LUQUILLO LONG-TERM ECOLOGICAL RESEARCH PROGRAM

UNDERSTANDING CHANGE IN ECOSYSTEMS OF NORTHEAST PUERTO RICO

A Renewal Proposal Submitted to the National Science Foundation

by

The Institute for Tropical Ecosystem Studies
University of Puerto Rico-Río Piedras

International Institute of Tropical Forestry
USDA Forest Service

February 1, 2006

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PROJECT SUMMARY

Intellectual Merit: The Luquillo Long-Term Ecological Research Program (LUQ) focuses on understanding factors driving long-term change in tropical forest ecosystems in the Luquillo Mountains of Puerto Rico. Building from an earlier emphasis on natural disturbance (hurricanes, landslides, droughts, floods) and ecosystem response to disturbance, LUQ will continue studies of ecosystem structure and processes in mid-elevation tabonuco forest, extend research into other forest types along an elevation gradient, and begin investigations of regional-scale processes affecting the Luquillo Mountains. Four approaches will be used: long-term measurements and experiments, comparative analyses among different forest communities, gradient analysis from forest to urban ecosystems, and synthesis using conceptual and simulation models.

Mounting evidence suggests that increasing hurricane intensity, declining rainfall in the mountains, and rising temperature in urbanized areas in the nearby lowlands can have significant effects on the ecosystems of the Luquillo Mountains. In this context, we ask:

How do changes in disturbance regime and climate alter biogeochemical cycles, biotic structure, and ecosystem services in the Luquillo Mountains and northeastern Puerto Rico?

This overarching question leads to three specific questions addressing key elements of our long-term conceptual framework, and nine hypotheses addressing these elements.

1) *What controls variation in C and nutrient fluxes, and how are these variations modified by disturbance?* Many ecosystem processes in the Luquillo Mountains exhibit well defined seasonality and links to climate. Understanding these relationships is essential for determining the sensitivity of tropical forest biota and biogeochemical cycling to climatic and environmental change. This question and associated hypotheses focus on how climate and disturbance history affect inter- and intra-annual variation in carbon and nutrient fluxes in the Luquillo Mountains.

2) *Are changes in temperature, rainfall, light and wind (climate) along the Luquillo elevation gradient sufficient to explain variation in biogeochemical processes and biotic structure?* We propose to study linear and non-linear trends in climate with elevation in the Luquillo Mountains as drivers of ecosystem processes and the distribution of organisms. By improving our understanding of the importance of biotic and abiotic factors in determining the distribution of organisms over spatial gradients in tropical mountains, we increase our ability to understand the effects of environmental change on biogeochemical processes and biotic structure.

3) *How important are changes in land-use in determining long-term ecosystem biogeochemistry, biotic structure, and services?* Land-use and land-cover are changing dramatically in northeastern Puerto Rico in response to socioeconomic changes. We propose to examine the long-term effects of land-use and land-cover change on a range of ecosystem features, including regional and local climate, tree species composition in forests, stream ecology, and a key ecosystem service and product: the delivery of clean water for humans.

Broader Impacts: The proposed research will provide an improved scientific framework for the management of tropical ecosystems and ecosystem services. It will do so both through conceptual advances and documentation of human disturbance and ecosystem response. The project will continue to produce a cadre of young and minority scientists who are versed in linking population and ecosystem approaches to evaluating environmental change, and will provide them with skills that can be applied in tropical regions or elsewhere. LUQ has developed a comprehensive education program involving teachers at a network of six high schools and with a web-based middle school curriculum for teaching ecology. Additional outreach activities are directed at improving the general public's appreciation of the water resources provided to surrounding towns by streams draining the Luquillo Mountains.

Section 1 Results From Prior NSF Support

Long-Term Ecological Research in the Luquillo Experimental Forest 3: NSF Grants DEB-0080538, 11/00–10/02 ($1,400,000) and DEB-0218039, 12/02–11/06 ($2,800,000)

The goal of the Luquillo Long-Term Ecological Research Program (LUQ) is to understand long-term patterns and processes in tropical forest and stream ecosystems, using the Luquillo Mountains and nearby developed areas of Puerto Rico (Fig.1). This region has a well-documented history of natural and human disturbances and ecosystem response (Fig. 2), a gradient in abiotic environmental variables and forest types from sea level to 1075 m, and a land-use gradient from undisturbed forests to a large city. LUQ began in 1988, building on forest management research starting in the 1940s (Wadsworth 1949) and systems ecology beginning in the 1960s (Odum & Pigeon 1970). In the first three phases of LUQ we showed how a diverse biota interacts with a varied disturbance regime and environmental gradients to determine habitat structure, nutrient cycling, community organization, and food web relations in terrestrial and aquatic ecosystems (Reagan & Waide 1996, Walker et al. 1996a, Walker 1999, Covich et al. 2004a). Our results show that we must study multiple disturbances interacting with climate to understand directional environmental change and effects on ecosystem services.

1.1 Disturbance and Response: Disturbance is a major driver of ecosystems in the Luquillo Mountains. Severe hurricanes strike the Luquillo Mountains on average every 50-60 yr (Scatena & Larsen 1991) but may become more frequent and intense (Section 2.2). Chronic hurricanes produce a forest with high tree density (stems $\geq$ 10 cm dbh), low canopy, and few woody vines (Brokaw et al. 2004, Rice et al. 2004, Thompson et al. 2004). Our long-term studies (Section 2.3.1) reveal resistance and resilience of ecosystems (Fig. 3), as well as species-specific differences in responses to disturbances that will likely result in directional change in communities if the hurricane regime changes. Three censuses of trees in the Luquillo Forest Dynamics Plot and other studies show that susceptibility to hurricane damage and regeneration of seedlings and saplings depend on previous damage and species-specific life-history characteristics, microsite preferences, and response to crowding (Walker 2000, Walker et al. 2003, Uriarte et al. 2004, Ostertag et al. 2005, Ogle et al. in press). Long-term observations of animal populations also reveal species differences in disturbance response (Bloch & Weiss 2002, Bloch & Willig in press). Species response to hurricane disturbance (Woolbright 1996, Covich et al. 1996) can feed back on ecosystem processes. For example, the abundant frog, *Eleutherodactylus coqui*, influences invertebrate abundance, herbivory, and nutrient cycling, and may ultimately affect primary production (Beard et al. 2002, 2003), while freshwater shrimp mediate exchanges at the terrestrial-aquatic interface (Crowl et al. 2001, Covich et al. 2004a).

Short-term droughts and floods, thought to be increasing (Larsen 2000), strongly affect stream communities and ecosystem processes (Covich et al. 2000, 2003, Covich & Crowl 2002). Floods alter the rate and composition of detrital inputs to streams (Covich et al. 2000), while droughts decrease connectivity between hydrologic units, altering local food-web structure, detrital processing dynamics, and predator-prey dynamics (Covich et al. 2000, 2006).

In mid-elevation tabonuco forest (site of most LUQ research, Fig. 1), detrital dynamics regulate carbon and nutrient fluxes and ecosystem response (Sanford et al. 1991, Silver & Vogt 1993, Lodge et al. 1994, Scatena et al. 1996, Ostertag et al. 2003). Recent studies show that the observed high soil organic matter (SOM) under hurricane debris affects P availability. Pulses of nutrients increase post-storm plant production (Zalamea Bustillo 2005) and shift the identity and diversity of decomposer organisms that affect decomposition rates (González & Seastedt 2001, González et al. 2001, Santana et al. 2005). Moreover, nutrient additions promote regeneration in landslides (Frizano et al. 2002, Shiels in press, Shiels et al. in press). In 2005 we established the Canopy Trimming Experiment, a 20-yr field experiment to understand the mechanistic basis of hurricane effects. Trimming of canopy trees occurs on a 6-yr cycle, with experimental treatments designed to mimic and separate the hurricane effects of altered microclimate versus debris deposition on detrital dynamics, ecosystem processes, and populations and to look at the effects of repeated disturbance (Section 2.3.1). In 30 x 30 m plots with canopy tree branches trimmed: light increased (Fig. 4); soil moisture increased (Fig. 5), probably due to decreased plant interception and uptake; virtually all trimmed trees sprouted new branches; understory plants put on new growth; pioneer tree seedlings established; and grasses and ferns flourished temporarily, as they do after hurricane damage. Recovery from canopy loss, measured as leaf area index (LAI), was rapid and may be promoted by an increased connectivity of fungal hyphae responding to debris deposition on the forest floor (Fig. 6), suggesting a mechanism of forest resilience via rapid nutrient cycling.

A synthesis of 10 years' observation and experimentation through hurricane and drought events showed that ecosystem processes, such as plant growth and decomposition rates, recovered faster than ecosystem structure, such as foliage and fine root biomass (Beard et al. 2005). Resistance and resilience of the measured response variables depended on the type (hurricane or drought) and intensity of disturbance. Lastly, site-specific land-use legacies (Section 1.2) were more important than natural disturbance in determining nutrient availability (Beard et al. 2005). These results underline the need to continue our studies of the cumulative effects of repeated disturbances on ecosystem processes, particularly interactions among natural and human disturbances, in order to foresee the consequences of changing disturbance regimes in Puerto Rico and other areas (Lugo 2000, Lugo et al. 2006).

1.2 Land-Use Impacts: Human disturbance has had significant impacts on the Luquillo Mountains and surrounding areas (Thomlinson et al. 1996, Foster et al. 1999, 2003, Grau et al. 2003, Silver et al. 2004). In the past 500 years the island of Puerto Rico changed from near total forest cover before Europeans arrived to near total deforestation by the mid 1950s (Fig. 2). Since then the island has recovered to about one third forest cover, but the area surrounding the Luquillo Mountains is now increasingly urbanized (Fig. 7, Thomlinson & Rivera 2000, López et al. 2001, Grau et al. 2003, Lugo et al. 2004). Land-use legacies are strong. In the 16-ha Luquillo Forest Dynamics Plot, where intensive land-uses ceased in the 1930s, tree species composition reflects past land-use more strongly than damage from recent major hurricanes in 1932, 1989 and 1998 (García Montiel 2002, Thompson et al. 2002). Second-growth forests in Puerto Rico rapidly converge in structure on historic forest types, but they differ in tree composition according to previous land-use and include many aliens (Pascarella et al. 2000, Grau et al. 2003, Lugo 2004b, Lugo & Helmer 2004, Lugo & Brandeis 2005). In the first 60 yr of reforestation of pastures, aboveground C accumulates, and more soil C accumulates than in pasture soil (Silver et al. 2000, 2004, Li et al. 2005). Soil C increases fastest in the first 20 yr but continues to increase for 40-80 yr and perhaps longer, as tree species change. Alien earthworms dominate soil fauna in secondary forests and affect ecosystem processes (Liu & Zou 2002, Hendrix et al. in press).

Land-use has affected climate in the Luquillo Mountains and surrounding areas. The urban heat island of San Juan (González et al. 2005) appears to be expanding with suburbanization (Fig. 8), and is undoubtedly affecting the Luquillo Mountains. Forest clearing upwind of the Luquillo Mountains apparently reduces rainfall in the mountains (van der Molen 2002, van der Molen et al. in press). Secondary forests with different land-use histories may respond differentially to a predicted increased severe hurricane disturbance (Thompson et al. 2002; Pascarella et al. 2004). Thus, to forecast directional environmental change in the Luquillo Mountains and other parts of Puerto Rico, it is essential to study both the effects of climate change on ecosystems (including increased severe hurricane frequency), and the separate effects of human disturbance on land-uses and regional climate.

1.3 Ecosystems and Climate: Our work in tabonuco forest established strong links between the abiotic environment, as modified by disturbance, and forest composition and function (Hall et al. 1992, Waide et al. 1998, Wang et al. 2002b). To increase our understanding of abiotic controls on ecosystems, we extended our work from tabonuco forest to other forest types along the climatic and forest gradient in the Luquillo Mountains (Section 2.3.2). Ascending the Luquillo Mountains, climate becomes cloudier, wetter (2500 to 4500 mm rain yr^{-1}), and cooler (c. 25 to 18.5 °C), and forests become shorter, denser, less species-rich, and less productive (Waide et al. 1998). From tabonuco forest at c. 250 m to the mountain peaks at c. 1075 m, plant species composition changes markedly; palms increase with elevation; and the uphill boundaries of many species are clustered together and distinct, indicating community change (Fig. 9). Riparian and upland forests are more similar with increasing elevation, as soil moisture increases and reduces the difference between upland and riparian soils (Heartsill Scalley 2005). In contrast, litter invertebrates respond to the changing plant community rather than to the direct effects of climate along the elevation gradient (Richardson et al. 2005).

Differences in temperature explain 87% of the variability in litterfall rates above 600 m. Litterfall net primary productivity (NPP) decreased from 9.0 Mg/ha/yr at the lower elevation sites to < 2.0 Mg/ha/yr at the upper elevation sites. Fine root mass and soil moisture increase with elevation, while respiration decreases (McGroddy & Silver 2000). Soil O_2 concentrations vary significantly in space and time along the gradient and anaerobic conditions may drive many ecosystem and community characteristics (Silver et al. 1999). We are synthesizing climate and ecosystem studies on the elevation gradient and at the landscape scale by developing spatially-explicit models of climate and evapotranspiration (Wooster 1989, Wu et al. in press a, b), carbon and soil dynamics, and aboveground productivity (Hall et al. 1992, Wang et al. 2002a, b, c).

Further study of ecosystems along the climatic gradient, together with work on effects of intra-annual climate variation, will give us mechanistic explanations and improve our ability to understand and predict the consequences of climate change (Chambers & Silver 2004, 2005), especially with regard to water delivery, an important ecosystem service rendered by the Luquillo Mountains.

1.4 Streams and Ecosystem Services: Our long-term, intensive work on stream ecology and terrestrial-aquatic links in the Luquillo Mountains (e.g., Crowl et al. 2001, McDowell 2001, March & Pringle 2003, Covich et al. 2004a, 2006) has enabled us to document the effects of natural and human disturbance (water diversion, damming, drought, and hurricanes) on detrital dynamics, aquatic populations, and water quality and delivery. The massive defoliation caused by Hurricane Hugo produced large but short-lived increases in nutrient export, with nitrate and potassium concentrations more than doubling in most streams but returning to background within 18 months, in synchrony with re-vegetation (Schaefer et al. 2000). Nitrogen retention and loss in riparian zones in the Luquillo Mountains strongly regulates nitrate export following disturbance (McDowell et al. 1992, 1996). At the scale of the whole Río Icacos basin, total dissolved N export would be 50% greater in the absence of riparian N retention (Chestnut & McDowell 2000, Madden 2004). Rapid dissimilatory nitrate reduction to ammonium by microbes probably has a significant role (Silver et al. 2001, 2005).

Detrital dynamics are significantly affected by the species composition and abundance of shrimp, fish, and snails in these streams (Crowl et al. 2001, 2006, March & Pringle 2003, Blanco & Scatena 2005). This assemblage varies with elevation (March et al. 2002), and is greatly affected by floods and droughts (Section 1.1), as well as by water diversion and damming, both of which impede upstream migration of stream biota (Benstead et al. 1999, March et al. 2003, Freeman et al. 2003, Greathouse 2005). In 2005 about 70% of the water draining the Luquillo Mountains was diverted for municipal use, compared to 50% in 1994 (Crook 2005). These diversions leave only 30% of the water draining the forest to flow freely into the ocean, which reduces the hydrologic connectivity along the river continuum, because these water withdrawals cause high mortality of migratory fishes and shrimps. Added to the effects of water diversion, streams above large dams have low abundances of shrimp and fish, and therefore high levels of epilithic algae, carbon, nitrogen, and particulate organic and inorganic matter (Greathouse et al. in press). Thus water diversion impoverishes aquatic fauna and reduces water quality, which has negative economic consequences (González Cabán & Loomis 1997, 1999). With these results we have developed water management recommendations that have been implemented by local government (Pringle et al. 1999, Scatena & Johnson 2001, Rivera Ramírez et al. 2002, Ortiz Zayas & Scatena 2004).

The possible drying in the Luquillo Mountains (Section 1.2) coupled with increased water use by suburban areas surrounding the Luquillo Mountains provides a strong impetus to continue our studies of this important ecosystem service.

1.5 Cross-Site Studies: As the only tropical, terrestrial LTER site, LUQ plays a valuable role in cross-site comparisons within the LTER network and with other tropical sites. For example, in the Long-term Intersite Decomposition Experiment (LIDET) our diverse, warm site had higher decomposition rates than less diverse, cooler sites (e.g., KNZ, CWT), but similar rates of nitrogen mineralization (Parton et al. in review). Comparative studies between LUQ and NWT show how the biota and climate affect decomposition and soil processes (González & Seastedt 2001, González et al. 2001). The Lotic Intersite Nitrogen Experiment (LINX) showed that in our N-rich site, ammonium turnover in streams is more rapid than in most temperate sites, due largely to high nitrification rates (Peterson et al. 2001, Merriam et al. 2002). Other ecosystem comparisons have included primary production (Clark et al. 2001a, b), stream metabolism (Mulholland et al. 2002), stream microbial biomass (Findlay et al. 2002), and a study showing that nitrous oxide fluxes increase with temperature and moisture along a latitudinal gradient (Silver, in prep.). LUQ maintains one of 15 sites in the Center for Tropical Forest Science (CTFS, Smithsonian Institution) network of large, long-term forest plots. Cross-site comparisons among these plots have produced much new understanding of tropical forests and biodiversity maintenance (Losos & Leigh 2004; Wills et al. 2006). This range of cross-site work underlines the importance of a site with a warm, wet environment and a diverse biota in establishing the core principles underlying ecosystem processes.

1.6 Mid-Term Review: In 2003 a mid-term review team enthusiastically endorsed the projects and direction of LUQ. They suggested we strengthen our conceptual framework, emphasize water as a link among studies, add more spatial analyses, and ensure necessary expertise in micrometeorology. We developed a conceptual framework that links scales, concepts, and models and will guide our work for decades (Section 2.2). Water connects our disturbance, climate, stream, land-use, and ecosystem services research (Section 2.4). We have published several papers that extend our work spatially (Wang et al. 2002a, b, c, Wu et al. in press a, b), and the Institute for Tropical Ecosystem Studies (home institution of LUQ) is hiring a landscape ecology/GIS expert (replacing Thomlinson) who will dedicate primary research efforts to LUQ. In the area of micrometeorology we have strengthened our micrometeorology work in our main experiment (CTE), and one of our Senior Investigators (Ramírez) focuses on this area.

1.7 Education and Outreach, Human Resources: In 2003 we named Steven McGee Education Coordinator for LUQ. He and LUQ scientists developed a bilingual school curriculum unit, *Journey to El Yunque* (Section 5), and he has organized LTER Network-level education efforts. LUQ's Schoolyard LTER has leveraged funds from NSF's IMD program and the Puerto Rico Department of Education, to develop programs that have reached some 900 Puerto Rico high school teachers. LUQ's REU programs include students supported on LTER supplemental funds, students in a site-based REU program, and students from other universities' REU programs, totaling about 65 students (mostly women and under-served groups) in the period 2000-2005. LUQ outreach includes workshops on water and ecosystem management with local municipalities surrounding the Luquillo Mountains, which are jointly sponsored by local government and the LUQ-HELP collaboration, a UNESCO/WMO global initiative aimed at improving the linkage between hydrology and society. Thirty students earned doctoral or masters' degrees working with LUQ during the past six years. Three current LUQ Senior Investigators were graduate students with LUQ Senior Investigator advisors.

1.8 Information Management: Since the last grant renewal the LUQ database has reached Level 3-4 implementation of EML (Ecological Metadata Language), and we have contributed data to Clim-DB, Hydro-DB, and Site-DB. Our information manager serves on the LTER-IM Executive Committee and is the current editor of *LTER DataBits*, the LTER newsletter for information management. We have contributed to the development of common information management frameworks and distributed knowledge networks (Meléndez Colom & Baker 2002, Andelman et al. 2003). LUQ maintains 104 datasets on its website for public use. All LUQ-funded datasets are made available within two years after collecting, with a few exceptions (usually for graduate students) that extend this period but ensure eventual access.

1.9 Publications: Since it began in 1988 LUQ has published 555 peer-reviewed journal articles, 124 book chapters, 10 books, 84 theses and dissertations, and 29 other publications, (see: http://luq.lternet.edu/ for a complete list). From 2000 to 2006 we published 273 peer-reviewed journal articles, 50 book chapters, 4 books, 31 theses and dissertations, and 15 other publications. The collaborative breadth of LUQ has produced many syntheses of results, which extend the relevance of its work and prove the synergistic value of LUQ. Recent examples of synthesis treat disturbance (Walker 2002, Grau et al. 2003, Walker & Del Moral 2003, Beard et al. 2005), carbon and nutrient budgets (Silver et al. 2000, 2002, Silver & Miya 2001, Grau et al. 2004, Chambers & Silver 2005), tree life histories (Lugo & Zimmerman 2002), forest ecology (McDowell 2002, Lugo 2005, Lugo et al. 2006), alien species (Lugo 2004b), bats (Gannon et al. 2005), ecological hierarchies (Scatena 2002), ecosystem services (Scatena 2000a, b, 2003, Scatena et al. 2002), stream ecology (Smith et al. 2003, Covich et al. 2004a), and general ecology (Belovsky et al. 2004). The LUQ synthesis book will be submitted to Oxford University Press in 2006. Scientists in LUQ have also published on forest restoration and conservation (Zimmerman et al. 2000, Lugo 2001, 2004a, 2005, Lugo et al. 2001, Shiels & Walker 2003, Walker 2005), on water management (McDowell 2001, Pringle 2001, 2005, Scatena 2001, 2003, March et al. 2003, Santos Román et al. 2003, Ortiz Zayas & Scatena 2004, Pringle & Collins 2004, Scatena et al. 2004), and on a new economics for the tropics (Hall 2000, Hall et al. 2001).

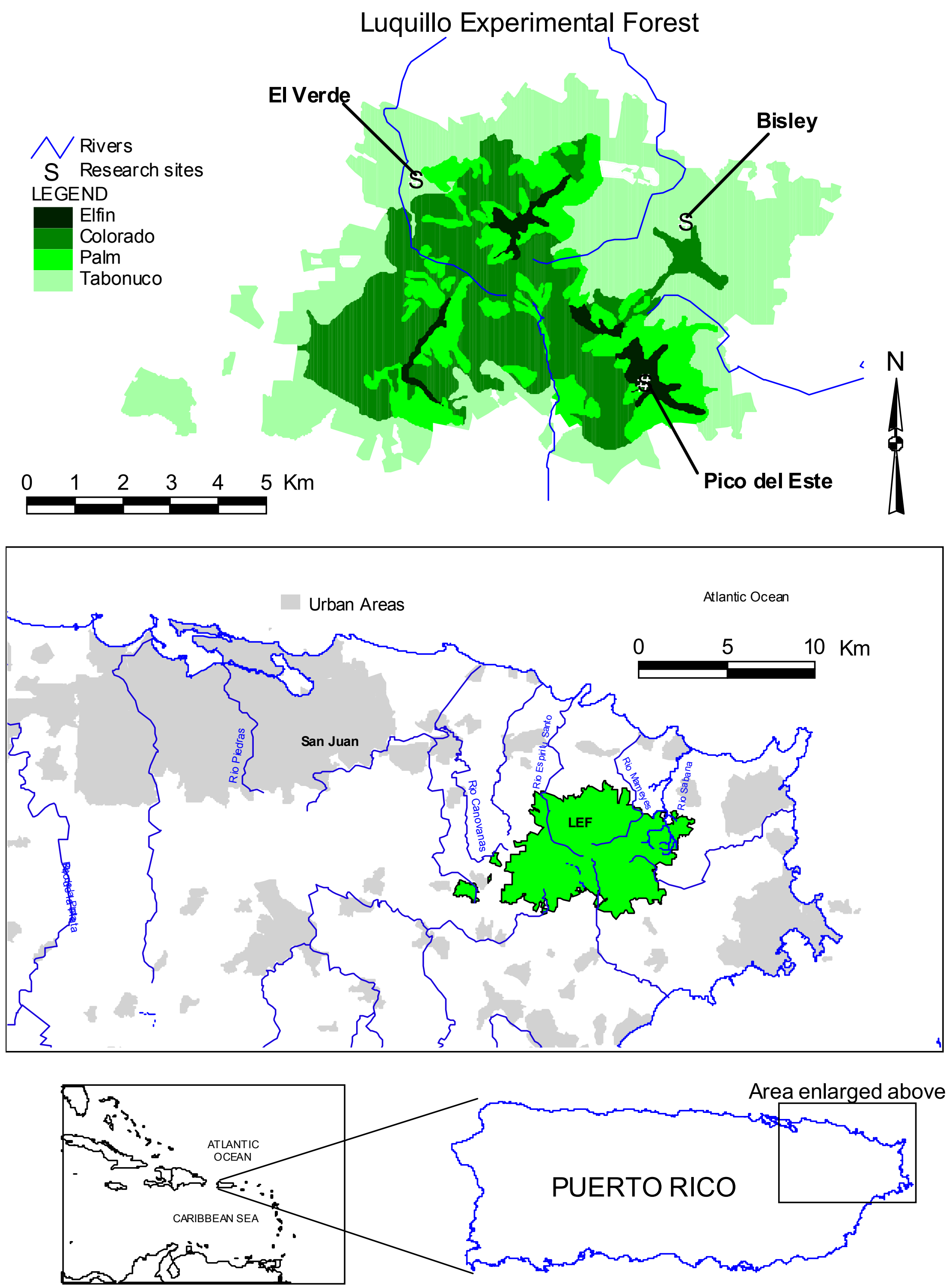

Figure 1 – Map of Puerto Rico and the Caribbean (lower panel), the northeastern portion of Puerto Rico (middle panel), and the Luquillo Experimental Forest in the Luquillo Mountains (upper panel). Note the river basins (Río Piedras, Río Canóvanas) that represent new urban study sites in the middle panel.

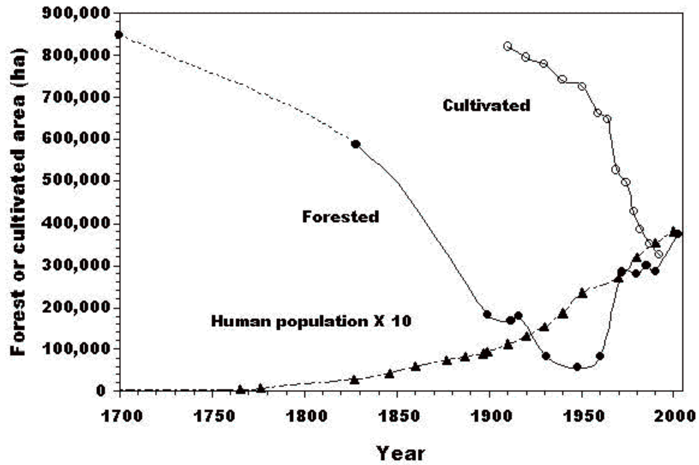

Figure 2 – Land-use and land-cover in Puerto Rico, showing trends in human population, forest area, and cultivated area over time. The earliest evidence of humans in Puerto Rico dates from the 1st Century A.D. (Morales Carrión 1983). Europeans settled on the island in 1508.

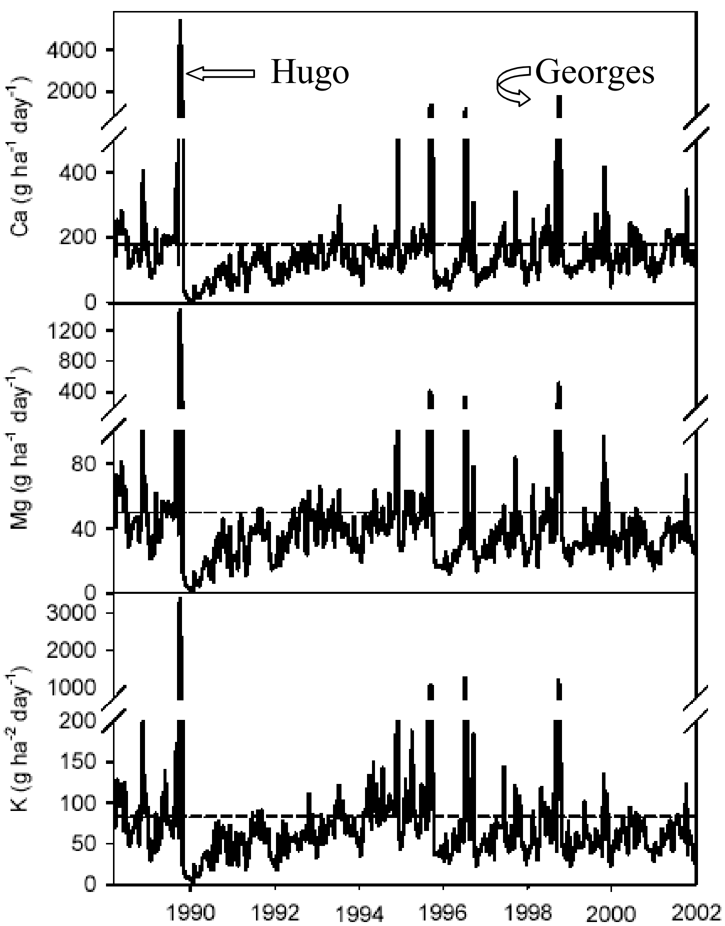

Figure 3 – Biogeochemical resilience evident in long-term nutrient flux in litterfall to the forest floor in the Bisley Experimental Watersheds. Hurricanes Hugo and Georges, the most powerful hurricanes of our study period, are indicated. Other storms resulted in additional peaks in litter mass and litter nutrient inputs. Note the breaks in scale.

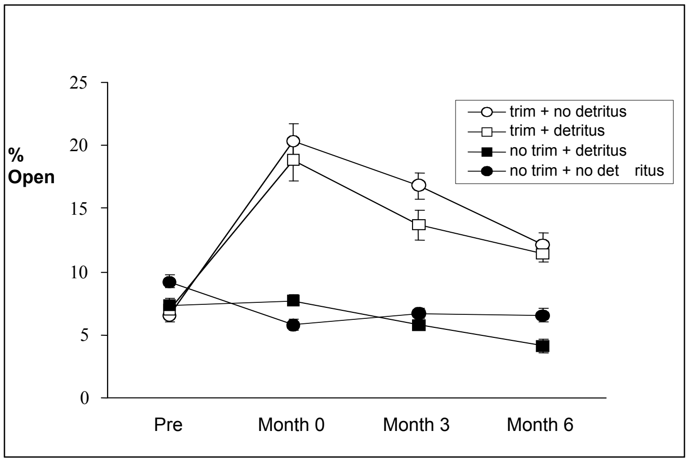

Figure 4 – Effects of canopy trimming on canopy openness (% of clear sky above randomly selected points) in the Canopy Trimming Experiment (Section 2.3.1). Open symbols are trimmed plots, filled symbols are untrimmed. Rapid regeneration is closing the canopy after the initial trimming. Bars represent 1 standard error about the means.

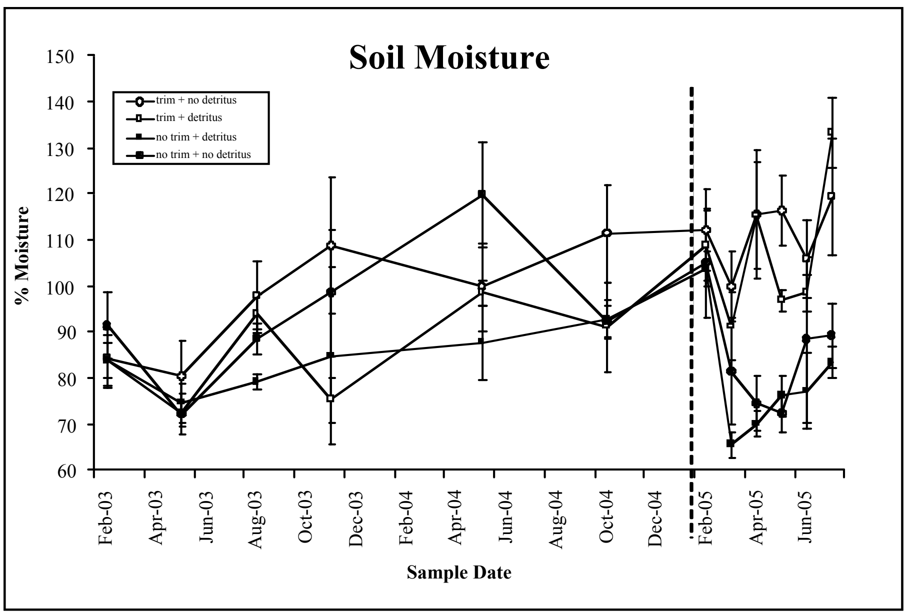

Figure 5 – Effects of canopy trimming on soil moisture (% of dry weight) in the Canopy Trimming Experiment (Section 2.3.1). Open symbols are trimmed plots, filled symbols are untrimmed. Bars represent 1 standard error about the means.

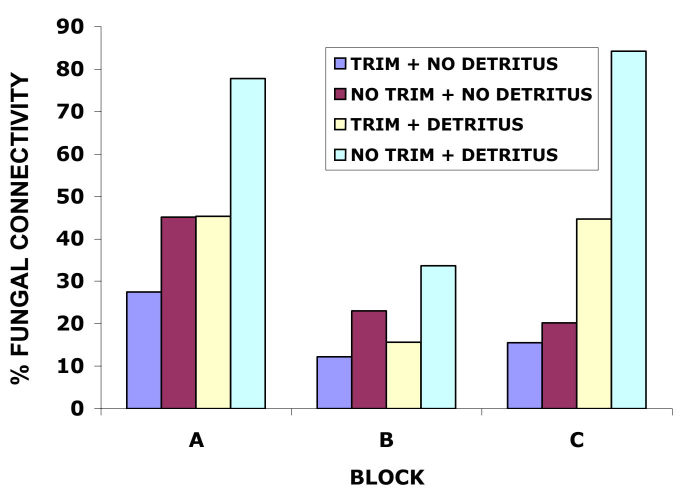

Figure 6 – Effects of Canopy Trimming Experiment (Section 2.3.1) treatments on hyphal connectivity (the percentage of leaves that are attached to the forest floor by fungal hyphae during the first 6 weeks of decomposition). Data are presented for each block separately. A randomized-block ANOVA shows both a block effect and a treatment effect, with block B being different from the other two, and fungal connectivity significantly highest in the trim + detritus treatment.

Figure 7 – View from the forested Luquillo Mountains toward San Juan, Puerto Rico, showing land use ranging from total forest cover (Luquillo Mountains), to agriculture mixed with forest, to suburban and urban development.

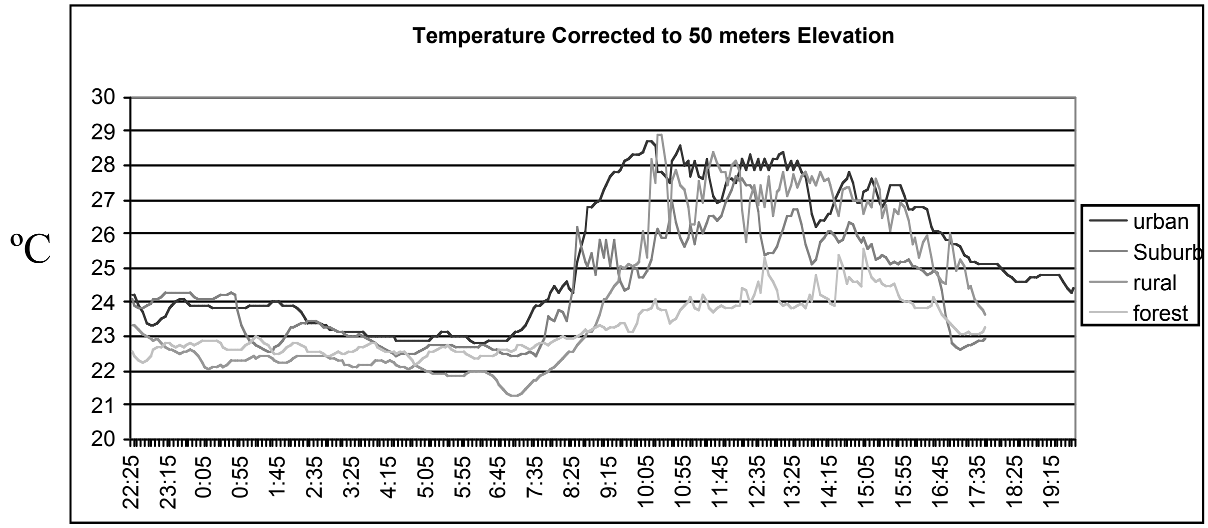

Figure 8 – Diel patterns in temperature (°C) at four sites along the urban-suburban-rural-forest gradient in northeastern Puerto Rico.

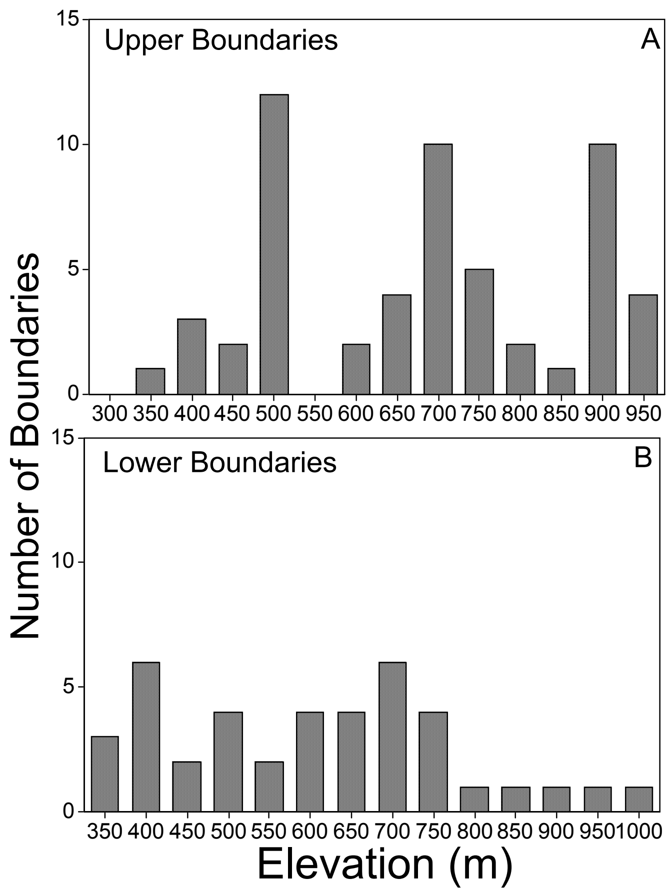

Figure 9 – Analysis of the distribution of woody plant species along an elevation gradient in the Luquillo Mountains (from Barone et al. in review). The bars represent the number of species that show an upper elevation distribution limit (A) and a lower elevation limit (B).

Section 2 Proposed Research

2.1 INTRODUCTION

Ecosystem change in the tropics is likely to have disproportionately large impacts on global climate, biodiversity, and ecosystem services (Millennium Ecosystem Assessment 2005, Wright 2005). The Luquillo Long-Term Ecological Research Program (LUQ) is dedicated to understanding ecosystem change in Puerto Rico as a means to better evaluate changes in similar tropical ecosystems (Lawton et al. 2001, Grau et al. 2003, Lovejoy & Hanna 2005, Wright 2005). We build from our growing knowledge of the ecosystems of the Luquillo Mountains to an examination of the coupling between the natural and human ecosystems of northeastern Puerto Rico. Coupled human-natural ecosystems represent large areas of the tropics as well as other regions of the globe (Aide & Grau 2004). An improved understanding of the linkages between human and natural ecosystems is critical to understanding and adapting to change at scales from local to global and from the immediate to the long-term.

The location of LUQ in a windward mountain range on the Atlantic coast and near a fast growing, major city, together with the program's existing long-term records, makes Puerto Rico an ideal site to answer questions about environmental change due to climate and land-use in the tropics. Indeed, the changes we study in Puerto Rico apply to many other areas of the tropics, where the environment and ecosystem services are strongly affected by complex direct and indirect interactions resulting from changing climate and human activity (e.g., Lawton et al. 2001, Parmesan & Yohe 2003, Aide & Grau 2004, Foley et al. 2005, Lovejoy & Hanna 2005, Wright 2005). The population density of Puerto Rico (c. 425 people km^{-2}) is higher than in any of the fifty states and exceeded by only a few places in the world. The Luquillo Mountains are a protected area in the midst of expanding human development, and as such provide an important laboratory for the study of coupled human-natural systems.

When LUQ began in 1988, we focused on changes in a particular tropical rain forest community (mid-elevation "tabonuco" forest) that were caused by natural disturbances such as hurricanes, landslides, and treefalls. The conceptual framework guiding this research (Fig. 10; Waide & Lugo 1992) focused on four elements:

1. Pattern, frequency, and intensity of disturbance.
2. Environmental properties that vary with disturbance size, age, and origin.
3. Biological properties that vary with environmental properties.
4. System properties that emerge from the effects of disturbance pattern and frequency on the interaction between abiotic environment and biota.

The occurrence of Hurricane Hugo in 1989 concentrated our focus temporarily (Walker et al. 1996a), but an increasing appreciation for the importance of legacies of land-use as well as the cumulative effects of droughts, floods, and additional hurricanes led us to seek a more generalized understanding of the effects of disturbance. Our studies on the impacts of natural disturbance showed how the resistance and resilience of the biota maintained ecosystem structure and function (Covich et al. 1991, Scatena et al. 1996, Silver et al. 1996, Walker et al. 1996a, Ostertag et al. 2003, 2005, Beard et al. 2005). Later phases of LUQ research revealed the strong and lasting impacts of human disturbance in the Luquillo Mountains (Zimmerman et al. 1995, Pringle 1997, Foster et al. 1999, Thompson et al. 2002). These long-lasting impacts suggested that human activities outside the Luquillo Mountains could cause regional changes in

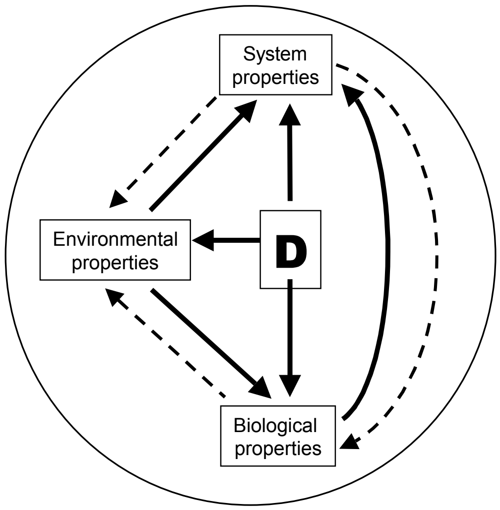

Figure 10 – Conceptual framework (*sensu* Pickett et al. 2005) linking disturbance with the properties of tabonuco forest in the Luquillo Mountains. At a particular locale, disturbances (D) of different pattern, frequency, and intensity will modify the environmental properties of the ecosystem in characteristic ways. Together, the modified environmental properties and direct effects of disturbance lead to changes in biological properties. The interaction among disturbance, the abiotic environment, and the biota influence the emergence of system properties, with feedbacks among the different ecosystem components (dashed lines). Cumulative changes in environmental, biological, and system properties after disturbance determine the subsequent behavior of the system (e.g., the successional trajectory that the ecosystem follows). This conceptual framework is explained in greater detail in Hall et al. (1992) and Willig and Walker (1999).

temperature and rainfall (Scatena 1998, van der Molen 2002, González et al. 2005). Our research focus progressed to an assessment of the ecosystem services, such as clean water, that are delivered to society by the Luquillo Mountains, as well as the impact of human actions on those services (González Caban & Loomis 1997, Scatena et al. 2002, Covich et al. 2004b, Ortiz Zayas & Scatena 2004).

The present proposal describes our continuing efforts to understand ecosystem responses to changing climate and disturbance regime in the Luquillo Mountains. We also begin extending our program to include interactions between the Luquillo Mountains and the surrounding human-dominated ecosystems. The fourth six-year cycle of research in the Luquillo LTER Program (LTER 4, 2006-2012) will focus on the major drivers of change in ecosystem structure and function, and on ecosystem response to those drivers. The drivers include both acute, pulse drivers, such as increased frequency and intensity of extreme events (hurricanes and droughts), and chronic, press drivers, such as gradual changes in rainfall and temperature following alterations in land-use and land-cover (Bender et al. 1984, Lodge et al. 1994). Research in LTER 4 will be based on the following overarching question:

How do changes in disturbance regime and climate alter biogeochemical cycles, biotic structure, and ecosystem services in the Luquillo Mountains and northeastern Puerto Rico?

The proposal includes four research approaches that address this overarching question: 1) maintaining **long-term measurements and experiments** in tabonuco forest, 2) applying our conceptual understanding of tabonuco forest to a **comparative analysis** of rain and elfin cloud forest communities along an elevation gradient, 3) initiating new measurements to characterize aspects of the **gradient from forest to urban ecosystems**, and 4) consolidating our knowledge through **synthesis and modeling**. In the context of these research approaches, three focal questions link nine hypotheses (Table 1) focusing on different spatial scales (Table 2).

2.2 CONCEPTUAL FRAMEWORK

The conceptual framework guiding LUQ research for the next six years builds on our core focus on disturbance and response by adding new projects on regional change and ecosystem services. This framework has developed from results of the previous three six-year LUQ grant cycles and forms part of a long-term plan covering the next four cycles (Section 2.4). As mentioned, research in earlier cycles of LUQ focused principally on the effects of different disturbance types and the response of the biota and ecosystem processes to disturbance (Fig. 11). In the last cycle, we expanded our research focus from tabonuco forest along an elevation gradient into other forest types (Fig. 12). In LTER 4, we will begin to incorporate changes in global climate and regional land-use as important drivers of the disturbance regime and local climate that impinge on the ecosystems of the Luquillo Mountains. In addition, we will further examine the important issue of the services produced by these ecosystems (Farber et al. 2006), and how the quantity and quality of these services change as system structure and functions change. We incorporate these new research goals into an existing conceptual framework (Chapin et al. 1997) that we modify for our purposes (Fig. 13) based on the following ideas:

1. Disturbance is a fundamental component shaping the climatic, biotic, and biogeochemical characteristics of the Luquillo Mountains (Waide & Lugo 1992, Walker & Willig 1999).
2. Models predict that the frequency and intensity of hurricane disturbance are changing in the Luquillo Mountains (Royer et al. 1998, Walsh & Pittock 1998, Goldenberg et al. 2001, Emmanuel 2005, Trenberth 2005, Webster et al. 2005). Both models and empirical data also suggest that rainfall and temperature are changing in the Luquillo Mountains (Scatena 1998, van der Molen 2002, Eastman unpublished, Schaefer 2003).
3. The drivers of these changes are regional and global climate change and human land-uses (deforestation, afforestation, urbanization) (Pielke et al. 1999, 2005, Kalnay & Cai 2003, Emmanuel 2005, Feddema et al. 2005, González et al. 2005, Pielke 2005).
4. The responses to changes in the disturbance regime and climate will be expressed as changes in biotic structure and biogeochemistry (Doyle 1981, Sanford et al. 1991, Covich et al. 1991, 1996, O'Brien et al. 1992, Erickson & Ayala 2004, Silver 1998, Wang et al. 2002a, b, c).
5. These changes will result in new ecosystems characterized by new species compositions and will likely alter structures, biogeochemistry, and ecosystem services in northeastern Puerto Rico.

We locate the three focal questions (Section 2.5) developed in this proposal at the appropriate places (shown in red) in the diagram (Fig. 13) to indicate where we will focus our efforts in LTER 4. Studies of other elements of the conceptual framework will be addressed in future proposals, as discussed below (Section 2.4).

Table 1 – Continuing experiments and measurements and new hypotheses in LTER 4. See Table 2 for the relationship between the categories of studies here (tabonuco forest, other forest types, and coupled forest-urban ecosystems) and scales of study, the LUQ conceptual framework, and modeling efforts.	Tabonuco forest	Other forest types	Coupled forest-urban systems
Canopy Trimming Experiment	X		
Luquillo Forest Dynamics Plot	X		
<u>Question I</u> – What controls variation in C and nutrient fluxes, and how are these variations modified by disturbance?			
Hypothesis 1. *Intra-annual patterns in rainfall or temperature drive temporal patterns in litterfall, litter decomposition, soil respiration, and losses of nutrients and dissolved organic matter (DOM).*	X		
Hypothesis 2. *Conditioning and transport of litter is controlled by extreme weather events.*	X		
<u>Question II</u> – Are climatic changes in temperature, rainfall, and light along the Luquillo Mountains elevation gradient sufficient to explain variation in biogeochemical processes and biotic processes?			
Hypothesis 3. *Litter, soil organic matter (SOM), and DOM fluxes can be explained by a combination of rainfall and temperature variation along the elevation gradient.*		X	
Hypothesis 4. *Distributions of organisms over the elevation gradient cannot be predicted solely by abiotic characteristics.*		X	
Hypothesis 5. *Resistance and resilience do not vary between high and low elevation forests*		X	
<u>Question III</u> – How important are changes in land-use in determining long-term ecosystem biogeochemistry, biotic structure, and services?			
Hypothesis 6. *Urbanization and changes in land-cover have a greater influence on local climate and ecosystem processes than regional or global climatic patterns.*			X
Hypothesis 7. *Increasing intensity of land-use selects tree species with particular life histories and creates new forest ecosystems.*	X		
Hypothesis 8. *Urbanization in a watershed controls the magnitude and variability of in-stream metabolism, detrital processing, energy flow within food webs, and dissolved inorganic N exports.*			X
Hypothesis 9. *Over the past 20 years the quantity of ecosystem products removed from the Luquillo Mountains has increased while the ecosystem processes supplying those products have been altered.*			X

Table 2 – LUQ research spans scales from ecosystem processes within tabonuco forest to coupled forest-urban ecosystems in northeastern Puerto Rico. A conceptual framework at each level of investigation provides a link to appropriately-scaled analytical and simulation models. At the scale of tabonuco forest, material flows in terrestrial and aquatic habitats are strongly driven by abiotic (e.g., the quantity of water moving through the systems) and biotic (e.g., litter quality) properties (Fig. 11). Changes in forested ecosystems within the Luquillo Mountains are related to disturbance patterns and frequency interacting with elevation changes in local climate and species composition (Fig. 12). In northeastern Puerto Rico, regional changes in land-use/land-cover (especially increasing urbanization), coupled with globally-driven changes in climate (e.g., hurricane intensity) and atmospheric deposition affect hydrologic and biogeochemical cycles and the ecosystem services they provide.

Scale	**Conceptual Framework**	**Modeling Framework**
Coupled forest-urban ecosystems	Regional relationships (Fig. 1)	Models under development
Forest zones of the Luquillo Mountains	Landscape relationships (Fig. 12)	CENTURY-L Metacommunity model
Tabonuco forest	Material flow relationships (Fig. 11)	CENTURY SORTIE-PR Trophic Interaction Model (TIM)

2.3 RESEARCH APPROACHES

A large part of LUQ research takes place in El Verde Research Area and the Bisley Experimental Watersheds in the tabonuco forest zone (c. 200-600 m asl) of the Luquillo Mountains (Fig. 1). Other studies are located along the elevation gradient (Section 2.3.2) and in the lowlands between the mountains and San Juan (Figs. 1, 7). Work will be conducted by a team of 25 researchers and educators, representing an array of disciplines (Table 3). Ten of these people have been on the project since it began in 1988. LUQ uses a set of complementary research approaches in its investigations:

2.3.1 Long-term measurements and experiments – The core of LUQ is a series of long-term measurements of environmental, biotic, and system properties designed to reveal the relationships between disturbance and response in the Luquillo Mountains (Table 4). These core measurements are complemented by hypothesis-driven experiments focused on improving our understanding of ecosystem processes related to disturbance in tabonuco forest. Chief among the long-term measurements is the Luquillo Forest Dynamics Plot (LFDP). Long-term plot studies of plants in forest ecosystems support research on: 1) long-term plant community dynamics in response to multiple disturbances (hurricanes, drought, past land-use), 2) niche and life-history characteristics, 3) species diversity and community organization, 4) forest biomass and architecture, and 5) animals and other groups. The LFDP covers 16 ha of tabonuco forest in which c. 70,000 woody plant stems ≥ 1.0 cm dbh are studied through time (Section 2.5.3, Thompson et al. 2004). This large plot is needed to study community ecology in a forest where species richness and the number of rare species are high, in order to include a full community and to study it at the scale on which mechanisms promoting species diversity and coexistence are thought to occur (Condit 1995, Wills et al. 2006, Zimmerman et al., in press). LUQ also includes long-term study plots in the Bisley Experimental Watersheds and along the elevation gradient (next section) in the Luquillo Mountains.

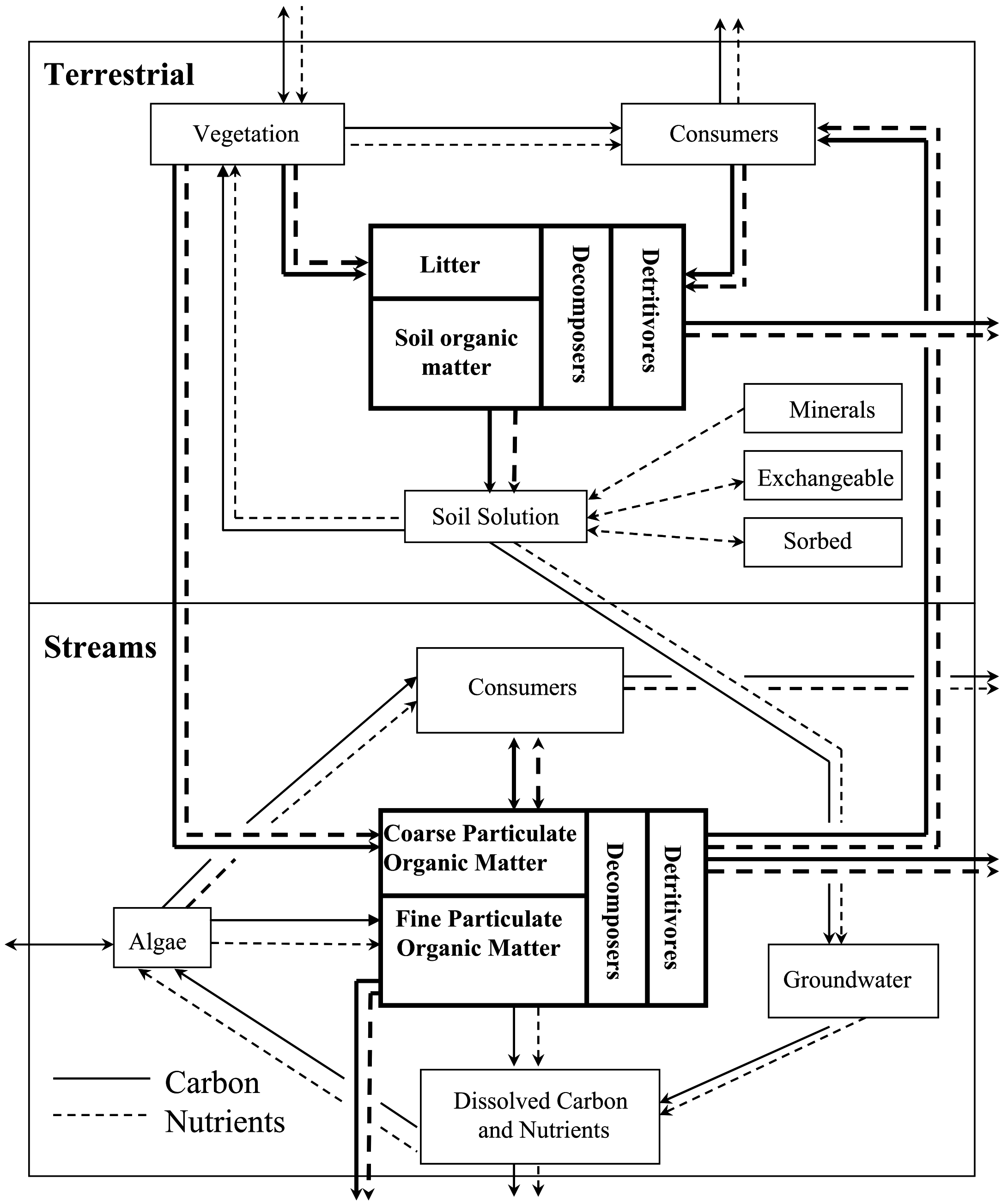

Fig. 11. Generalized box model of material flow in terrestrial and aquatic forested landscapes in the Luquillo Mountains. Compartments and arrows in bold indicate major pools and fluxes of carbon (solid lines) and nutrients (dashed lines) associated with detrital dynamics.

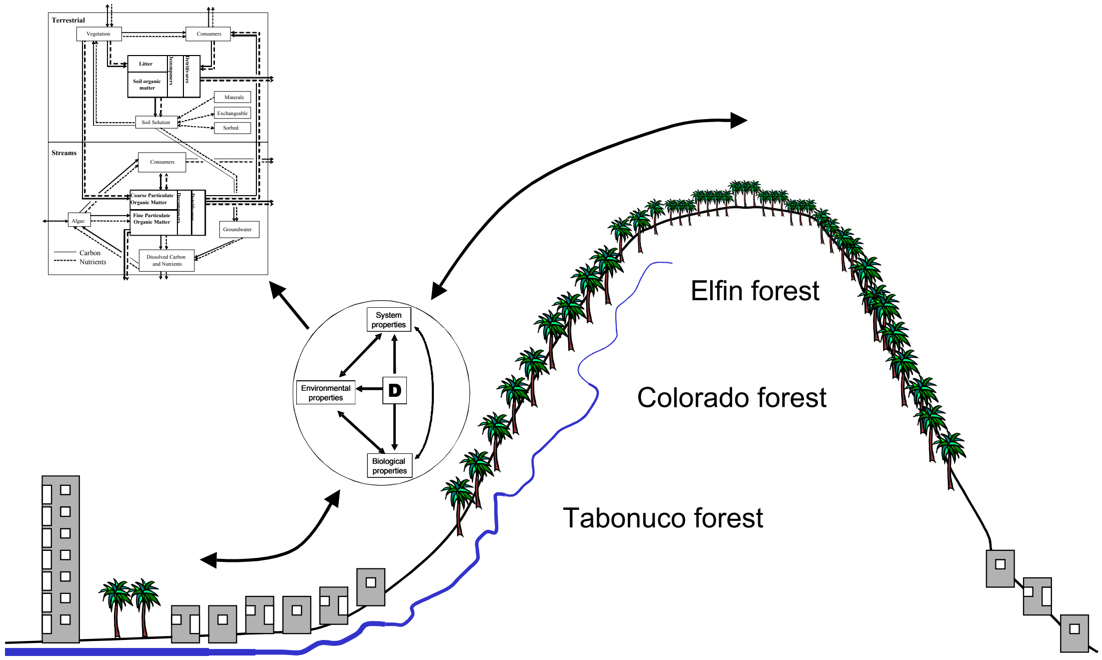

Figure 12 – Conceptual framework linking flows of energy and nutrients (Fig. 11) with changes in disturbance regime and environmental, biological, and system properties (Fig. 10) along an elevation gradient in the Luquillo Mountains. Our conceptual approach addresses the manner in which environmental and biological changes interact with disturbance to affect the storage and processing of carbon and nutrients.

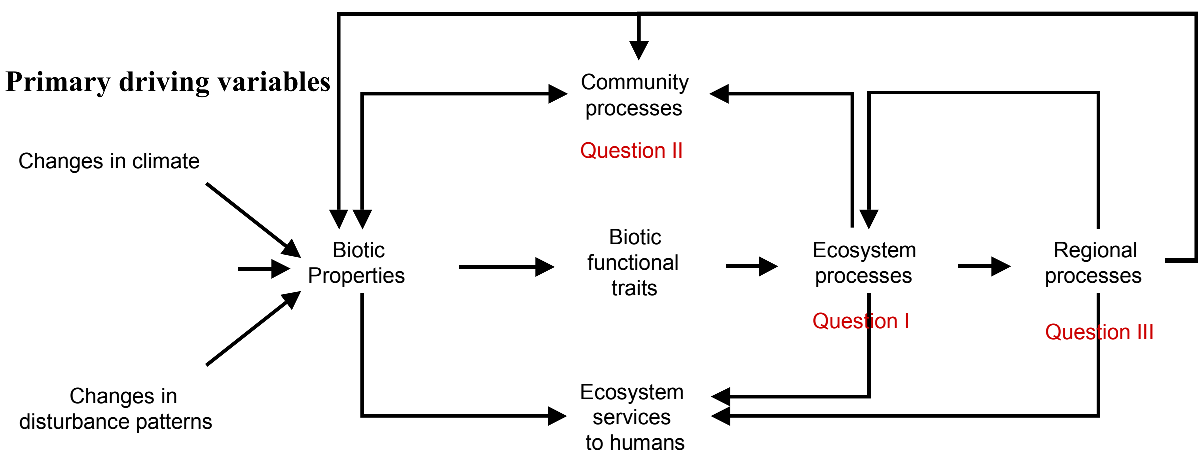

Figure 13 – Changes in primary driving variables affect community, ecosystem, and regional processes directly (not shown for simplicity) as well as indirectly through changes in the biota. In this framework, biotic properties (e.g., species composition, diversity), community processes (e.g., predation, competition), ecosystem processes (e.g., production, decomposition), and regional processes (e.g., land-use/land-cover, urban heat island effects) interact to determine ecosystem services. Ecosystem services are "…the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997). Hypotheses addressed in this proposal focus on questions addressing ecosystem, community, and regional processes (Table 1). Modified from Chapin et al. (1997).

Table 3 – Luquillo LTER researchers. New members in italics. Executive Committee (Section 3) members in bold. Participation in ongoing research and new hypotheses is shown. CTE = Canopy Trimming Experiment (Section 2.3.1); LFDP = Luquillo Forest Dynamics Plot (Section 2.3.1); New hyp. = LTER 4 hypotheses (Section 2.5)

Name	Affiliation	Discipline	CTE	LFDP	New hyp.
Nicholas Brokaw PI	U. Puerto Rico	forest ecology and disturbance	X	X	4, 5, 7
Ariel Lugo PI	IITF, USDA-FS	ecosystem analysis, nutrient cycling, education		X	4, 5, 6, 7, 9
Gary Belovsky	Notre Dame U.	food web modeling	X		4
Sharon Cantrell	U. Turabo, PR	microbial ecology	X		3, 4
Alan Covich	U. Georgia	stream ecology	X	X	2, 4, 8, 9
Todd Crowl	Utah State U.	quantitative analysis, food web dynamics	X	X	2, 4, 5, 8, 9
Grizelle González	IITF, USDA-FS	decomposition, nutrient cycling	X		1, 3, 4
Charles Hall	SUNY-ESF	modeling, climate change	X		6, 9
D. Jean Lodge	IITF, USDA-FS	nutrient cycling, fungal systematics	X	X	1, 2, 3, 4
Olga Mayol	U. Puerto Rico	atmospheric chemistry, climate change			1, 6
William McDowell	U. New Hampshire	aquatic biogeochemistry	X	X	1, 2, 3, 5, 8
Steven McGee	The Learning Partnership	education			–
Eda Meléndez Colom	U. Puerto Rico	information management	X	X	–
Jorge Ortiz Zayas	U. Puerto Rico	urban stream ecology, hydrology, education			8, 9
Catherine Pringle	U. Georgia	stream ecology, water budgets	X	X	4, 8, 9
Alonso Ramírez	U. Puerto Rico	aquatic entomology, climatology	X		1, 4, 6, 8
Barbara Richardson	independ., Edinburgh UK	invertebrate community ecology			4, 5
Frederick Scatena	U. Pennsylvania	geomorphology, climatology	X		1, 2, 5, 7, 8, 9
Whendee Silver	U. California-Berkeley	terrestrial biogeochemistry, climate change	X		1, 3, 5
Jill Thompson	U. Puerto Rico	forest ecology and production	X	X	4, 7
Robert Waide	U. New Mexico	Population ecology, LU/LC		X	4, 5, 6, 7
Lawrence Walker	U. Nevada-Las Vegas	succession, primary production			5, 7
Michael Willig	U. Connecticut	invert. ecology, quantitative analysis	X	X	4, 5, 7
Jess K. Zimmerman	U. Puerto Rico	Forest dynamics, education	X	X	4, 5, 7
Xiaoming Zou	U. Puerto Rico	nutrient dynamics, earthworm ecology	X		1, 2, 3

Table 4 – Long-term observations in the Luquillo LTER. B = Bisley, E = El Verde, L = landslides, P = Pico del Este, LM = other areas in the Luquillo Mountains, CTFS = Center for Tropical Forest Science, Smithsonian Institution.

Measure	Initiation	Source / funding	Site	Frequency
Meteorology				
Rainfall	1975, 1987 1994	NSF, DOE, USFS, Mellon	E, B, P, LM	hourly and daily totals daily NOAA records to c. 1900
Temperature (air and soil)	1975, 1987 1994, 1997	NOAA, NSF, USFS, USGS, Mellon	E, B, P, LM	hourly and daily totals; level-3 stations
Humidity, wind speed and direction	1988, 1994	NSF, USFS, USGS, Mellon	B, E, P, LM	continuous; level- 3 stations
Light (PAR, total radiation, albedo)	1988, 1994	NSF, USFS, USGS	E, B, P, LM	continuous at 4 stations
Hydrology				
Stream discharge	1945	USGS, USFS	LM	daily: 18 historical streams, 12 active
Throughfall	1987	USFS, NSF	B, LM	daily, weekly
Chemistry (*major cations and anions*)				
Rain	1983, 1988	NADP, NSF	E, B, P	weekly samples, bulk and wet only
Throughfall	1988, 1994	UPR, NSF	B	weekly
Streamwater	1983, 1988, 1997 (DON)	UPR,NSF, NASA	B, E, LM	weekly at 8 sites; periodic at 13
Litterfall	1989, 1994	NSF, USFS, Mellon	B, E, P	2 week sampling
Groundwater, soil water, soil oxygen	1988, 1994	NSF, USFS, Mellon, USGS	LM	weekly to periodic
Plants				
Forest structure, biomass, tree species composition	1988	NSF, USFS, Mellon	B, E, LM	1-5 year intervals
Belowground biomass	1988	NSF, Mellon	B, E	yearly
Canopy structure and leaf area index	1989	NSF	E, B	every 3 years
Coarse wood distribution	2002	NSF, USFS	B	every 3 years
Seedling dynamics	1989	NSF, USFS, CTFS	B, E	monthly to yearly
Flowering phenology	1989	NSF, USFS	B, E,	weekly to monthly
Herbivory	2002	NSF	E	yearly
Litterfall, litter decomposition	1987, 1994, 1996	NSF, USFS	B, E, L, P, LM	weekly to periodic
Landslide revegetation	1988	NSF	LM	yearly
Abandoned pasture revegetation	1996	NSF	LM	yearly
Understory structure & composition	1988	NSF	E	yearly
Animals				
Key species inventories	1988	NSF	E, B	yearly
Disturbance				
Treefall gaps, landslides, stream channel change	1988	NSF,USFS, USGS	B, E, LM	yearly to periodic

Chief among the long-term experiments is the Canopy Trimming Experiment (CTE). Hurricanes remove plant biomass from the forest canopy and deposit it as detritus on the forest floor, which in turn alters a range of biotic and biogeochemical processes (Lodge et al. 1991). The CTE will help distinguish the effects of microclimate, detrital inputs, and different functional groups of decomposers in detrital processing and ecosystem resilience after hurricanes. The CTE will also assess the effects of a possible increase in hurricane frequency (Royer et al. 1998) and evaluate long-term predictions of the CENTURY model of soil organic matter accumulation and nutrient dynamics, as parameterized for the tabonuco forest (Sanford et al. 1991). The experiment includes four treatments in each of three blocks. To simulate an increased frequency of hurricanes the treatments will be repeated every six years to at least 18 years total. Each treatment covers a 30 x 30 m area, and these include: 1) canopy trimmed, with trimmed biomass distributed on the forest floor, simulating changes in microclimate and redistribution of biomass, 2) canopy trimmed, with trimmed biomass removed from the plot, simulating changes in microclimate created by the hurricane but without the associated redistribution of biomass, 3) canopy not trimmed, but canopy biomass from a trimmed plot distributed on the forest floor, simulating the changes in redistribution of biomass created by the hurricane but without the associated change in microclimate, 4) canopy not trimmed and no canopy biomass added to forest floor, as a control. Measurements in the CTE plots began one year before treatments were applied and will continue for the duration of the experiment at variable intervals. Measurements include microclimate, soil nutrients, trace gas fluxes, microbial communities, litter inputs and decomposition, and plant and animal community dynamics (Section 2.5.1).

2.3.2 Comparative analyses – We seek to link our conceptual understanding of tabonuco forest derived from long-term experiments and measurements with knowledge of changes in disturbance patterns and driving variables along an elevation gradient in the Luquillo Mountains (Table 5). The Luquillo Mountains, ranging from sea level to 1075 m, present a gradient of climate and vegetation change that extends through five life zones (*subtropical moist forest* to *lower montane rain forest*; Ewel & Whitmore 1973). In addition to tabonuco forest, these life zones include colorado forest (600-900 m asl), elfin forest (900-1075 m asl), and palm forest (edaphic formation at all elevations; Fig. 1). By comparing emergent ecosystem properties along this gradient, we focus on general properties that underlie the dynamics of ecosystems.

2.3.3 Gradients from forest to urban ecosystems – The 23-km distance from the fully protected, 11,000-ha Luquillo Experimental Forest (congruent with the Caribbean National Forest, a U.S. National Forest) in the Luquillo Mountains to the center of San Juan, a city of 1.3 million, represents a steep gradient of land-use, as San Juan expands up against the mountains (Fig. 7). Previous research on land-use conducted by LUQ scientists provides us with the understanding to project future land-use scenarios during the next century (Thomlinson et al. 1996, Thomlinson & Rivera 2000). In LTER 4, we will establish two carefully selected studies along this gradient. By measuring key variables and processes along this spatial gradient, we will gain sufficient understanding to build an integrated model of how changes in climate and land-use are likely to affect tropical ecosystems more generally (Section 2.7).

Table 5 – Luquillo LTER current studies along the elevation and land-use/land-cover gradients in northeastern Puerto Rico.

Climate: elevation: mountain peaks to coastal plain, models; land-use: forest to urban
Soils and nutrients: elevation: soil nutrients, descriptions; land-use: pasture to forest chronosequence
Aquatic physical factors: elevation: physical habitat variables along the stream continuum; land-use: physical factors in forest versus urban streams
Biotic structure - invertebrates: elevation: microbial communities, microarthropod communities, earthworms and soil arthropods, litter animals, invertebrates in bromeliads, terrestrial snail communities, butterflies; land-use: pasture to forest earthworm chronosequence
Biotic structure - plants and vegetation: elevation: tree and shrub populations, composition and structure by forest type, including riparian forest, various animal species; land-use: pasture to forest chronosequence, post-coffee and old-field succession chronosequences, land cover changes
Biotic structure - aquatic communities: elevation: algal communities, food webs and detrital processing along river profiles, macroinvertebrate communities, freshwater snail migration, riparian tree communities land-use: fauna of forest and urban streams
Biogeochemistry - productivity: elevation: primary productivity, total ecosystem respiration, litterfall production; land-use: pasture to forest chronosequence, primary productivity
Biogeochemistry - decomposition: elevation: soil respiration and litter decomposition, role of micro-invertebrates, SOM accumulation, soil labile carbon; land-use: pasture to forest chronosequence
Biogeochemistry - nutrient cycling: elevation: soil carbon modeling and CO_2 efflux, carbon dynamics in upper elevation forests, methane dynamics, soil phosphorus fractions and phosphorus cycling, nitrogen cycling, soil oxygen, C, N, Fe, Al, and texture, soil redox dynamics and biogeochemical cycling, Fe (III) reduction rates, concentrations of Fe, watershed dissolved organic carbon and nutrient fluxes, relationship between soil and streamwater dissolved organic carbon export
Biogeochemistry - aquatic: elevation: changes in algal production, relationship between soil and streamwater DOC export, spatial distribution of streamwater chemistry, changes in food webs and detrital processing; land-use: chemical features of forest versus urban streams

2.3.4 Synthesis and modeling – We emphasize synthesis of existing research results within our own site and across sites in accordance with the emerging goals of the LTER Network strategic plan. Our approaches to synthesis include working groups focused on specific research agendas, implementation of new analytical approaches to existing data, and simulation modeling (Section 2.7, Table 2). The Trophic Interaction Model (TIM) captures the relationships between biotic interactions and material flows within an ecosystem, and it links forests and streams. CENTURY is an ecosystem model that we have adapted for use over the entire Luquillo Mountains landscape (CENTURY-L; Wang & Hall 2004). A simulation model describing community response to disturbance (SORTIE-PR, Section 2.5.3), as well as analyses using a metacommunity framework, provide information to parameterize CENTURY over space and time.

2.4 LONG-TERM PLANNING IN THE LUQUILLO LTER

The research we propose for the next six years is the first phase of ongoing, adaptive planning to link the dynamics of forest and urban ecosystems. It has been evident since the inception of LUQ that some major drivers of forest dynamics arose from human activities outside of the forest (Section 1.2). In a plenary address at the recent meeting of the Ecological Society of America, José Sarukhán emphasized the importance of changing natural systems: "Conversion of natural systems into human-managed systems is by far the most important driving force in the loss of genes, species, populations, or whole ecosystems, locally and globally." Further research on the ecosystems of the Luquillo Mountains must incorporate these links between forest and urban ecosystems for a complete understanding of ecosystem change.

The natural communities of the Luquillo Mountains provide many ecosystem services to humans in surrounding urban areas. The provision of clean water for human consumption and industrial use is the most important of these services. Water is already a major component of our research, and in this proposal we strengthen our focus on water as a unifying theme. Each of our nine hypotheses considers water either as: 1) an important component of the climate (precipitation); 2) an important regulator of biogeochemical processes, which in turn influence biotic structure; 3) an essential element affecting community structure and dynamics in aquatic and terrestrial systems, or 4) a critical and limiting ecosystem product of the Luquillo Mountains. Initial efforts to link water and ecosystem services have been implemented through a recent Biocomplexity grant that focuses on stream drainage and road networks in the Luquillo Mountains that influence human access to river-based recreation and harvest of riverine fishes, shrimps, and crabs (<http://biocomplexity.cnr.colostate.edu/articles.htm>).

We do not underestimate the challenge inherent in building links between urban and forest ecosystems (Farber et al. 2006). Our current proposal represents the first step in a long-term research plan. Such an expansion of LUQ research will require the incorporation of new disciplines, measurements, and experiments linked in a multi-dimensional framework (Pickett et al. 2005). As with our past work, future work will benefit from a range of funding sources, with LTER as the anchoring project, and will involve existing (e.g., Forest Service) and new partners (e.g., USGS, US EPA, University of Puerto Rico-Mayagüez). We are convinced that a long-term, detailed understanding of the Luquillo Mountains and environs will require us to address not only the acute, pulse disturbances inherent in forest ecosystems, but also the chronic, press disturbances arising from coupled human systems that can result in complex, non-linear, cascading dynamics (Pielke et al. 1999, Peters et al. 2004, Burkett et al. 2005).

2.5 LUQUILLO LTER 4 RESEARCH: Questions, Hypotheses, & Workplans

The following questions and hypotheses will be addressed in LTER 4 to build on our past research on disturbance, directional ecosystem change, and ecosystem processes and services in northeastern Puerto Rico. The selected projects focus on key components of the conceptual framework described above. These projects include studies of how climate and disturbance control biogeochemical processes and biotic structure, how these vary along the elevation gradient and with past and present land-use, and how environmental change is affecting streams, and a key product – water. (Names in parentheses after hypotheses below indicate project leader [first name given] and other team members.)

2.5.1 <u>Question I</u> – What controls variation in C and nutrient fluxes, and how are these variations modified by disturbance?

The Luquillo Mountains are characterized by warm temperatures and high rainfall throughout the year (García Martinó et al. 1996). Such tropical climates are often referred to as aseasonal and are thought to have little temporal variation in ecosystem processes. However, many ecosystem processes in the Luquillo Mountains exhibit well defined seasonality and links to climate (Odum & Pigeon 1970, Scatena et al. 1996). Quantifying and understanding these relationships is essential for determining the sensitivity of tropical forest biota and biogeochemical cycling to climatic and environmental change (note "Question I" in Fig. 13).

This question and associated hypotheses focus on how climate and disturbance history affect inter- and intra-annual variation in carbon and nutrient fluxes in tabonuco forest in the Luquillo Mountains. They explore a critical nexus of interactions that link abiotic and biotic variability with ecosystem processes (Fig. 12).

Hypothesis 1. *Intra-annual patterns in rainfall or temperature drive temporal patterns in litterfall, litter decomposition, soil respiration, and losses of nutrients and dissolved organic matter* (*DOM*). *Disturbance alters the intra-annual patterns in litterfall, soil respiration, and DOM and nutrient losses independently of rainfall and/or temperature*. (Silver, Mayol, McDowell, González, Scatena, Ramírez, Lodge, Zou)

Background – LUQ research has documented intra-and inter-annual variation in rainfall and stream flow (Scatena 2001, Schaefer 2003), rainfall chemistry (McDowell et al. 1990), litterfall and phenology (Lugo & Frangi 1993, Zou et al. 1995, Scatena et al. 1996), soil oxygen and respiration (Silver et al. 1999 and in prep.), soil nutrient pool size (Silver et al. 1996), soil microbial biomass (Ruan et al. 2004), stream water chemistry (McDowell & Asbury 1994, Schaefer et al. 2000), and the life-history cycles of terrestrial and aquatic organisms (Reagan & Waide 1996, Covich & McDowell 1996). Our previous research has also demonstrated how these processes are linked to disturbance and land-use. Moreover, weather events (e.g. wind storms, heat waves) and catastrophic disturbances such as hurricanes can cause pulses of litter (Lodge et al. 1991, Scatena et al. 1996, Ostertag et al. 2005), microbial activity (Lodge et al. 1994), tissue growth or mortality (Silver & Vogt 1993, Beard et al. 2005), changes in soil chemistry (Silver et al. 1994) and changes population structure (Walker et al. 1991). Data collected in the previous LUQ cycles indicate that several factors can contribute to within-year variability in ecosystem processes and response to disturbance. Rainfall, daily air temperature, cloud cover, and solar isolation oscillate over the course of a year (Wang et al. 2002b). Although the magnitude of these seasonal differences is relatively low compared to other environments, they can drive patterns in biogeochemical cycling and phenology (Lodge et al. 1994). Nevertheless, relationships between seasonal environmental conditions, disturbance history, and biogeochemical or biotic processes are complex. For example, the high thermal capacity of soils decouples mean monthly soil and air temperature (Brown et al. 1983, LUQ website data). Whereas the litter layer can dry in a few days, soil drying is also buffered by hill slope drainage patterns and can take three to six weeks to respond to drought (Lodge 1993, 1996). Likewise, temporal variability in nitrate flux is influenced by variations in stream flow, but also correlates with seasonal variation in litterfall (McDowell & Asbury 1994) and time since watershed scale disturbance (Schaefer et al. 2000). Soil oxygen concentrations are driven by rainfall at a landscape scale, but by soil hydrology and microbial populations at the landform scale (Silver et al. 1999, Wang et al. 2002c, Ruan et al. 2004).

Data recently collected during a 21-month pre-treatment calibration period designed to quantify any inherent variability among the CTE plots (Section 2.3.1) demonstrate both considerable temporal variability in many ecosystem response variables and strong spatial synchronization among plots. Flux of CO_2, for example, is highest in July and August and lowest in January and February (Fig. 14), and appears to be driven primarily by seasonal differences in temperature. This seasonality suggests that if long-term climate alone is driving these patterns in intra-annual variability, then addition of litter alone will not change the temporal variability of CO_2 flux, although it may change the magnitude of the flux (the "disturbance effect"). Alternatively, both the flux magnitude and temporal variability may change with disturbance, suggesting that intra-annual patterns in CO_2 flux are not solely due to temperature but are related to a complex combination of temperature and C availability.

Workplan – We will use experiments associated with the CTE and data collected as part of our ongoing environmental modeling efforts to evaluate this hypothesis. In the CTE we will continue to monitor soil and air temperature and relative humidity continuously, litterfall every two weeks, and soil solution chemistry and trace gas flux monthly. Trace gas fluxes (CO_2, CH_4, N_2O) are measured from surface chambers. Infrared detection of CO_2 will be conducted *in situ* (LiCor 6400) and samples are taken for gas chromatographic analysis of CH_4 and N_2O, using FID and ECD detectors, respectively. Soil solution nutrient chemistry is measured in porous cup ceramic tension lysimeters installed at 40 cm depth. Samples are analyzed for pH, NH_4^+, NO_3^-, PO_4^{3-}, Na^+, K^+, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Cl^-, DOC, and DON using spectrophotometric analysis, ion chromatography, and high-temperature combustion, respectively. Litterfall is measured in litter baskets placed 1 m above the forest floor. To test this hypothesis we will compare intra-annual variability with and without changes in microclimate and detrital inputs. Because there is no *a priori* reason that intra-annual variability should follow strictly seasonal patterns, or follow any other regular periodicity, we will compare treated plots to controls both before and after initiation of the experiment. Our pre-treatment results show no statistically significant difference between treatment and control plots for any of our response variables, using repeated measures ANOVA.

Environmental data collected during and before LTER 4 will also be analyzed to address this hypothesis. While all of these data have been analyzed to address specific problems, environmental data collected at the same time but in different places in the forest have not been thoroughly cross-analyzed. Fortunately we have overlapping time series of litter production (Scatena et al. 1996 and in prep, González et al. in review, Silver et al. in prep), litter decomposition (Bloomfield et al. 1993, LIDET data set), soil respiration (Silver et al. in prep.), and nutrient concentrations and fluxes of rainfall, throughfall, and streamflow (McDowell & Asbury 1994, Schaefer et al. 2000, McDowell et al. in prep.) from various locations in the Luquillo Mountains. These data sets will be combined and used to explore intra-annual patterns in ecological processes in relation to climate, weather, and disturbance events.

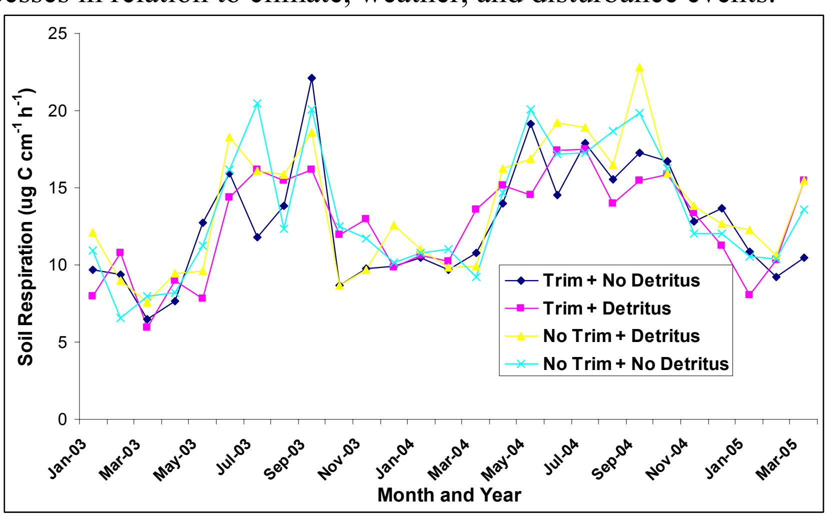

Figure 14 – Flux of CO_2 from soils in the Canopy Trimming Experiment (Section 2.3.1) before experimental manipulations. Note the good agreement between plots prior to treatment, and the seasonality in fluxes.

During LTER 4 we will compare trends in temperature, wind speed, rainfall and throughfall with trends in litterfall, stream water chemistry, soil gas fluxes, and litter decomposition, using parametric and non-parametric correlative analyses. Time series and multiple regression approaches will also be used to examine the effects of lagged environmental variables on biogeochemical responses. Similar approaches have been successfully used in the past and indicate that antecedent environmental conditions can explain a significant amount of variation in soil and water chemistry (McDowell & Asbury 1994, Silver et al. 1999, Ruan et al. 2004).

Hypothesis 2. *The intra- and inter-annual variation in the conditioning of litter and its transport from hill slopes to headwater streams is controlled by prolonged droughts, floods and other extreme weather events. This temporal variation influences detrital structure and quality, nutrient cycling, and stream invertebrate communities. Predicted changes in the intensities of droughts and floods will likely have long-term effects on stream biodiversity and detrital processing in headwater streams*. (Covich, Lodge, Crowl, Scatena, McDowell, Zou)

Background – Leaf litter enters stream channels through direct inputs from adjacent riparian forest plants and from downstream transport throughout the drainage network during base flows and storm flows. In addition, fallen leaves decay on the forest floor and move downslope into streams, where they enter the aquatic detrital food web (Lodge & Asbury 1988, Scatena et al. 1996, Vogt et al. 1996). Thus the movement of litter from hill slopes to stream channels links terrestrial and aquatic food webs. Export from forested slopes increased stream litter export about 20% in a temperate forest (McDowell & Fisher 1976), but export from slopes in tabonuco forest may be less (Scatena et al. 1996, Vogt et al. 1996), partly because litter fungi create terrestrial debris dams (Lodge & Asbury 1988).

Both the litter delivery rate to streams and its quality as detritus for stream invertebrates are affected by patterns of rainfall, especially extreme events (Schaefer 2003). The rate of this leaf-detrital flux to streams reflects rainfall variability because litter accumulates and slowly decomposes during dry periods and is washed into permanent stream channels during the next large storm flow. The quality and quantity of the detritus for stream invertebrates depend on the species composition of the litter and the type of "pre-conditioning" by fungi before it enters streams (Crowl et al. 2006). Pre-conditioning depends on fungal species, which in turn depends on soil and litter wetness, which is a function of topography and recent variations in rainfall. Climate models predict a future of more variable rainfall and increased inter-storm periods (Schaefer 2003). This increased variability and intensity of flood- and drought-events is expected to affect both the variability in quantity and frequency of leaf flux across the forest floor into streams and the quality of detrital leaf flux.

Increased variability in rainfall and resulting changes in detrital leaf flux may also affect hill slope erosion and fluvial sedimentation. Hill slope erosion is influenced by litter dynamics because basidiomycete fungi bind together to form "litter mats", which shield soil surfaces from rain impact and erosion (Lodge & Asbury 1988). Mat-forming litter fungi, however, are sensitive to droughts that dry the litter layer and reduce its protective function (Lodge 1993, 1996; Lodge & Cantrell 1995; Miller & Lodge 1997). More variable rainfall may not only influence the binding effect of basidiomycetes litter mats but also produce more variable temporal pattern in the formation and breakup of detrital dams on land and in streams. These debris dams affect nutrient availability and habitat structure for stream invertebrates. Sediment inputs can periodically accumulate and bury leaf litter and thus decrease the availability of leaf-litter food resources to benthic detritivores. More variable sequences of droughts and floods will likely break down fungal mats and increase the export of leaf litter and sediments from the forest floor to the stream. This export of leaf litter input may have negative effects on aquatic life, due to the altered quality of leaf litter for detritivores (Crowl et al. 2006) and to the associated increases in sedimentation (Gellis 1993). Increased leaf transport can also have negative effects on ecosystem services, due to increased reservoir sedimentation.

Workplan – To quantify the detrital linkages between hill slopes and aquatic systems we will determine the detrital quality of forest floor leaves, measure the amount of leaf and surface soil movement downslope from the forest floor into and through the network of streams, and compare detrital food webs across this network. Litter mat density will be manipulated on some slopes above pools in a stream at El Verde and in the Bisley watersheds to increase or decrease the density of terrestrial debris dams formed by the mats and simultaneously alter the detrital quality. Effects on soil erosion of litter mat manipulation and fluctuations in mat density in response to moisture will be assessed using a combination of Gerlach troughs and erosion pins (Basnet 1992, Larsen et al. 1999). Sediment export is measured more readily at the slope-stream interface than in streams, because sediments tend to accumulate behind organic matter debris dams in stream channels and are flushed out episodically during extreme high-flow events (Gellis 1993). Sample collection will be done to overlap with the 2 week collections of litter transport at the Bisley stream gauge. Additional stream litter traps will be deployed on other small and temporary steams to increase replication. Rates of leaf and soil export from selected steep slopes to stream channels will be measured at biweekly intervals, using upslope facing litter traps, and correlated with rainfall patterns. Intra-annual variation in rainfall effects will be correlated with expansion or contraction and extinction of individual mats. Effects of microbial preconditioning on detrital quality for stream invertebrates (freshwater shrimps and crabs) will be determined using feeding choice experiments in experimental streams as well as in aquaria, and correlated with changes in decapod densities in pools below manipulated slopes (Covich et al. 2003, 2006, Wright & Covich 2005a, 2005b). Marked leaves and branches entering the stream channels will be tracked as they are transported downstream to determine changes in leaf breakdown and in formation and breakup of aquatic debris dams. These organic accumulations increase retention of litter associated with rocky substrata and stream-bank root wads relative to changes in rainfall and stream flow and alter habitat for benthic invertebrates (Pyron et al. 1999).

Litter flow in the Bisley streams has been monitored every two weeks since the start of LUQ. This effort has focused on quantifying the annual carbon flux from watersheds (Scatena et al. 1996). During LTER 4, these data will be analyzed and compared with new data to determine relationships among the flux of litter detritus in streams, rainfall, and streamflow. Additional studies in El Verde streams have quantified differences in leaf deposition and export in streams by tree species (Crowl et al. 2006). During LTER 4 we will collect additional data to determine relationships between rainfall, streamflow, the hill slope collections described above, and the nutrient quantity of litter flow. The goal of this effort is to explicitly link terrestrial disturbance to stream ecosystem function.

2.5.2 Question II – Are climatic changes in temperature, rainfall, light and wind along the Luquillo Mountains elevation gradient sufficient to explain variation in biogeochemical processes and biotic processes?

Here we propose to explore linear and non-linear trends in climate with elevation in the Luquillo Mountains as drivers of ecosystem processes and the distribution of organisms ("Question II" in Fig. 13). By improving our understanding of the relative importance of biotic and abiotic factors in determining the distribution of organisms over spatial gradients in tropical mountains, we will increase our ability to understand the effects of projected future temporal changes in these factors resulting from climate change and increased disturbance frequency. By examining resistance and resilience of low- and high-elevation forests, we link our studies of disturbance and spatial gradients.

Hypothesis 3. *Changes in rates of litter decomposition, soil organic matter* (*SOM*) *decomposition, and DOM fluxes can be explained by mean annual temperature, rainfall, or both combined, along the elevation gradient*. (González, McDowell, Silver, Cantrell, Lodge, Zou)
Background – There are distinct trends in several ecosystem attributes along the elevation gradient in the Luquillo Mountains. Some pools and processes change linearly; for example litterfall rates decrease linearly along the elevation gradient (Weaver & Murphy 1990), while soil organic matter pools increase linearly (McGroddy & Silver 2000, Wang et al. 2002c). However, litter decomposition and soil CO_2 effluxes follow a stepwise trend that suggests threshold effects (McGroddy & Silver 2000, Silver et al. in prep.).

Work plan – In studies along a climate gradient it is difficult to distinguish the effects of climate per se from the effects of changing plant community composition. Fortunately, in the Luquillo Mountains forests strongly dominated by sierra palm (*Prestoea montana*) occur all along the elevation gradient; whereas tree composition in dicotyledonous forest changes (Brown et al. 1983). For our studies of ecosystem processes on the elevation (climate) gradient, plots in palm forests will be a control for plant community composition along the climate gradient, while paired plots in the dicot forests will allow us to determine the interaction among plant community composition, climate, and ecosystem processes (cf. Richardson et al. 2005). We will characterize each plot for soil decomposer communities, soil microbial communities, and soil chemical and physical properties. To determine potential climate controls on soil C and N fluxes we will install replicate intact soil cores in each plot, fitted with Prenart disk lysimeters to capture leachate at the bottom of the core. Cores will be incubated *in situ* for 1 to 4 years during which time we will sample soil respiration, soil CH_4 and N_2O fluxes, and DOM in leachate six times per year. Harvested cores will be analyzed for microbial community composition, soil nutrients, and C fractions. Our goal is not to determine a highly precise annual flux rate, but to compare relative rate processes across treatments at several different points throughout the year and across years. To determine potential controls on litter decomposition we will conduct a factorial litter transplant experiment. Treatments will include: 1) litter collected *in situ* (palm or mixed dicotyledonous plants) as a control, 2) litter transplanted between palm and dicotyledonous sites within an elevation to estimate the impacts of cover type while controlling for climate, 3) control litter (palm) transplanted to all sites along the elevation gradient to estimate the effects of climate within a given litter type, and 4) mixed litter decomposed at all sites along the elevation gradient to determine the interactions of climate and litter quality. Replicate bags will be collected five times over two years and analyzed for decomposer community composition, mass loss, and nutrient and C chemistry. We will use regression approaches, path analytical techniques, and canonical correspondence analysis to determine axes of variation for climate, biotic structure, and biogeochemistry among treatments along the elevation gradient.

Hypothesis 4. *Distributions of terrestrial organisms over the elevation gradient of the Luquillo Mountains are more closely related to changes in biotic characteristics* (*e.g., forest composition and physiognomy*) *than they are to patterns in abiotic characteristics* (*e.g., temperature, rainfall, light, and wind*). *Similarly, the distributions of aquatic organisms are more closely related to geomorphological discontinuities in the stream channel and changes in the quality of leaf litter* (*e.g., a higher proportion of palm leaves*) *than to patterns in abiotic characteristics*. (Willig, Waide, Brokaw, Belovsky, Cantrell, Covich, Crowl, González, Lodge, Lugo, Pringle, Ramírez, Richardson, Thompson, Zimmerman)

Background – We have used a multivariate approach incorporating abiotic and biotic ecosystem attributes to explain the distribution and abundance of organisms along environmental gradients in the Luquillo Mountains (Willig & Walker 1999). A framework that coupled this concept with disturbance provided a useful method for understanding and predicting the trajectory of disturbance-initiated succession. In this framework, future ecosystem states are derived from present abiotic and biotic system characteristics through successional processes in response to disturbance. Ecosystem change is a function of the cumulative effects of changes in forcing functions arising from the disturbance regime (Walker & Willig 1999). In this section, we extend these ideas from tabonuco to other forest types by examining the relative importance of biotic and abiotic factors in determining species distributions along an elevation gradient.

As our focus expanded from tabonuco forest to the whole mountain landscape, we needed more information about the relationship between species distributions, community composition, and changes in climate with elevation. We focused first on the distributions of trees with elevation and the driving variables that influenced these distributions (Barone et al. in review, Gould et al. in review). Measures of tree community composition at 50 m intervals along three elevation transects indicated that upper elevation communities are nested subsets of lower elevation communities (Barone et al. in review). Upper boundaries of species distributions were significantly clustered near 500, 700, and 900 m on the transects (Fig. 9). Species turnover and coherence (Leibold & Mikkelson 2002) were also significant on all transects. These results suggest a distributional pattern that conforms to neither a Clementsian nor the Gleasonian community model, but a level of structure between these two views. One key species, the sierra palm (*Prestoea montana*) occurs in pure stands at all elevations wherever appropriate conditions exist.

While many studies have documented the distributions of organisms along the elevation gradient in the Luquillo Mountains, few attempts have been made to compare these distributional patterns to theoretical models and link them to causal mechanisms (but see Silver et al. 1999). In general, species density and richness decline with elevation and correlate with a decline in net primary productivity along elevation gradients, but this is not true for all taxa (cf. Rosenzweig 1995, Brown & Lomolino 1998). Details of distribution patterns along the gradient in the Luquillo Mountains are known only for trees (Fig. 9, Barone et al. in review), aquatic snails, shrimps (Lugo 1985, Greathouse & Pringle in press), land snails (Alvarez 1997), bromeliad inhabiting invertebrates (Richardson 1999, Richardson et al. 2000), and litter invertebrates (Richardson et al. 2005). These studies show variation in patterns of distribution, growth rates and body size with elevation. Adaptations to increasing elevation appear to be responses to secondary biotic and abiotic factors, and not simply responses to the direct effects of climate.

The plots established in LTER 3 for tree surveys and adjacent stream reaches provide the infrastructure necessary for studies of other taxonomic groups along gradients of abiotic and biotic change. In the present proposal, we expand the range of target organisms to include vertebrates (birds, amphibians, reptiles), invertebrates (aquatic and terrestrial understory insects), soil and leaf microbes, understory plants, and the communities inhabiting tank bromeliads. In addition, we expand existing work in the distribution of families of litter invertebrates (Richardson et al. 2005) to include patterns of species distribution. We build on work showing that characteristics of litter invertebrate communities in the Luquillo Mountains (abundance, species richness, uniformity of communities) are more strongly related to biotic factors (e.g., forest composition) than to the direct effects of abiotic factors (e.g., temperature and rainfall; Richardson et al. 2005). In stream ecosystems, the distributions of aquatic organisms are related to breaks in geomorphology (e.g., waterfalls; Greathouse 2005) and changes in the characteristics of leaf litter (Crowl et al. 2001). The goal of the proposed measurements is to establish the relationship between the distribution of organisms and the driving variables of climate, forest type, geomorphology, and food source and to determine how far this relationship varies among taxa.

In addition to our focus on distributional patterns, we will link community characteristics to ecosystem processes along the elevation gradient (Fig. 12) through the Trophic Interaction Model (TIM), a food-chain model developed in the present grant period. Using TIM, we will examine the relative importance of biotic interactions and abiotic factors in determining changes in the abundances of fast and slow decomposing plant species, nutrient cycling, and NPP along the elevation gradient. We will use measurements of plant, consumer, and decomposer functional groups and climate made under Hypotheses 3 and 4 to parameterize TIM at different elevations and to evaluate the relative influence of these factors on carbon and nutrient dynamics (Fig. 11). In addition, we will compare carbon and nutrient dynamics in matched dicotyledonous forest and palm plots at the same elevation (as part of Hypothesis 3). The palm *Prestoea* is a C3 plant whose leaf anatomy (with nodules of silica) makes it difficult for invertebrates to consume and microbes to break down. Palm forest litter has lower decay rates, post-hurricane, than all other forest litter types (Ostertag et al. 2003). Therefore, we would expect differences in C and N dynamics between palm and dicotyledonous forest plots.

<u>Workplan</u> – We will use plots established in the present grant period (Barone et al., in review) for tree measurements (0.1 ha plots at 50 m elevation intervals from 250-1000 m asl in two watersheds) and other plots to survey and map the distribution of terrestrial taxa with elevation. For a subset of these plots located in tabonuco, colorado, and elfin cloud forest, we will select matching plots in palm forest at the same elevation. Nearly pure stands of the sierra palm (*Prestoea montana*) occur through the elevation gradient adjacent to forest stands. We will use these matched plots to separate the effects of changing biotic structure (e.g., forest composition and physiognomy) from the abiotic factors that vary with elevation (Richardson et al. 2005). Surveys of each target organism will be based on methods that we are using for our long-term population monitoring in tabonuco forest. We will also measure the distribution and abundance of stream organisms in watersheds containing our study plots. Measurements of temperature, rainfall, soil moisture, soil oxygen, and other abiotic factors will be conducted in a subset of the plots to provide information to correlate with the distribution of organisms.

Results from the surveys will be used to test predictions from competing models of community structure from the literature (e.g., checkerboard, nested subsets, Clementsian, Gleasonian, even spacing, and random; Leibold & Mikkelson 2002) and will provide data to establish the relationships between driving climate variables, forest structure, and distribution of organisms. We will use the approach of Leibold & Mikkelson (2002) to examine the structure of meta-communities along the gradient by calculating coherence, species turnover, and boundary clumping for species and sites. Using path analytical techniques and canonical correspondence analysis we will extract axes of variation for climate, biotic structure, and biogeochemistry for comparison with changes in community characteristics along the elevation gradient. These analyses will provide future opportunities to examine the effects of disturbance on meta-community structure.

Hypothesis 5. *Resistance and resilience, as measured by changes in abiotic environment, biotic structure, and biogeochemistry over the past 16 years, have not varied between high and low elevation forests over a series of recent hurricanes, despite large differences in community composition, forest structure, and rates of ecosystem processes*. (Waide, Brokaw, Crowl, Lugo, McDowell, Richardson, Scatena, Silver, Walker, Willig, Zimmerman)

Background – The repeated disturbances in the Luquillo Mountains since Hurricane Hugo in 1989 provide the chance to examine differences in ecosystem resistance and resilience over an elevation gradient. Resistance can be measured as the inverse of displacement in abiotic or biotic space (Hall et al. 1992), whereas resilience is the time required to return to a reference state (or the instantaneous rate of return in that direction). Moreover, theory and observation suggest that resistance and resilience are inversely related (Holling 1973, Grimm 1996, Herbert et al. 1999).

Previous, short-term results from LUQ suggested that lower elevation, more productive tabonuco forest was less resistant and more resilient to the effects of Hurricane Hugo than the upper elevation, less productive elfin forest. For example, leaf-fall returned to pre-hurricane levels more quickly in tabonuco forest than in elfin forest (Walker et al. 1996b, Zimmerman et al. 1996). Comparisons of the recovery of biomass after road abandonment also indicates that the cloud forest recovers at a much slower rate than roads at lower elevations (Olander et al. 1998). However, the elfin forest appears to be more resistant to invasions by non-native species than the lower elevation forests. In contrast, longer-term measurements of response to disturbance in these forest types suggest that a spurt of growth in elfin forest 15 years after disturbance compensates for earlier slower rates and results in roughly similar rates of biomass resilience after about 20 years (Weaver & Murphy 1990). Moreover, when we control for disturbance intensity and initial biomass, resistance may also be similar in these two forest types, if not higher in the elfin forest. We have sufficient data to examine other ecosystem characteristics for similar patterns.

Our approach facilitates comparison at different points along the elevation (climatic) gradient by allowing us to quantify differences in the intensity of response as the length of the vector of net change in multi-dimensional biotic space or abiotic space (Willig & Walker 1999). Response to disturbance can be quantified as the rate of return to a previously specified reference state in multidimensional 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.

Work plan – Using long-term monitoring observations collected by LUQ and associated projects, we will characterize the resistance and resilience of tabonuco and elfin forest plots to repeated disturbance in terms of the following characteristics: 1) forest structure (tree height, density), 2) forest composition, 3) nutrient cycling, 4) productivity and decomposition, 5) flower and fruit phenology, and 6) the abiotic environment (temperature and wind speed). For example, we will test the proposed inverse relationship between resistance and resilience by quantifying hurricane damage to, and recovery of, forest structure along the elevation gradient. In 1988, before Hurricane Hugo, we measured three-dimensional forest structure in three hectare-sized plots, one each at 350 m, 700 m, and 1000 m. We have remeasured structure in these plots after Hurricane Hugo and at intervals since then (Brokaw & Grear 1991, Brokaw et al. 2004). These before-and-after hurricane data, with additional data to 20 years after Hurricane Hugo, will enable us to assess immediate structural damage by the storm (resistance) and post-hurricane time needed for recovery to pre-hurricane structure (resilience) at these three elevations.

Resistance and resilience of the hydrologic cycle will be quantified by analyzing stream flow hydrographs and changes in water chemistry. Hydrograph separation techniques have already been used to identify flow patterns and watershed responses in Luquillo watersheds (Rivera Ramírez et al. 2002, Schellekens et al. 2004) and will be extended to other gauged sites in different forest types and elevations. Moreover, runoff per unit precipitation, and the response and the recovery times of hydrographs will be calculated and compared to quantify the resistance and resilience of different watersheds. The long-term response of stream chemistry to disturbance in tabonuco and elfin forest sites will be quantified by comparing changes in chemistry in our long-term gauged sites in tabonuco forest (Table 4) with samples taken periodically from high-elevation elfin forest sites since 1984 (McDowell & Asbury 1994, Schaefer et al. 2000, McDowell unpub.).

We will assess the resistance and resilience of litter nutrient cycles by comparing the response of litter nutrient cycles to specific climatic events in tabonuco, colorado, and elfin forests (Scatena et al. 1996, Silver et al. 1999). Specifically, we will compare and contrast our long-term time series of litter fall and climate from different forest types to assess the relationship between specific climatic events (e.g. rainfall, wind speed) and litter fall. During LTER 4 we will also compare nutrient re-translocation rates and changes in fluxes following specific meteorological events.

This approach will require collection of new, event-specific data, maintenance of our long-term data collection, manipulation of existing long-term data sets from multiple projects to quantify resistance and resilience, and the application of appropriate statistical comparisons. One of the end results will be an integrated database of measures of resistance and resilience that we will add to after future disturbances.

2.5.3 Question III – How important are changes in land-use in determining long-term ecosystem biogeochemistry, biotic structure, and services?

Land-use and land-cover is changing dramatically in northeastern Puerto Rico (Thomlinson & Rivera 2000, Thomlinson et al. 1996) in response to well-documented socioeconomic changes occurring island-wide (Grau et al. 2003). The forests in these changing landscapes and the streams that drain them have undergone extensive and directional change that affects important community and ecosystem characteristics. The work proposed here is the beginning of a new initiative by LUQ to examine the impact of land-use and land-cover change on a broad range of ecosystem processes ("Question III" in Fig. 13). We propose to extend our elevation gradient to coastal urban areas outside the Luquillo Mountains. Understanding this gradient is essential to separating local from regional changes, needed for a foundation on which to build LUQ work in urban and coastal plain areas. However, documentation of functional differences imposed by human land-use on forest and streams has only just begun. In turn, understanding the relative influence of these stresses and management mitigations is critical to evaluating long-term ecosystem services, particularly water availability, provided by the Luquillo Mountains.

Hypothesis 6. *Urbanization and associated changes in land-cover have a greater influence on local climate and ecosystem processes than do changes from global processes* (*such as increased* CO_2). (Hall, Lugo, Mayol, Ramírez, Waide)

Background – Several lines of evidence suggest that the Puerto Rican climate has and will continue to change. Local surface temperatures in urban San Juan have also been increasing at a greater rate than nearby vegetated areas (González et al. 2005). This urban heat-island effect in Puerto Rico may be greater than in temperate areas (Kalnay & Cai 2003, González et al. 2005, Murphy 2005), and local urban influences on climate may be greater than the changes predicted from global climate change (Hulme & Viner 1995, Scatena 1998, Brazel et al. 2000). For the Luquillo Mountains, modeling suggests that both gross and net primary productivity will decrease with a doubling of CO_2 and with the projected increases in temperature and decreases in precipitation (Wang et al. 2002b, c). In fact, there is evidence of shifts in the major forest zones in the Luquillo Mountains (Scatena 1998).

At the regional scale, the island's annual precipitation decreased by 16% during the 20th century (van der Molen 2002). All eight of the precipitation stations with records starting around 1900 have recorded downward trends in total annual precipitation. Furthermore, 1997, 1994, and 1991 were the 2nd, 3rd and 6th driest years in the 20th century (Larsen 2000). Island-wide simulations suggest that coastal plain deforestation can alter the island's cloud base and decrease the island's total rainfall (van der Molen 2002). At the global scale, model simulation of future CO_2-induced climate change indicates that Puerto Rico may experience an increase in hurricane activity (Emanuel 1987, 2005), decreases in soil moisture, and increases in dry season length (Hulme & Viner 1995).

Workplan – Research will focus on two goals: 1) quantifying the urban and suburban heat-island effect around the Luquillo Mountains; and 2) extending our existing spatially explicit ecosystem models of the Luquillo Mountains into the surrounding suburban and urban areas. To do this we will link our existing LTER-based weather stations to a series of weather stations and temperature sensors at 20 or more stations that extend from the lower Luquillo Mountains to the center of San Juan. Scientists from UPR-Mayagüez and University of California-Santa Clara are partners in this venture (González et al. 2005). These stations will be used to measure temperature, relative humidity, and incoming, outgoing, and net energy balance. Existing high-resolution aerial photography and Airborne Thermal and Land Applications Sensor (ATLAS) imagery will be used to calculate the percent vegetative cover for the regions around the climate stations and to develop maps and models of heat abnormalities and night-time cooling. The changes in values of various climatic variables, such as temperature, rainfall, and evapotranspiration due to urbanization (and suburbanization) from our map analyses and models will be compared with projected climate change for this region derived from global climate models. Preliminary analysis of four calibration and four control stations indicates that the techniques proposed are robust.

During LTER 4 we will extend our existing spatially explicit ecosystem models to cover eastern Puerto Rico. Currently these models predict climate and evapotranspiration, river flow, carbon and soil dynamics, and above ground productivity (Hall et al. 1992, Wang et al. 2002a, b, c, Wu et al. in press a). Combined, they model spatial variations in major meteorological parameters, energy balance, and ecosystem processes within the forested Luquillo Mountains. By the end of LTER 4 they will be able to model these variables for all of eastern Puerto Rico, including forested and urban environments, and we will make projections with and without further urbanization and global climate change.

***Hypothesis** 7. Human land-use selects tree species with particular life histories and creates new forest communities. These new communities have different successional pathways and distinct community equilibria after hurricane disturbance compared to forests not subjected to human disturbance.* (Thompson, Brokaw, Lugo, Scatena, Waide, Walker, Willig, Zimmerman)
Background – The impact on forests of natural disturbances interacting with climate and land-use changes is a worldwide issue (Dale et al. 2001, Hansen et al. 2001). The 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde Research Area (Section 2.3.1) provides a case study of the dual effects of natural and human disturbance on tree species composition. We established the LFDP to study the long-terms impacts of hurricane disturbance, but discovered a legacy of historic land-use in forest composition across the plot (Thompson et al. 2002), which is typical of the tabonuco zone in the Luquillo Mountains (Scatena 1989, García Montiel & Scatena 1994, Foster et al. 1999, Aide et al. 2000, Pascarella et al. 2000). It is unclear, however, how those land-use legacies will interact with altered hurricane frequency or intensity to determine future community composition.

After severe hurricane damage, tree community composition seems to be stabilized by resprouting and seedling establishment, by life history trade-offs in colonization and competitive ability, and by density-dependent mortality (Fig. 15, Walker 1991, Zimmerman et al. 1994, Walker et al. 2003, Uriarte et al. 2004, 2005). However, these stabilizing processes may operate differently in communities whose tree compositions are shaped by human land-use. Such communities shaped by human land-use may have unique dynamics that perpetuate the compositional differences indefinitely (Ogle et al. in press). Alternatively, seed dispersal and the stabilizing mechanisms we have documented may drive communities with different land-use histories to converge in composition in the long term. These processes may interact with the effects of changes in hurricane frequency and intensity that are predicted to alter relative abundances and diversity of tree species (Doyle 1981, Overpeck et al. 1990, O'Brien et al. 1992).

Workplan – In LTER 4 we will test this hypothesis by applying the SORTIE forest model (Pacala et al. 1993) to long-term census data on the Luquillo Forest Dynamics Plot (LFDP). As mentioned above, the LFDP covers 16 ha of forest, in which all self-supporting woody plants ≥ 1.0 cm dbh are identified, measured, mapped and permanently tagged every five years (c. 70,000 stems in each census). The 16 ha covers two areas that have known, contrasting land-use histories: one portion (~10 ha) of the plot was subject to clear-cutting and some agriculture (ending in the 1930s), while another portion (~6 ha) has never been cut over and has only been subject to selective harvest of a few trees (ending in the 1950s) (Thompson et al. 2002). These historic land-use areas have distinct tree communities.

Results of three previous censuses of the LFDP (1990, 1995, 2000) and the ongoing fourth census will be used to parameterize a version of the spatially-explicit simulation model SORTIE that is specially restructured as SORTIE-PR (census and modeling funded by NSF-DEB 0517186). The three census intervals span three distinct periods of forest dynamics overlying the two areas of different historical land-uses (Thompson et al. 2002). During the interval 1990 to 1995 the forest was recovering from Hurricane Hugo (struck in 1989); 1995-2000 included forest damage from Hurricane Georges; and 2000-2005 included only recovery. Thus the 15-yr dataset from the LFDP will enable us to describe variation in tree population and community dynamics as a function of historic land-uses in the different land-use areas of the LFDP, interacting with different phases of hurricane damage and recovery. Response variables include species-specific susceptibility to hurricane damage, survival, growth, and ability to profit

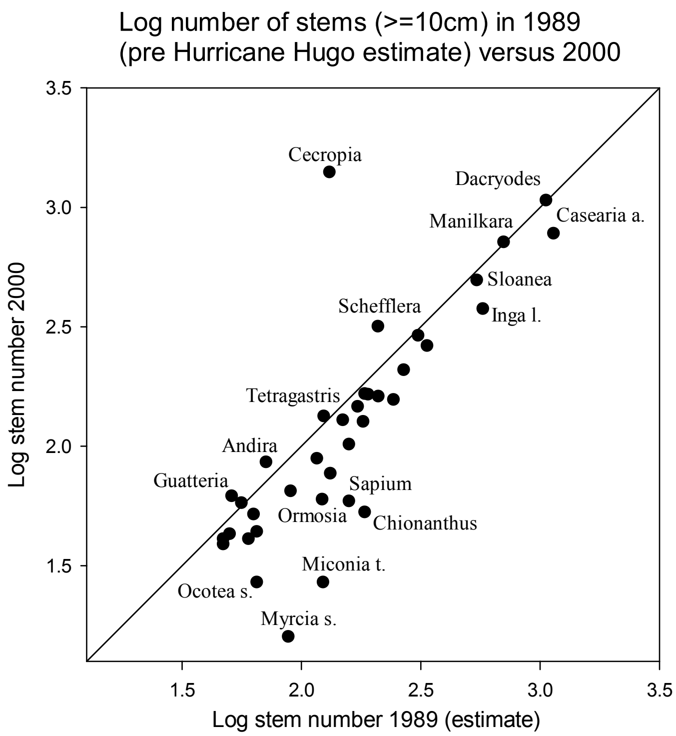

Figure 15 – Abundance of the most common tree species (≥10 cm dbh) in the Luquillo Forest Dynamics Plot before (ordinate) and 10-11 yr after (abscissa) Hurricane Hugo struck the forest.

from damage to neighboring trees, depending on the spatial configuration, sizes, and species of those neighbors. Using these long-term, empirical data, we will parameterize the functional relationships that govern tree demography of dominant species at the site, using likelihood-based analytical methods (Canham et al. 2001, Johnson & Omland 2004). These relationships will be used in SORTIE-PR to integrate the results of our analysis into simulations of long-term forest dynamics. We can then test the hypothesis of convergence versus divergence of successional pathways and tree community equilibria. We do this by having SORTIE-PR explore a range of scenarios varying in both land-use history and different frequencies and intensities of hurricane disturbance.

Hypothesis 8. *Urbanization causes changes in stream nutrients, discharge variation, and light that result in increased magnitude and variability of in-stream metabolism, detrital processing, energy flow within food webs, and dissolved inorganic N exports*. (Ramírez, Ortiz Zayas, Covich, McDowell, Pringle, Scatena).

<u>Background</u> – The phrase "urban stream syndrome" has been coined to describe patterns in degraded streams draining urban land (Walsh et al. 2005). This definition is based on information from temperate zone urban streams (e.g., Meyer et al. 2005), as relatively little data has been collected from their tropical counterparts (Moyo & Phiri 2002, Brasher 2003, Santos-Román et al. 2003). Urbanization alters many physical and chemical characteristics of streams, including canopy cover, nutrient inputs, and hydrologic regime. Removal of riparian vegetation increases temperature and the amount of light reaching the stream channel (Baer & Pringle 2000, Paul & Meyer 2001). When combined with the increased nutrient inputs typical of urbanized streams, increased primary production is likely to occur. Preliminary work from the LINX II project shows that primary production is greater in most urban/suburban streams than in forested sites (Potter et al. in prep.), suggesting a shift in food resources in those streams. Urban streams also have low biodiversity relative to forest streams (Grubaugh & Wallace 1995). Therefore,

stream ecosystem processes that are normally dominated by biota (e.g., detrital processing) are also likely to be altered in urban settings. We know that macrobiota (shrimps and crabs) strongly influence detrital processing in the Luquillo Mountains, and that decomposition is rapid in these streams (e.g., O'Connor et al. 2000, Crowl et al. 2001, March et al. 2001). Generally, leaf litter decomposition rates increase in urban streams, even though stream biota are less abundant and diverse in these systems. This is thought to be due to physical factors that accelerate decomposition in urban streams, such as more frequent and severe flooding (Paul 1999).

Stream water NO_3^- concentrations are an important index of water quality. High stream water NO_3^- loads negatively affect human and ecosystem health, causing eutrophication of downstream reservoirs and coastal zones (NRC 2000), and thus represent an important degradation of ecosystem services. Because dominant processes in the N cycle appear to vary considerably between temperate and tropical regions (Matson et al. 1999), relationships between people and water quality in small tropical basins may differ from the temperate model (Pierels et al. 1991; Caraco et al. 2004). Our initial work in Puerto Rico on urban streams has addressed in-stream NO_3^- retention and denitrification as part of the multi-site LINX II project (http://www.biol.vt.edu/faculty/webster/linx/). The proposed work represents a new initiative to examine the impact of urbanization on a broad range of ecosystem processes.

Workplan – We will address linkages between urbanization and stream ecosystem function (e.g., metabolism) and services (e.g., water quality), using two related projects. The first involves new measurements of stream metabolism, algal communities, and litter decomposition in three watersheds (Mameyes, Canóvanas, Río Piedras) with different degrees of urbanization, extending our previous work (Ortiz Zayas et al. 2005). The Mameyes watershed drains the Luquillo Mountains and has urban impacts on its lowermost reaches only; it will serve as a reference (Fig. 1). The Río Piedras watershed is completely immersed in the San Juan Metropolitan Area and will serve as our most urbanized end member. The Río Canóvanas watershed drains both forest and urban areas, and thus is a transitional watershed. In each watershed we will have a high-, mid-, and low-elevation site that is a second or third order reach of similar width and flow. Stream attributes (width, depth, velocity, canopy openness, and nutrient concentrations) will be measured in the field, and watershed attributes (soils, land cover, human population density, and impervious surfaces) will be determined using available GIS layers.

At each of the nine study sites we will measure stream metabolism, algal standing crop (chlorophyll *a*, AFDM) and community composition, and leaf litter decomposition rates. Each site will be sampled and characterized during low-flow and high-flow periods (February and July). We will also examine relationships between C:N:P stoichiometry of basal resources (algae and organic matter) and invertebrate consumers at each site (Sterner & Elser 2002).

Whole-stream metabolism (photosynthesis and respiration) will be measured with the open-channel technique (Odum 1956, Marzolf et al. 1994, McCutchan et al. 2002, Ortiz Zayas et al. 2005), and propane injections (Kilpatrick et al. 1989) will be used to directly measure re-aeration rates. Primary production will be related to canopy openness, nutrient levels in stream water, and algal biomass. Community respiration will be related to nutrient levels and the lability of dissolved organic carbon. We will determine carbon lability twice at each site (February and July) using *in vitro* bioassays of organic carbon decomposition (Ebdrup 2001). Algal standing crop and community composition will be determined following standard procedures (Lowe & Labiberte 1996, Steinman & Lamberti 1996). Leaf litter decomposition rates will be determined at each site by measuring organic matter loss over time in leaf packs.

Because riparian species composition also changes with urbanization (Heartsill Scalley & Aide 2003), we will use litter obtained from each stream in litter packs as well as a standard litter pack of the same species composition for comparison.

The second project will examine the impacts of urbanization on water quality by expanding our existing network of stream water chemistry stations using a combination of new LUQ sites and analysis of water quality data collected by the USGS WEBB program. We will add two stream sampling sites, the Río Sabana and lower Río Espíritu Santo, to the existing Río Mameyes site for our ongoing weekly analysis of water quality, making three LUQ monitoring stations with significant human land-use in some portion of their watershed. We will relate stream water chemistry to land-use (TM coverage of urban and agricultural lands), population density (Census 2000), and % impervious cover in these sites and the USGS WEBB sites.

Hypothesis 9. *Over the past 20 years the absolute quantity of water and other ecosystem products removed from the Luquillo Mountains has increased, while the ecosystem processes that supply those products have been altered*. (Scatena, Covich, Crowl, Pringle, Lugo, Ortiz Zayas, Hall)

<u>Background</u> – Historically, the Luquillo Mountains have been a source of many economic products and commodities, including, timber, agricultural goods, metals, minerals, and water (Wadsworth 1949, Scatena 1989). Currently the main economic products provided by the Luquillo Mountains are clean water (Ortiz Zayas et al. 2004) and recreation (González Caban & Loomis 1997). Major services provided are carbon fixation (Silver et al. 2000), water purification (Scatena et al. 2002), maintenance of regional biodiversity (Lugo 1994, Blanco & Scatena 2005), research, and education.

While the socio-economic value of these products and services is recognized, they are undergoing increased pressures and stresses from surrounding land-use changes. From a near absence of urban cover in 1936, the lowlands and adjacent areas surrounding the Luquillo Mountains have undergone both reforestation and urbanization (Thomlinson et al. 1996, López et al. 2001, Lugo et al. 2004). The rate of change to urban cover was 400 ha yr^{-1} during 1994-2000 and continued at 160 ha yr^{-1} during 2000-2005 (Lugo et al. 2004, López and others, pers. comm.). By 2002, 19% of land immediately surrounding the Luquillo Mountains area was urban. These increases in urban areas have also increased demands on the forest's natural products and resources (Thomlinson & Rivera 2000). For example, on an average day in 1994, 50% of the stream flow from the Luquillo Mountains was diverted before it reached the ocean (Nauman 1994). By 2004, diversions had increased to 70% (Crook 2005). Reduced flow has decreased the ecosystem services provided by instream flow, including maintenance of aquatic habitats and water quality in the coastal streams and along shores. Dams and physical and chemical modifications to aquatic habitats have likely reduced the migration and abundance of freshwater shrimp and snails (Benstead et al. 1999, Blanco & Scatena 2005, Greathouse et al. in press). The larva and juveniles of these species are a major food source for coastal fish, have traditionally been harvested by humans from Luquillo Mountains streams, and provide ecosystem services by processing instream carbon and periphyton (Pringle 1996, Pringle et al. 1999).

The increased pressure on the region's resources has already provoked lawsuits, and more are expected in the future (Ortiz Zayas et al. 2005). At the same time, there has been increased vigilance regarding the management and use of the region's natural resources, and LUQ research has been instrumental in supporting ecosystem-based management (Scatena

2001), in developing ecosystem-friendly water withdrawal structures (March et al. 2003), and in improving public outreach (Section 5).

Workplan – We will address this hypothesis by quantifying the historic and present ecosystem services provided by the Luquillo Mountains. This work will build on our existing valuation studies (González Cabán & Loomis, 1997, 1999, Loomis & González Cabán 1997, Odum et al. 2000, Scatena et al. 2002, NRC 2000) and be linked to on-going biocomplexity studies at LUQ and efforts at other LTER sites (Farber et al. 2006). The research will focus on: 1) quantifying the magnitudes and spatial distribution of major ecosystem products and services currently provided by the Luquillo Mountains; 2) evaluating changes that have occurred in the services and products over the past 20 years; and 3) developing metrics than can be used to evaluate and monitor ecosystem services. Emphasis will be on ecosystem services and products associated with clean water. Information will be analyzed and synthesized during a workshop on ecosystem services of the Luquillo Mountains that is planned for 2008 (Section 2.7).

Changes in the production of clean water will be analyzed by continuing and extending our analysis of water-use budgets for the forest (Nauman 1994, Crook 2005). These water budgets not only provide estimates of the amount of fresh water provided by the Luquillo Mountains, but also needed background information for our long-term ecological studies. During LTER 4 we will obtain a five year update of previous budgets and also work on methods to improve the quantification of water diversions in ungauged intakes. In addition, we will develop and test metrics of riverine connectivity and aquatic quality (Crook 2005), using combined geomorphic, biochemical, and biotic variables. Our initial research indicates that migratory tropical shrimps and snails are ideal species to use for gauging riverine connectivity and biointegrity because they: 1) regulate important in-stream ecological processes (Pringle 1996, March et al. 2001), 2) are sensitive to water quality and quantity (Blanco & Scatena 2005), and 3) migrate to and from coastal zones and headwater streams. We will combine our probability-based metrics (Crook 2005) with population-based metrics (Blanco & Scatena 2005) and new GIS-based maps of aquatic habitat (Pike in prep.) into an integrated method that managers can use to evaluate and monitor aquatic health and connectivity.

2.6 CROSS-SITE STUDIES

LUQ is involved in a range of cross-site research projects, including studies on primary productivity, nutrient cycling, water management, primary succession, forest dynamics, fragmentation, plant phenology, invertebrate ecology, and biodiversity (Table 6). Many of these studies compare LUQ with other LTER sites, while others are international, especially connecting LUQ with other tropical sites. Notable are LUQ's productive membership in the Center for Tropical Forest Science (Wills et al. 2006), publication of a special issue of *Biotropica* on Asian tropical forests with comparisons to the Luquillo Mountains (Zou et al. in press), and developing cooperative studies with sites in mainland China. With supplemental NSF funds in 2005, LUQ Senior Investigators and students organized a workshop in southern China on land-use change in the tropics, which produced a submitted manuscript (Cao et al. in review) and plans to reconvene in 2006 to establish cross-site studies. LUQ is leading a team (Puerto Rico-Mexico-Costa Rica) to study nutrient recycling by stream consumers across a gradient of precipitation, hydrology, and stream connectivity. Other cross-site initiatives are LUQ-sponsored conferences on alien species invasions (Lugo), environmental flows of tropical streams (Pringle, Scatena), tropical landslides (Walker, Zou), and belowground ecology (González, Lodge). LUQ is hosting the 2007 LTER Network-level meeting on social science.

Table 6 – Ongoing and recent cross-site projects conducted at Luquillo LTER, including collaborating sites and colleagues (italics indicate current LUQ Senior Investigators).

1. Methods for measurement of net primary productivity (*Waide*, Fahey, Knapp).
2. Long Term Ecological Trends in the LTER network (*Meléndez Colom*, *Lugo*, Peters and many others).
3. Species-time relationship across ecosystems and taxonomic groups (*Waide*, White, Adler, Lauenroth, Gill, Greenberg, Kaufman, Rassweiler, Rusak, Smith, Steinbeck, Yao).
4. Characterizing forest structure for assessments of carbon cycling and biodiversity (*Waide*, R. Dubayah, S. Goetz, D. Clark).
5. Development of a common information management framework for LTER; PAL (*Meléndez Colom*, Baker).
6. TEAM - Tropical Ecology, Assessment, and Monitoring Initiative – network of tropical sites to monitor and forecast change in biodiverisity (*Willig*, Conservation International).
7. UNDERC - Leaf decomposition; Michigan (*Belovsky, Crowl*, REU students).
8. Landscape fragmentation and forest fuel accumulation; BNZ, Idaho (*González*, *Scatena*, Gould, Hudak).
9. SORTIE forest dynamics model; HFR *(Thompson*, *Brokaw, Zimmerman,* Uriarte, Canham).
10. Earthworm invasions in the tropics; Nanjenshan, Taiwan; Xishuanbanna, China (*Zou*, P. C. Hou, Yang).
11. DONIC (Dissolved Organic Nitrogen Intersite Comparison); NWT, SBC, others (*McDowell*).
12. Canopy herbivory and soil processes in temperate and tropical forest; CWT (Schowalter, Lowman, Hunter).
13. Dissimilatory nitrate reduction in humid ecosystems; BNZ, La Selva (*Silver*, Firestone, Chapin).
14. LIDET (Long-Term Intersite Decomposition Experiment Team); 28 LTER and international sites (*Silver, Lodge*, Harmon).
15. LINX (Lotic Intersite Nitrogen Experiment); 10 LTER and other sites (*McDowell*, Mulholland).
16. WW-DECOEX (World Wide Aquatic Leaf Decomposition Experiment); 11 tropical sites (*Crowl, Covich,* Wantzen).
17. Carbon, nitrogen, and phosphorus dynamics in tropical ecosystems; Tapajós, Brazil (*Silver*, Keller).
18. Earthworms and soil processes in tropical ecosystems; Xishuangbanna, China (*Zou*).
19. Relationship between nutrient inputs and faunal diversity; Dominica, Costa Rica (*Richardson*, Srivastava).
20. Bromeliad phytotelmata in tabonuco and elfin forests; Dominica (*Richardson*).
21. Aquatic insect emergence; La Selva (*Ramírez*, *Pringle*).
22. Tropical forest dynamics - CTFS (Center for Tropical Forest Science); 15 international sites (*Thompson, Brokaw, Zimmerman,* Davies, Condit, others).
23. Tropical tree phenology; Ecuador, Panama (*Zimmerman, Thompson*, Wright, Muller-Landau, Garwood).
24. Primary succession; five international sites (*Walker*).
25. Tropical Montane Cloud Forest Network (*Scatena, Silver*).
26. SCOPE Resiliency network (*Lugo, Scatena, Silver*).
27. FRIEND/AMIGO, UNESCO network on Caribbean hydrology (*Scatena*).
28. UNESCO-HELP watershed program (*Scatena*, Ortiz).
29. Consumer-driven nutrient recycling in streams; CWT (*Ramírez*, Cross, Benstead, March, Rosamond).

2.7 SYNTHESIS

Our synthesis activities will build upon our growing knowledge of ecosystem change in Puerto Rico to understand the coupling of natural and human-dominated ecosystems at scales from local to global. To facilitate this synthesis and the development of emerging principles, we have planned a series of formal synthesis activities that will involve researchers and stakeholders from Luquillo and other LTER sites and organizations (Table 7). These activities include workshops that are focused on the major activities and hypotheses of the project. During these workshops, multidisciplinary groups will review protocols and research progress, exchange and compare data, and develop integrated synthesis papers and education products.

Table 7 – Timeline of major events in LTER 4 (not including regular LUQ-LTER meetings). PI or Senior Investigator organizer in parentheses. In addition to these events LUQ has annual and monthly meetings and an annual REU meeting, in which REU students report on their research. Luquillo-HELP (Section 2.7); LFDP = Luquillo Forest Dynamics Plot (Section 2.3.1); IITF = International Institute of Tropical Forestry USDA Forest Service.

2006
- LUQ synthesis book to publishers (Brokaw)
- Luquillo-HELP workshops with local municipalities (Ortiz Zayas)
- Fourth LFDP census (now underway, Thompson)

2007
- Canopy Trimming Experiment synthesis workshop (Zimmerman)
- LUQ hosting Network LTER social science meeting (Brokaw)
- Luquillo-HELP workshops with local municipalities (Ortiz Zayas)
- Five-year Bisley Experimental Watersheds census (Scatena, IITF)

2008
- Ecosystem services and evaluation workshop (Scatena, Pringle, Lugo)
- LFDP workshop (Thompson, Brokaw)
- Trophic interactions and biodiversity workshop (Waide, Willig, Ramírez)
- Luquillo-HELP workshops with local municipalities (Ortiz Zayas)

2009
- Elevation gradient workshop (González, Silver, Waide)
- Mid-Term Site Review (Brokaw)
- Stream ecology and biogeochemistry workshop (Covich, McDowell, Pringle)

2010
- Second treatment for Canopy Trimming Experiment, and workshop (Zimmerman)
- Urbanization and urban heat island workshop (Hall, Lugo, Waide)
- Fifth LFDP census (Thompson)

2011
- Renewal proposal workshop (Brokaw)
- Resistance and resilience workshop (Lugo, Waide, Scatena)

2012
- Renewal proposal (Brokaw)
- Five-year Bisley Experimental Watersheds census (Scatena, IITF)

Increasing the incorporation of social science perspectives and outreach into our research is an additional goal for LTER 4. This incorporation will build upon our existing strengths in environmental history, ecologic evaluations, and community outreach. A long-term goal is to develop a multi-dimensional biophysical-economic model of eastern Puerto Rico (Hall 2000) that is linked to our educational tools (http://elyunque.net/journey.html) and outreach activities. To promote this effort we will expand our dialogs on water and ecosystem management with the local municipalities and urban areas surrounding the forest. This dialog has been facilitated by workshops that are jointly sponsored by local municipalities and the LUQ-HELP collaboration (Table 7). During these meetings local environmental managers, community leaders, LUQ scientists and graduate students discuss and work toward incorporating scientific research into the management of the region's natural resources. The design and implementation of a new type of water intake structure that reduces the impacts to migrating aquatic fauna (March et al. 2003) was an outcome of earlier meetings between LUQ scientists and local resource managers.

It has also been the tradition of LUQ to provide synthesis and outreach through the publication of edited volumes and participation in cross-site activities. These effort will continue in LTER 4, and several products are already in progress, including a collection of papers on forest succession and restoration (Walker et al. in prep.) and on tropical montane cloud forests (Bruijnzeel et al. in press), and the LUQ synthesis book (Brokaw et al. in prep.).

Section 3 Site Management

3.1 Luquillo LTER Research Team

The LUQ research team consists of two PIs, 23 Senior Investigators (Table 3), 26 Associate Researchers (Table 8), and many graduate and undergraduate students. Ten of the PIs and Senior Investigators live in Puerto Rico, and 14 live in many locations elsewhere. This diverse, distributed membership produces an energetic cross-fertilization of ideas and many publications (345 in 2000-2006), and brings the resources of 14 different institutions to LUQ.

LUQ maintains a strong research team by continually evaluating the contribution of current Senior Investigators and by recruiting new ones. Senior Investigators are evaluated by the LUQ Executive Committee (Section 3.2) in terms of number and impact of publications, need for a their particular expertise and experience, participation in program planning, cooperation with information management practices (Section 4), graduate student participation, cross-site activities, and ability to attract complementary funding.

LUQ has a broad field from which to add new investigators, because its diverse and distributed Senior Investigators are associated with many colleagues, students, and institutions. As potential new investigators, all interested people are invited to attend LUQ meetings and learn about the program (Section 3.3). LUQ also seeks to expand the diversity of its research team when adding new investigators. Three Puerto Ricans (Cantrell, Ortiz, Mayol) have been added to the roster of Senior Investigators for LTER 4. LUQ also benefits from continuity among generations: three current Senior Investigators were graduate students under other LUQ Senior Investigators.

Associate Researchers in LUQ add expertise and data to LUQ. Associates are provided seed funds (materials, travel) to continue their participation.

3.2 Program Management

Nicholas Brokaw and Ariel Lugo are the PIs of LUQ. Brokaw is a professor in the Institute for Tropical Ecosystem Studies (ITES), University of Puerto Rico-Río Piedras (UPR). He has been with LUQ since it began in 1988 and has been Lead-PI since 2002. Brokaw is in charge of day-to-day LUQ operations, while ITES and UPR handle LUQ administration. Lugo is Director of the International Institute of Tropical Forestry, USDA Forest Service, in Puerto Rico. He is in charge of Forest Service participation in the LUQ program. Previous Lead-PIs, Jess Zimmerman and Robert Waide, are Senior Investigators in LUQ.

An Executive Committee (EC) guides LUQ and makes the major decisions. The EC consists of Brokaw and Lugo and five Senior Investigators. The Senior Investigator members rotate, each serving about two years. Current Senior Investigator members of the EC are Fred Scatena, Whendee Silver, Catherine Pringle, Bob Waide, and Bill McDowell. EC membership is intended to represent the various disciplines in LUQ and to include members who live in Puerto Rico and those who reside on the mainland. The EC meets frequently via conference call and in person at LUQ general meetings (see below).

Brokaw and two Senior Investigators (Jean Lodge, Alonso Ramírez) form the Data Management Committee with the Information Manager, Eda Meléndez Colom. The Data Management Committee reviews and plans development of information management in LUQ.

During LTER 4 LUQ will obtain outside review from visiting scientists selected for their expertise in LUQ research areas. These scientists will come to Puerto Rico for several days of interaction with LUQ. They may come during a LUQ general meeting, or when LUQ convenes the synthesis groups described in Section 2.7, or at other opportune times. This will be a fluid system; these advisors will not constitute a standing committee, though some advisors may be retained for several years to gain perspective on LUQ.

3.3 Research Management, Meetings

LUQ PIs and Senior Investigators are grouped in teams to address the research questions and hypotheses of LTER 4 (Section 2.5). The teams and their leaders for the three questions in LTER 4 are:

Question I: Silver (leader), Covich, Crowl, González, Lodge, Mayol, McDowell, Ramírez, Scatena, Zou

Question II: Brokaw (leader), Cantrell, Covich, Crowl, McDowell, González, Lodge, Lugo, Ramírez, Richardson, Pringle, Waide, Walker, Willig, Scatena, Silver

Question III: Scatena (leader), Brokaw, Hall, Lugo, McDowell, Ortiz, Pringle, Ramírez, Scatena, Thompson, Waide, Walker, Willig

Leaders and teams for each hypothesis are given in Section 2.5.

Field work is coordinated through El Verde Field Station (administered by ITES) and Sabana Field Station (USDA-FS) near the Bisley Experimental Watersheds (see facilities section of proposal). Alonso Ramírez is currently the Director of El Verde and coordinates administration of this facility. Grizelle González is Director of Sabana ,and Fred Scatena manages research at Bisley.

LUQ scientists meet twice during the year to review research progress, plan new research, and discuss management issues related to the site. January meetings are devoted to research, interaction with visiting advisors, and site business. Parts of this meeting are open to anyone interested in LUQ. June meetings are devoted mainly to research planning, and are attended mainly by the PIs, Senior Investigators, and other researchers. During LTER 4 there will be a series of synthesis meeting (Section 2.7, Table 7). LUQ also has regularly scheduled meeting in most months to review progress and discuss particular projects presented by a speaker. This meeting is open to anyone who is interested.

Table 8 – Luquillo LTER Associate Researchers. Scientists associated with the Luquillo LTER program. These scientists contribute to the program with complementary research, usually funded through outside grants. These individuals receive occasional travel money or seed funds from LUQ.

Juan Felipe Blanco-Libreros – Universidad de Colombia – Antioquia (stream ecology)
Karen Beard – Utah State University (animal and ecosystems ecology)
L. A. Bruijnzeel – Vrije Universiteite of Amsterdam (hydrology, elfin forest ecology)
Charles Canham – Institute of Ecosystem Studies (forest ecology, modeling)
Stephen B. Cox – National Center for Ecological Analysis and Synthesis (community ecology)
Robert Edwards – Independent (spider systematics and ecology)
Heather Erickson – Lewis and Clark College, Washington (nutrient cycling)
Ned Fetcher – University of Scranton (plant physiology, carbon gain)
Mary Firestone – University of California - Berkeley (biogeochemistry)
Michael Gannon – Pennsylvania State University - Altoona (ecology of bats)
Jorge González – University of California - Santa Clara (climate)
William Gould – International Inst. of Tropical Forestry, USDA-FS (landscape ecology)
Bruce Haines – University of Georgia (nutrient cycling in plants)
Tamara Heartsill Scalley – University of Pennsylvania (terrestrial/aquatic links)
Arthur H. Johnson – University of Pennsylvania (biogeochemistry)
Paul Klawinski – William Jewell College (animal ecology)
Matthew C. Larsen – USGS (biogeochemistry)
Randall W. Myster – University of Central Oklahoma (plant ecology)
Timothy Schowalter – Louisiana State University (plant-insect interactions)
Joanne Sharpe – Independent (fern ecology)
Aaron Shiels – University of Hawaii (vegetation development, restoration)
John Thomlinson – California State University - Dominguez Hills (landscape ecology)
María Uriarte – Columbia University (forest dynamics, modeling)
Hans F. Vugts – Vrije Universiteite of Amsterdam (meteorology)
Sheila E. Ward – University of Puerto Rico (forest dynamics, Meliaceae genetics)
Lawrence Woolbright – Siena College (herpetology)
Joseph Wunderle – International Inst. of Tropical Forestry, USDA-FS (avian ecology)

Section 4 Data and Information Management

4.1 Mission and Scope: The Information Management (IM) program for the Luquillo LTER (LUQ) is dedicated to preserving the data collected by LUQ scientists and making it accessible to the scientific community. The LUQ IM program also helps LUQ researchers design data gathering and formatting for efficient entry to databases, trains users to employ IM and network tools, provides local network and systems administration technical support, maintains the LUQ Web site, and participation of LUQ in the LTER Network. LUQ's IM program has been developed with the following components:

1. Computer and network infrastructure that provides hardware, software, and telecommunication tools.
2. Up-to-date LUQ datasets, metadata, database catalog, publication references, and personnel information.
3. Information management protocols, security procedures, data submission policies, data accessibility policies, and a flexible system structure assuring the continuity of the system and its development.
4. Administrative and technical personnel who ensure the functionality of the system and the security, preservation, and enhancement of the components of the system.

4.2 Background: Beginning in 1988, a centralized, computer-based IM system served as the central depository and metadata center, as well as the data entry, management, and sharing facility for all the data sets generated by LUQ. LUQ now has a Local Area Network (LAN) on which the Intranet is defined, with at least 20 computers and one or more file and program servers used by the local scientific community. The system evolved from a centralized system in 1992 to a decentralized and distributed networking-based system in 2001.

LUQ's metadata standards were developed in 1989, and by 1991 these standards and guidelines were made available online. Since 1990 a database catalog holding these metadata has been maintained at the site as the IM framework. In 2005, these metadata standards were translated to the level between 3 and 4 of the Ecological Metadata Language (EML) standards, following the EML Best Practices Guidelines. EML packages are harvested periodically from LUQ's Web site by the EML-based metadata catalog harvesting engine of Metacat.

Since 1995, the LUQ Web site (http://luq.lternet.edu/) has provided an updated list of all available datasets (linked to their metadata), data in an ASCII-comma delimited format, and a Data Management Policy (http://luq.lternet.edu/datamng/imdocs/dmpolicy.htm). A total of 104 datasets are available on the Web, 24 more than in 2001. In 2001 this Web site was re-designed with the help of the LTER Network Office. Our Web site hosts all data, metadata, protocols, forms and guidelines of the LUQ IM. The IM office includes the full-time Information Manager and one full-time and one part-time data entry specialist.

4.3 IM Design and Implementation: The LUQ IM infrastructure reflects the present state of technology at the University of Puerto Rico and the Institute for Tropical Ecosystem Studies (ITES). The design of the data procedures is dictated by the needs of field technicians, research methods, computer technology, and the scientific community that uses the data. The basic information elements of a common data management framework (publication and personnel databases, data catalog, and data with its metadata) are accessible both at the Internet and Intranet levels (ITES LAN). The ITES LAN is part of a wider network of computers controlled at the University of Puerto Rico's main Office of System Administration, in addition to the Río

Piedras campus system administration office. The data management and Web standards established also result from interaction with other IM communities, including the information managers at other LTER sites and the LTER Network Office. A LUQ Information Management Committee periodically reviews LUQ IM operations, implementation, and plans.

4.3.1 Hardware, software and networking – Seven distributed, password-protected computer systems constitute the LUQ IM Intranet. They host two Web sites, the data and information managed at the site, the publication database, and software. The LAN has a network printer/scanner that can be accessed remotely and from any location in the LAN. Software packages for data manipulation, analysis, graphing, and Web page design and maintenance are available on the system and are used by the IM staff and visiting research staff. A wireless mini LAN capable of holding four wireless connections at a time is located at the IM office and is available for visitors to ITES.

4.3.2 Security – Each data and metadata file is updated on their host computer and on two 250MB zip backup disks every time the information is updated. Backup media with data files in their original computer format are kept in a fire-proof file cabinet. A third backup on a CD is updated every 4-5 weeks and is carried home by the IM staff person in charge of entering the data. Identical copies of two separate file systems, one holding all original data, metadata, and catalog files, and the other holding the Web site files, are kept in two of the IM office computers. Zip files of individual sections of the Web site are periodically updated and saved on two CDs as additional backups. Completed data sets remain in their host computer for Intranet access, and their corresponding backups are also kept safely. Copies of the updated data files are distributed to their owner every time the data goes through the process of entry or quality control.

4.3.3 Data and metadata encoding, query capability – Data are encoded using various types of software, usually in spreadsheet format by the investigators. All data files in the IM program are converted to a DBMS format to facilitate their query capability, graphing, and manipulation. When data structures are transformed in this process, the data owner's approval is requested. Data can be searched for from the Intranet as well as from the Internet using the local database catalog and the Web site's search engine or by browsing several online lists that group data by different categories. Metadata is also searchable from Metacat, which provides users with the location of the data and metadata on LUQ's Web site.

4.4 IM Procedures and Protocols:

4.4.1 Database design, data entry – LUQ investigators are asked to meet with the LUQ Information Manager at the beginning of a project to discuss the dataset design and software for entering and manipulating the data. Metadata forms for the each of the datasets that will be generated by the project are completed by the investigator and Information Manager. Database design, data entry, quality control, review, and revision are completed as in Fig. 16.

4.4.2 Required data submission from LUQ; data from other sources – Researchers who use LUQ resources for their projects are required to submit their data and metadata to the LUQ IM program (Section 4.4.4 for data availability practices). Researchers working in the LUQ study area but not supported by LUQ are encouraged to submit their data to the LUQ IM program . Inducements to these researchers include help with dataset design, data entry services, secure archiving, help with analysis, and increased interaction with other researchers. The LUQ Web site hosts 16 of these data sets.

4.4.3 IM protocols documentation and planning documents – LUQ IM protocols for data, metadata, data filing, production of EML packages, and publication data entry have been published on the Web (http://luq.lternet.edu/datamng/index.html).

4.4.4 Data updates and availability – Data are updated on the Web at intervals whose length depends on the data set. Data sets are made available on the Web, with no restrictions to other researchers, not later than two years after the data are first gathered, as required by the NSF and stated in the LUQ Data Management Policy (http://luq.lternet.edu/datamng/imdocs/dmpolicy.htm). Some exceptions to the two-year rule are made for especially large data sets that take a long time to "clean" and organize, and for graduate student thesis data. However, all LUQ datasets are eventually made completely available. Researchers who want to download LUQ data from the Web are asked to agree to a users' policy (Data Management Policy, URL above), which includes informing LUQ and the researcher who gathered the data that they (the user) has downloaded the data, and informing us as to how the data will be used. A Web tool to track data access is in place for the use of the Information Manager.

4.5 IM Support for Science: The LUQ Web site provides information in addition to data, including: LUQ research program and project descriptions, an indexed list of publications in an End Note database file, LUQ personnel list, LUQ proposals, forms for submitting publications, photograph records, metadata guidelines, protocols, and IM development documents (Table 9).

The server's system log files that record Web hits are periodically backed up and archived for future inspection and analysis. The LUQ Web site is referenced by a range of other Web sites within the Internet. When the Internet is searched for "Luquillo Experimental Forest", at least seven sites list the Luquillo Web site in their selection of Ecology resources and three others list it as a reference to get specific data from or for data that has been used in the analysis of a paper. Additional sites indicate that university classes are using LUQ data for projects, presentations, and teachers' guides.

4.6 LUQ IM Participation in Network Activities: The LUQ IM program participates actively in LTER Network Information System (NIS) projects. Distributed databases are maintained locally as part of our participation in the NIS, including: a Data Table of Contents (DTOC), the All-site Bibliography, up-to-date LUQ personnel information, network-harvested hydrology data from nine stations in NIS Hydro-DB, and meteorological data from three stations in NIS Clim-DB. The LUQ Information Manager was elected member of the Information Managers Executive Committee (IMEXEC) and was the *LTER DataBits* Newsletter co-editor and editor from August 2004 to August 2005. She is the contact person for the IMEXEC for this Newsletter. She is a member of the "Best Web Practices" sub-committee and participated in the "Site Review" sub-committee.

4.7 Future Developments: Plans for the development of the LUQ IM program include: 1) new mechanisms to allow investigators to remotely deposit their data in the LUQ IM system (implemented by August 2006); 2) a scroll down Web site map with links to other U.S. LTER sites, and other Best Web Practices' features; 3) translation of the already existing metadata to EML level 5 standards to allow data as well as its already harvested metadata retrieval by the LTER Network Office's data warehouse; (4) Completion of a database containing GIS referenced list of all LUQ project sites (LUQ GIS database at: http://ites.upr.edu/thomlinson/spatialdata/index.html).

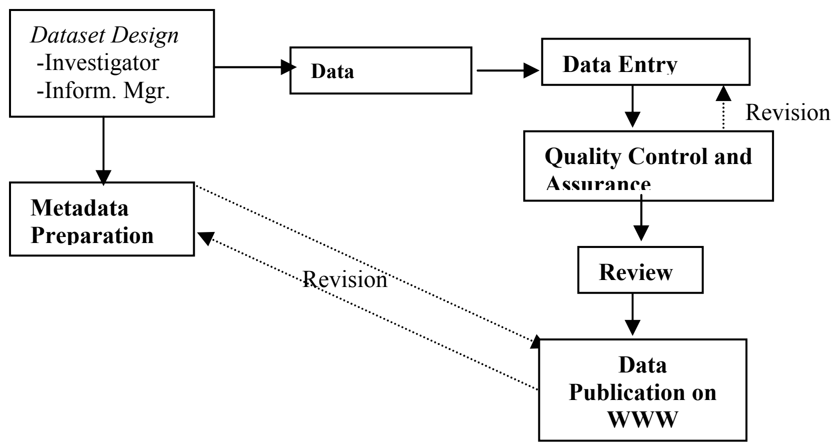

Figure 16 – Steps involved in the LUQ IM process of dataset design, data entry, quality control, and data publication on the Web for the use of the scientific community.

Table 9 – Information and other features provided in the LUQ Web site.

Document type	**Document Web location or URL**
Indexed list of publications	http://luq.lternet.edu/publications
Searchable personnel listing	http://luq.lternet.edu/people
Information management Web page including list of LUQ NIS databases	http://luq.lternet.edu/datamng/
LUQ program and Project descriptions	http://luq.lternet.edu/research/
Publication End Note database file	http://luq.lternet.edu/datamng/ForMembersOnly/EndNoteLTERBiblio/
Level 3-4 EML files of LUQ's metadata	http://luq.lternet.edu/EcologicalMetadataLanguage/LUQEMLFiles/
Past proposals	http://luq.lternet.edu/publications/
Photo records	http://luq.lternet.edu/data/lterdb09/metadata/lterdb09.htm#DATA
Form to submit references	http://luq.lternet.edu/cgi-bin/publication_submit/mewebkey.html
Metadata, guidelines, IM development documents and protocols	http://luq.lternet.edu/datamng/

Section 5 Education and Outreach

5.1 Education

In 2003, Dr. Steven McGee, an education researcher and President of The Learning Partnership, was named the education coordinator for Luquillo LTER (LUQ). He coordinates LUQ education activities with Jorge Ortiz Zayas at the Institute for Tropical Ecosystem Studies, University of Puerto Rico (ITES) and Ariel Lugo at the International Institute of Tropical Forestry (IITF).

5.1.1 Network-level – At the LTER All Scientists Meeting in September 2003, McGee organized a workshop on LTER curriculum development. As a result of that workshop, he organized an LTER network-funded grant-writing workshop for LTER education coordinators. This resulted in the submission of two grant proposals to ESIE. In summer 2004, Dr. McGee attended the annual meeting of education coordinators at the Andrews Forest. He contributed to the revision of the LTER Education Handbook released in fall 2005. These activities have laid the foundation for greater collaboration among the education activities across the LTER network.

5.1.2 Schoolyard LTER – For nearly 20 years, the U.S. Forest Service and the University of Puerto Rico have collaborated to promote K-12 curriculum development in science and mathematics throughout Puerto Rico. Over this period, six schools have been consistently involved in the LUQ Schoolyard LTER program. Teachers and students from each of these schools have established long-term research plots near their schools. In some schools, the outcomes of these investigations have led to teachers producing peer-reviewed journal articles. (Lugo 1999). The primary focus during the LUQ funding cycle has been providing equipment and training to support teachers to continue study of the long-term plots. In addition, the LUQ Schoolyard program provided support to one of the teachers to develop spreadsheet templates to standardize data management. We are currently integrating two new middle schools to represent urban forest settings.

5.1.3 *Journey to El Yunque* – With funding from NSF's Instructional Materials Development (IMD) program, LUQ researchers have supported the development of a four-week bilingual middle school curriculum unit called *Journey to El Yunque* (see http://elyunque.net/journey.html). Students use LUQ data to investigate the effects of Hurricane Hugo and Hurricane Georges on the Luquillo Mountains and consider the long-term implications of increased hurricane activity. Early results suggest that students using *Journey to El Yunque* perform better on state ecological test items than students using traditional textbooks. With funding from the Puerto Rico Department of Education, the *Journey to El Yunque* program has expanded to include literacy activities for elementary students and activities with productivity tools for high school students. In summer 2005, they provided training to over 900 Puerto Rican K12 teachers. Over 500 of those teachers returned for a follow-up event at the end of October.

5.1.4 Future K-12 plans – For the Schoolyard LTER program, we are currently working to incorporate GLOBE data collection protocols to more efficiently support schools in their data collection efforts. We are also investigating the expansion of summer activities at each of the sites. The *Journey to El Yunque* program is seeking to expand the program into high school biology and expand the role of modeling in the program. The Learning Partnership, UPR, SRI

International, and Computer Learning Centers are preparing a proposal to the applied research strand of the IMD program for a 3-year $1.5 million project.

5.1.5. Graduate and undergraduate education – LUQ has been successful at incorporating graduate and undergraduate students in research at our site and at participating institutions on the mainland. UPR has had a site REU program at El Verde Field Station for six years, which is currently up for renewal. One-half of the students participating during the last three years of funding have been Puerto Rican. The REU program is part of a long-term effort at LUQ to incorporate more Puerto Rican students in graduate research—an issue LUQ has recognized for some time and was also noted at LUQ's 2003 Mid-Term Review. LUQ is a victim of the success of other federal programs operating in Puerto Rico (e.g., EPSCOR). The UPR system as a whole is very successful at producing Puerto Ricans with advanced degrees (e.g., 10% of UPR undergraduates eventually earn a Ph.D.), due in large part to federally-funded programs that target U.S. minority students. However, UPR's overall success has not translated into increased Puerto Rican graduate students in the LUQ program. At this moment in time there are more funding opportunities targeting Puerto Rican students than there are interested Puerto Rican students. Funding for LUQ graduate students has primarily gone to mainland graduate students and international students. Therefore it is essential that LUQ increase the number of Puerto Rican students interested in ecology. LUQ's success at increasing the number of Puerto Rican REU students should pay dividends down the road. The strong representation of Puerto Rican students in our REU program, our strong local K12 program, the recruitment of new Puerto Rican LTER faculty at ITES (Ramírez, Ortiz Zayas, and Mayol), combined with the new focus on urban ecology, should all contribute towards increasing the number of students from the increasingly environmentally-minded Puerto Rican student population.

5.2 Outreach

Since 2000, the Luquillo Mountains have been included in the HELP Program (http://www.luquillohelp.upr.edu), a global network of water catchments whose goal is to improve the linkages between hydrology and society. HELP is sponsored by UNESCO and the World Meteorological Organization. The project has a strong outreach component. For instance, in 2005 two water dialogues were held in Puerto Rico between federal, state and municipal authorities, non-governmental community groups and universities to discuss water-related problems, propose solutions, and identify future research needs. Six more dialogues, for each municipality in the Luquillo Mountains, are planned in the next three years.

To improve dissemination, aquatic research findings in the Luquillo Mountains, the University of Georgia, the University of Puerto Rico, and the U.S. Forest Service have been developing educational posters. Electronic versions of these posters can be accessed at http://www.arches.uga.edu/~cpringle/EnvOutTools.html. "El Yunque and Water" is a colorful poster with vivid examples of how human water needs should be in balance with the water needs of ecosystems. The poster "A tropical stream continuum: protect our native plants and animals" represents how the River Continuum Concept (Vannote et al. 1980) applies to a densely populated island such as Puerto Rico, stressing the impact of low head dams on migratory aquatic fauna.

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Luquillo LTER Online Data Sets (January 2006)

TITLE	DATES	originator / contact
Climate and stream flow		
Daily rainfall (Bisley area, 5 stations)	December 26, 1989 to ongoing	F.N. Scatena
USDC NOAA's National Climatic Data Center daily precipitation (5 stations)	PE1969 to 1992, RG1956 to 1984, RBU1955 to 1974, RBL1955 to 1992, Fajardo 1931 to 1992	NCDC / D.A. Schaefer
Rainfall and throughfall at Bisley tower	July 30, 1987 to ongoing	F.N. Scatena
Maximum temperature at El Verde since 1975	January 1, 1964ongoing	W.H. McDowell / A. Ramírez
Meteorological data from El Verde Field Station: NADP Tower	January 1, 2001 to ongoing	W. Lawrence / A. Ramírez
Meteorological data from towers (pre-Hugo) or rooftop (post Hugo) at El Verde	(1)October 6, 1989 to 1991, (2)October 6, 1989 to 1995	W. Lawrence / A. Ramírez
Minimum temperature at El Verde since 1975	January 1, 1964 to ongoing	W.H. McDowell / A. Ramírez
Rainfall at El Verde since 1975	January 1, 1964 to ongoing	W.H. McDowell / A. Ramírez
Temperature and humidity in the LFDP (40 points)	February 6, 2000 to ongoing	R.B. Waide
USDC NOAA's National Climatic Data Center daily maximum temperature (5 stations)	PE1969 to 1992, RG1956 to 1984, RBU1955 to 1974, RBL1955 to 1992, Fajardo 1931 to 1992	NCDC / D.A. Schaefer
USDC NOAA's National Climatic Data Center daily minimum temperature (5 stations)	PE1969 to 1992, RG1956 to 1984, RBU1955 to 1974, RBL1955 to 1992, Fajardo 1931 to 1992	NCDC / D.A. Schaefer
Bisley Tower I Meteorological data (Bisley Tower)	January 1, 1994 to ongoing	F.N. Scatena
USGS Long-term daily streamflow data at several LEF locations	July 1, 1945 to ongoing	D.A. Schaefer
Water and atmospheric chemistry, soils, nutrients		
NADP/NTN precipitation chemistry data	1989 to 1996	D.A. Schaefer / A. Ramírez
El Verde atmospheric deposition data from Nov. 21, 1983 to Sep. 22, 1987	November 21, 1983 to September 22, 1987	W.H. McDowell
Rio Icacos hyporheic and riparian chemistry	June 6 to July 26, 1996	W.H. McDowell
Chemistry of rainfall, throughfall and stream water from El Verde and Bisley	(1)June 3, 1983, (2)October 10, 1998(1)December 19, 1983, (	W.H. McDowell
Spatial Variation of Soil Carbon, Nitrogen and Phosphorus in the Luquillo Experimental Forest (LEF) (LEF_SOIL_CNP)	June 29,1998 to June 15, 1999	H. Wang / C.A.S. Hall

Water and atmospheric chemistry, soils, nutrients (continued)		
Patterns in soil and physical properties of the Bisley Watersheds 1 and 2 (Big Dig 1988, Big Dig 1990)	1988 to 1990	W. Silver
Soil organic matter dynamics in the tabonuco forest, a plantation and a secondary forest in Guzman	July 1996 to June 1997	Y. Li / X.Zou
Litterfall and coarse woody debris, decompostion		
Coarse Woody Debris in Bisley Experimental Forest and the Rio Icacos Basin	February 19, 2002 to ongoing	W.H. McDowell / Jordan Macy
Aboveground litterfall data at Bisley	August 1989 to May 1995	K.A. Vogt
Litter decomposition in tabonuco forest before Hugo	November 1980 to October 1981	X. Zou
Litterfall in tabonuco (subtropical wet) forest in the Luquillo Experimental Forest, Puerto Rico (MRCE Litterfall data)	March 26, 1990 (EV) to December 31, 2003; April 2, 1990 (PE) to ongoing	J.K. Zimmerman
Litterfall of the tabonuco forest before Hurricane Hugo	November 1980 to October 1981	C. Zucca / X. Zou
Short-term disappearance of foliar litter of three tree species native to rain forest of Puerto Rico	Feb 6, 1989 to Oct 20, 1990	W.H. McDowell
Long-term Intersite Decomposition Experiment (LIDET)	September 12, 1990 to April 15, 1993	D.A. Schaefer
Habitat		
Physical environment of the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico	February, 1990 to January, 1991	E. Everham / J. Thompson
Bisley 40 X 40 grid vegetation and site characteristics	March 1, 1988	F.N. Scatena
Canopy gap survey at (El Verde)	November 1988	N.V.L. Brokaw
Vegetation profile and canopy height of Tabonuco, Colorado and Cloud Forests	July 1, 1989 to ongoing	N.V.L. Brokaw
Bisley Grid Habitat data 1994, 1999	June 1, 1994 to August 31, 1999	M.R. Willig / C. Bloch
Canopy height in the Luquillo Forest Dynamics Plot	April 9, 1992 to 1997	E. Everham / J. Thompson
Luquillo Forest Dynamics Plot		
Species names and codes of the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico	February 1, 1990 to January 31, 1991	E. Everham / J. Thompson
Census of species, diameter and location at the Luquillo Forest Dynamics Plot	August 1, 1990 to ongoing	E. Everham / J. Thompson

Luquillo Forest Dynamics Plot (continued)		
Elevation at grid points on the Luquillo Forest Dynamics Plot	June 15, 1990 to January 30, 1992	E. Everham / J. Thompson
Tree damage by Hurricane Hugo on the Luquillo Forest Dynamics Plot	August 1990 to September 1993	E. Everham / J. Thompson
Location of trees in the Hurricane Recovery Plot	June 15, 1990 to ongoing	E. Everham / J. Thompson
Plant community, tree regeneration, plant phenology		
Altitudinal transects vegetation data along three rivers in the Luquillo Experimental Forest	September 17, 2001 to July 31, 2002	J.A. Barone
Germination in three R/FR light environments (El Verde)	Germ.: 28 Jan to 3 Jul, 1995 Light: 29 Feb to 11 Mar 1995	J. Jardine / B. Haines
Regeneration after Hurricane Hugo woody species > 10cm tall (9ha grid, El Verde)(Small 9Ha Grid)	June 6, 1990 to Nov 1, 1994	N.V.L. Brokaw
Regeneration after Hurricane Hugo woody species > 1m tall (9ha grid, El Verde) (Large 9Ha Grid)	June 6, 1990 to Nov 2, 1994	N.V.L. Brokaw
Regeneration after Hurricane Hugo woody species > 1m tall (9ha grid, El Verde) Percent cover below 3m (9 ha grid, El Verde)	June 6, 1990 to June 30, 1992	N.V.L. Brokaw
Regeneration after Hurricane Hugo woody species > 1m tall (9ha grid, El Verde)(Wood fall from Hurricane Hugo 9Ha Grid)	June 6, 1990 to Dec 31, 1991	N.V.L. Brokaw
Seedling and sapling dynamics of treefall pits and undisturbed florest floor in El Verde, Puerto Rico	May 1991 to May 1992	L.L. Walker
Phenologies of the Tabonuco Forest trees and shrubs	8 July 1992 to ongoing	J.K. Zimmerman
Cecropia growth in gaps (El Verde)	August 1, 1989 to August 31, 1989	N.V.L. Brokaw
Regrowth in pastures, coffee plantations, landslides		
Ecuador old fields permanent plot vegetation sampling	March 1998 to ongoing	R.W. Myster
El Verde Coffee Plantation permanent plot vegetation sampling	December 8, 1998 to October 28, 1999	R.W. Myster
Sabana pasture permanent plot vegetation sampling	November 16, 1995 to ongoing	R.W. Myster
Landslide Removal Experiment vegetation cover and pole touches	Nov 1997 to May 2000	L.L. Walker
Above ground biomass in landslides	April 27, 1990	L.L. Walker
Landslide revegetation measurements	June 1988 to ongoing	D.J. Lodge
Revegetation of landslides, vegetation > 0.1 m	June 1988 to ongoing	L.L. Walker

Regrowth in pastures, coffee plantations, landslides (continued)		
Revegetation of landslides, vegetation > 1.0 m	June 1988 to ongoing	L.L. Walker
Soil sample from landslide ES1 (Espíritu Santo, El Verde), ES2, and RB2 (Río Blanco)	December 27, 1988; January 1 to March 15, 1992	D.J. Lodge
Fungi and herbaceous plants, epiphytes		
Fungi of the Greater Antilles	1 April, 1996 to 29 March 2000	D.J. Lodge
Bromeliad chemistry at different elevations in the LEF	February 1996	B.A. Richardson
Bromeliad collection data at different elevations in the LEF	December 1993 to March 1997	B.A. Richardson
Bromeliad invertebrate counts at different elevations in the LEF	December 1993 to March 1997	B.A. Richardson
Fern distribution in El Verde MRCE plots	October 11, 1995 to November 28, 1995	J.M. Sharpe
Fern sporophyte growth observation at the Luquillo Experimental Forest (LEF)	September 10, 1991 to ongoing	J.M. Sharpe
Invertebrates, decomposers, herbivory		
Heliconia invertebrate counts	February 1, 1996 to March 31, 1998	B.A. Richardson
Heliconia collection data	February 1996 to March 1998	B.A. Richardson
Heliconia fluid and organic matter analyses	March 1998	B.A. Richardson
Invertebrate dry weight data in the Luquillo Experimental Forest	2004	B.A. Richardson
Canopy invertebrate responses to Hurricane Hugo	February 23, 1991 to ongoing	T.D. Schowalter
Effect of plant density and light availability on leaf damage in Manilkara bidentata	April, 1995 to March 1996	M.P. Angulo
Herbivory of eight common species at El Verde from 1994 to 1996	November 1994 to October 1996	M.P. Angulo
Leaf miners (*Acrocercops* sp.)larvae performance on young leaves of Manilkara bidentata	April, 1995 to March 1996	M.P. Angulo
Litter invertebrate communities at different elevations in the Luquillo Experimental Forest	February 1999 to February 2001	B.A. Richardson
El Verde Grid invertebrate data	June, 1991 to ongoing	M.R. Willig / C. Bloch
Grid invertebrate data 1989 and 1990 (Bisley)	July 28, 1989 to August 29, 1990	M.R. Willig / C. Bloch
Habitat selection/*Caracolus caracolla* and other snails	March 27, 1991 to ongoing	M.R. Willig / C. Bloch
Earthworms in tropical tree plantations and secondary forests	January to May 1994	G. Gonzalez

Vertebrates		
Earthworms in abandoned tropical pastures	January to May 1994	X. Zou
Frog abundance in fertilization plots	June 1993	L.L. Woolbright
Frog grid data (Bisley)	Summer 1989 (pre Hugo)	L.L. Woolbright
Frog population plots (El Verde + Bisley)	Jan 2, 1987 to Jan 9 1997	L.L. Woolbright
Frog spatial distribution data (El Verde + Bisley)	Aug 1, 1991 to May 30, 1993	L.L. Woolbright
Frog transect data	June 14, 1989	L.L. Woolbright
Anole El Verde 9Ha and Bisley grids study	November 24, 1989 to October 26, 1990	D.P. Reagan
Anole food habits	October 30, 1989	D.P. Reagan
Anole ground level transects (Bisley and El Verde)	February 21, 1989 to 1992 (wet season)	D.P. Reagan
Anole multiple mark and resight studies	February 18, 1989 to 1992 (wet season)	D.P. Reagan
Anole treefall gap transects (Bisley & El Verde-H10 Gaps)	February 18, 1989 to 1992 (wet season)	D.P. Reagan
Anole vertical transects (tower data)	January 9, 1989 to 1992 (wet season)	D.P. Reagan
Bird point counts	May 10, 1989 to ongoing	R.B. Waide
Food web		
Experimental Understory Food Web data in El Verde	September 1999 to July 2000	P. Klawinski
Stream ecology		
Neritina snails hierarchical distribution	August 22, 2000 to January 9, 2003	J. Blanco
Neritina snails upstream migrations	January 8, 2000 to June 30, 2002	J. Blanco
Bisley/Prieta algae monitoring	June 1, 2002 to ongoing	E. Greathouse
Río Mameyes diatoms 1998-2000	May 1998 to June 26, 2001	B. Bryan
Does the River Continuum Concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream	June 2001 to August 2001	E. Greathouse
Conservation and management of migratory fauna and dams in tropical streams of Puerto Rico	19902005	E. Greathouse
Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico	June 2001 to June 2003	E. Greathouse
Shrimp populations in Quebrada Prieta (Pools 0,1)	January 5, 1988 to ongoing	A.P. Covich

Stream ecology (continued)		
Shrimp populations variability in numbers and sizes in response to disturbance and seasons on 20 pools along the reach of Quebrada Prieta, Luquillo Experimental Forest	July 10, 1990 to July 19, 1991	K.M. Buzby
Spatial and temporal differences in shrimp numbers (1 year, 20 pools)	July 1990 to July 1991	K.M. Buzby
Recovery of a tropical stream after a harvest-related chlorine poisoning event	June 1999 to July 1999	C.M. Pringle
Effects of biotic (shrimp) and abiotic (discharge) factors on the depositional environment quantified in a montane stream in Puerto Rico.	September 5 to 14, 1992	C.M. Pringle
Enclosure/exclosure experiments in a montane Puerto Rican stream examining direct and indirect effects of two dominant taxa of atyid (Atyidae) shrimp, *Atya lanipes Holthius* and *Xiphocaris elongata* Guerin-Meneville	February 23, 1990 to July 27, 1990	C.M. Pringle
Experimentally manipulated biota over a 30-40d period in two streams with distinctly different macrobiotic assemblages	June 20, 1994 to August 13, 1994	C.M. Pringle
Photo records		
Photo records from Luquillo Experimental Forest	February 1988	D.J. Lodge

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Year 2000 to the Present

Journal articles (Total 273)

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