enhancement and predator control (*sensu* Osenberg & Mittelbach 1996). Thus, in terms of our overall model, we can relate trophic interactions in streams to changes in light availability. In some pools, the riparian canopy was damaged only slightly so that shading has persisted and algal growth has been minimal. In other pools, major gaps have been opened by tree falls and tree mortality so that algal growth increased rapidly in response to intense light (and an initial pulse of nutrients from leaf leachates). We will manipulate the presence or absence of predators and detritivores in these pools to determine how the fish and benthic invertebrate assemblages interact to affect primary production and detrital processing (Covich et al. 1991; 1996; 1998, Johnson et al. 1998, Crowl et al. 2000a). From experiments completed during LTER 2, we already know that the detrital pathway is an important component of stream function, strongly affecting nutrient availability and cycling as well as the overall stream community (Crowl et al., 2000a). We anticipate that primary production will be limited to gap areas. Our previous behavioral studies demonstrate that freshwater shrimp avoid brightly illuminated areas and may feed on periphyton primarily at night when fish predators are present.

To investigate the interactions between fish, shrimp, insect larvae, algal production, benthic organic matter and detrital transport, we will perform an *in situ* experiment in the Bisley watershed. A two by two cross-classified design will be employed in which fish and shrimp presence will be manipulated in three replicate pools. Replicate stream pools will receive: no shrimp or fish; shrimp (5 m-2) and no fish; fish (2 m-2) and no shrimp; and fish and shrimp (2 and 5 m-2 respectively). Fish and shrimp densities are based on pre-hurricane densities and will be maintained by fencing off the pools (using 5 mm mesh plastic screens) to prevent migration. Tiles will placed into the pools and will be harvested weekly over a 3-6 week period for algal and benthic organic matter standing crop and amounts of carbon and nitrogen in benthic organic matter (BOM). The quality and quantity of BOM will be compared to pre-hurricane levels (Pringle et al. 1999). Drift nets and Surber samplers will

be used weekly to measure the responses of mayflies and caddisflies in all pools. Nutrients (DOC, N and P) will continue to be monitored weekly in this stream.

Hypothesis 2C. Pivotal plant and fungal species control rates of litter decomposition and nutrient mineralization when environmental variables are held constant. (Lodge, Silver)

Rationale - This project seeks to identify the interactive effects of plant and fungal species on release of nutrients from decomposing litter. These effects are thought important in the response of tabonuco forest to disturbance because of the large amounts of green litter produced by hurricanes (Lodge et al. 1994) and other disturbances to the canopy. Although it often is assumed that litter decomposition and nutrient mineralization can be predicted from the additive rates and proportions of constituent species in the litter, a growing body of evidence suggests that this is not always true (Harrison 1971, Berg 1986, Klemmedson 1987, Taylor et al. 1989, Blair et al. 1990, Montagnini et al. 1993, Berg et al. 1995, Byard et al. 1996, Wells et al. 1998). Because decomposer basidiomycete fungi link various litter components on the forest floor, and litter types differ in nitrogen, phosphorus and labile carbon content, the translocation of nutrients among different food bases by basidiomycetes may contribute to the accelerated rates of litter decomposition or mineralization that are sometimes observed in mixed-litter systems (McClaugherty et al. 1985, Lodge 1993). In litter mixtures that have both high nitrogen and high polyphenolic concentrations, the chemical interaction of nitrogen with phenolic rings can sometimes inhibit decomposition (Berg 1986, Berg et el. 1995). The loss of pivotal species from the decomposer community may affect the rates of ecosystem processes if there are no other species that play the same critical role. Some detrital species may be uniquely adapted to a particular substrate and set of environmental conditions whereas other species that are either generalists or are adapted to different substrates may not be as efficient as the specialists in decomposing a substrate. Members of the detrital food chain are often taxonomically host-specific at the level of plant genus or family, and therefore mis-matches of decomposers and detritivores with leaf genera or families might result in slower rates of decomposition or different rates of mineralization.

Workplan - Leaf litter from four tree species contrasting in nutrient and polyphenol content will be decomposed in litterbags placed in a communal tabonuco forest plot, singly and in all combinations of species, to determine if they interact synergistically in terms of decomposition or mineralization. Positive synergistic effects caused by fungi are more likely during early decomposition, whereas negative effects caused by chemical interactions are more likely during the late phases of decomposition. We will use microcosm experiments to determine whether the dominant early-stage litter decomposer fungi in a particular leaf species are more efficient at decomposing or mineralizing their preferred substrates than leaves from other tree species. Only the primary leaf decomposers will be studied (first 2 months of decomposition) because they are not dependent on other microorganisms, and they previously have been used successfully in other microcosm studies (Verhoeff 1996). Freshly fallen leaf litter of the four selected species will be gathered and placed in litterbags in a communal plot so that they are colonized under the same environmental conditions. After six weeks, the fungi will be isolated from each of the litter types using the particle filtration method (Polishook et al.1996). The two most frequently isolated species from each leaf type will then be used to inoculate freshly fallen, sterilized leaf litter of the selected tree species in microcosms. A congener of one of the tree species will be added to this experiment to compare variation in leaf quality and taxonomic identity (five leaf types x 10 species of fungi x 3 reps). The microcosms will be misted with sterile water and the leachates collected from a drain in the bottom to

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determine the effects of matched and mismatched fungi on rates of N-leaching and N and P mineralization. Rates of decomposition will be measured using CO_2 traps that are replaced and sampled weekly and final dry weight after 8 weeks of decomposition.

Hypothesis 2D: Earthworms improve phosphorus availability in highly weathered soils through increasing the solubility of inorganic phosphorus and accelerating the mineralization of organic phosphorus. Experimental removal of earthworms from tropical pastures will reduce soil phosphorus availability more than in tabonuco forest because of differences in earthworm abundances between the two habitats. (Zou).

Rationale - Using already established earthworm exclosures (under separate funding), we will investigate the impacts that earthworms have on the availability of soil phosphorus. Human disturbance, here represented by the contrast of high earthworm abundance in pastures versus low abundance in forest soils (Zou & Gonzalez 1997, Gonzalez & Zou 1999, Gonzalez et al. 1999), will be used to assess the degree to which disturbance and earthworm presence affects the critical soil nutrient phosphorus. Soil phosphorus availability in highly-weathered soils is tightly controlled by geochemical processes (Lindsay 1979). Inorganic phosphorus is strongly tied to the hydroxides and oxides of aluminum and iron in these soils with low pH. One mechanism to increase the solubility of aluminum or iron phosphate is to elevate soil pH. Earthworms typically maintain pH values ranging between 5.6 and 6.0 in their guts through physiological processes that are not well understood (Lee 1985, Edwards & Bohlen 1996). This pH range has the highest solubility for inorganic phosphorus compounds (Lindsay 1979). Earthworms are also recognized to accelerate the decomposition of soil organic matter (Bohlen et al. 1997), thus the mineralization of organic phosphorus. There are about 100 and 850 earthworms within a square meter area in the tabonuco forest and an adjacent tropical pasture, respectively (Zou and Gonzalez 1997, Gonzalez & Zou 1999, Gonzalez et al. 1999). These earthworms can process a large quantity of soil each day through their guts. The rise in pH from 4.8 in soils to 5.6 in earthworm guts can increase the solubility of inorganic phosphorus by several orders of magnitude. Earthworms can accelerate the mineralization of organic compounds through direct comminution and digestion of organic materials and indirect mixing of organic materials with soil minerals and soil organisms (Lee 1985, Edwards & Bohlen 1996).

Workplan - We established earthworm exclusion plots in a pasture near the Bisley watershed and in the tabonuco forest at El Verde research area in 1997. At each site, we trenched eight plots of 1 x 2 m in size down to 0.5 below soil surface. Four plots were randomly assigned as control plots and four as exclusion plots. These plots were separated from the surrounding area using soil barriers. Earthworm exclusion was achieved using a modified electro-shocking technique (Bohlen et al. 1997). This experiment was originally used to quantify the effect of earthworms on plant litter decomposition (Liu & Zou, unpublished data). We will sample soils from the 0-10, 10-25, and 25-50 cm layers. Soil phosphorus availability will be evaluated using a resin extraction technique (Zou et al. 1992, 1995a). Potential rates of soil inorganic phosphorus solubilization and organic phosphorus mineralization will be assessed using an irradiation-autoclaving-incubation procedure developed by Zou et al. (1992, 1995a). These analyses will be performed once a year through LTER 3.

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Hypothesis 2E. In areas previously disturbed by landslides, three sets of colonizing species (woody pioneer species, climbing ferns, tree ferns) modify ecological space in a way that inhibits or facilitates later successional tree species (Walker).

Rationale - The mechanisms that drive successional recovery of plant communities following disturbances are, despite a century of investigation, still only understood in general terms (Glenn-Lewin et al. 1992). Connell & Slatyer (1977) compiled evidence that early colonizers often resist invasion by later arrivals (inhibition model), thereby slowing succession. Recent studies have suggested colonizing species may also facilitate the establishment of later arrivals (Callaway 1995), especially in primary succession (Walker 1999). However, very little is known about the relative balance of inhibitory and facilitative interactions (Callaway & Walker 1997), particularly in primary succession in tropical ecosystems. Landslides are an example of primary succession (where the biotic legacy of plants and soils is largely removed), and they represent the most extreme form of disturbance in the LEF-LTER (Larsen & Simon 1993, Zarin and Johnson 1995a,b, Walker & Boneta 1995, Fetcher et al. 1996 Walker et al. 1996b). We propose an experimental study of the roles of three sets of early colonizing plants on LEF landslides.

Workplan - Removal experiments are an excellent way to examine the mechanism of competitive inhibition (Aarssen & Epp 1990), particularly when species can be kept out of experimental plots as they invade nearby control plots. Removals of existing (aboveground) biomass must be interpreted with caution, however, as the removal of a potential competitor can have complex secondary impacts on remaining vegetation in addition to removal of competitive effects. However, by pairing removal plots with controls and monitoring light and soil variables over time, the successional implications of the removal can be judged effectively.

Species or species groups have been removed from plots ranging in size from 3x3 m to 8x8 m on 2 to 4 replicate landslides (Table 4. These treatments were established in 1997. Vegetation is removed every 6 mos and dried and weighed. Soils (gravimetric moisture, pH, particle size, organic matter, bulk density, total N and P), microclimate (air and soil temperatures, PAR, hemispherical photos), and vegetation (cover, species composition, height growth) is characterized for each plot before removals and at subsequent 6-12 mo intervals. Thus, the potential facilitative or arresting effects of colonizing vegetation will be assessed not only in terms of their impact on plant community dynamics but also in terms of key environmental variables believed essential to the mechanisms of facilitation and arrested succession.

Research Theme 3: The Influence of Climate and Physical Constraints on the Distribution and Abundance of Organisms and Related Ecosystem Processes in the Luquillo Mountains

Background - This Research Theme represents a new initiative by the LEF-LTER to address the variation in climate and the distribution of organisms throughout the LEF. As in many montane landscapes, a distinct zonation of vegetation has been recognized in the Luquillo Mountains (Beard 1941, Wadsworth 1951, Brown et al. 1983; Fig. 1). How variation in climate affects the distribution of species (Fig. 18) has not been addressed at the landscape level the LEF (Smith 1970, Crow & Grigal 1979, Weaver 1991). Numerous hypotheses have been put forward to explain changes in forest composition, productivity (Fig. 13), structure, and species richness with elevation in tropical mountains (Waide et al. 1998). Key factors include low light levels and increased wind exposure (Fetcher et al. 1999) as well as increased rainfall (Garcia-Martino et al. 1996), soil water-logging and low soil O_2 levels (Silver et al. 1999) at higher elevations. An understanding of these relationships is critical

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to understanding how disturbance regulates the distribution of organisms and ecosystem structure and function in a tropical montane landscape.

For stream environments, analogous changes in communities and ecosystems with elevation are predicted by the River Continuum Concept (Vannote et al. 1980, Cummins et al. 1985). A fundamental tenet of the River Continuum Concept is that changes in the relative importance of energy inputs (light energy vs. detrital inputs from the surrounding landscape) produce predictable patterns at various trophic levels as one moves downstream, from first to higher-order streams. Corresponding changes in other trophic levels and stream chemistry are hypothesized to occur in response to this primary gradient. Light limitation is the common thread linking changes in both aquatic and terrestrial communities with elevation in a montane landscape.

The distribution of organisms in terrestrial and aquatic habitats in the Luquillo Mountains is complicated by the history of human disturbance (Foster et al. 1998; Fig. 2c). Much of the upper elevations (corresponding to colorado, palm, and cloud forests) have little history of human disturbance (with the exception of road building and communication facilities; Scatena 1993, Olander et al. 1998) and are considered primary forest. In stream environments, human disturbance manifests itself through the construction of dams and water abstraction, both of which have strong effects on the distribution of organisms far upstream of the site of disturbance (Benstead et al. 1999).

Approach - The Luquillo Mountains can be roughly divided into relatively undisturbed areas from as low as 300 m elevation to the summit of the mountains and areas disturbed by humans from as high as 700 m down to the coastline. Both of our prime study areas at El Verde (250-480 meters) and Bisley (260 - 400 meters) are in tabonuco forest at the upper end of the zone of human disturbance. During the next six years, we will describe for both terrestrial and aquatic habitats the distribution of organisms and key ecosystem variables in areas of relatively little human disturbance (above 300 m elevation; Fig. 2a, c). The impact of human disturbance on lower elevation forests is relatively well-studied (Crow and Gigal 1979, Garcia-Montiel and Scatena 1994, Zimmerman et al. 1995a, Foster et al. 1998, Thompson et al. submitted) and is the subject of Research Theme 1. Studies of aquatic habitats will include stream portions extending down in elevation to the coast because of the profound effects of natural and human barriers on the migration of stream organisms. The long-term goal of this program, carrying our research well into the new century, is a mechanistic understanding of variation in ecosystem processes (primary production and biogeochemistry), distributions of populations, community structure, and food webs across the entire montane landscape. A long-term monitoring program is being established as part of this new initiative to assess the impacts of disturbance (e.g., hurricanes, Fig. 2d) on these montane communities.

Hypothesis 3A: The distribution of woody species and other key organisms in the Luquillo Mountains follows an individualistic pattern with respect to ecological space. (Zimmerman, Brokaw, Hall, Herbert, Lodge, Lugo, Melendez, Sabat, Thomlinson, Waide, Willig, Woolbright)

Rationale - Early investigators categorized the vegetation of the Luquillo Mountains into discrete communities arranged along gradients of elevation and slope (Beard 1941, Wadsworth 1951). This classification has been perpetuated in subsequent

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reviews (Brown et al. 1983; Fig. 1), but no empirical study has demonstrated the existence of distinct communities. Investigations of forest composition have focused on tabonuco (Crow & Grigal 1979), colorado (White 1963, Weaver 1991), or elfin forest (Howard 1968) zones, but have generally failed to examine the transition zones between the purported forest types (but see Smith 1970; Fig. 12). Moreover, no study has examined the distribution of plant species over the entire range of primary gradients that exist in the Luquillo Mountains.

Given the present state of knowledge about the distribution and abundance of organisms with elevation in the Luquillo Mountains, we are unable to determine whether a community-unit (Clements 1936), a continuum (Whittaker 1951, Curtis 1959), or another kind of model (e.g., the hierarchical continuum model; Collins et al. 1993, Hoagland & Collins 1997) is more appropriate. A null approach using species randomly placed in ecological space predicts the absence of distinctive community types and a peak in species richness at intermediate elevations (Willig & Lyons 1998, Hofer et al. 1999; Fig. 16). We propose to compare the empirical distribution of woody plants in the Luquillo Mountains to predictions from the null model as well as the other models indicated above. Repeated surveys over time allow the assessment of the spatial and temporal dynamics of species, an important factor in the hierarchical continuum and related models (Hoagland & Collins 1997). Measurements of primary gradients in parallel with vegetation sampling (Hypothesis 3B) will facilitate characterization of changes in ecological space along the elevational gradient.

Workplan - To begin our studies of climate, the distribution of plant and animal species, and ecosystem properties, we will initially focus on the least human-disturbed areas of the LEF (above 300 m elevation; Fig. 2c). Sampling locations along the elevational gradient will be placed at 100 m intervals in three principal watersheds, the Mameyes, Espiritu Santo, and Icacos, which represent the variation in geologic parent material in the LEF (Fig. 2b). Within each sampling location, individual plots will be placed on ridges, slopes, and in valleys to sample variation due to catena (ridge-slope-valley complex) position. Because catenas include streams and riparian zones, this approach will allow us to link terrestrial and aquatic research programs. The first phase of this new project, the establishment of plots along altitudinal gradients, the measurement of woody vegetation, and the establishment of climate stations at a subset of locations will begin in Year 2 of LTER 3. Data from the Luquillo Forest Dynamics Plot and preliminary sampling will be used to determine the appropriate plot shape and size to sample woody vegetation. Measurement of woody vegetation will include all stems > 1 cm DBH and will be conducted every six years to determine community dynamics and long-term growth patterns. Results from vegetation studies will be used to request funds from other sources to measure other key populations and communities. We will analyze three characteristics of species distributions: 1) patterns of species boundaries; 2) patterns of modes of species response curves; and 3) the hierarchical structure of species distributions (Collin et al. 1993, Hoagland & Collins 1997, Hofer et al. 1999).

To make predictions about the potential effects of disturbance on the vegetation of the LEF, we will develop a landscape dynamics model for the entire LEF starting from a relief sensitive gap model (FACET) and scaling it up to a cover-type based MOSAIC model (Acevedo et al. 1995, Acevedo et al. 1996, Urban et al. 1999). FACET will incorporate knowledge from previous gap models for the tabonuco forest (ZELIG by Pulliam, personal communication, and FORICO by Doyle [1982]) and existing data on forest dynamics and disturbance in the LEF (e.g. Crow 1980, Weaver 1991, Zimmerman et al. 1994,

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Boose et al. submitted). FACET will be expanded to include species response to soil water-logging and O2 (hypothesis 3B), and susceptibility to disturbance. Gradient space will be partitioned in many classes by combining several levels of each of the environmental factors (elevation, aspect, slope, soil water retention and fertility) and disturbances (hurricane intensity, frequency and directionality; landslides, treefalls, and drought). Physiological drivers (temperature, water, light) are incorporated via lapse rates (Meléndez-Colom 1999). Scaling-up will be accomplished by SEMAPAR (Acevedo et al., submitted) which will run FACET for each one of the gradient classes and determine MOSAIC parameters for each class. Time series of MOSAIC output maps for the entire LEF, under a variety of disturbance scenarios, will constitute a predictive integration of gradient (physical template and physiological drivers) and disturbance effects on patterns of community distributions in the entire LEF.

Hypothesis 3B: Variation in climate at higher elevations in the Luquillo Mountains affects patterns of soil carbon via effects on soil oxygen (Silver, Hall).

Rationale - Silver et al. (1999) have shown that soil O2 content provides a robust index linking climate with key biological resources in the soils of the LEF. As rainfall increases, soil O2 content decreases. This triggers several biogeochemical changes including 1) increased soil C content (Wang et al., submitted), 2) an increased proportion of the labile soil C pool (McGroddy & Silver 2000), 3) the potential for increased P availability due to Fe reduction, and 4) changes in soil bacterial communities from dominantly aerobic to a mix of aerobic and anaerobic communities, resulting in greater rates of methanogenesis and denitrification (Silver et al. 1999). Using a spatially explicit version of the CENTURY Ecosystem Model, Wang et al. (submitted) have shown also increased SOM content with increasing rainfall in the LEF, but the mechanistic components of the model are still not developed fully .

Workplan - The total soil organic C pool, soil C fractions, and monthly soil O2 concentrations and soil CO2 and CH4 efflux will be measured in a subset of plots established under Hypothesis 3A and compared to monthly measurements of soil microbial C along the elevation gradient. This will allow us to determine the degree to which, and the scale at which, these variables are interrelated as rainfall and temperature change along the elevational gradient. Using field data and the CENTURY model, we will develop stronger mechanistic links and incorporate soil O2 and associated biogeochemical cycling into the model structure. This will refine predictions of the soil chemical and physical properties along environmental gradients in the LEF, and determine the best indices to measure to determine spatial and temporal patterns of soil C dynamics.

Hypothesis 3C: Spatial variability in stream chemistry reflects watershed-scale patterns in biogeochemical processes (McDowell)

Rationale - Linkages between watershed biogeochemistry and stream chemistry are well documented following large-scale disturbances such as clear-cutting and wildfires in tropical watersheds (Malmer & Grip 1994, Williams & Melack 1997, Williard et al. 1997). In the Luquillo Mountains, we have shown that large-scale disturbance causes significant changes in stream chemistry over time (Schaefer et al. 2000). In addition to the temporal changes in stream chemistry associated with disturbance, we have also shown that there are consistent differences in nutrient losses among watersheds. For example, nitrate concentrations in the Mameyes drainage (Bisley watersheds) are typically double those of the Espiritu Santo drainage, and these differences persisted following Hurricane Hugo (Schaefer et al. 2000). These differences in concentration and flux occur despite similarities in elevation, runoff, vegetation, and bedrock in the two basins.

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We will use an empirical approach to test the hypothesis that differences in stream chemistry and flux among watersheds are related to patterns in biogeochemical processes across the terrestrial landscape. Using linear regression, nutrient losses in stream water will be related to the biogeochemical characteristics of the drainage basin. This sort of approach has been used recently to predict global riverine DOC fluxes from watershed soil C:N ratios (Aitkenhead & McDowell 2000), and nitrate concentrations from watershed N mineralization rates (Williard et al. 1997).

Workplan - Biogeochemical characteristics (soil chemistry, N mineralization rates, soil O2) will be sampled on three altitudinal transects (Mameyes, Espiritu Santo, and Icacos drainage basins) in support of Hypotheses 3A and 3B above. Stream chemistry will be sampled biweekly at 7 points between 300 and 900 m elevation (resulting in 7 sub-basins) along each altitudinal transect, with additional samples taken during periods of high flow. Samples will be analyzed for dissolved organic carbon, dissolved organic nitrogen, NH4+, NO3-, PO43-, Cl-, SO42-, base cations, and SiO2. Based on previous results (McDowell & Asbury 1994), we anticipate that seasonal variability in stream water chemistry will be minimal, but that for some elements (particularly Na+, Ca2+, Mg2+, and SiO2) large changes will be associated with changes in stream flow (McDowell & Asbury 1994). Nutrient fluxes will be calculated as the product of elemental concentrations and stream flow for daily time steps. For elements which are highly responsive to stream flow, regressions between concentration and flow will be used to estimate concentrations during days which were not sampled (McDowell & Asbury 1994). Each of our study watersheds has two or more long-term stream gauging stations, and stream flow will be estimated for ungauged sub-basins using previously published relationships between elevation, rainfall, and runoff for the Luquillo Mountains (García-Martino et al. 1996).

Hypothesis 3D: Boundaries of aquatic communities cannot be predicted by the same primary and secondary gradients associated with terrestrial organisms and stream chemistry because of geomorphic and human barriers to dispersal. (Crowl, Pringle, Covich, McDowell).

Rationale - Alterations of streams in their lower reaches can produce effects in upstream reaches on levels from genes to ecosystems (Pringle 1997). The dispersal of shrimps, fishes, and snails along stream corridors creates a critical functional linkage between tropical rivers and their estuaries. These linkages are naturally disrupted by geomorphic characteristics such as waterfalls which limit the spatial distribution of part of the fauna (Covich & McDowell 1996). Linkages are being further disrupted by small-scale damming and water abstraction during dry periods (March et al. 1998; Benstead et al. 1999). Model simulations estimate that the long-term mean daily entrainment mortality at a dam on the Espiritu Santo River ranges between 34% and 62% depending on estimates of the amount of water that is extracted from the river (Benstead et al. 1999). These research results have posed many new questions including: 1) to what extent are stream biota and associated ecological processes at high elevation a legacy of natural versus anthropogenic disturbances (hurricanes and droughts vs fishing, shrimp trapping, and downstream pollution)? 2) How have stream communities of the LEF been affected by natural (waterfalls) vs anthropogenic (dams) barriers along the stream continuum? 3) What are the effects of water withdrawals on shrimp and/or fish

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recruitment and how are these effects transmitted upstream? and 4) How can we apply our knowledge of downstream-upstream linkages to the development of management solutions to mitigate anthropogenic effects on stream communities?

Workplan - We will build upon research that we have conducted at stations established along the lower elevations of the Espiritu Santo and Mameyes (at ~300, 90 and 10 m.a.s.l.; **P**ringle and Blake 1994, March et al. 1998, March et al. dissertation in progress, Scatena et al. in preparation, Crowl and Scatena, in preparation) and add sites at higher elevations (500 and 700 m) adjacent to the terrestrial long-term study sites. Macrobiotic assemblages (fishes and shrimps) at each of these sites will be sampled each year using a combination of electroshocking, snorkeling and trapping. We will also measure canopy cover, water temperature, stream width, insect abundance, algal standing crop, and benthic organic matter at the same time. Water chemistry (major elements, inorganic nutrients, dissolved organic carbon and dissolved organic nitrogen) will be sampled intensively at the lower elevation sites in conjunction with higher elevation sites (Hypothesis 3C). Dams and natural barriers to migration (waterfalls) will be mapped, and rates of water abstraction and stream flow will be tabulated on a long-term basis. This long-term data set will provide us with a template for analysis of the effects of disturbances such as hurricanes, landslides, and pollution and spill events that might affect the abundance and diversity of stream biota. Parallel with our efforts to determine the impact of water withdrawals on drifting larval mortality (Benstead et al. 1999; March et al. in prep.), we will continue to quantify the effects of dams and water withdrawals on upstream shrimp migration using videography techniques developed during LTER 2. These data will be used to both determine the spatial and temporal variation of aquatic biota in a heavily human impacted watershed (Espiritu Santo) and a relatively unimpacted one (Mameyes), and to determine the effects of downstream barriers to long-term population dynamics.

SYNTHESIS

Our research program presents a critically designed array of studies linked by a simple conceptual model which views the biota in the context of ecological space defined by primary gradients of light, water, and nutrient availability. Disturbance affects the biota directly or indirectly via changes in the physical template or by changes in ecological space. Feedback is provided by the biota through trophic interactions and effects on primary gradients. This research program combines long-term monitoring with short- to long-term experiments designed to provide a mechanistic understanding of the interactions among disturbance, the biota, and primary gradients. Where field research does not directly address the issue of how disturbance influences the dynamics of LEF ecosystems and landscapes, this question will be initially approached using simulation models (Table 5). Models have been specifically chosen which best represent the components of the ecosystem under consideration, which accommodate well our conceptual model and which can be easily modified to take into account new monitoring data and experimental results. During the next phase of research we will solidify our understanding of the disturbance regime and the complex interactions among the biota in tabonuco forest that are, among other things, important in the response of the ecosystem to disturbance. A new research effort is directed at extending our understanding of disturbance and the biota to all forest communities in the LEF, thus positioning our research program to become the first to fully describe tropical montane forest in a manner that integrates population, community, biogeochemical, and landscape perspectives.

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LITERATURE CITED

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SITE MANAGEMENT

Site management of the LEF-LTER will continue in a manner similar to LTER 1 and 2 (Fig. 23). Changes in personnel have resulted in some refinements as to how the program is lead. Robert Waide, who was lead-PI for the program in LTER 1 and 2, has left UPR but will continue as a Co-PI. In his place, Jess Zimmerman (with the LEF-LTER since 1991 and PI since 1994) is now lead-PI and guides the program on a day-to-day basis. Also, Fred Scatena has stepped down as signatory PI and has been replaced by D. Jean Lodge. Lodge has been with the LEF-LTER since its inception. Ariel Lugo remains as signatory PI.

During LTER 3, Zimmerman, Lugo, and Lodge will guide the program as an Executive Committee (EC) with the participation of two other rotating members chosen from among the Co-PI's at mainland institutions. The decision to include off-island collaborators on the Luquillo EC was made so that they would have more influence on decision making in the program. Each rotating member will have a term of two years and will be chosen by the extant EC. Rotating members will meet with the rest of the EC at bi-annual investigator meetings (see below) and at two other times during the year.

The Executive Committee is aided by a National Advisory Committee (NAC). Currently, this committee is composed of Julie Denslow, Richard Wiegert, and John Porter.

Investigators in the LEF-LTER will meet twice during the year to review research progress, consider new research opportunities, and to discuss management issues related to the site. January meetings will include only signatory PIs and Co-PIs and will be devoted to assessing research progress and site management with the aide of the Advisory Committee. A second meeting will be held each summer and will be devoted entirely to research reports, focusing primarily on the participation of graduate and undergraduate students.

Associate researchers (Table 3) provide critical added expertise and data to the LEF-LTER monitoring program. Beginning in LTER 3, Associates will be provided seed funds (materials or travel) to continue their participation. Funds will be awarded on an annual basis by the EC on a competitive basis.

Research is coordinated through the El Verde Field Station (UPR) and Sabana Field Station (USDA-FS) near the Bisley Experimental Watersheds. Elvia Melendez-Ackerman is Director of El Verde and coordinates administration of this facility. Fred Scatena will continue to coordinate research activity at the Bisley Experimental Watersheds.

DATA AND INFORMATION MANAGEMENT SYSTEM

The Data and Information Management System at the LEF-LTER made research results available to other scientists, policy makers, and the general public in a timely manner and with sufficient accompanying information (metadata) so as to optimize their utility. Data Management at the LEF-LTER is guided by Eda Melendez with the assistance of two data entry technicians. Data Management at Luquillo has profited greatly from the assistance of John Porter, a member of the National Advisory Committee.

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During LTER 2, the Luquillo Data Management group has had 10 principal tasks: 1) acquire and implement new hardware and software for data management; 2) acquire existing long-term data sets from other projects or agencies; 3) identify, document, archive, and update LTER data sets; 4) enter data; 5) perform quality control on data entry; 6) manipulate data; 7) fill requests for data from LTER and non-LTER scientists; 8) maintain inventories of data sets and publications; 9) implement a web-based program to provide data services to interested parties, and 10) document their activities in reports and presentations. .The protocols established since 1991 for filing, managing, and requesting data from the LEF-LTER site are accessible on our Web site at http://www.sunites.upr.edu/sunceer/datamng/division.htm. To date, 115 LTER data sets have been file with Data Management , 83 of which are documented with the standard LUQ LTER documentation forms. Additional 98 data sets from non-LTER studies are relevant to the LTER program and are catalogued separately. The most recent ones are documented with our standard documentation forms. The data base for the LTER therefore contains 215 data sets. In LTER 1 & 2 we received a total of 247 data requests from LTER and non-lTER people.

Several types of data archived by LEF-LTER present special challenges, because of size, complexity, or nature of the data, and because they may be added to sequentially by different LTER investigators. These include animal populations, plant spatial distribution and growth, rain and stream water chemistry, meteorological records, and remotely sensed imagery. In each of these cases the investigators in charge must work closely with Data Management in the maintenance of data utility. Besides the data itself, long term archives of water samples and soil and plant material are maintained for addressing research questions that have not yet been posed.

The activity of archiving data and its corresponding metadata is an on-going project. A manual that contains all the protocols, forms, and guidelines to file data sets and publications with Data Management has been published in our annual reports and on our web page (http://luq.lternet.edu/datamng/imdocs/division.html), and the data sets and publications lists are updated regularly. These guidelines were originally intended as an aid to assist off-island scientists, but more generally, they have been used to stimulate the communication between the data manager and the investigator. This communication has been eased substantially by the facilities provided by the Internet including our web page, where all the forms, data management protocols are made available to the Investigator without direct intervention of the Data Manager.

In order to include their data sets in the official LTER Data Catalog (which is published in our reports and on our Web site), the investigators must file the documentation forms with Data Management. A committee of LEF-LTER investigators recently reviewed all metadata for the LEF-LTER data sets, identifying incomplete or incorrect information and sent notifications to individual researchers. This process will soon be reviewed to ensure that all investigators have replied.

The use of the Luquillo web site is now essential in developing mechanisms to facilitate the contribution of the investigators to the LTER Data Bases. The contributions are made as a separate data files and are available on the Web as downloadable files (most commonly in ASCII format). If the data are not made readily available for other users, a description of the data posted in our on-line Catalog along with its metadata. Data Management is currently entering metadata for the data that were catalogued before the development of the on-line documentation forms (available at: http://luq.lternet.edu/datamng/imdocs/division.html

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The Data Manager is involved in the design of those projects for which Data Management provides data entry services. At the present, Data Management collaborates in seven projects that involve data entry for 14 data sets, the bibliography on the Web, and project specific species lists. At the beginning of a project ,the investigator and the Data Manager meet to discuss the data file structure as well as the software to be used for the entry of the data to produce an output suitable for the analysis of the data. The involvement of the Data Manager is greater at the beginning of the project since she designs the procedures and trains Data Entry Technicians in data entry, quality control and report preparation. On certain occasions, the investigator requests the data in a special format which requires the intervention of the Data Manager since programming or a knowledge of sophisticated computational methods may be required.

A data management protocol developed at the LEF-LTER in 1992 provides guidelines to the investigators at our site for making the data available to other researchers. Meteorological data are available on the Web and updated annually for the El Verde and Bisley weather stations. For other projects, investigators are required to provide their meta-data initially to Data Management, and to make the data itself available after QA/QC review and within two years for each of their data sets. Since the LTER Catalog is updated annually, any new data sets are made available to the general public on our Web site at that time. In the event of an external request for data not yet published, a form is available to the requester (on the Web at: http://luq.lternet.edu/datamng/datareq.asc). The Data Manager then obtains direct written authorization, either from the investigator or from the LTER PI to release the data. To date, all the special requests received by Data Management have been approved for release.

OUTREACH

Educational Activities - The LEF-LTER is participating in education at the K-12 levels in two ways. We have established a Schoolyard LTER program in Puerto Rico involving teachers at six high schools. Expanding on a program established by the USDA Forest Service at two rural high schools, the additional four schools will form a network that adds two rural and two urban schools. The focus of the activities will be on factors that affect water quality and quantity, and the role of forests in maintaining both of these ecosystem services. An additional focus of the urban schools will on the effect of urban forests on local climate. As part of this program, schools are provided with materials to establish their own weather stations. Each school also will have research programs associated with their own nearby forests or streams. Teachers are given guidance in curriculum development and research goals at weekend retreats at El Verde Field Station. LEF-LTER researchers provide workshops on research projects in the classroom and at field localities and teachers are instructed in data management techniques. Supplemental NSF LTER funding will provide Internet connections to schools that do not already have them so that schools can easily share data collected at each of their sites. Yearly symposia are planned where teachers and students from the network of schools will come together to share the results of their individual programs.

A second outreach program directed at K-12 students is being conducted in collaboration with the Center for Educational Technologies (CET), Wheeling Jesuit University in West Virginia. LEF-LTER researchers are assisting CET in the development of interactive software for middle school students that will teach students the ecology of the rain forest in the LEF. This software development builds on CET's experience developing the NASA Classroom of the Future. Seed funding for project was obtained through a SGER grant obtained by CET. The new program will consider the impacts of hurricanes, and teaching students the basic ecology of the main groups of fungi, plants, and animals in the forest. Focusing on life history variation and trophic interactions among species, students will investigate the impacts of hurricanes on individual study organisms by collecting their own data and then comparing it to long-term data maintained by LEF-LTER data management. Then, combining their data sets, the students will assess the impact and recovery of the entire rainforest system as a group. Progress to date has included the identification of critical components to be developed in this program and the use of coqui frog population dynamics as a first subject.

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The Howard Hughes Program at Texas Tech University has supported 13 undergraduate students (5 female and 4 Hispanic) who participated in ecological research assessing effects of disturbance on invertebrate populations and communities in a spatially explicit fashion. Both Puerto Rican and mainland students first went to the Texas Tech campus for orientation and methodological training, and then spend between 12 and 15 weeks doing research in the Tabonuco forest at LEF-LTER.

Local activities - The LEF-LTER has been instrumental in the management and monitoring of the lower Mameyes River, the largest unregulated river draining the LEF. The Puerto Rico Water Company (PRWC) had intended to dam the lower Mameyes and install a water intake that would frequently reduce water flow to levels below those in the long-term record. Research by LTER investigators indicated this would impede the migration of shrimp and fish along the river corridor, and that low water levels would allow water with abnormally high salinity to enter the lower river basin. In response to these results, the PRWC redesigned the water intake such that waters are withdrawn from the hyporheic zone without the use of a dam, and agreed not to reduce water flow to below the natural minimum levels. Modeling studies (Scatena and Johnson, 2000) indicated that this design would have mimimum impact on shrimp and fish populations and would maintain normal salinity levels in the lower basin. LEF-LTER researchers continue to participate in a monitoring program aimed at assessing the impacts of water withdrawals on the stream ecosystem.

Ariel Lugo and John Thomlinson continue to serve on the Science Technical Advisory Committee for the Federal San Juan Bay Estuary Program. This committee is currently reviewing a Comprehensive Conservation and Management Plan, various long-term monitoring activities, and the results of all the studies conducted as part of the program. Jess Zimmerman, Fred Scatena and John Thomlinson have participated in activities of the Eastern Ecology Coalition, a grass-roots environmental group in eastern Puerto Rico. Fred Scatena continues to consult with local government groups on issues related to public water supply in Puerto Rico.

International activities - Our Data Manager has participated in two symposia of the Latin American International LTER Network. Her presentations were directed at the development of data management systems in a tropical setting. A copy of her presentation can be found at http://luq.lternet.edu/datamng/ilter/sld001.htm

Mike Willig, as a member of the Steering Committee of Conservation International for "Assessing and Monitoring the Status of Biodiversity in Tropical Forest Habitats" has participated in workshops to develop a global network of tropical field sites and to validate models for assessing threats to biodiversity.

BUDGET (not on-line)

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LEF-LTER Proposal 2000: Figures

Descriptions:

Fig. 1. Vegetation types of the Luquillo Experimental Forest showing the location of two major research areas, El Verde and Bisley.

Fig. 2. The physical template of the LEF: a) elevation; b) geology. ES, MA, and IC denote focal watersheds. Landscape patterns of disturbance in the LEF: c) forest cover in 1936 (Foster et al. 1998), and d) cumulative hurricane exposure between 1886 and 1996 (Boose et al.1994; Boose et al., in prep.).

Fig. 3. Legacies of human disturbance in the LEF. a) Data from a small plot study conducted at three sites (BS=Bisley, EV=El Verde, and CB=Cubuy) showing variation in forest composition among three land uses circa 40 years hence (Zimmerman et al. 1995); b) The 16 ha Luquillo Forest Dynamics Plot at El Verde showing the replacement of tabonuco (*Dacryodes excelsa*) by

Casearea arborea in the northern (upper) portion of the plot. Information indicates that this area was clear-cut in the 1920=s (Thompson et al., submitted).

Fig. 4. Distribution of hurricane impacts to Puerto Rico between 1886 and 1996 (Boose et al., submitted; see http://www.lternet.edu/hfr/research/region/hurrican.htm). Data are the number of storms exhibiting damaging winds at least a strength of F2 on the Fujita scale.

Fig. 5. a) Hurricanes affecting the LEF since 1988, and b) the impacts of wind on litterfall at the Bisley research area.

Fig. 6. Recurrence interval of droughts in the LEF and impacts to flora, fungi, and fauna.

Fig. 7. Five year summary of the effects of Hurricane Hugo on various groups of plants and animals and ecosystem processes (Zimmerman et al. 1996).

Fig. 8. The effects of Hurricanes Hugo and Georges on stream chemistry in one monitored stream (Bisley 3). Upper pair of panels show increases in nitrate and potassium concentrations following Hurricane Hugo (September 18, 1989; Schaefer et al. in press). The middle pair of graphs show the same ions for six months following Hurricane Georges. The lower pair of graphs show changes with both ions plotted against one another to show variation in ecological space experienced by stream organisms following a hurricane.

Fig. 9. Changes in the mean density of adult *Euletherodactylis coqui* in four 400 m^2 plots located at El Verde and Bisley in response to Hurricanes Hugo and Georges. Frogs increase in density because of the increased cover provided by hurricane debris. Less of this debris was produced during Hurricane Georges than during Hugo (X. Zou, unpublished data, L. Woolbright, personal observation).

Fig. 10. Changes in tree abundance on the Luquillo Forest Dynamics Plot from 1989 to 1996.

Fig. 11. Flowchart of spatial modeling of soil organic carbon (SOC) in the LEF. This diagram illustrates the intercorporatoin of a topographically-related climate model (TOPOCLIM, Wooster 1989), a forest Gross Primary Production model (TOPOPROD, Marley 1998), and a soil carbon model, CENTURY (Parton et al. 1987, 1988, Sanford et al. 1991). These models are integrated with a GIS (IDRISI) to simulate the distribution of SOC storage and fluxes over the entire LEF.

Fig. 12. Stream pools available to shrimp (*Atya lanipes*) in the lower Mamayes River, estimated using historical stream flow data, under differing schemes of water level management (Scatena and Johnson, in press). Q95 and Q99 refer to flow exceedence: Q95 is the stream flow that is exceeded 95% of the time and Q99 is the flow exceeded 99% of the time.

Fig. 13. Changes in aboveground litter production as a function of elevation in the LEF. Data are from Weaver and Murphy 1986, Zou et al. 1995, Scatena et al. 1996 and primarily Silver et al., submitted.

Fig. 14. Guiding questions for research in the Luquillo LTER.

Fig. 15. Central model for the Luquillo LTER showing the relationship between disturbance, physical template, primary gradients of water, light, and nutrients (abiotic factors), and the biota.

Fig. 16. A schematic example showing how geographical space can be interpreted in ecological space to make a prediction concerning changes in species richness with ,mlelevation. L and M refer to light and moisture levels, respectively and S refers to species richness.

Fig 17. Long-term rainfall and streamflow data for the Bisley Watersheds and the Mameyes River showing major weather events during the period.

Fig. 18. Data on arthropod abundances collected monthly since Hurricane Georges (September 1998) showing the interaction between sites differing in human disturbance and canopy status (Klawinski, unpublished). Areas of little human disturbance were selectively logged as late as the 1940's while coffee and clear-cut areas were abandoned in the 1920's. Arthropods are sampled using pitfall traps, malaise traps, and blacklights. Data are pooled numbers for the 6 most common taxa (Hymenoptera, Diptera, Acari, Homoptera, Collembola, Coleoptera).

Fig. 19. Interpretation of the overarching model described in the Theoretical Foundations applied to guiding questions of the Luquillo LTER (Fig. 14) which will be continued under Research Theme 1; a) What is the spatial and temporal distribution of disturbance types? and b) What is the role of the biota in the response to disturbance? This theme focuses on specific hypotheses related to hurricane and human disturbance.

Fig. 20. Research Theme 3 considers the influence of elevation (geophysical template) on primary factors (light, water, and soil nutrient availability) on the distribution of organisms. Long-term monitoring and models are directed at incorporating effects of disturbance on the LEF landscape.

Fig. 21. Management scheme for the Luquillo LTER program.

Fig. 22. Research Theme 3 considers the influence of elevation (geophysical template) on primary factors (light, water, and soil nutrient availability) on the distribution of organisms. Long-term monitoring and modeling incorporate effects of disturbance on the LEF landscape.

Fig 23. Management scheme for the Luquillo Experimental Forest LTER

Figures:

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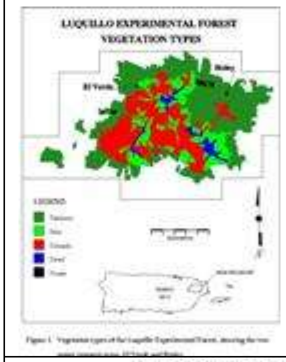

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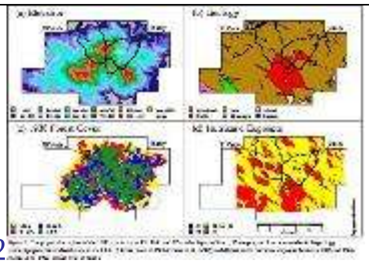

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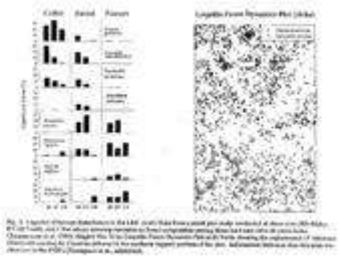

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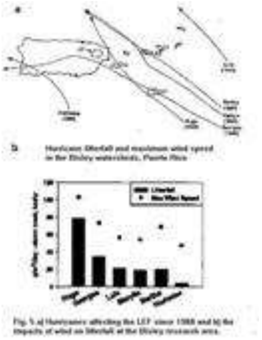

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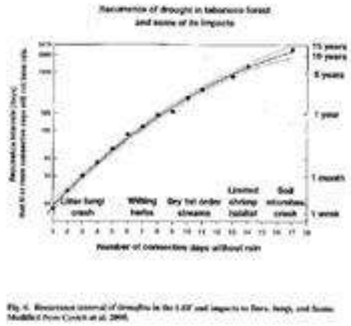

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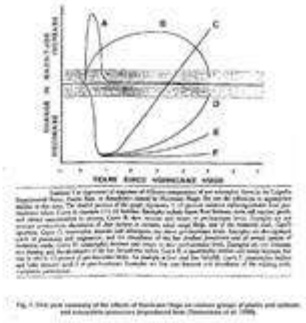

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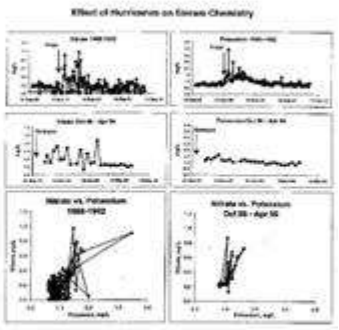

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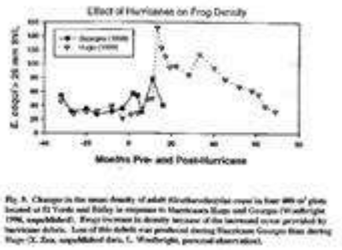

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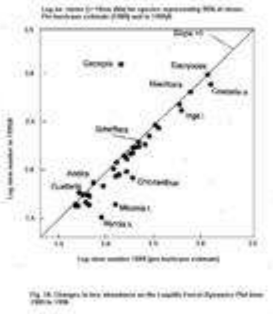

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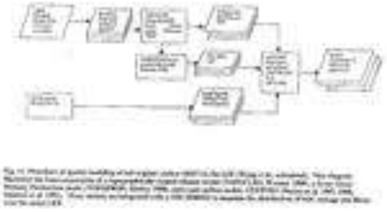

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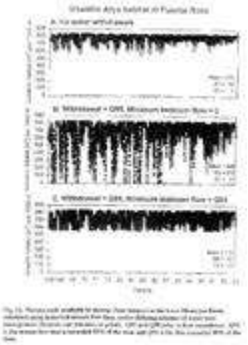

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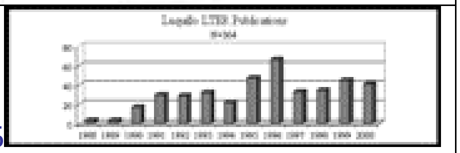
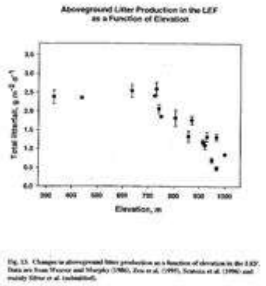
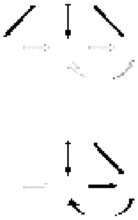
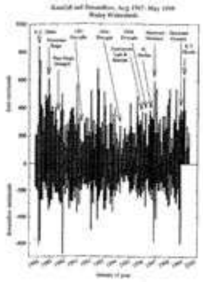
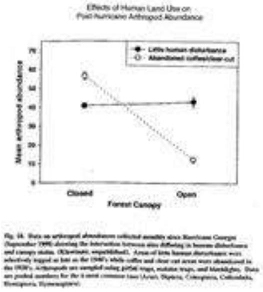
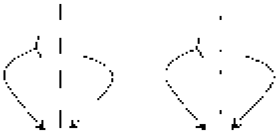
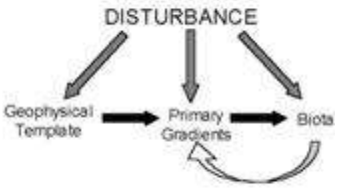
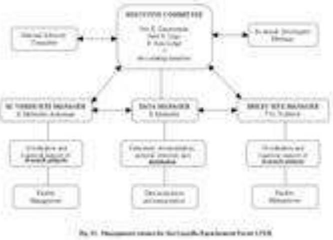


		
 16	17 	18 
19 	20 	21 
 22	23 	

LEF-LTER Proposal 2000: Tables

Table 1. Research Themes to Be Addressed in LEF-LTER 3.

Table 2. Participants in LTER 3. PI=s have responsibility for directing the research program as part of an Executive Committee (EC) comprising the PIs and two Co-PIs. Co-PI=s will serve two year terms on the EC and will be chosen by the PI=s (see Site Management). Co-PI=s are funded

directly from the core grant. Unless otherwise indicated, PI=s and Co-PI=s have been with the LEF-LTER program since its inception.

Table 3. Summary of long-term experiments established in the LEF that will be continued by LTER researchers. Experiments in bold are discussed in the text.

Table 4. Description of species removed from landslides and their potential for facilitating and arresting primary succession.

Table 5. A summary of models to be employed for synthesizing results of monitoring and experiments in LTER 3.

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Table 7. Tree species selected for detailed study of ecological characteristics and for modelling of community dynamics. species were chosen by their combined relative abundances on the Luquillo Forest Dynamics Plot before and after Hurricane Hugo. Life history grouping is based on Zimmerman et al. (1994).

Table 8. Affiliations of scientists involved in LTER 3

Tables:

Table 1. Research Themes to Be Addressed in LEF-LTER 3.

Research Theme 1:	**Cumulative Effects of Disturbance – Hurricanes Hugo and Georges and Legacies of Human Land Use (Continuation of LTER 2)**
Research Theme 2:	**The Role of the Biota in Controlling Community and Ecosystem Processes that Affect Nutrient Availability and Organic Matter Processing**
Research Theme 3:	**The Influence of Climate and Physical Constraints on the Distribution and Abundance of Organisms and Related Ecosystem Processes in the Luquillo Mountains**

Table 2. Participants in LTER 3. PI's have responsibility for directing the research program as part of an Executive Committee (EC) comprising the PIs and two Co-PIs. Co-PI's will serve two year terms on the EC and will be chosen by the PI's (see Site Management). Co-PI's are funded directly from the core grant. Unless otherwise indicated, PI's and Co-PI's have been with the LEF-LTER program since its inception.

	Participant	Present Affiliation	Specialty	Years of Tropical Experience
PIs	J. K. Zimmerman*	University of Puerto Rico	Plant ecology	15
	A.E. Lugo	Int. Inst. Tropical Forestry, USDA FS	Ecosystem analysis, nutrient cycling	40
	D.J. Lodge	Forest Products Lab, USDA FS	Nutrient cycling, fungal systematics	18
Co-PI’s	G. Belovsky***	Utah State University	Population and ecosystem modeling	0
	N. Brokaw	Manomet Observatory	Regeneration patterns, disturbance	27
	A. Covich	Colorado State University	Stream ecology	24
	T. Crowl*	Utah State University	Stream ecology	12
	C. Hall	SUNY-ESF	Modeling, stream ecology	14
	D. Herbert	University of Puerto Rico	Ecosystem dynamics, modeling	18
	W. McDowell*	University of New Hampshire	Soil solution chemistry	18
	E. Melendez	University of Puerto Rico	Data management	12
	E. Melendez-Ackerman**	University of Puerto Rico	Plant population biology	14
	C. Pringle**	University of Georgia	Stream ecology	18
	A. Sabat*	University of Puerto Rico	Population ecology, modeling	18

	F. Scatena	Int. Inst. Tropical Forestry, USDA FS	Geomorphology	13
	W. Silver*	University of California - Berkeley	Decomposition, productivity	19
	J. Thompson**	University of Puerto Rico	Forest ecology	13
	J. Thomlinson*	University of Puerto Rico	Landscape ecology, GIS	7
	D. Vogt*	Yale University	Nutrient cycling	11
	K. Vogt*	Yale University	Ecosystem dynamics, decomposition	11
	R. Waide	University of New Mexico	Avian ecology	29
	L. Walker	University of Nevada – Las Vegas	Succession, primary production	16
	M. Willig	Texas Tech University	Ecology and behavior of bats, invertebrates. functional diversity	24
	L. Woolbright	Siena College	Ecology and behavior of frogs	28
	X. Zou*	University of Puerto Rico	Soil and earthworm ecology	11

*Joined the program during LTER 1

**Joined the program during LTER 2

***Joining the program in LTER 3

Table 3. Summary of long-term experiments established in the LEF that will be continued by LTER researchers. Experiments in bold are discussed in the text.

Experiment	Researchers	Goals	Funding	Citations

(Initiation Date)			source	
Controls on Primary Productivity (1989-90)	X. Zou, J. Zimmerman D.J. Lodge	Describe interactive effects of nutrient availability and hurricane disturbance on productivity in tabonuco and cloud forest.	NSF-CREST, NSF-LTER, NSF (pending).	Zimmerman et al. (1995), Walker et al. (1996)
Effect of wood decomposition on soil organic carbon (SOC; 1998)	D.J. Lodge	Compare SOC and N-availability under logs felled by Hurricanes Hugo and Georges	USDA Forest Service	Zimmerman et al. (1995)
Experimental Forest Biomass Removal (1989)	W. Silver F. Scatena	Describe experimental removal of forest biomass and hurricane disturbance on soil nutrient pools.	USDA Forest Service, NSF-LTER	Silver and Vogt (1994), Silver 1996
Experimental Treefalls (1995)	F. Scatena	Describe the effect of treefall gaps on dynamics of understory vegetation	USDA Forest Service	
Riparian wood decomposition (Hypothesis 1B-1995)	D., K. Vogt, A. Covich J. Lodge F. Scatena	Measure effects of coarse woody debris on linked terrestrial - stream ecosystem processes.	NSF and NSF-LTER	Zimmerman et al. (1995), Vogt et al. (1996)
Food Web Exclosures (Hypothesis 2A-1999)	R. Waide M. Willig	Describe impacts of secondary consumers on arthropod communities, herbivory, and litter decomposition	NSF-LTER UPR	Reagan and Waide (1996)
Earthworm Exclosures (Hypothesis 2D - 1998)	X. Zou	Describe the effects of experimental removal of earthworms on litter decomposition and soil phosphorus dynamics	NASA, NSF-LTER	
Removal of Landslide Pioneer Vegetation	L. Walker	Describe impacts of removing colonizing vegetation in landslides	NSF-LTER	Walker et al. (1996)

(Hypothesis 2E - 1997)		on soil characteristics		

Table 4. Description of species removed from landslides and their potential for facilitating and arresting primary succession.

Species	Landslide location	Potential Facilitative Effects	Potential Arresting Effects	References
Climbing Ferns *(Gleichenia bifida*, *Dicranopteris pectinata*)	Upper portion (exposed mineral soil)	Promote tree seedling germination	Retard tree seedling and sapling growth	Walker (1994), Russell et al. 1998
Tree ferns *Cyathea arborea*	Upper portion (exposed mineral soil)	Improve SOM	Sequester important nutrients	Vitousek et al. (1995), Walker et al. (1996)
Woody pioneer shrubs/trees/herbs *Cecropia schreberiana* *Pyschotria bertieriana* *Solanum torvum* *Phytolacca rivinoides*	Lower portion (forest floor high in SOM)	Shade, improve soil nutrient availability and SOM	Competition for light and nutrients.	Walker et al. (1996)

Table 5. A summary of models to be employed for synthesizing results of monitoring and experiments in LTER 3.

Model	**Researchers**	**Application**	**References**
SORTIE	Canham, Brokaw, Thompson,	Hypothesis 1A: Use patterns of crown damage	Pacala et al. (1993, 1996)

	Fetcher, Haines	and recovery, sapling light-growth response curves, and seedling shadows to predict dynamics of key tree species in response to hurricane disturbance.	
MEL	Herbert, Zimmerman	Hypothesis 1D: Determine dynamics of forest communities in soils with contrasting nitrogen content	Rastetter et al. (1997), Herbert et al. (1999)
Trophic interactions and limiting nutrients	Belovsky, Waide, Willig, Covich, Crowl	Hypotheses 2A,B: Address how consumers impact nutrient cycling that limits plant production	DeAngelis (1992), Belovsky and Slade, submitted
ZELIG, MOSAIC	Acevedo, Melendez, Thomlinson	Hypothesis 3A: Address the role of disturbance in landscape dynamics of LEF forests.	Doyle (1982), Acevedo et al. (1995, 1996)
CENTURY	Hall, Silver, McDowell	Hypothesis 3B, C: Address mechanistic links between soil O_2 levels, soil biogeochemistry, and stream chemistry.	Sanford et al. (1991), Wang et al. submitted

Table 6. Summary of long-term experiments established in the LEF that will be continued by LTER researchers. Experiments in bold are discussed in the text.

Experiment (Initiation Date)	Researcher(s)	Goals	Funding source	Citations
Controls on Primary Productivity (1989-90)	X. Zou, J. Zimmerman J. Lodge	Describe interactive effects of nutrient availability and hurricane disturbance on productivity in tabonuco and cloud forest.	NSF-CREST, NSF-LTER, NSF (pending).	Zimmerman et al. 1995, Walker et al. 1996
Experimental Forest Biomass Removal (1989)	W. Silver F. Scatena	Describe experimental removal of forest biomass and hurricane disturbance on soil nutrient pools.	USDA Forest Service, NSF-LTER	Silver and Vogt 1994, Silver 1996

Experimental Treefalls (1995)	F. Scatena	Describe the effect of treefall gaps on dynamics of understory vegetation	USDA Forest Service	
Riparian wood decomposition (Hypothesis 1B – 1995)	D., K. Vogt, A. Covich J. Lodge F. Scatena	Measure effects of coarse woody debris on linked terrestrial - stream ecosystem processes.	NSF and NSF-LTER	Vogt et al. 1996
Earthworm exclusion (Hypothesis 2B – 1997)	X. Zou	Describe the effects of experimental removal of earthworms on litter decomposition and soil phosphorus dynamics	NASA, NSF-LTER	
Food Web Exclosures (Hypothesis 2C – 1999)	R. Waide M. Willig	Describe impacts of secondary consumers on arthropod communities, herbivory, and litter decomposition	NSF-LTER UPR	
Removal of Landslide Pioneer Vegetation (Hypothesis 2E – 1997)	L. Walker	Describe impacts of removing colonizing vegetation in landslides on soil characteristics	NSF-LTER	

Table 7. Tree species selected for detailed study of ecological characteristics and for modelling of community dynamics. species were chosen by their combined relative abundances on the Luquillo Forest Dynamics Plot before and after Hurricane Hugo. Life history grouping is based on Zimmerman et al. (1994).

Species	**Life History**
Alchornea latifolia	Nonpioneer
Buchenavia capitata	Nonpioneer
Casearia arborea	Nonpioneer
Cecropia schreberiana	Pioneer
Cordia borinquensis	Nonpioneer

Dacryodes excelsa	Nonpioneer
Guarea guidonia	Nonpioneer
Inga laurina	Nonpioneer
Manilkara bidentata	Nonpioneer
Matayba domingensis	Nonpioneer
Prestoea montana	Nonpioneer
Schefflera morototoni	Pioneer
Sloanea berteriana	Nonpioneer
Tabebuia heterophylla	Nonpioneer

Table 8. Scientists associated with the Luquillo LTER program. These scientists contribute to the program with complementary research studies. These individuals are not funded from the core grant, except for seed funds (see Site Management).

Participant	Present Affiliation	Specialty
C. Canham	Institute for Ecosystem Studies	Forest ecology, modeling
Ned Fetcher	Scranton University	Light dynamics, carbon gain
R. Edwards	Retired	Spider systematics and ecology
M. Gannon	Penn State - Altoona	Ecology of bats
B. Haines	University of Georgia	Nutrient cycling in plants
P. Klawinski	University of Puerto Rico	Insect population ecology
H.T. Odum	University of Florida	Ecosystem studies,

		modeling
B. Richardson	Retired	Insect systematics and ecology
J. Sharpe	No present affiliation	Fern ecology
Tim Schowalter	Oregon State University	Plant-insect interactions
J. Wunderle	Int. Inst. Tropical Forestry, USDA FS	Avian ecology

Table 9. A summary of models to be employed for synthesizing results of monitoring and experiments in LTER 3.

Model	Researchers	Application	References
SORTIE	Canham, Brokaw, Thompson, Fetcher, Haines	Hypothesis 1A: Use patterns of crown damage and recovery, sapling light-growth response curves, and seedling shadows to predict dynamics of key tree species in response to hurricane disturbance.	Pacala et al. 1993, 1996
Trophic interactions and limiting nutrients	Belovsky, Waide, Willig, Covich, Crowl	Hypotheses 2A,B: Address how consumers impact nutrient cycling that limits plant production	DeAngelis 1992, Pastor and Cohen 1997, Belovsky and Slade submitted
Sierra Palm	Sabat	Hypotheses 3A, B: Predict the distribution of palm populations based in the LEF based on history of hurricane disturbance and soil conditions.	Sabat, submitted

ZELIG, MOSAIC	Acevedo, Melendez, Thomlinson	Hypothesis 3A: Address the role of disturbance in landscape dynamics of LEF forests.	Doyle 1982, Acevedo et al. 1995, 1996
CENTURY	Hall, Silver, McDowell	Hypothesis 3B, C: Address mechanistic links between soil O_2 levels, soil biogeochemistry, and stream chemistry.	Sanford et al. 1991

Methods:

LEF-LTER Proposal 2000: Methods

Riparian Studies
Research Theme 1:

- **Hypothesis A**
- **Hypothesis B**
- **Hypothesis C**
- **Hypothesis D**

Research Theme 2:
- **Hypothesis A**
- **Hypothesis B**
- **Hypothesis C**
- **Hypothesis D**
- **Hypothesis E**

Research Theme 3:
- **Hypothesis A**
- **Hypothesis B**
- **Hypothesis C**
- **Hypothesis D**

METHODS
Research Theme 1: Cumulative effects of Hurricane Hugo and Georges and Legacies of Human Disturbance

Hypothesis 1A:

"Census of the Luquillo Forest Dynamics Plot (LFDP)" Jill Thompson
The census will follow standard Center for Tropical Forest Science (CTFS) methods for the international network of large forest plots (Condit 1998). All free standing woody stems ?1 cm

D130 will be measured for diameter, identified and mapped to 0.5 m within each 5 m x 5 m subplot in the 16 ha Forest Dynamics Plot. Our method is slightly modified as we tag all stems on multiple stemmed individuals while CTFS only requires one tag per individual woody plant. All stems tagged in the previous censuses will be located by tag number, and all new stems which have grown since the last census will be tagged with an aluminum number tag. Data on stem and species survival, mortality, growth and recruitment will be calculated in relation to soil type, previous land use history and the distribution of damage from Hurricanes Hugo and Georges.

In 150, 1 m x 2 m seedling plots in the LFDP all seedlings with stems ?10 cm in height and ? 1 cm D130 will be tagged and measured for height and root collar diameter. The growth, mortality and survival of these seedlings will be assessed in relation to parent tree distribution, soil type, previous land use history and the distribution of damage from Hurricanes Hugo and Georges.

Hypothesis 1C:

"The reforestation of tropical pastures will lead to an increase in surface soil carbon derived from forest vegetation, but this will be offset by a loss of pasture soil carbon from deeper soil depths. Over time, the amount of soil carbon lost from the previous land use will approximate the amount of soil carbon gained through reforestation." Whendee Silver, Ariel Lugo.

Methods will follow Silver et al (in review) who estimated the rate of C accumulated following reforestation at one site in the LEF. We will use two sets of chronosequences of secondary forest recovering from pasture and current pasture within and near the LEF, where the land use history, plant species composition, and aboveground biomass have been well documented (Aide et al. 1995, Zimmerman et al. 1995). Eight sites ranging from 1 to 80 years since abandonment will be selected along each chronosequence, and paired with a pasture of approximately the same age. At each site, we will excavate five 0.5 x 0.5 x 1 m depth soil pits and collected two quantitative soil cores at 10 cm depth increments. One core will be used to estimate bulk density and the second will be used for total C and C isotope analyses.

Cores for bulk density will be dried at 105 ^{o}C and weighed to determine mass per unit volume. Soils for C analyses will be ground to a fine powder. Previous analyses with 5 % HCl have indicated no evidence of carbonates in this area. Triplicate 45 mg subsamples will analyzed for d ^{13}C on an Europa 2020 continuous-flow mass spectrometer at U.C. Berkeley. The C isotope ratio will be expressed in d units relative to a PDB standard such that the d ^{13}C = ($R_{sample} – R_{standard}$) x 1000.
We will estimate the proportion of C_3- and C_4-C in the soil using a modified version of the standard mixing equation proposed by Vitorello et al. (1989):

Equation 2:

% C_4 = (d - d $_L$ / d $_g$ - d $_L$)*100
% C_3 = 100 - % C_4

Where d = the d ^{13}C of the soil sample, d $_L$ is the d ^{13}C of a composite sample of forest litter and roots, and d $_g$ is a composite sample of pasture grass. The percentages of C_3- and C_4-C will then be multiplied by the total C pool to estimate the proportion of C derived from the forest or pasture by depth. Values will be corrected for bulk density by depth (Veldkamp 1994). We will estimate a net rate of C accumulation or loss following reforestation as the difference in the C pools in the reforested sites by depth and the adjacent pasture.

(Return to Outline)

Research Theme 2: The Interactive Roles of Disturbances and the Biota in Controlling Community and Ecosystem Processes (e.g., Nutrient Availability and Organic Matter Processing)

Hypothesis 2A:

"Consumer populatins in tabonuco forest are limited by predation. Exclusion of predators will have cascading effects on the abundance of detritivores and rates of decomposition." Paul Klawinski

Because rates of litter decomposition can be significantly increased by the presence of micro- and macro-arthropods (Heneghan et al. 1998, 1999), we propose to examine the cascading effect of top predators on arthropod detritivores and rates of leaf litter decomposition. We have established 32 exclosures, 3.3 m in length, width and approximate height, which have been distributed over eight spatial blocks in tabonuco forest with a history of little human disturbance. Each exclosure is covered with 1 cm square plastic mesh which preliminary studies showed excluded all Anolis lizards and Eleutherodactylus frogs except juvenile Eleutherodactylus size classes. Each block contains an open control (to test for the effect of added understory structure caused by the exclosures) and four exclosures: Closed Control (netted exclosure with field densities of Anolis and Eleutherodactylus); Anolis Exclusion (field densities of Eleutherodactylus; no Anolis); Eleutherodactylus Exclusion (field densities of Anolis; no Eleutherodactylus); Total Exclusion (neither Anolis nor Eleutherodactylus). We have used these exclosures to examine the effect of frog and lizard predation on arthropod herbivores and the resulting rates of herbivory and propose to continue to use these exclosures after the herbivory experiment is completed in order to examine the effect of frog and lizard predation on arthropod detritivores and rates of litter decomposition. We are currently monitoring flying, foliar and litter arthropods within these exclosures as well as measuring rates of herbivory. Also, as leaf litter accumulates on the roof of the exclosures, it is removed (every 2 weeks) and evenly spread in the exclosures. When we shift the focus of these experiments to studies of decomposition, we will discontinue flying and foliar arthropod monitoring and will begin weighing the amount of litter collected on the roof prior to placing it in the exclosure. At regular time intervals, random quadrats of litter (0.25 m2) will be collected (each quadrat sampled only once) from within each exclosure, placed in Tullgren funnels for litter arthropod extraction, dried to constant mass, weighed, and analyzed for nutrient content. Leaf litter decomposition will be measured through the use of leaf litter decomposition bags. These bags will be constructed of 2.5 cm plastic mesh to allow the entrance of macroarthropods and will be placed at the litter/humus interface on 1 mm nylon mesh sheets which will effectively capture decomposed fragments of litter. Each litter bag will contain 5 g of air dried tabonuco (Dacryoides excelsa) leaves. Twelve litter bags will be distributed in each plot (480 bags total) and one bag will be collected from every plot each month, be placed in Tullgren funnels for arthropod extraction, oven dried, weighed, ground and analyzed for nutrient content. All arthropods will be identified to species and counted to test for the effects of predation regime on arthropodd abundance and the effects of arthropod abundance on rates of decomposition. This experiment will give us information on the relative effects of both frog and lizard predation (separate and combined) on litter arthropod communites and what effect this, in turn, has on litter decomposition.

Because Anolis lizards seldom forage in leaf litter (Reagan 1996), we expect that Eleutherodactylus frogs will be the dominant predator in leaf litter communities, especially juvenile size classes which primarily occupy the litter layers (Stewart and Woolbright 1996). Therefore, we propose a second experiment that will specifically examine the effect of juvenile frogs on litter arthropods and rates of litter decompostion. This experiment will involve smaller exclosures (2 m x 1 m) which will be covered in 1 mm nylon mesh which should effectively control the movements of even juvenile frogs. Because the mesh will also control the movement of many litter arthropods, the plots will be made long and thin as well as relatively low to the ground (ca. 1 m in height) such that the entire plot can be sampled from the outside of the plot. Each exclosure will have a removable roof which is also covered in 1 mm nylon mesh. We propose three treatments: Control (exclosures containing field densities of juvenile frogs (3 frogs/m2); Frog Exclusion (litter hand sifted and frogs removed); Total Exclusion (frogs removed and arthropods repelled by the addition of naphthalene). These treatments will allow us to quantify the rate of decomposition in the presence of frogs (low arthropod abundance), absence of frogs (high arthropod abundance) and in the absence of frogs and arthropods (decomposition due to microbial activity). As above, litter collecting on the surface of the roof will be removed, weighed, and spread within each plot. Arthropod abundance will be assessed as above using small quadrats of leaf litter extracted with Tullgren funnels. These litter samples will be returned to the plots after extraction due to the small size of the plots being used. Litter decomposition will also be assessed using leaf litter decomposition bags as described above (12 bags/exclosure; 360 total). Plots will be arranged in 10 blocks on undisturbed ridge tops as previous data on litter arthropod communities has revealed small-scale spatial variation which will be assessable through spatial blocking.

Hypothesis 2D:

"Earthworms improve phosphorus availability in highly weathered soils through increasing the solubility of inorganic phosphorus and accelerating the mineralization of organic phosphorus. Experimental removal of earthworms from tropical pastures will reduce soil phosphorus availability more than in tabonuco forest because of differences in earthworm abundances between the two habitats." Xiaoming Zou

Soil samples will be collected from each plot at the depth of 0-10, 10-25, 25-50 cm. Each sample will be analyzed for resin extractable organic and inorganic phosphorus and the potential rates of phosphorus transformations. The resin extractable inorganic and organic phosphorus will follow the procedures proposed in the LTER standard soil method book (Lajtha et al. 1999).

Potential rates of phosphorus transformations will be estimated using the irradiation-autoclaving-incubation procedures developed by Zou et al. 1992 and 1995. Three treatments will be applied to each fresh soil sample: control, irradiation, and irradiation plus autoclaving. Soils will then be incubated with resin bags under aerobic conditions. The control treatment allows for the occurrence of three processes: net inorganic P solubilization, microbial immobilization of orthophosphate, and the mineralization of organic phosphorus. The irradiation treatment will kill microbes, thus terminate microbial immobilization process. The irradiation plus autoclaving treatment will kill microbes and denature phosphatase enzymes, thus terminate both microbial immobilization and organic P mineralization processes. Difference in resin extractable P after the incubation among the three treatments will give estimates of net mineral P solubilization, microbial P immobilization, and the mineralization of organic P.

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Research Theme 3: The Influence of Climate and Physical Constraints on the Distribution and Abundance of Organisms and Related Ecosystem Processes in the Luquillo Mountains

Hypothesis 3A:
"Top Down Versus Bottom-Up Control of Food Web Dynamics" D. Jean Lodge

Workplan - Given that most habitats are spatially patchy, pools along the same reach often differ in resources and predators. These differences may influence energy flow within headwater streams. Some pool habitats are likely to have higher primary and secondary productivity than others. Since the recent impact of Hurricane Georges on Puerto Rico in September, 1998, we have identified some large, persistent riparian gaps that allow us to test new hypotheses regarding both detrital and algal resource enhancement and predator control (*sensu* Osenberg and Mittelbach 1996). In some pools, the riparian canopy was only slightly damaged (or quicky grew back) so that shading has persisted and algal growth has been minimal. In other pools there have been major gaps opened by tree falls and tree mortality so that algal growth increased rapidly in response to intense light (and an initial pulse of nutrients from leaf leachates). We can manipulate the presence or absence of different predators and nutrients in these pools and comprehensively determine the relative importance of top-down or bottom-up regulation. Because of the large-scale disturbances from the recent hurricane, we are in a position to test hypotheses regarding individual-, population- and community-level responses. These predictions are based both on current theory regarding top-down versus bottom-up control in aquatic communities and on observations following Hurricane Hugo in 1989 (Covich et al. 1991; 1996; 1998, Crowl et al., **In review**, Johnson et al. 1998).

To investigate the interactions between fish, shrimp, insect larvae, and algal production and detrital loading, we will perform an in situ experiment in the Bisley watershed. A two by two cross-classified design will be employed in which fish and shrimp presence and absence will be manipulated in three replicate pools. Replicate stream pools will receive: no shrimp or fish; shrimp (5 m^{-2}) and no fish; fish (2 m^{-2}) and no shrimp; and fish and shrimp (2 and 5 m^{-2} respectively). Fish and shrimp densities are based on pre-hurricane densities and will be maintained by fencing off the pools (using 5 mm mesh plastic screens) to prevent migration. Tiles will placed into the pools and will be harvested weekly over a 3-6 week period for algal and benthic organic matter standing crop and amounts of carbon and nitrogen in benthic organic matter (BOM). The quality and quantity of BOM will be compared to pre-hurricane levels (Pringle et al. 2000). Drift nets and Surber samplers will be used weekly to measure the responses of mayflies and caddisflies in all pools. Monitoring of nutrient pools (dissolved organic carbon, nitrogen and phosphorus) have been monitored weekly in this stream and will be continued. All response variables will be analyzed using a repeated measures, multiple ANOVA model. We will also include a nested experiment in which we use electrified hoops to exclude shrimp and/or fishes from small patches within the pools. This will allow us to determine the spatial extent of the shrimp/fish effects and more directly test the hypothesis that shrimp grazing is the primary cause of algal and detrital BOM decreases in the absence of fish.

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Hypothesis 3B:

"Consumer populations in tabonuco forest are limited by predation. Increases of pivotal predators will affect productivity and biomass of lower trophic levels." Robert Waide, Michael Willig

Workplan - The food web in tabonuco forest has four trophic levels and is characterized by the absence of large consumers and predators (Reagan and Waide 1996). The top predators are birds which consume lizards and frogs, which have the greatest animal biomass. An experiment using predator exclosures that was initiated at the end of the last LTER cycle will be completed. The exclosure experiments had been dropped because of flat funding in the LTER budget but were initiated recently using other funds. These exclosures were designed to include or exclude coqui frogs and anolis lizards, which are thought to play a pivotal role in controlling herbivory as well as nutrient mineralization by detritivores (primarily fungus gnats). While nitrogen is generally abundant in undisturbed tabonuco forest, immobilization of N by microbial biomass following Hurricane Hugo (Zimmerman et al. 1995) suggests that frogs could play a pivotal role in controlling N-avialability after disturbance. New long-term experiments on predator augmentation will be initiated during this funding cycle.

"Variation in climate as a function of elevation in the Luquillo Mountains affects patterns of soil carbon via effects on soil processes" Charles A.S. Hall, Hongqing Wang and Wei Wu (SUNY-ESF, Syracuse NY 13210)

Further development of simulation models:

We have built a spatially explicit tropical ecosystem model base on the FOREST-BGC (Running and Coughlan 1988) and the CENTURY (Parton et al. 1987, 1988) ecosystem models for the Luquillo Experimental Forest (Marley 1998, Wang et al. Submitted). Our model is process-based and is already a good predictor of spatial pattern of photosynthesis and soil carbon in the Luquillo Mountains. What we need to do is to examine the spatial reliability of the model. We need spatially selected field data to calibrate and validate the model. For simulation of photosynthesis, we need to measure the physiological response of vegetation (e.g.. stomatal conductance) to changing environmental gradients over the Luquillo Mountains. For soil carbon pools, we will develop techniques for direct measurement of soil carbon pool sizes in order to initialize each pool, monitor the fluxes of carbon through each pool and then validate simulations. We will incorporate soil oxygen concentration and biogeochemical cycling into the model structure as determinants of soil decomposition and mineralization rates. Meanwhile, we will incorporate models of hurricane influence on landscapes in the Luquillo Mountains, e.g. EXPOS, HURRECON models (Boose et al. 1994) and RECOVER model (Everham, 1996) to simulate the long term hurricane impacts on the spatial and temporal patterns of soil carbon over the Luquillo Mountains. Finally, we will combine GIS tools and graphic techniques into our simulation to determine and display the scale and degree of the spatial and temporal dynamics of carbon cycling in this tropical forest ecosystem.

Model validation

a) Soil sampling and field measurements
We will collect soil samples from different depths (0-10, 10-30, 30-100 cm) from 7 randomly selected sites along an elevation gradient over the entire Luquillo Mountains. At or near each elevation site, we will select 4 subsites that represent topographic gradients (i.e. ridge, slope, upland valley and riparian valley in this tropical mountain area) (Garcia-Montiel and Scatena, 1994; Scatena and Lugo, 1995). For representative purposes, we will mix samples at each site. In order to examine the variability at each site due to laboratory analysis, quality control (i.e. duplication of samples and blanks) will be conducted (Anderson and Ingram 1989). We will obtain monthly air and soil temperature and rainfall data from nearby climatic stations or by field measurements.

b) Field measurement of photosynthetic rates
We will select 10 trees for 3 dominant species at each sampling site to measure photosynthetic rates using Lci (the Ultra Compact Photosynthesis Measurement System), ADC2250 Advance Gas Exchange Management System and DEX Electronic Dendrometers (www.dynamax.com). Measurements will be conducted on a monthly basis.

c) Soil chemical analysis:
Total soil organic carbon (SOC) will be determined on air-dried soils using the Modified Walkly-Black method (Anderson and Ingram, 1989). Microbial biomass carbon will be determined by the $CHCl_3$ fumigation-direct extraction method (Motavalli et al., 1994; Vance et al., 1987). Carbon contained in a 0.5 M K_2SO_4 extract of unfumigated soils is considered a

measure of soluble carbon. The sum of microbial biomass carbon plus soluble carbon will be treated as an estimate of the active carbon pool. The slow carbon pool will be determined using the suspension method (Motavalli et al., 1994). The passive carbon pool is calculated as the total organic carbon minus the active and slow carbon pools. Monthly soil oxygen concentration will be measured using an oxygen electrode (Farrell et al., 1993). Measurements of fluxes of CO2 and CH4 will be measured monthly using plastic chamber method (Steudler et al. 1991). In the meantime, we will analyze for gravimetric moisture content (g H2O/ 100 g dry soil), bulk density (g dry soil/ cm ^3), soil pH (using pH meter) and exchangeable cations (Anderson and Ingram, 1989).

d) Statistical analysis of data:

We will apply spatial statistical analysis technique (Griffith and Layne 1999) to determine the spatial dependence of soil carbon storage and fluxes and the spatial relation between soil carbon and other soil physical and chemical properties in order to make precise prediction of patterns in soil carbon dynamics. In addition, we will use conventional statistical techniques (e.g. SAS) to examine the basic statistical features of variables used in our simulations.

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Hypothesis 3C:

All samples will be filtered with a pre-combusted Whatman GF/F glass fiber filter prior to analysis; a subsample for silica and cations will be held refrigerated, and a subsample for other analyses will be held frozen until analysis. Dissolved organic carbon will be measured as non-purgeable organic carbon using automated high temperature platinum-catalyzed combustion (Shimadzu TOC 5000 with autosampler). Total dissolved N will be measured using high temperature platinum-catalyzed combustion followed by analysis of total NO in the combustion gas stream using an Antek Model 720C chemiluminescent detector (Merriam et al. 1996). Ion chromatography (Dionex micromembrane chemical suppression and conductivity detection) anions (sulfate, chloride, and nitrate). Single column non-suppressed ion chromatography will be used to measure base cations (sodium, calcium, magnesium, and potassium). Ammonium (phenol hypochlorite method), orthophosphate (ammonium molybdate method), and total dissolved P (persulfate digestion followed by ammonium molybdate for orthophosphate) will be measured with a flow injection analyzer (Lachat QuikChem). Dissolved organic N will be estimated as the difference between total dissolved N and DIN.

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Hypothesis 3D:

Riparian Studies

"**Relationship between primary gradients, disturbance and riparian species distribution along Sonadora Creek, El Verde**" E. Meléndez-Ackerman, R. Tremblay, J. Sharpe.

Little is known about what regulates the distribution of lithophitic plant species in riparian zones. One posibility is that their populations are mainly controlled by primary gradients in environmental factors (i.e. light, temperature, humidity) with dominant species exhibiting either different or analogous responses to changes in these factors along elevational gradients. Aside from changes in elevation, changes in the microenvironment along streams may also be regulated by the frequency and intensity of disturbance events (e.g. floods, droughts, hurricanes) on forest streams. Thus, disturbances may also play an important role in the distribution of plant species in riparian zones.

We will explore the role of primary gradients and disturbances by monitoring 3 dominant lithophitic species (*Lepanthes rupestris* (Orchidaceae), *Pitcarnia angustifolia* (Bromeliaceae), , (Polypodiaceae) along Sonadora Creek near the El Verde Field Station Research Area. We will monitor populations of these species along a 400 m stretch on both sides of the Sonadora creek between 300 m and 700 m in elevation. As part of another project we have already marked all patches (i.e. rocks and trees) containing *Lepanthes rupestris* plants for a total of 200 occupied sites. Since occupied patches have on average a number of 45 plants growing on them (Tremblay, 1997) our total number of plants is likely to be in the order of 9,000. In addition, we have randomly selected and marked 4 unocupied patches in the vecinity of every occupied site for an additional 800 marked sites. We will complete surveying and marking on the remaining strech of Sonadora this summer so that the area surveyed on both sides of the creek is symetrical. We will also use marked patches to census the fern species. We will survey the area to determine the locations of *P. angustifolia* populations which tend to occupy larger areas than our study orchid and fern populations.
For each species we will initially tag or map all individuals regardless of life history stage in marked patches as well as all newly recruited plants throughout the duration of the study. Every 4 months we will census all sites to obtain individual data on survival, life history stage (seedling, juvenile, non-reproductive adult and reproductive adult) and reproductive output. We intent to count the number of new recruits and as well as the presence or absence of live plants in all marked sites. At every census and for every site we will also collect data on environmental variable that may influence population performance (i.e. temperature, % relative humidity, light intensity). Additional censuses will be performed after disturbance events (i.e. floods, droughts, hurricanes) and rainfall data from the El Verde weather Station will be recorded for each census period. For every flood event we will obtain data on stream flow from the Sonadora US Geological Survey water gauge.

The above data will serve various purposes. First it will allow us to construct life tables that will be used to estimate the intrinsic growth rates of individual patches using a matrix-based demographic analysis (Tremblay, 1997) which will be used to determine relationship between the primary gradients and disturbance events with the degree of local population persistence. Second, it will help us estimate the rates of colonization and extinction of patches and how these relate to changes in environmental parameters. With these data we hope to determine the extent by which riparian lithophitic populations behave as metapopulations where persistence is likely to be achieved at the landscape level.

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